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(Continued on back cover)

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CONTENTS

Vol. 82, No. 1 January 1984

(Continued on next page)

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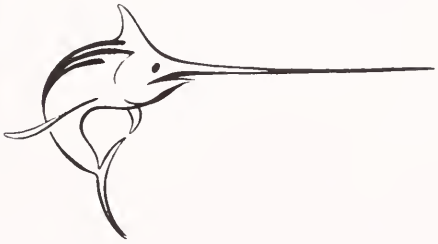
Notes

Best NMFS Publications for 1982

The Publications Advisory Committee of the National Marine Fisheries Service has announced the best publications authored by the NMFS scientists and published in the *Fishery Bulletin* and the *Marine Fisheries Review* for 1982. Only effective and interpretive articles which significantly contribute to the understanding and knowledge of NMFS mission-related studies are eligible, and the following papers were judged as the best in meeting this requirement.



"Development of the vertebral column, fins and fin supports, branchiostegal rays, and squamation in the swordfish, *Xiphias gladius*" by Thomas Potthoff and Sharon Kelley appears in *Fishery Bulletin* 80(2):161-186. Thomas Potthoff, fishery biologist, and Sharon Kelley, research assistant, are from the Southeast Fisheries Center's Miami Laboratory, Miami, Fla.

"A review of the offshore shrimp fishery and the 1981 Texas closure" by Edward F. Klima, Kenneth N. Baxter, and Frank J. Patella, Jr. appears in *Marine Fisheries Review* 44(9-10):16-30. Edward F. Klima, Director of the Galveston Laboratory, Kenneth N. Baxter, supervisory fishery biologist, and Frank J. Patella, Jr., fishery biologist, are also from the Southeast Fisheries Center but from the Galveston Laboratory, Galveston, Tex.

DOCUMENTATION OF ANNUAL GROWTH LINES IN OCEAN QUAHOGS, *ARCTICA ISLANDICA* LINNÉ

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ABSTRACT

About 42,000 ocean quahogs, *Arctica islandica* Linné, were marked and released at a deep (53 m) oceanic site off Long Island, New York, in 1978. Shells of live specimens recovered 1 and 2 years later were radially sectioned, polished, and etched for preparation of acetate peels and examination by optical microscopy or microprojection; selected specimens were similarly prepared for examination by scanning electron microscopy. Specific growth line and growth increment microstructures are described and photographed. An annual periodicity of microstructure is documented, providing a basis for accurate age analyses of this commercially important species.

Numerous bivalve species form periodic growth lines in their shells (Rhoads and Lutz 1980). Internal growth lines found in the shells of ocean quahogs, *Arctica islandica* Linné, have stimulated interest in using these markings to determine age and growth (Thompson et al. 1980a, b), since fishery exploitation has increased significantly within the past decade (Serchuk and Murawski 1980[3]).

Documentation of age and growth of ocean quahogs has been incomplete. Some studies included no account of aging methodologies (Thorson *in* Turner 1949; Jaeckel 1952; Loosanoff 1953; Skuladottir 1967); in others, concentric "rings" or "bands" formed in the periostracum of small quahogs (<ca. 60 mm in shell length) were considered annuli, but validation of the annual periodicity of these markings was not provided (Lovén 1929; Chandler 1965; Caddy et al. 1974; Chéné 1970[4]; Meagher and Medcof 1972[5]). Microstructure of ocean quahog shells has been studied, but the analyses did not specifically distinguish growth lines from growth increments (Sorby 1879; Bøggild 1930; Taylor et al. 1969, 1973; Lutz and Rhoads 1977, 1980). A means of clearly separating such shell features was needed.

Recent investigators of age phenomena in ocean quahogs have microscopically examined the shells and acetate peel images produced from sectioned, polished, and etched shells. This method greatly aided separating the many crowded growth layers in the hinge plate and near the ventral valve margin of large, old specimens. Lutz and Rhoads (1977) found alternating bands of aragonitic prisms and complex-crossed lamellar microstructures in the inner shell layer of ocean quahog shells that they believed were related to periods of aerobic and anaerobic respiration. Thompson et al. (1980a, b) reported that internal growth bands corresponded to external checks on the valves and that the internal growth bands were formed by successive deposition of two repeating growth layers or increments. Jones (1980) labelled the growth increments (GI) as GI I and GI II, since each was microstructurally distinct, had thickness, and was formed within a time frame of several months. For these reasons, he considered the GI I layer to be unlike minute "growth lines" or "striations" appearing as subdaily deposits in the shells of other bivalves (Gordan and Carriker 1978); the GI II layer became thinner and ill-defined from the GI I layer with ontogeny.

Since growth bands in ocean quahog shells seem to lack microstructures of possible subannual periodicities, the definitions of a growth line and growth increment formulated by Clark (1974a, b) have general application. Clark (1974b:1) defined the former as "abrupt or repetitive changes in the character of an accreting tissue" and the latter as "the thick-

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[3]Serchuk, F.M. and S.A. Murawski. 1980. Evaluation and status of ocean quahog, *Arctica islandica* (Linnaeus) populations off the Middle Atlantic Coast of the United States. U.S. Dep. Commer., NOAA, NMFS, Woods Hole Lab. Doc. 80-32, 4 p.

[4]Chéné, P.L. 1970. Growth, PSP accumulation, and other features of ocean quahog (*Arctica islandica*). Fish Res. Board Can., St. Andrews Biol. Stn., Orig. Manuscr. Rep. 1104, 34 p.

[5]Meagher, J.J., and J.C. Medcof. 1972. Shell rings and growth rate of ocean clams (*Arctica islandica*). Fish Res. Board Can., St. Andrews Biol. Stn., Orig. Manuscr. Rep. 1105, 26 p.

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FISHERY BULLETIN: VOL. 82, NO. 1, 1984.

ness or volume of tissue formed by accretionary growth between successive growth lines." In fact, Jones (1980:333) identified the layers as a "consistently thin, dark gray, translucent increment" of prismatic microstructures which was "easily distinguished from" homogeneous and crossed microstructural layers.

Assessment research on ages of ocean quahogs requires accurate counts and measurements of growth increments. Age observations are customarily made of acetate peel images under optical microscopes with transmitted light. An important assessment requirement is that an annual increment has a distinct beginning and end. The concept of a growth line forming between successive growth increments fulfills that requirement.

Counts of supposed annual growth bands seen in the shells of ocean quahogs by Thompson et al. (1980a, b) resulted in slow growth rates and an extreme longevity estimate of 150 yr. Slow growth rate and suspiciously long life for a bivalve seemed to invalidate the thesis of only a single growth line and growth increment being formed annually. Supportive evidence included finding similar bands in surf clams; finding a low number of bands formed during the onset of sexual maturity that were not explained by less than an annual frequency; finding an expected number of bands in small specimens of known age; finding an expected number of bands formed sequentially in samples taken frequently during 2 yr that had only an annual periodicity; finding a line deposited during the fall-winter, a period coinciding with spawning; and finding ages determined by radiometric analyses that were comparable with band counting. The latter three types of investigation have been expanded by Jones (1980) and Turekian et al. (1982) with the same results. As part of the study, I. Thompson (pers. comm.) marked and released ocean quahogs in the natural environment, but none was recovered. Direct and readily comprehended observations of shell growth after marking were considered to be important additional evidence in support of the thesis of an annual periodicity of growth line and growth increment deposition.

In 1978, the National Marine Fisheries Service marked large numbers of ocean quahogs for release and recovery at a site 53 m deep and 48 km south-southeast of Shinnecock Inlet, Long Island, N.Y., (lat. 40°21'N, long. 72°24'W). Details of this project have been reported in Murawski et al. (1982). Periodicity of growth line formation and shell accretion after notching of recovered ocean quahogs and the microstructure of unmarked and marked shells are described herein with photographic documentation.

METHODS

A commercial clam dredge vessel, the MV *Diane Maria*, was chartered for the marking operation during 25 July to 5 August 1978. The knife of the hydraulic dredge was 2.54 m wide, and the cage was lined with 12.7 mm square-mesh hardware cloth to retain small clams. Ocean quahogs for marking were collected within 9 km of the planting site and released during a 10-d period (ca. 17,000 on 26 July, 3,000 on 2 August, and 21,000 on 4 August 1978). Two 0.7 mm thick carborundum discs, spaced 2 mm apart and mounted in the mandrel of an electric grinder, produced distinctive parallel, shallow grooves from the ventral margin up onto the valve surface (Ropes and Merrill 1970). Four operators of grinders marked about 1,600 clams/h. Groups (ca. 3,000-8,000) of marked clams were released at loran-C coordinates within a rectangular area of about 3 by 6 μs.

Marked clam recoveries were made in conjunction with annual clam resource surveys. During recovery operations, a Northstar 6000[6] loran-C unit and Epsco loran-C plotter aided in a systematic search of the planting site. Marked clam recoveries were highly variable. On 20 and 21 August 1979 and about 387 d after the marking operation, 43 hydraulic dredge tows at the planting site captured 14,043 ocean quahogs and 74 (0.5%) were marked; on 9 September 1980 and 773 d after the marking operation, 1,899 ocean quahogs were captured in 2 dredge tows and 249 (13.1%) were marked. Some marked specimens were damaged, but 67 recovered in 1979 and 200 recovered in 1980 were alive and had intact paired valves.

Recaptured specimens were frozen to prevent periostracum loss from drying and to facilitate opening without shell damage. Microscopic examination of 267 notched shells was made to assess the effects of marking and to obtain growth measurements. Shell measurements were made to the nearest 0.1 mm by calipers; growth after marking was measured to the nearest 0.01 mm by an ocular micrometer in a dissecting microscope. Acetate peels of all marked ocean quahogs were prepared by the procedures described by Ropes (1982[7]). Briefly, radial sections from the umbo to ventral margin were produced on left valves, oriented to include the broadest surface of the single prominent tooth in the hinge. This exposed the internal growth lines in the valve and hinge tooth for later treatment. The paired notch marks in a valve

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

[7]Ropes, J. W. 1982. Procedures for preparing acetate peels of embedded valves of *Arctica islandica* for aging. U.S. Dep. Commer., NOAA, NMFS, Woods Hole Lab., Doc. 82-18, 8 p.

were not usually oriented in the above plane of radial sections, so additional radial cuts were made to expose growth lines in the notch area. Subsequently, shells were embedded in an epoxy resin, and the cut shell edge ground on wetable carborundum paper and polished. Acetate peels were produced after etching the shell cut surfaces in a 1% HCl solution for 1 min, followed by microscopic examination of the peels that were sandwiched between slides.

Preparation of polished and etched radial sections of marked and unmarked ocean quahog valves were further examined by scanning electron microscopy (SEM)[8]. These examinations included vertical transects from the periostracum to the shell's interior and specific sites affected by the marking operation. Shell microstructure was diagnosed by using the classification scheme of Carter (1980), wherein shell microstructures are elucidated on the basis of their major (i.e., first-order) structural arrangement, independent of genetic or optical crystallographic criteria.

RESULTS

Whole Shells

Notch marks showed clearly on wet shells but periostracum obscured the ventralmost ends extending well beyond the ventral valve margin on all specimens (Figs. 1-4). Cuts made in the shell-free periostracum beyond the ventral margin of some large quahogs had not been repaired after 2 yr (Fig. 4a); small individuals, however, had completely formed yellowish-brown periostracum (grayish white in the photographs) over new shell growth, which contrasted sharply with darker, earlier deposition (Fig. 3a).

In some specimens, the mark formed U-shaped notches at the marginal edge of the old shell. New shell deposition was obviously disrupted for quahogs with deep U-notches, since the marginal shell between the notches was outlined in relief over new shell (Fig. 3b, c). Faint paired bulges were also found on the ventral inner surface of the notched valve of a few shells and occasionally the notches extended part way onto the opposite valve. An occasional live quahog was found with a cracked valve caused from handling during the marking operation. The blackened margins of the cracks, suggestive of reducing conditions, indicated that the cracks were old. There was no evidence of repair by shell covering the cracks in quahogs recovered 2 yr after marking.

Sectioned Shells

An interruption of shell deposition from notching in some sectioned shells was visible without magnification in the cut surfaces. Microscopic examination revealed a depression that curved dorsally back into the shell from the external surface and became increasingly attenuated until it was unrecognizable from the usual shell features along the inner margin. This type of interruption was greatest in shells of small quahogs, probably due to some mantle tissue incision. Periostracum penetrated into the interruption to a depth of about 1 mm. The thicker and tougher periostracum of large clams was less easily incised during marking and probably served to minimize incision of mantle tissue.

Acetate Peels of Sectioned Shells

Acetate peels enhanced detection of interruptions in shell deposition due to notching (Figs. 1d, 2d, 3d, 4d). In small clams (<80 mm shell length), the interruption was immediately followed by a line similar to a succession of lines formed throughout the valve before marking. No additional lines were evident thereafter to the marginal tip in shells examined from the late August 1979 recovery, but in 34 shells of small clams recovered in early September 1980, a second line occurred about midway to the tip in all shells and a third line had formed very near the marginal valve tip and along the inner margin in 47% (Fig. 3d). These were all considered to be annual growth lines for reasons dicussed later. Shell deposition between growth lines in the outer layer had a granular appearance, which was sometimes broken by a faint line of uncertain origin (Figs. 1d, 3d). The interruption of shell deposition from marking was also evident in large ocean quahogs (Figs. 2d, 4d), although an infiltration of the depression with periostracum was not clearly evident. The separation of shell deposits was more definite and extended deeper into the shell of large clams, sometimes to a depth of 2 mm (Figs. 2d, 4d). Growth lines were very closely spaced (ca. 100 μm) and the shell depositional texture in between lines appeared similar to that seen in smaller clams. In large ocean quahogs, new shell was formed laterally beyond the notch mark and was an indication that the notching operation had little effect on shell deposition and growth (Figs. 5a, 6a).

None of the marked quahogs had as severe an

[8]SEM work was performed on an ETEC Autoscan instrument at the Dental Research Center, University of North Carolina, Chapel Hill, N.C.; on the JEOLJSM-35 of the Biology Department, Princeton University, Princeton, N.J.; and on the ISI 1200 of the Department of Geology, University of Florida, Gainesville, Fla.

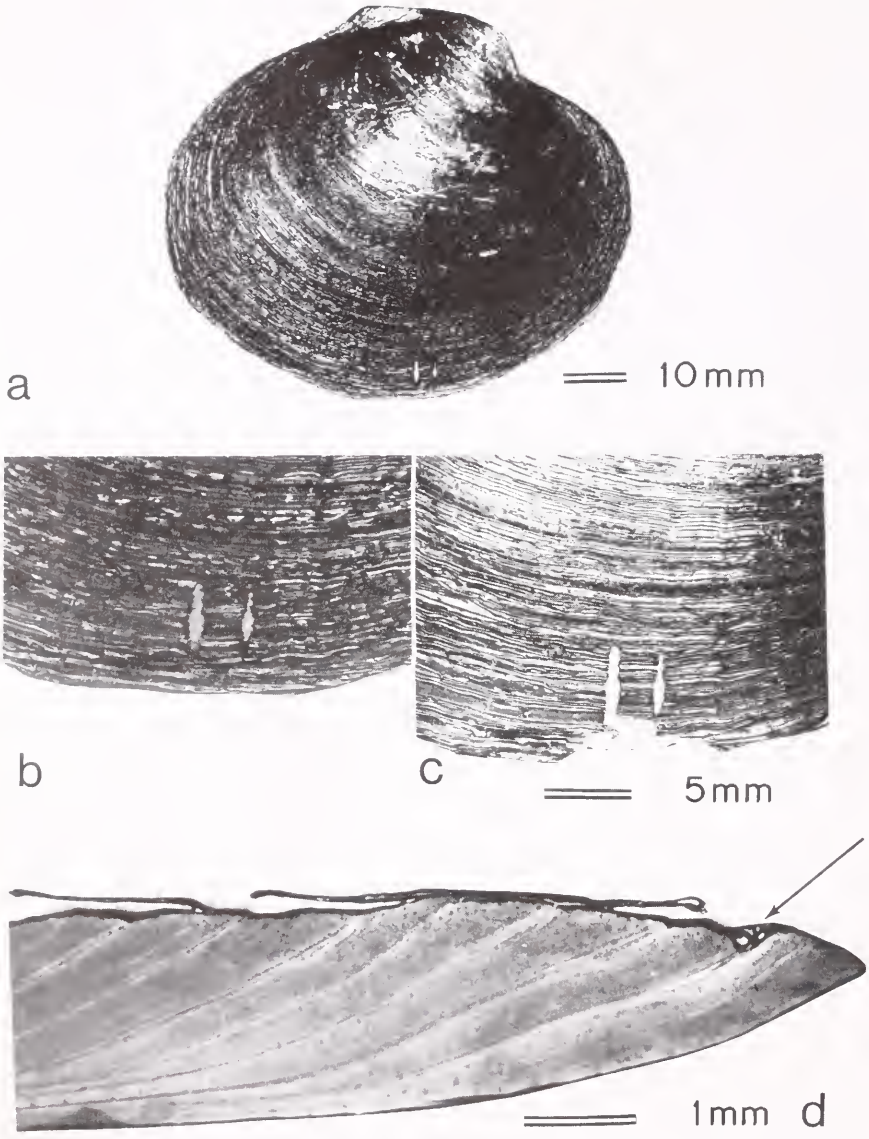
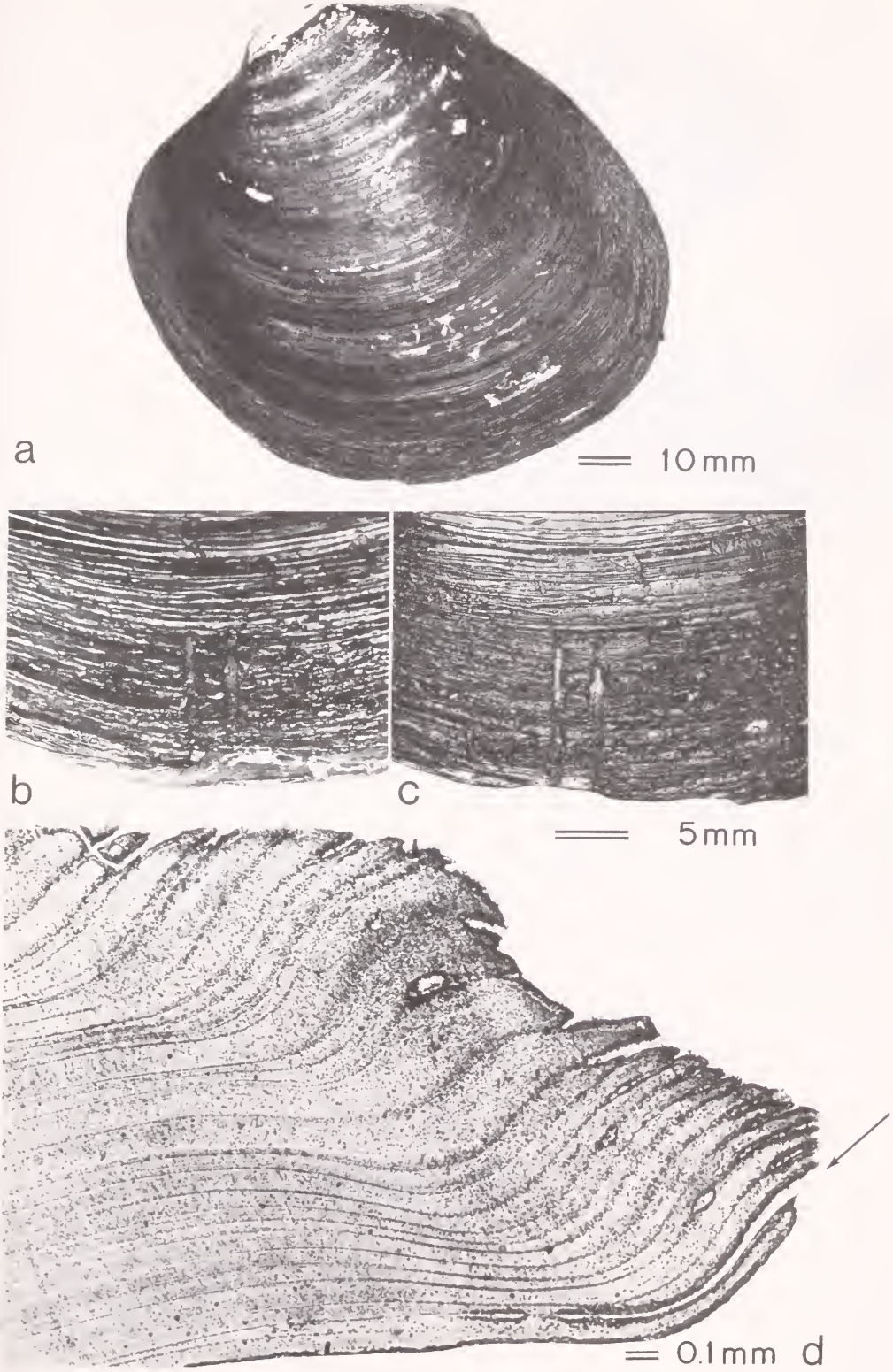


FIGURE 1.—(a) Right valve of an 18-yr-old ocean quahog, *Arctica islandica*, 71.4 mm in shell length recovered on 21 August 1979. Estimated annual growth was 1.3 mm. The notch-mark area is shown before (b) and after (c) peeling off the periostracum. (d) Optical photomicrograph (microprojector) of seven repetitive growth lines in an acetate peel of the valve margin. An arrow points to an interruption of growth and growth line formed at or soon after marking the clam in 1978. An internal line is evident between the mark-induced line and the valve edge. This line is the normally occurring age mark probably formed in late autumn-early winter. Scale bars of magnification are included.

FIGURE 2.—(a) Left valve of an ocean quahog, *Arctica islandica*, about 110 yr old and 100.5 mm in shell length recovered on 20 August 1979. Estimated annual growth in 1 yr was 0.1 mm. The notch-mark area is shown before (b) and after (c) peeling off the periostracum. (d) Optical photomicrograph (compound microscope) of many repetitive growth lines in an acetate peel of the valve margin. An arrow points to an interruption of growth and growth line formed at or soon after marking the clam. Scale bars of magnification are included.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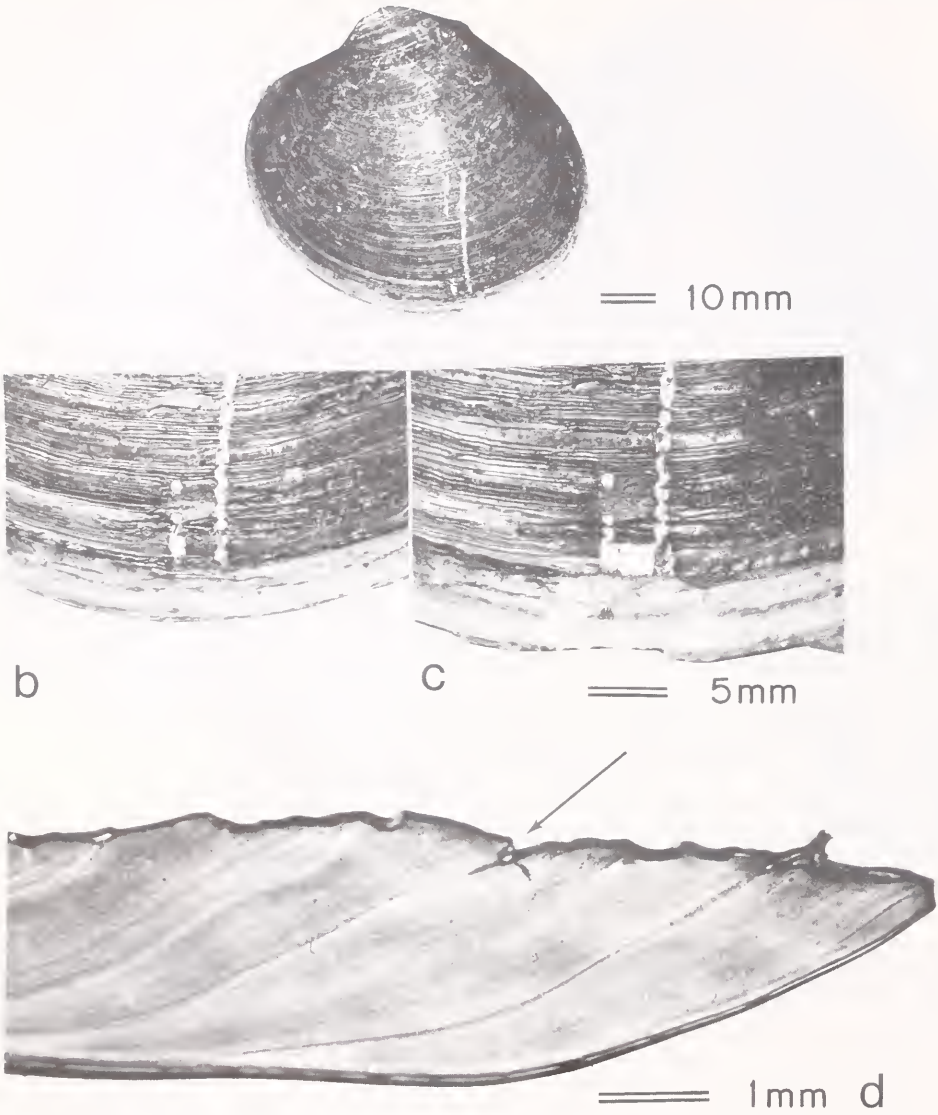
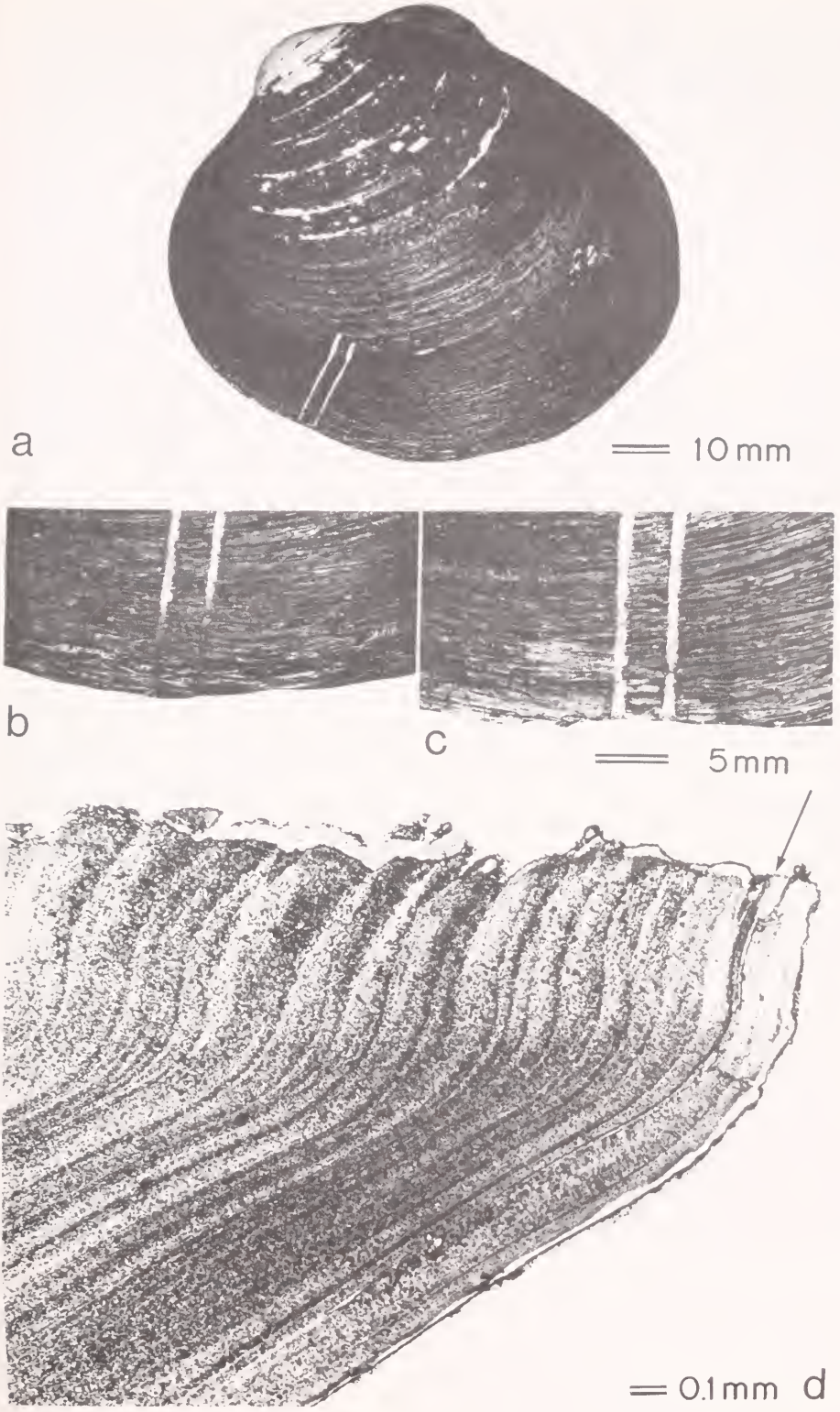


FIGURE 3.—(a) Left valve of a 15-yr-old ocean quahog, *Arctica islandica*, 61.7 mm in shell length recovered on 9 September 1980. Estimated 2-yr growth increment was 3.2 mm. The notch-mark area is shown before (b) and after (c) peeling off the periostracum. (d) Optical photomicrograph (microprojector) of five repetitive growth lines in an acetate peel of the valve margin. An arrow points to an interruption of growth and growth line formed at or soon after marking the clam. Two additional lines, one midway to the valve tip and one near the valve tip, were formed after marking the quahog. Scale bars of magnification are included.

FIGURE 4.—(a) Left valve of an ocean quahog, *Arctica islandica*, about 95 yr old and 91.7 mm in shell length recovered on 9 September 1980. Estimated 2-yr growth increment was 0.3 mm. The notch-mark area is shown before (b) and after (c) peeling off the periostracum. (d) Optical photomicrograph (compound microscope) of many repetitive growth lines in an acetate peel of the valve margin. An arrow points to an interruption of growth and growth line formed at or soon after marking the clam. Scale bars of magnification are included.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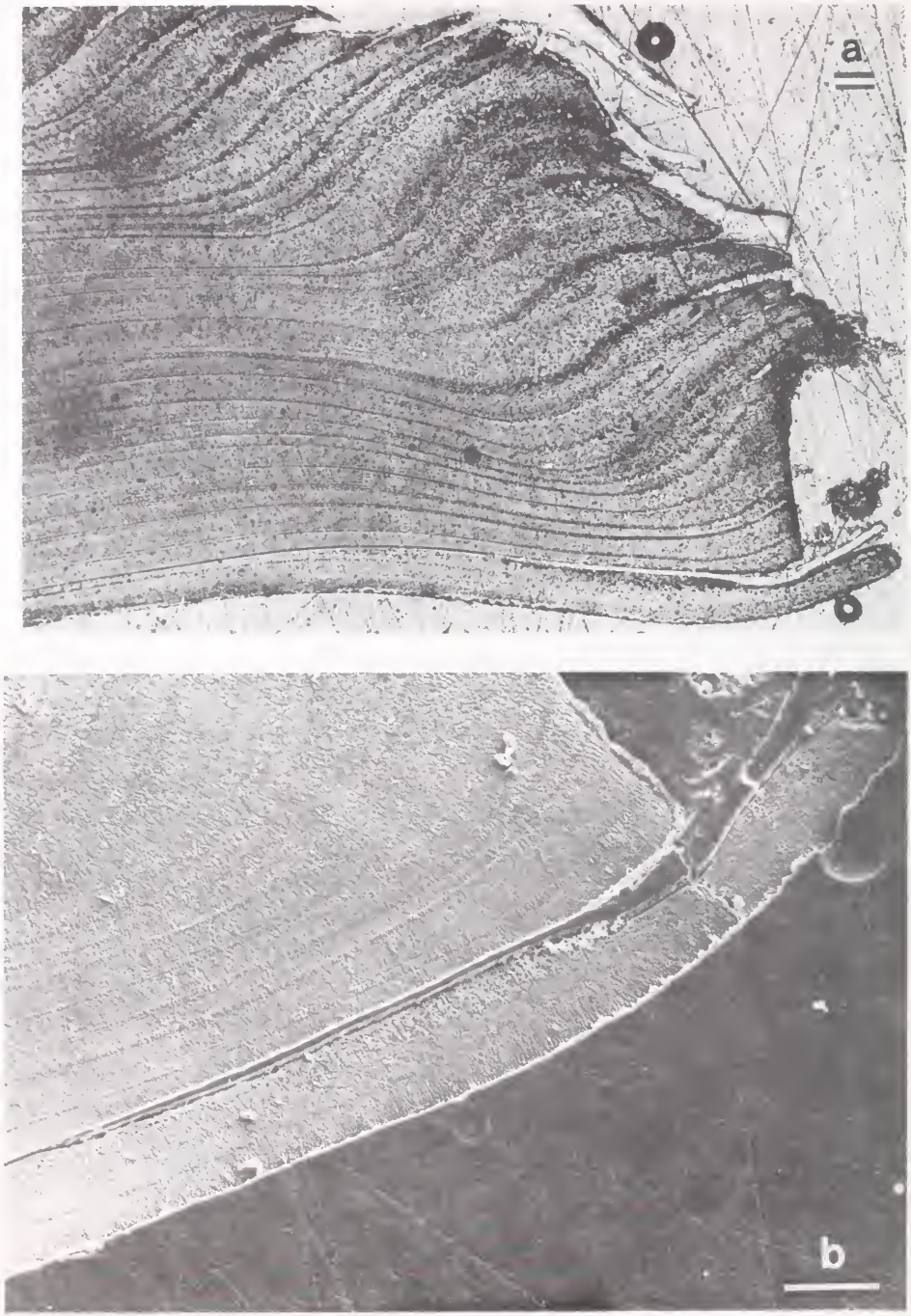
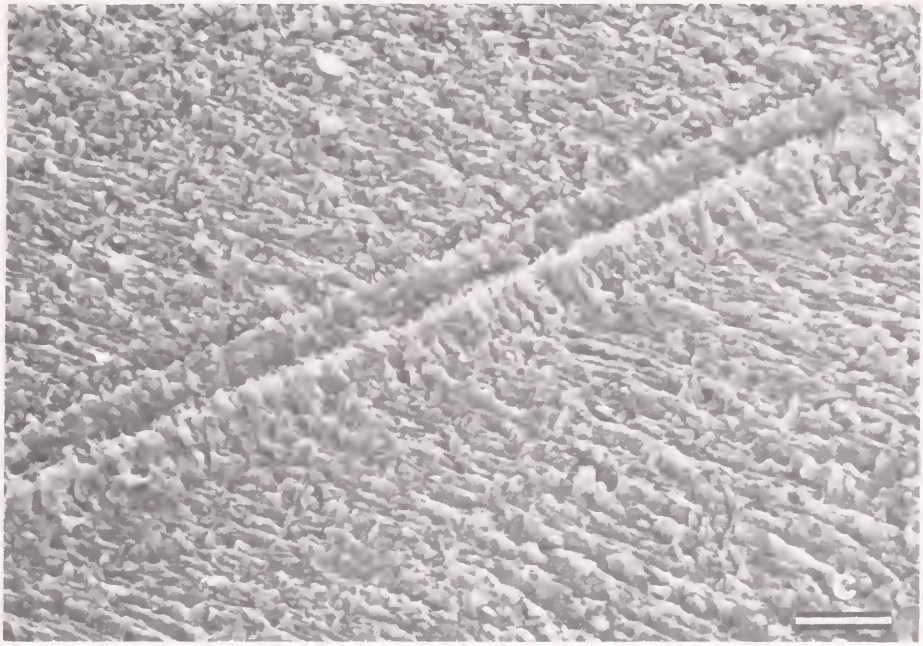
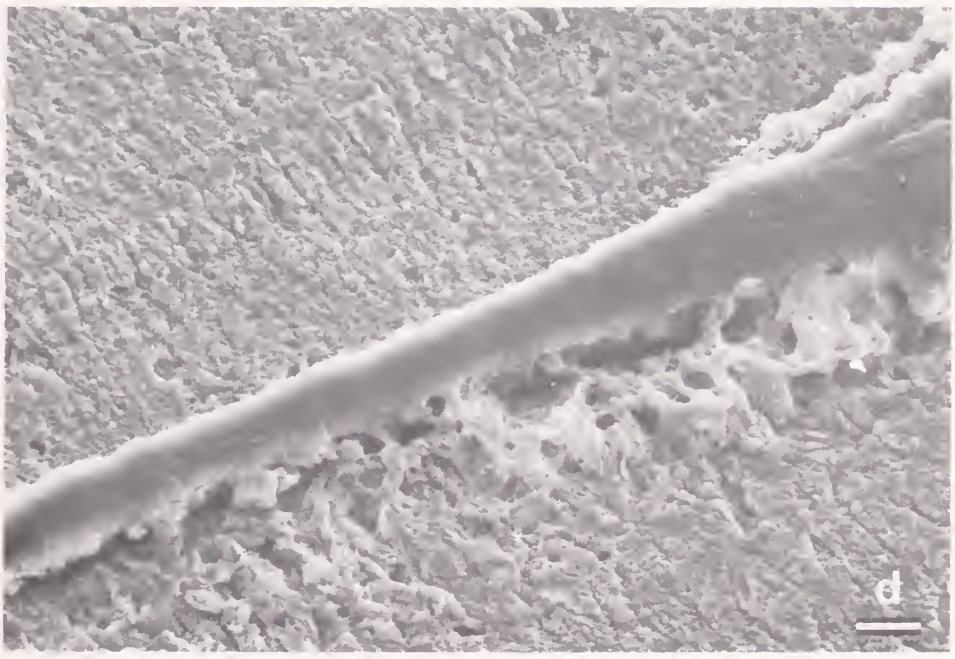


FIGURE 5.—(a) Optical photomicrograph (compound microscope) of an acetate peel at a notch-mark in the ocean quahog, *Arctica islandica*, shown in Figure 2 (scale bar = 100 μm). Note the single annual increment of growth formed laterally beyond the notch-mark. (b) SEM photomicrograph of the same shell specimen (scale bar = 100 μm). Abbreviatons of shell microstructural terms in this and subsequent figures are expalined in this text. (c) Transitional CA-CL microstruc-





ture interrupted by an ISP band that extends from the notch-line seen in (b) (scale bar = 10 μm). This photomicrograph was taken beyond the field of view of (b), to the lower left and beyond the zone of epoxy penetration. (d) Enlargement of epoxy penetration zone from (b) interrupts normal shell microstructure followed by a zone of cavernous, poorly organized, disrupted shell growth (scale bar = 10 μm).

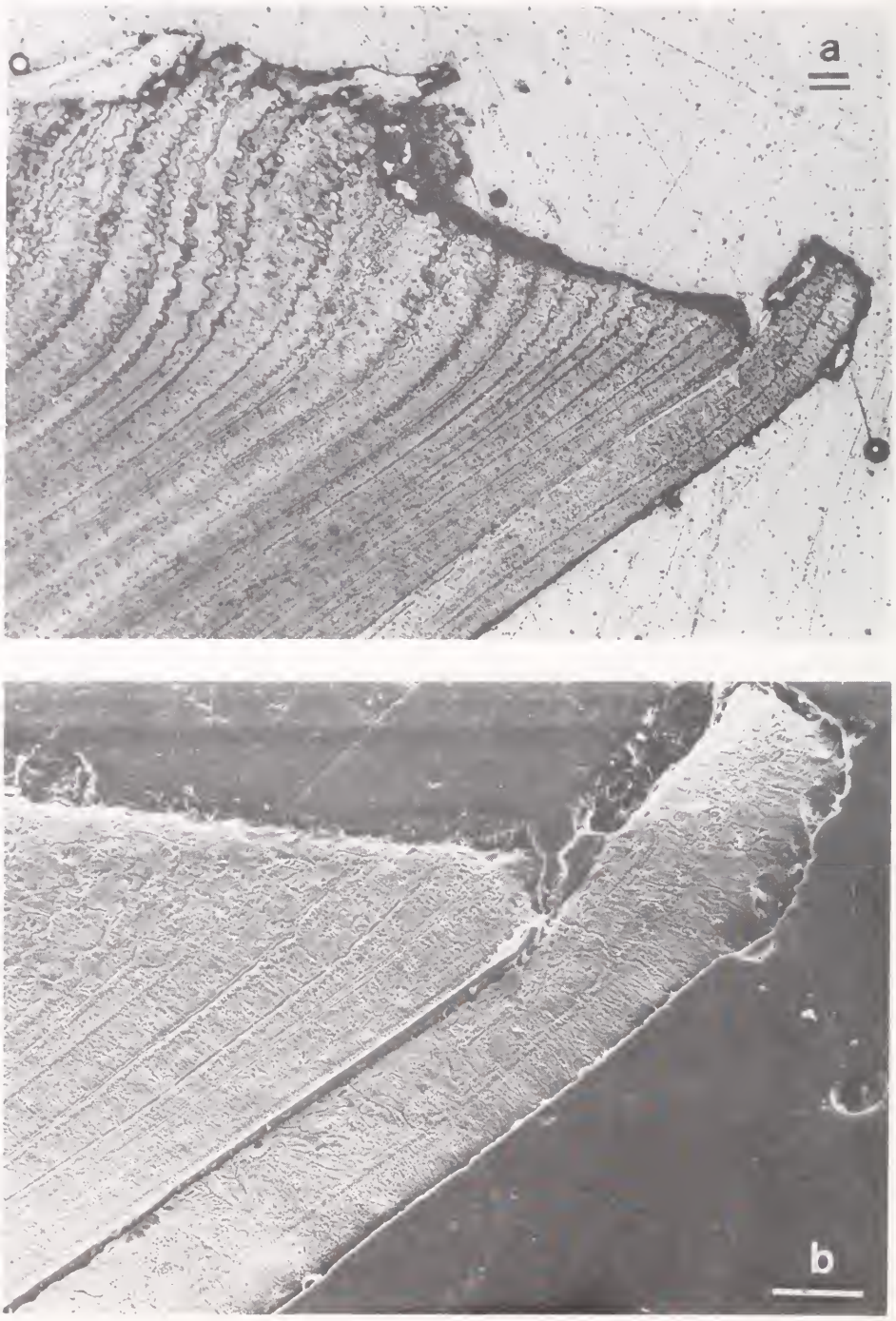
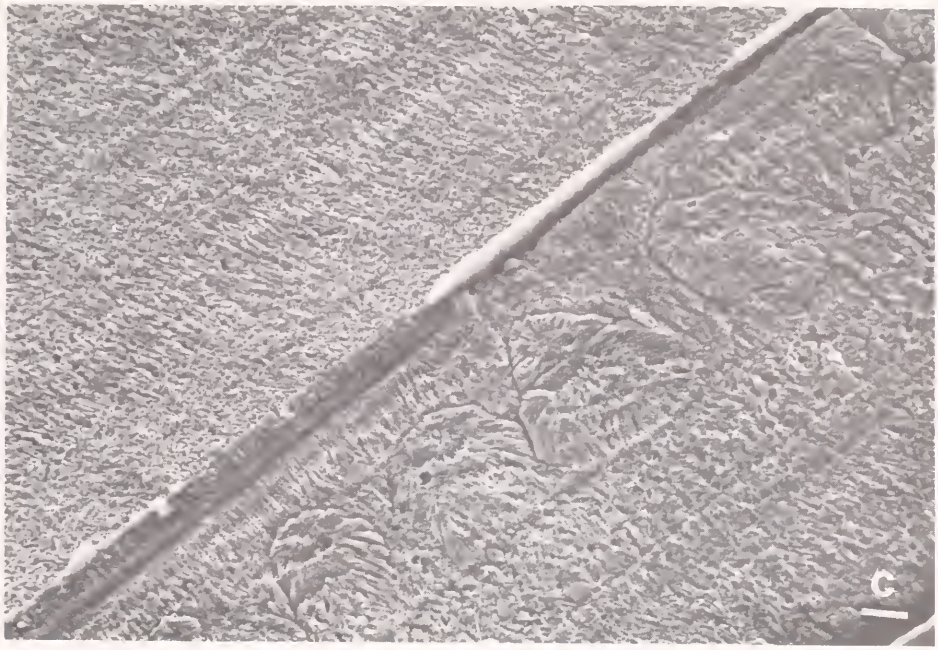
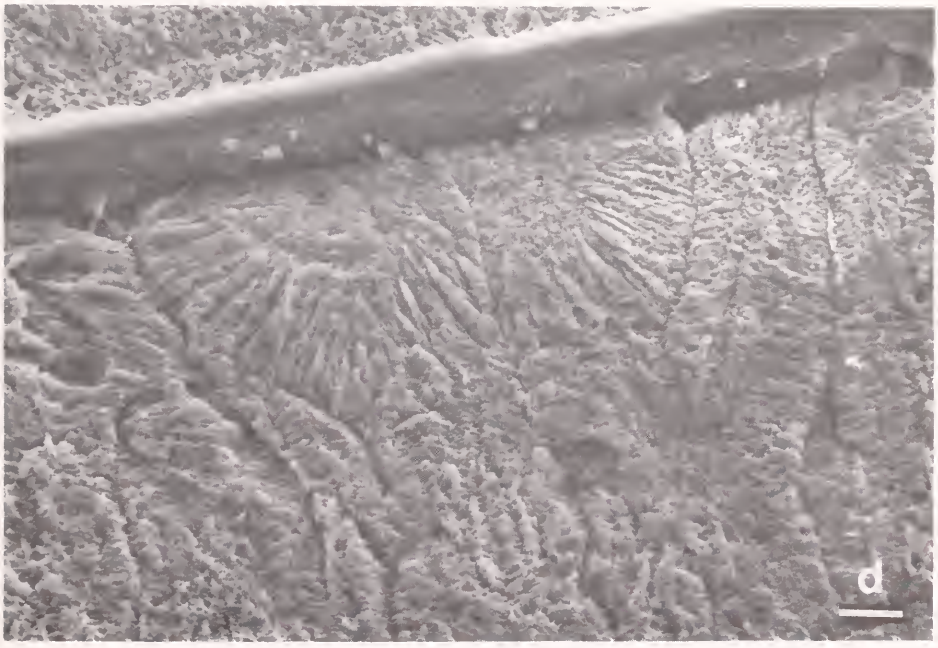


FIGURE 6.—(a) Optical photomicrograph (compound microscope) of an acetate peel at a notch-mark in a 100.3 mm long ocean quahog, *Arctica islandica*, about 110 yr old recovered on 9 September 1980. Note two annual increments of growth formed laterally beyond the notch-mark, estimated to be 0.1 mm (scale bar = 100 μm). (b) SEM photomicrograph of the same specimen (scale bar = 100 μm). The penetration of epoxy medium corresponds to the marking event. (c) Tran-





sitional CA-CL microstructure in the upper left interrupted by the penetration of epoxy into the shell along the line corresponding with the notching event (scale bar = 10 μm). Beyond the zone of epoxy penetration this line is recognized as an ISP band. Following this line is a zone of SphP disruption growth which gradually gives way to transitional CA-CL. This photomicrograph was taken off the field of view of (b), to the lower left. (d) Disruption growth of SphP microstructure following the line which corresponds to marking of the clam (scale bar = 50 μm).

interruption in shell deposition as did a 66.4 mm shell-length specimen collected during a 1980 winter clam survey (Fig. 7 a, b). A depression outlined the entire shape of the clam at the time of its formation and at 25.9 mm shell length. The shell formed before the depression was raised laterally above that formed afterwards in a shinglelike fashion. Both valves of the clam showed the interruption. The smaller shell shape was only slightly atypical for ocean quahogs, and no irregularity was found as an indication that an injury had occurred. The ratio between the greatest shell height (21.4 mm) and shell length (25.9 mm) of the smaller shell was 0.826, and for the entire shell (50.2 mm shell height; 66.4 mm shell length) was 0.756. These values suggest that growth after the depression departed from the more typical, isomet-

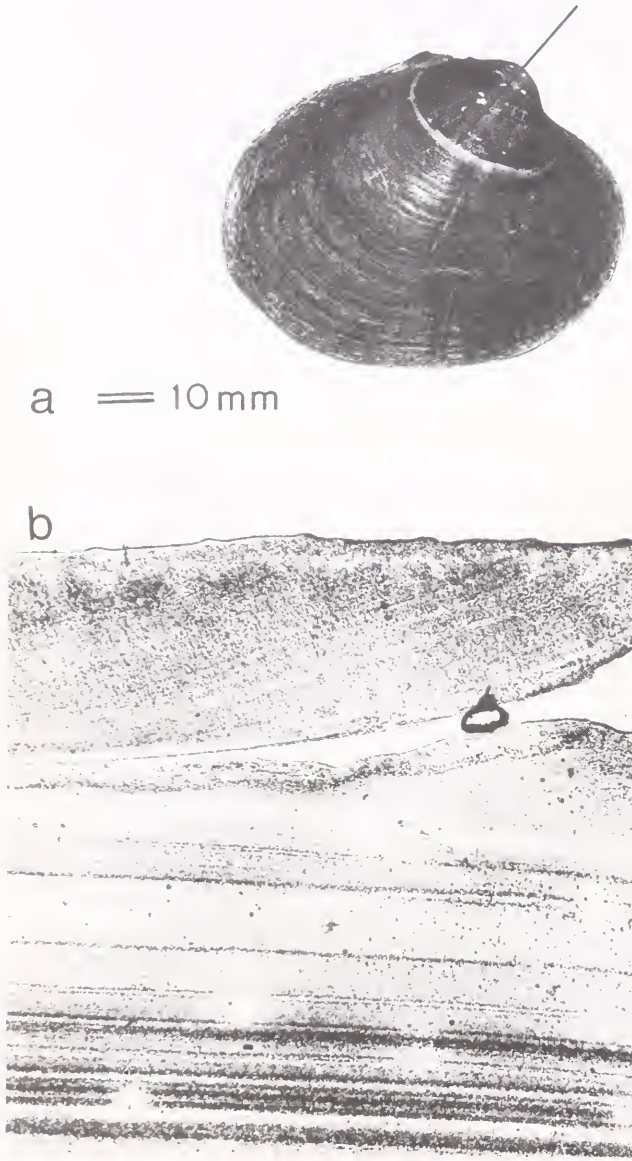


FIGURE 7.—(a) Right valve of an ocean quahog, *Arctica islandica*, 23 yr old and 66.4 mm in shell length collected near the marking site during 1980. An obvious interruption of growth (arrow) and radiating lines in the anterior half of the valve are shown. (b) Optical photomicrograph (compound microscope) of an acetate peel of the sectioned valve at the site of growth interruption. Scale bars of magnification are included.

ric growth reported for ocean quahogs by Murawski et al. (1982). Light radial lines extended from the umbonal area to valve margin in the periostracum of the anterior half of the shell formed after growth had been interrupted, but their significance was not evident.

Microstructure of Unmarked Shells

The ocean quahog shell is entirely aragonitic with an inner and outer layer separated by an extremely thin prismatic pallial myostracum. The latter is composed predominantly of irregular simple prisms (ISP) and occasionally a few fibrous prisms (FP). Both principal shell layers contain two growth sublayers: The thin annual growth line and the wider annual growth increment. Significant variations were found in the microstructure of each during examinations by SEM.

The distribution of microstructures in a typical ocean quahog shell may be seen by considering a transect from the exterior to interior depositional surfaces. The thick, dark brown or black periostracum is an obvious exterior surface covering, but it is intimately associated with the shell. Some aragonitic shell material is invariably removed when peeling off the periostracum and granules of aragonite were found embedded in it during examination of unetched thin sections under the crossed nicols of a polarizing microscope. The aragonite is dissolved by etching the polished surfaces of sectioned shells, leaving cavities, some with angular faces in the periostracum (Fig. 8a).

Important microstructures for aging purposes are found mostly in the outer shell layer. The dominant growth increment sublayer beneath the periostracum exhibits a granular homogeneous (HOM) microstructure which is very cavernous and has bleblike isolated crystal morphotypes (ICM) (Fig. 8b, c). These microstructures typically grade into incipient ISP (Fig. 8d). Below the prisms is a layer of crossed microstructures which appear to be transitional between simple crossed lamellar (CL) and crossed acicular (CA) structures (Fig. 8d). The latter predominates in the middle portion of the outer shell layer with occasional occurrences of fine complex-crossed lamellar (FCCL) microstructure. Transitional CA-CL microstructures are also seen in Figure 8e.

In the thin growth lines of the outer shell layer, FP near the external surface soon give way to very distinctive spherultic prisms (SphP) (Fig. 9a-d). These SphP themselves grade into composite prisms (CompP) which are comprised of first-order prisms with the second-order prisms radiating toward the depositional surface from a central, longitudinal axis. Closer toward the inner shell layer the FP, SphP, and CompP microstructures are gradually replaced by ISP bands.

The inner shell layer is characterized by growth lines composed of ISP which alternate with growth increment bands of FCCL microstructures. The hinge plate and tooth region have microstructures recognizable as distinct sublayers that are important for aging purposes. Here growth lines are constructed of narrow ISP (Fig. 9e). These alternate with growth increment bands that are composed of transitional CA-CL, FCCL, and HOM microstructures (Fig. 9e).

In summary, ocean quahog shells are composed largely of HOM, CA-CL, and minor amounts of FCCL microstructures with prismatic bands of local importance. The latter constitute the growth line layer; the former the growth increment layer. Figure 10 is a diagrammatic sketch of the distribution of microstructures in the two principal layers of the valve of a typical ocean quahog.

Microstructure of Marked Shells

Variations in the shell microstructure associated with notching and subsequent shell growth of ocean quahog specimens were studied by examining the ventral margins of six quahogs. The same basic pattern described for unmarked shells was observed in these specimens. Optical and scanning electron photomicrographs of two shells illustrate the salient features (Figs. 5, 6).

The notching event in both shells was accompanied by a disruption of the normal growth pattern and a resumption of shell growth at a new orientation. This is seen in Figures 5a and 6a as a prominent flattened surface in the exterior shell surface from the marking operation followed by a lateral extension of the shell margin out beyond the notch mark and old shell surface. The extension represents renewed growth at a new orientation. Retraction of the mantle during the marking process and resumption of shell growth at a slightly new orientation resulted in a zone of either loosely calcified or uncalcified shell paralleling the shell margin and extending from the notch inward toward the depositional surface. This zone is filled with epoxy medium during the embedding process and is seen in Figures 5b and 6b, c, and d as the resistant, unetched material penetrating several millimeters into the outer shell layer. The penetration zone disappeared shortly beyond the field of view in Figures 5b and 6b. Where this happened (Fig. 5c), a

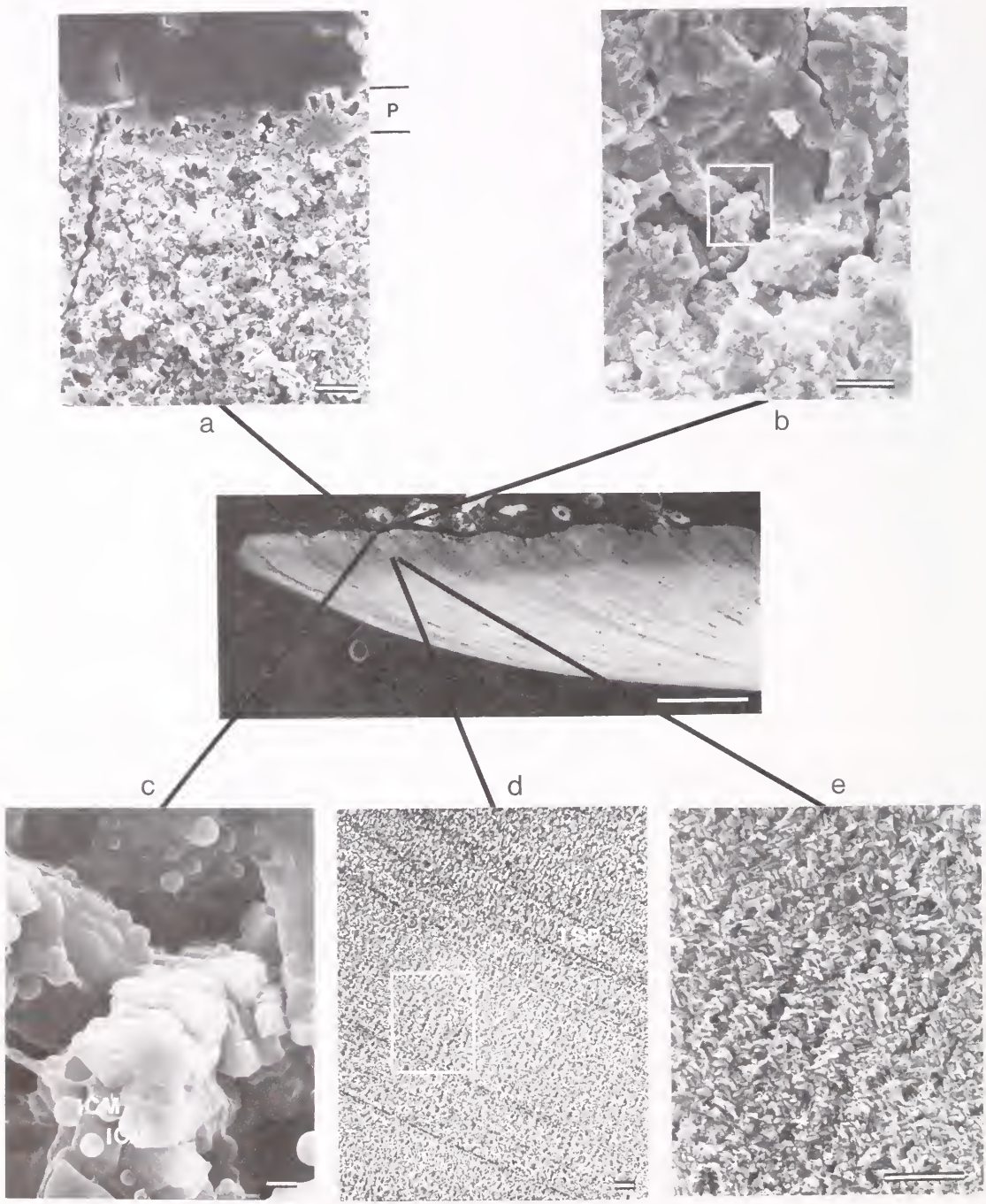


FIGURE 8.—Microstructural variation in the shell of a 97.5 mm long, 92-yr-old ocean quahog, *Arctica islandica*. The central photograph is of an acetate peel from a radial, polished, and etched section through the valve at the ventral margin. Black lines locate SEM photomicrographic enlargements of specific polished and etched areas in the section valve (scale bar = 1 mm). (a) Periostracum ("P") with angular cavities and HOM microstructure (scale bar = 10 μm). (b) Cavities in HOM microstructure of outermost valve surface. White rectangle encloses are enlarged in (c) (scale bar = 10 μm). (c) Cavities showing bleblike ICM structures (scale bar = 1 μm). (d) HOM microstructure at top trending to ISP, then to transitional CA-CL toward the bottom. White rectangle encloses the area enlarged in (e) (scale bar = 10 μm). (e) Transitional CA-CL microstructure at higher magnification (scale bar = 10 μm).

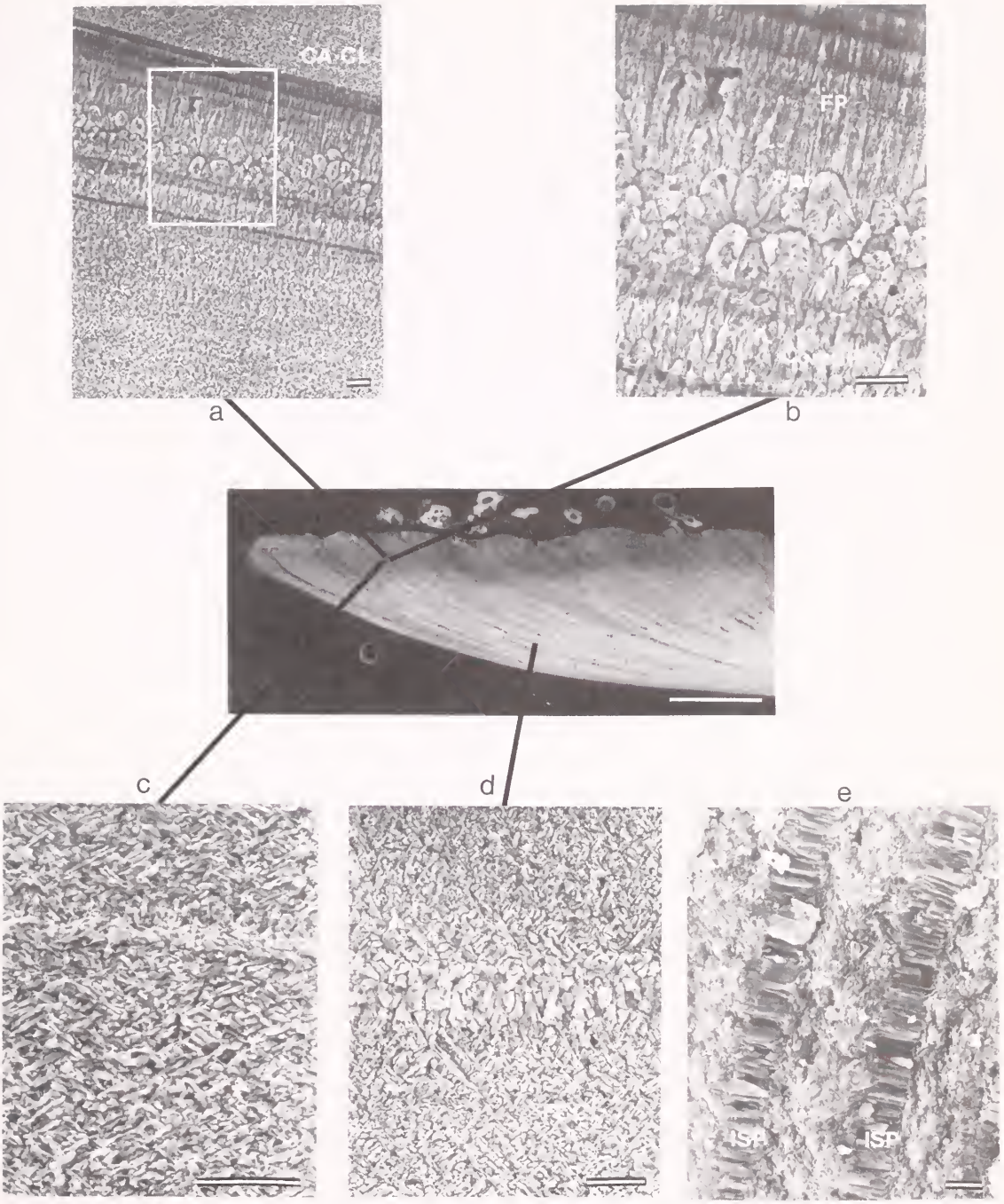


FIGURE 9.—Microstructural variation in the shell of ocean quahog, *Arctica islandica*, continued from Figure 8. (Central photograph scale bar = 1 μm). (a) Annual growth line sublayer (region between upper and lower-most dark bands) in outer shell layer, located beneath the CA-CL microstructure of Figure 8e. White rectangle encloses the area enlarged in (b) (scale bar = 10 μm). (b) The center of the growth line sublayer showing FP, SphP, and CompP microstructures (scale bar = 10 μm). (c) Transitional CA-CL microstructure of the growth increment sublayer below (b) (scale bar = 10 μm). (d) ISP forming growth line sublayer within FCCL microstructure. Photomicrograph from area closer to the depositional surface than previous photos (scale bar = 10 μm). (e) HOM microstructure interrupted by two prominent ISP bands from a section through the hinge plate (scale bar = 10 μm).

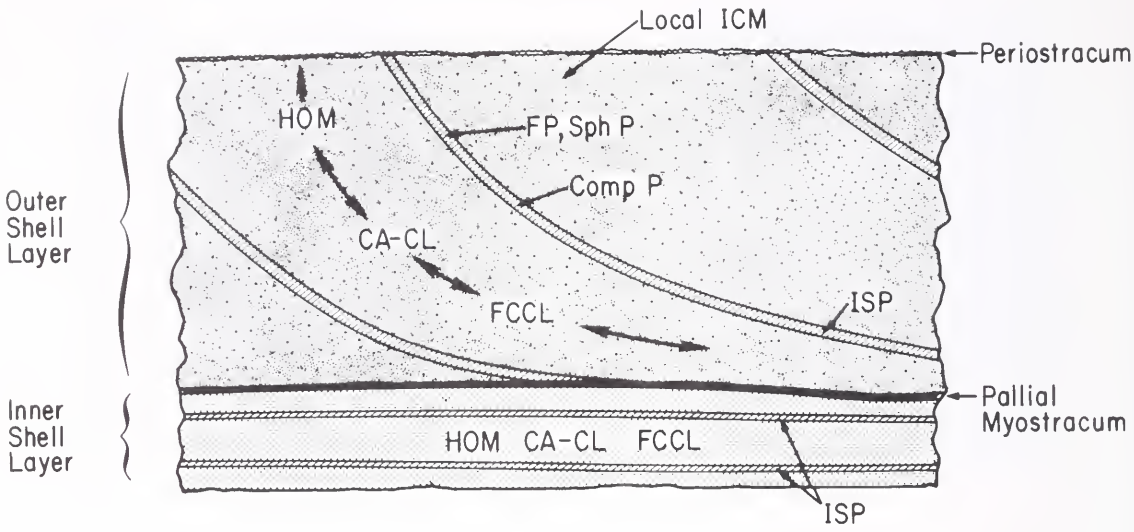


FIGURE 10.—Idealized, partial, radial cross section through the shell of a typical ocean quahog, *Arctica islandica*, showing the distribution of shell microstructures. Ventral margin is toward the left. Section is located inside the pallial line. Legend of acronyms: ICM = isolated crystal morphotypes; FP = fibrous prisms; SphP = spherulitic prisms; CompP = composite prisms; ISP = irregular simple prisms; HOM = granular homogeneous; CA = crossed acicular; CL = crossed lamellar; FCCL = fine complex crossed lamellar.

growth line of ISP continued parallel to the earlier growth lines.

The typical outer shell layer structure formed by the time of marking is noted in Figures 5b and 6b. These figures clearly show the alternation of the growth line and growth increment sublayers. However, immediately following the marking event all specimens showed a disruption in microstructural development, especially out near the shell surface. This coincided with the presence of loosely organized SphP immediately following the marking event line (see particularly Fig. 6c, d). The disruption zone consisted of cavernous, poorly organized, microstructure (Fig. 5d).

In all six shells examined, the growth line associated with the marking event continued inward toward the shell interior, even beyond the zone of epoxy penetration (Figs. 5b, 6b). When this line was traced inward, it was indistinguishable from the many earlier formed growth lines. Such a view is seen in Figure 5c located well off the field of view Figure 5b, to the bottom left. Here the growth line consisted of a diagonal ISP band bounded on both sides by transitional CA-CL microstructure.

DISCUSSION

The layering and separation between growth lines and growth increments of small ocean quahogs (< ca 60 mm shell length) are often visible macroscopically on the external surfaces of whole valves and in the cut surfaces of radial sections. However, macro- or microscopic examinations of large ocean quahog valves are consistently frustrated by a lack of clear differentiation of the same growth phenomena. Preparation of acetate peels of shell cross sections, as has been described and photographically documented, greatly enhances discrimination of the lines and increments of growth throughout the range of shell sizes.

Past investigators of the microstructure of ocean quahog shells described some of the basic components, but did not clearly elucidate differences between the lines and increments of growth. Sorby (1879: 62) appears to have given the first description of the structure of the *Arctica* (= *Cyprina*) *islandica* shell: "In *Cyprina islandica* we have another extreme case, in which the fibres perpendicular to the plane of growth are so short as to appear like granules, though the optic axes are still definitely oriented in the normal manner." Bøggild (1930:286) reported that he was unable to confirm Sorby's observations. Instead he stated that *Arctica islandica* belongs to a group of species within the Arcticidae (= Cyprinidae) having the least visible structure among all the bivalves. He terms this structure homogeneous but suggests there are small traces of other structures in the shell. Bøggild (1930) goes on to point out that the lower

part of the shell (inner layer) is perhaps more "... representative of the common, complex structure ... and ... there are alternating layers of more transparent layers and finely grained ones." More recently Taylor et al. (1969, 1973) examined the shell microstructure of *Arctica islandica*, which they adopted as their "type species" to illustrate homogeneous shell microstructure. Basically, the general picture by Bøggild (1930) agrees with that of Taylor et al. (1969), who used electron microscopy in their investigation. However, they disagreed sharply with Bøggild that the inner shell layer was "representative of the common complex structure." After examining unetched fractured sections and polished and etched sections of both shell layers, Taylor et al. (1969, 1973) concluded that both shell layers in *Arctica islandica* are built of minute, irregular rounded granules, quite variable in size (1.5-3 μm across), having highly irregular contacts with their neighbors and being poorly stacked. Taylor et al. (1969:51) further reported: "In peels and sections of the inner layer, within the pallial line there is a marked colour banding, in greys and browns. The only fine structure that can be resolved is a suggestion of minute grains, which are most conspicuous in the translucent, grey-colourless parts of the shell. These grains are arranged in sheets parallel to the shell interior. In the outer layer grains can also be resolved, but are arranged in sheets parallel to the margin of the shell and growth lines." They also noted that these features are more clearly seen in the umbonal region where the orientation of grains normal to layering is very conspicuous. Taylor et al. (1969) suggested that the layering is a reflection of repeated (?diurnal) deposition of carbonate (a prospect deemed very unlikely by Thompson et al. 1980a). Also in the umbonal region are thin (2-3 μm) prismatic bands which parallel the layering. Outside the pallial line, Taylor et al. (1969) reported the outer shell layer to be very dense and opaque, with the most obvious structural features being fine grains arranged in sheets giving the layer a finely banded appearance.

Analyses under SEM of oriented fractured, and polished and etched sections of ocean quahog shells revealed that microstructural variation is more complex than had been proposed by Bøggild (1930) or Taylor et al. (1969, 1973). Thin sections of isolated periostracal fragments examined under crossed nicols confirmed the presence of embedded aragonite granules in the periostracum of ocean quahogs reported for other recent bivalves (Carter and Aller 1975). These granules probably form a layer like that described for the blue mussel, *Mytilus edulis*, by Carriker (1979). After special treatment of the valves for examination by SEM, he found "a thin discrete calcareous layer continuous over the outer surface of the valves between the periostracum and the outermost shell layer." The layer is called mosaiostracum. The shell microstructure in the growth increment sublayer beneath the periostracum is HOM, as Bøggild (1930) and Taylor et al. (1969, 1973) reported. The "... minute, irregular, rounded granules ... have highly irregular contacts ..." (Taylor et al. 1969:51) that are particularly well exposed in fracture sections. An abundant transitional CA-CL microstructure was found in the middle portion of the outer shell layer and growth increment sublayer. This study confirmed its presence in ocean quahogs as reported by Carter (1980). The growth line sublayer of the outer shell layer had four grades of prismatic structure (FP, SphP, ComP, and ISP). Lutz and Rhoads (1977) examined the inner shell layer near the umbo of ocean quahogs and found bands of simple aragonitic prisms alternating with complex-crossed lamellar and homogeneous structures. We found similar microstructures in the inner shell layer of the valve of ocean quahogs. Our analyses identified distinct microstructures, not unlike those found in the valve for the growth line and growth increment layers in the hinge plate.

Growth line deposition more nearly approximates an annual event than any shorter or longer interval. Marked clams recovered in late August 1979 had formed only one growth line other than the mark-induced check soon after the notching operation in 1978. They had been free about 22 d longer than a calendar year. Those recovered in early September 1980 all had formed the growth line soon after the notching operation, like those recovered in 1979, and a second line appeared midway to the ventral valve edge, which in all probability had been formed after the late August 1979 recovery effort. These clams were free about 33 d more than 2 calendar years since the notching operation. A feature of the specimens recovered in 1980 was that about half had formed a third line very near the ventral valve edge and along the inner margin. All of the narrow growth lines were separated by relatively even, broad areas of growth increment deposits suggestive of no more or less than an annual interval for the deposition of growth lines, even though the time of formation of such lines may not correspond to an exact number of calendar days. These observations confirm similar conclusions of an annual periodicity of growth line formation by Thompson and Jones (1977), Thompson et al. (1980a, b), and Jones (1980).

Radiometric techniques for aging bivalve shells have recently been applied to ocean quahogs.

Thompson et al. (1980a) reported that the predicted radiometric age of an ocean quahog having 22 bands corresponded exactly to 22 yr when aged using ^{228}Ra. Turekian et al. (1982) concluded that age determinations of ocean quahogs from radiometric analyses are compatible with counts of bands formed annually. Thus, radiometric studies support the contention of an annual periodicity of growth lines in ocean quahogs.

Various environmental disturbances have been implicated in the formation of shell abnormalities and atypical growth lines in other bivalve species (Weymouth et al. 1925; Shuster 1957; Merrill et al. 1966; Clark 1968; Palmer 1980). It is therefore, conceivable that the stress imposed by dredging, marking, and returning the ocean quahogs to the ocean floor and their burrowing activities hastened the formation of a growth line in 1978. Thereafter, natural events affecting the metabolism of shell deposition are more likely stimuli. Such events apparently did not occur during the period after the formation of the growth line in 1978 and recovery of clams in late August 1979. Instead a growth line that in all probability had formed in 1979 was found in the shells of clams recovered on 9 September 1980. Its formation may have occurred in late August 1979, but the third line found in half of the clams recovered on 9 September 1980 suggests the possibility of its formation in early September 1980. By inference, then, growth line formation in 1979 and 1980 occurred in September.

The reported life span (150 yr, Thompson et al. 1980a) of ocean quahogs surpasses similar estimates for other bivalves. Age and growth of the far east mussel, *Crenomytilus grayanus*, have been determined from examinations of shell structure, an oxygen-isotope method, and notching experiments (Zolotarev 1974; Zolotarev and Ignat'ev 1977; Zolotarev and Selin 1979). These investigations indicated that longevity of the mussel may exceed 100 yr. Turekian et al. (1975) proposed a longevity of about 100 yr for a deep-sea nucoloid, *Tindaria callistiformis*, after determining ages by radiometric means and counting regularly spaced bands in the shell of one of the largest (8.4 mm in shell length). It seems likely that longevity of ocean quahogs may exceed 150 yr. Murawski and Serchuk (1979) reported a maximum shell length of 131 mm for ocean quahogs in extensive collections taken from the Middle Atlantic Bight. A specimen of this size is half again as large as the 88 mm example of a 149-yr-old ocean quahog reported by Thompson et al. (1980a).

In conclusion, the foregoing description of annual growth line formation in marked ocean quahogs and analyses of growth in the same specimens by Murawski et al. (1982) present significant supporting evidence for the hypothesis of slow growth and a long life span in the species. Ocean quahogs apparently live longer than any other bivalve known to man.

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FOOD OF SILVER HAKE, *MERLUCCIUS BILINEARIS*

RAY E. BOWMAN[1]

ABSTRACT

Stomach contents of 2,622 silver hake collected in the Northwest Atlantic have been analyzed. Fish were collected on bottom trawl surveys conducted from 1973 to 1976. The mean fish fork length (FL) was 20 cm and the average stomach content weight was 1.5 g. Silver hake <20 cm FL prey mostly on amphipods, decapod shrimp, and euphausiids. Fish 20 cm FL and longer take increasing proportions of fish and squid as part of their diet. Stomach contents of male and female fish of similar size indicate that females eat larger quantities of food (particularly more fish) than the males. The females are also, on the average, longer than the males. Silver hake feed primarily at night. Feeding begins near dusk and continues until just after midnight. In the spring a second feeding period seems to occur near noon. Silver hake feed intensively during spring. Their stomachs contain almost twice as much food in spring as they do in autumn. Significant differences were noted in the intensity of feeding between areas. Stomachs of fish, caught in the Middle Atlantic, contain the largest quantities of food. The species of prey taken by silver hake are highly variable and likely reflect prey availability during different years and seasons in various areas. When silver hake spawn, their dietary intake is reduced. The diet of fish taken in deep water (>150 m) is mostly euphausiids and squid, and the quantity of food found in their stomachs is less than that in stomachs taken from fish collected at depths <150 m.

Silver hake, *Merluccius bilinearis* (Mitchill 1814), is a Northwest Atlantic gadiform fish whose range extends from continental shelf waters off South Carolina to the Newfoundland Banks. It is most abundant in offshore waters extending from New York to Cape Sable, Nova Scotia (Bigelow and Schroeder 1953).

Previous investigations have shown that large silver hake eat mostly fish and/or squid, while smaller silver hake feed on euphausiids, amphipods, and decapod shrimp. Among the first to report these findings were Nichols and Breder (1927), who noted 75 herring about 7 cm long in the stomach of a 59 cm fish. Bigelow and Schroeder (1953) reported that silver hake are extremely voracious and will prey on smaller silver hake or any other of the schooling fishes such as young herring, mackerel, menhaden, alewives, or silversides. Evaluation of other studies on the diet of silver hake caught in various areas and during different years establishes that the prey of silver hake is very predictable in that it is usually comprised of a variety of fish, squid, and crustaceans (Jensen and Fritz 1960; Schaefer 1960; Vinogradov 1972; Noskov and Vinogradov 1977; Bowman and Langton 1978; Langton and Bowman 1980). Investigations by Swan and Clay (1979), Edwards and Bowman (1979), and Bowman and Bowman (1980) have shown that silver hake feed mostly at night.

Until recently the potential impact of silver hake on the Northwest Atlantic ecosystem had not been determined. Edwards and Bowman (1979) estimated the annual consumption of the principal predators in the Northwest Atlantic. They concluded that silver hake alone could potentially consume almost 10% of the standing crop of all fish within the study area annually, the bulk of which would be small or juvenile fish. They suggested that silver hake, more than any other species, plays the principal predatory role in regulating the Northwest Atlantic ecosystem. The purpose of this report is to document the quantities and types of food eaten by silver hake during the years 1973-76, and further, to identify feeding trends which may be of consequence when attempting to precisely determine silver hake's impact on other fish populations.

METHODS AND MATERIALS

A total of 325 samples from 2,622 silver hake stomachs was collected during eight MARMAP (Marine Resources Monitoring, Assessment, and Prediction) bottom trawl survey cruises conducted by the National Marine Fisheries Service during spring and fall 1973-76 (Table 1). The cruise periods were as follows: 16 March-15 May 1973; 26 September-20 November 1973; 12 March-4 May 1974; 20 September-14 November 1974; 4 March-12 May 1975; 15 October-18 November 1975; 4 March-8 May 1976; 20 October-23 November 1976. On spring cruises a two-seam modified Yankee No. 41 trawl was

[1]Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

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TABLE 1.—Number of silver hake stomachs examined from each geographic area by year and season.

Year	Season	Number examined		
		Middle Atlantic	Southern New England	Georges Bank
1973	Spring	39	105	48
	Fall	144	129	191
1974	Spring	189	93	103
	Fall	54	117	157
1975	Spring	68	100	92
	Fall	91	120	146
1976	Spring	111	125	63
	Fall	93	129	115
Totals		789	918	915

fished, and during fall cruises a standard Yankee No. 36 was used. The cod end and upper belly of both trawls were lined with 13 mm mesh netting to retain smaller fish. A scheme of stratified random trawling was conducted within the study area (Fig. 1), and fishing continued over 24 h/d[2]. All tows were 30 min in duration at a vessel speed of 3.5 kn in the direction of the next station.

Sampling of stomachs was concentrated in three areas: Middle Atlantic, Southern New England, and Georges Bank (Fig. 1). Fish within two length groups (≥20 cm and <20 cm) were randomly selected (50 fish/group) during each cruise from the bottom trawl survey catches in each area. At each station within a particular area no more than 10 fish were taken for each of the two length groups, and fish were not sampled at two consecutive stations. The only exception to this collection method occurred when it appeared (during the cruise) that 50 large or 50 small fish would not be collected within a particular area. In this case, all fish caught were collected in an attempt to obtain the minimum sample size. Stomachs of large fish were excised aboard ship; individually wrapped in gauze with a label denoting vessel, cruise, species, fork length (FL), sex, and maturity; and preserved in 3.7% formaldehyde (small fish were preserved whole).

In the laboratory the preserved stomachs were individually opened, and their contents emptied onto a 0.25 mm mesh opening screen sieve to permit washing without loss of any food items. The stomach contents were sorted, identified, counted, and damp dried on absorbent paper. Major prey items and commonly occurring but relatively minor prey, in terms of weight, were identified to species whenever possible. The wet weight of all stomach content groups was determined to the nearest 0.001 g and all information recorded. A stomach was considered empty when no food items could be identified and the material found in the stomach weighed <0.001 g. Data were analyzed with FORTRAN IV programs written for use on a Honeywell SIGMA 7[3] computer system located in Woods Hole, Mass.

Food data are presented in terms of the mean stomach content weight, adjusted stomach content weight (discussed below), and the percentage weight

[2]Further details of the bottom trawling techniques may be obtained from the Resource Surveys Investigation, Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

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

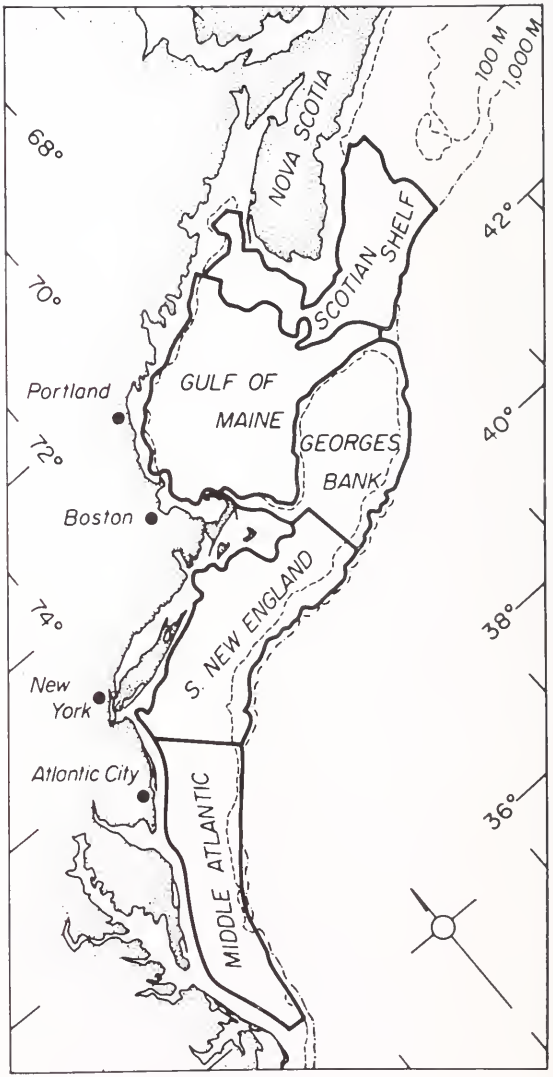

FIGURE 1.—Offshore areas sampled during bottom trawl surveys conducted by the Northeast Fisheries Center between the years of 1973 and 1976, inclusive.

each prey group made up of the total stomach contents weight. All tables follow a standard format to aid in making comparisons. In the tables, subtotals of the percentage weight of major stomach content groups are offset to the left. The minor prey groups are discussed in further taxonomic detail in the text.

Adjusted stomach content weights are weights adjusted by a correction factor which allows direct comparison of the stomach content weights of different-sized fish. Adjustment of the stomach content weights was necessary, before any quantitative comparisons could be made between variables such as sex or area. Observations on stomach tissue weight (excluding contents), mean stomach content weight, and whole fish weight (Fig. 2) revealed that neither the mean stomach content weight nor the stomach tissue weight is proportional to the body weight of different-sized fish. Stomach tissue weights of 526 silver hake were gathered during a study jointly conducted by American and Soviet scientists on Georges Bank, September 1978, aboard the Soviet RV *Belogorsk* (operated by the Atlantic Research Institute of Marine Fisheries and Oceanography, Kaliningrad, USSR). Mean stomach content weight data were derived from the 1973-76 food data given in this report, and the fish body weights were calculated using the silver hake length-weight equation described by Wilk et al. (1978). Silver hake weighing <100 g, or >300 g, have larger stomachs (stomach tissue weight being an indication of stomach size), and stomachs which contain on the average more food in terms of percentage body weight, than fish weighing between 100 and 300 g. Since both the stomach tissue weight and the mean stomach content weight were disproportionate when presented as percentage body weight for different-sized fish (but were generally proportionate relative to each other), and because the mean stomach content weight data was much more variable than the stomach tissue weight data, the data adjustment was based on stomach tissue weight rather than on body weight or mean stomach content weight. The following equation was used to adjust the stomach content weights:

$$\bar{A}_L = \frac{\bar{x}l}{\bar{w}l}$$

where $\bar{A}_L$ = Adjusted stomach content value. The adjusted stomach content value was converted to grams by multiplying it by the stomach tissue weight of a 30 cm FL fish.

$\bar{x}l$ = Mean stomach content weight of all fish at a given length.

$\bar{w}l$ = Mean stomach tissue weight of silver hake at a given length.

The adjusted stomach content data for fish 4 (0.3 g) to 15 (21 g) cm FL and 24 (90 g) to 35 (292 g) cm FL are presented separately in forthcoming sections.

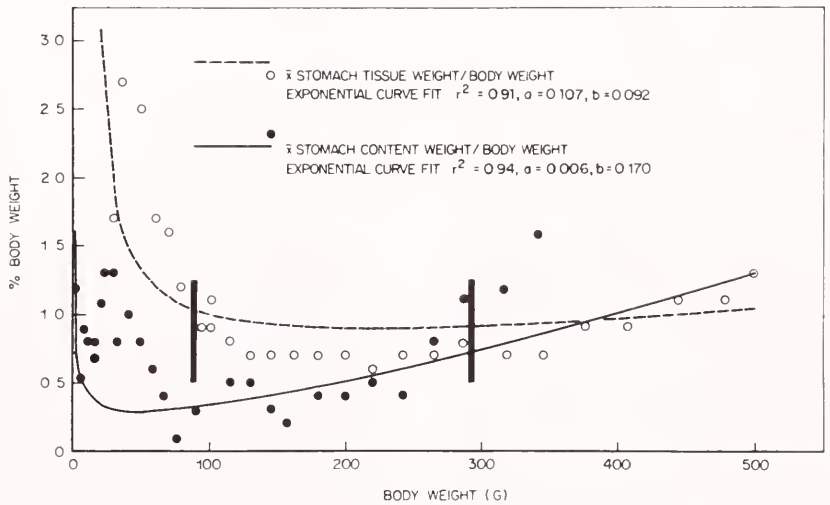

FIGURE 2.—Percentage body weight made up by the stomach tissue weight and the stomach content weight of different size silver hake. Area enclosed by solid lines represents more than 80% (excluding juveniles) of the silver hake population (fish 2-7 yr old), based on survey data. Stomach tissue weight/fish length and stomach content weight/fish length data were fit to an exponential curve (form $y = ae^{bx}$). The data are presented in terms of body weight for illustrative purposes.

These two length groups were chosen because the food consumption of fish <1 yr old (4-15 cm FL) differs substantially from the food consumption of older fish (evident from Figure 2). In addition, too few fish outside these length ranges were sampled to warrant inclusion in any of the calculations dealing with comparisons between data sets. An analysis of variance (one way) was used to test the observed differences among sample means (e.g., between geographic areas).

RESULTS

The contents of 2,622 silver hake stomachs, of which 803 (30.4%) were empty, were analyzed. Fish sampled averaged 20 cm FL and had, including the empty ones, a mean stomach content weight of 1.5 g. Sources of potential variation in the data presented below include size, sex, and maturity stage of fish, as well as the time of day, area, year, season, bottom depth, and temperature when or where the fish were caught. Each variable considered in this analysis is treated separately, i.e., the data were pooled over other variables with no attempt to determine the possible confounding effects of different variables on the results. Dietary trends noted within each particular variable examined should be considered only as preliminary observations.

Composition of the Diet

Overall, in terms of percentage weight, the diet of silver hake consists almost entirely of fish (80.0%), crustaceans (10.2%), and squid (9.2%), as can be seen in Table 2. The importance of crustaceans to the diet is overshadowed by the fish portion because large silver hake eat heavier meals consisting primarily of fish. However, Table 2 is useful because it serves as a composite list of the prey types commonly found in the stomachs of silver hake. Fish such as silver hake, *Merluccius bilinearis*; Atlantic mackerel, *Scomber scombrus*; butterfish, *Peprilus triacanthus*; herring (Clupeidae); American sand lance, *Ammodytes americanus*; scup, *Stenotomus chrysops*; Atlantic saury, *Scomberesox saurus*; and longfin hake, *Phycis chesteri*, each make up >0.1% of the stomach contents. The "Other Pisces" category, most of which could not be identified, accounts for a substantial portion (52.0%) of the "Pisces" group. Fishes which could be identified within this category (all contributed <0.1% to the diet) include summer flounder, *Paralichthys dentatus*; redfish, *Sebastes marinus*; codfishes (Gadidae); and flatfishes (Pleuronectiformes).

Crustacea in the diet is represented principally by euphausiids (mostly *Meganyctiphanes norvegica*, 3.7%, and *Euphausia*, <0.1%) and decapods such as the Crangonidae (mainly *Crangon septemspinosa*, 1.4%, and *Sclerocrangon boreas*, <0.1%), Pandalidae (almost exclusively *Dichelopandalus leptocerus*, 2.0%, although some *Pandalus borealis*, <0.1%, was also found), Pasiphaeidae (only *Pasiphaea multidentata*, 0.1%), and other unidentified decapods (0.4%) which were mostly shrimp (0.3%). Amphipods found in the stomachs consist primarily of the families Ampeliscidae (<0.1% each of *Ampelisca agaxxizi*, *A. spinipes*, *A vadorum*, and *Byblis serrata*), Oedicerotidae (<0.1% of *Monoculodes edwardsi* and *M. intermedius*), and Hyperiidae (exclusively the genus *Parathemisto*, 0.1%). The remaining crustacean groups are the Mysidacea (comprised of *Neomysis americana*, 0.7%, and *Erythrops*, <0.1%), Cumacea (mostly *Leptocuma*, <0.1%, and some unidentified diastylids, <0.1%), Copepoda (almost all identified as calanoids, <0.1%), and "Other Crustacea" (all of which was well-digested crustacean remains, 0.3%).

The only other stomach contents identified were the cephalopods (*Loligo pealei*, 4.7%, and *Rossia*,

TABLE 2.—Dietary composition of 2,622 silver hake caught in the Northwest Atlantic during the years 1973-76. (+ indicates <0.1%.)

Prey	Percentage weight	
Polychaeta	0.1	
Crustacea	10.2	
Amphipoda	1.3	
Ampeliscidae		1.0
Oedicerotidae		0.1
Hyperiidae		0.1
Other Amphipoda		0.1
Decapoda	3.9	
Crangonidae		1.4
Pandalidae		2.0
Pasiphaeidae		0.1
Other Decapoda		0.4
Euphausiacea	4.0	
Mysidacea	0.7	
Cumacea	+	
Copepoda	+	
Other Crustacea	0.3	
Cephalopoda	9.2	
Loligo		7.6
Other Cephalopoda		1.6
Pisces	80.0	
Scomberesox saurus		1.5
Clupeidae		2.7
Merluccius bilinearis		9.2
Phycis chesteri		0.2
Ammodytes americanus		1.8
Scomber scombrus		7.5
Stenotomus chrysops		1.6
Peprilus triacanthus		3.5
Other Pisces		52.0
Miscellaneous	0.5	
No. of stomachs examined	2,622	
No. of empty stomachs	803	
Mean stomach content weight (g)	1.477	
Mean fish FL (cm)	20.3	

<0.1%), Polychaeta, and the "Miscallaneous" category, which consisted of small amounts (<0.1%) of Echinodermata, Chaetognatha, unrecognizable digested matter, and sand.

The percentage weights of various prey of silver hake within specified length groups are listed in Table 3. Silver hake <20 cm FL eat mostly crustaceans (>80% on the average), whereas the food of individuals >20 cm FL is mostly fish and squid (average over 50%). Stomachs of silver hake 3-5 cm FL contain the largest percentages of smaller crustacean forms, such as amphipods and copepods. Decapods, euphausiids, and mysids, which are generally larger organisms (see Gosner 1971), make up the largest percentage of the diet of fish 6-20 cm FL.

Diet Differences Between Males and Females

The diet of male and female silver hake differs in both quality and quantity of food (Table 4). The stomachs of males have the largest percentage of crustaceans, while those of females have the largest percentage of fish and squid. The mean stomach content weight of the males is only about one-fifth that of the females. Males also occur less frequently in the samples (42% of the fish collected were males) and are generally smaller than the females (mean FL males, 28.4 cm; females, 32.1 cm). Since female fish are, on the average, longer than the males, the differences noted above had to be dealt with in considerably more detail.

A comparison of the data in Tables 5 (food of males) and 6 (food of females) indicates that males and females within the same size groupings consume different types and amounts of food. The same dietary patterns noted for male and female fish in the preceding paragraph can be seen within most of the individual length groups in these two tables (e.g., when males and females within the same size group are compared, the stomachs of the females contain larger quantities of food and higher percentages of fish and squid). The number of males sampled generally exceeds the number of females for length groups <30 cm, while females dominate the length groups >30 cm.

A subset of the data were analyzed separately using only fish lengths for which 20 or more individuals each of males and females were sampled (Fig. 3). This group of fish (ranging in FL from 24 to 34 cm) is fairly representative of the adult silver hake population sampled. The mean stomach content weight (Fig. 3A), percentage crustaceans (Fig. 3B), and percentage fish and squid (Fig. 3C) data presented graphically illustrate the differences between the diet of male and female silver hake of the same length. The stomachs of females contain more food, on the average, than those of males; the stomachs of males contain higher percentages of crustaceans than females; and the stomachs of females contain more fish and squid than those of males. Adjustment (by stomach tissue weight) of the mean stomach content weights given in Figure 3A revealed that the stomachs of females contain, on the average, 1.5 times the quantity of food found in the stomachs of males.

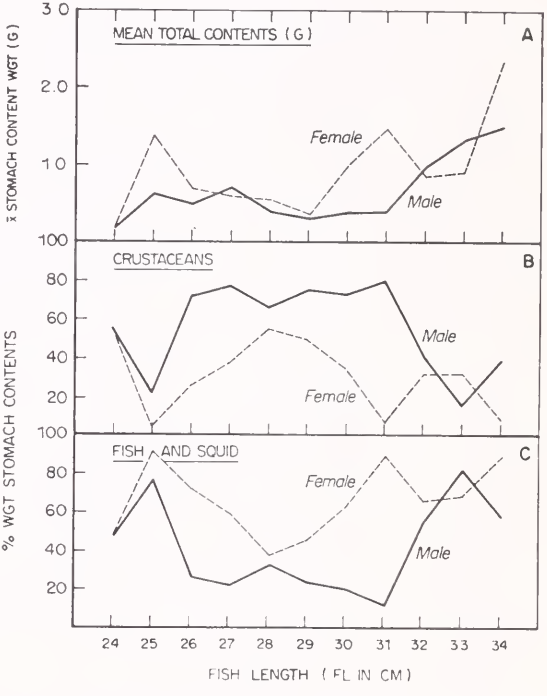

FIGURE 3.—A) Mean stomach content weight of male and female silver hake versus fish length, B) percentage of total stomach content weight made up by crustaceans for male and female silver hake, C) percentage of total stomach content weight made up by fish and squid for male and female silver hake.

Diurnal Variation in Feeding Intensity

The adjusted mean stomach content weight data presented in Figures 4 and 5 indicate the feeding periods of silver hake vary by season and size of fish. In autumn, the stomachs of larger fish (24-35 cm FL) are fullest just after midnight, while smaller fish (4-15 cm FL) have the fullest stomachs in late afternoon

TABLE 3.—Percentage composition (by weight) of the diet of silver hake versus fish length for silver hake collected in the Northwest Atlantic from 1973 through 1976. (+ indicates <0.1%.)

Prey	Length category (cm)										
	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	>50
Polychaeta	—	0.4	0.5	—	0.1	0.3	0.2	+	0.1	—	—
Crustacea	89.7	80.3	81.6	77.3	28.0	55.5	21.3	2.3	0.5	0.2	0.2
Amphipoda	58.7	18.9	6.1	1.2	1.7	1.3	0.7	+	+	—	+
Ampeliscidae	11.0	4.9	0.1	0.5	0.6	0.5	0.2	+	—	—	+
Oedicerotidae	3.1	3.4	4.1	0.1	+	0.2	0.1	+	—	—	—
Hyperiidae	42.1	6.2	0.3	0.4	0.6	0.4	0.3	—	—	—	—
Other Amphipoda	2 5	4.4	1.6	0.2	0.5	0.2	0.1	+	+	—	—
Decapoda	11.8	23.9	31.1	7.0	16.2	20.0	10.5	1.6	0.3	0.1	0.1
Crangonidae	7.7	16.0	18.7	3.7	4.3	6.1	4.3	0.3	0.1	—	+
Pandalidae	—	1.7	5.3	2.1	10.7	12.0	4.3	1.2	0.2	—	0.1
Pasiphaeidae	—	—	—	—	—	—	0.8	—	—	—	—
Other Decapoda	4 1	6.2	7.1	1.2	1.2	1.9	1.1	0.1	—	0.1	—
Euphausiacea	1.9	5.7	23.7	64 4	7.8	26.4	8.8	0.6	0.2	0.1	—
Mysidacea	4.2	22.1	12.8	3.9	0.2	6.7	0.6	+	+	—	0.1
Cumacea	0.8	1.1	0.2	+	0.2	+	+	—	—	—	—
Copepoda	1.7	+	+	—	+	—	—	—	—	—	—
Other Crustacea	10.6	8.6	7.7	0.8	1.9	1.1	0.7	0.1	+	+	+
Cephalopoda	—	—	—	—	17.8	3.4	14.9	14.3	0.1	12.0	—
Loligo	—	—	—	—	15.3	—	13.5	10.0	—	12.0	—
Other Cephalopoda	—	—	—	—	2.5	3.4	1.4	4.3	0.1	+	—
Pisces	4.8	13.9	14.0	19.9	52.8	38.7	62.4	83.4	98.9	99.8	
Scomberesox saurus	—	—	—	—	—	—	—	5.6	—	87.8	—
Clupeidae	—	—	—	—	—	—	3.5	3.5	8.0	—	—
Merluccius bilinearis	—	2.0	4.0	—	22.1	5.0	6.9	24.2	5.9	—	—
Phycis chesteri	—	—	—	—	—	—	1.2	—	—	—	—
Ammodytes americanus	—	6.3	2.0	—	—	+	3.1	0.4	7.7	—	—
Scomber scombrus	—	—	—	—	—	—	7.8	8.8	6.1	—	15.5
Stenotomus chrysops	—	—	—	—	—	—	—	—	10.5	6.8	—
Peprilus triacanthus	—	—	—	—	—	—	2.7	3.4	—	—	20.6
Other Pisces	4.8	5.6	8.0	19.9	30.7	33.7	37.2	37.5	60.7	—	63.7
Miscellaneous	5.5	5.4	3.9	2.8	1.3	2.1	1.2	+	0.4	+ 81.0	—
No. of stomachs examined	344	603	216	86	243	444	428	147	61	28	22
No. of empty stomachs	60	75	38	26	108	192	189	63	29	11	12
Mean stom. cont. wt. (g)	0.066	0.025	0.104	0.370	0.452	0.545	1.440	7.278	10.321	32.081	20.262
Mean fish FL (cm)	4.5	7.7	12.5	18.0	23.5	28.2	32.6	37.7	42.8	47.9	54.4

and just after midnight (Fig. 4). During springtime, large silver hake have substantial quantities of food in their stomachs (almost twice as much as during autumn) for two time periods, one near dusk and the other just before noon. Smaller fish have the most food in their stomachs just after midnight during spring (Fig. 5). No indication of a particular prey being eaten at a particular time of day was noted.

Diet Within Geographic Areas

Stomach content data for silver hake collected in various geographic areas (i.e., Middle Atlantic, Southern New England, and Georges Bank) are presented in Table 7. Fish is by far the dominant prey of silver hake within all geographic areas. Silver hake caught in the Middle Atlantic have the highest percentage of fish in their diet (Middle Atlantic, 87.5%; Southern New England, 78.4%; Georges Bank, 76.4%), but most was unidentified (60.4%). Silver hake (20.8%) and herring (Clupeidae, 3.2%) make up

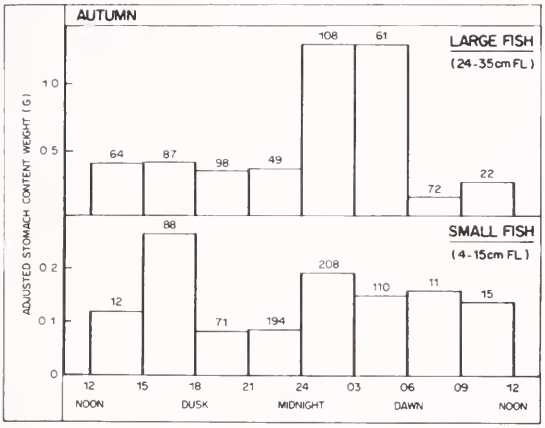

FIGURE 4.—Adjusted mean stomach content weight of large (24-35 cm FL) and small (4-15 cm FL) silver hake collected in the autumn versus time of day. The number of fish sampled in each time period is given just above the histogram.

TABLE 4.—Stomach contents of male and female silver hake collected in the Northwest Atlantic during 1973-76. Data are expressed as a percentage weight. (+ indicates <0.1%.)

Prey	Male	Female
Polychaeta	0.2	+
Crustacea	35.0	4.5
Amphipoda	0.6	0.2
Ampeliscidae	0.2	0.1
Oedicerotidae	0.1	+
Hyperiidae	0.2	0.1
Other Amphipoda	0.1	+
Decapoda	11.9	2.3
Crangonidae	5.1	0.6
Pandalidae	5.5	1.5
Pasiphaeidae	—	+
Other Decapoda	1.3	0.2
Euphausiacea	18.8	1.7
Mysidacea	2.7	0.2
Cumacea	+	+
Copepoda	+	—
Other Crustacea	1.0	0.1
Cephalopoda	4.3	10.4
Loligo	3.4	8.6
Other Cephalopoda	0.9	1.8
Pisces	59.1	84.6
Scomberesox saurus	—	1.8
Clupeidae	—	3.2
Merluccius bilinearis	22.6	7.6
Phycis chesteri	—	0.2
Ammodytes americanus	1.4	2.0
Scomber scombrus	3.8	8.4
Stenotomus chrysops	—	1.9
Peprilus triacanthus	3.3	3.7
Other Pisces	28.0	55.8
Miscellaneous	1.4	0.5
No. examined	613	842
No. of empty stomachs	252	354
Mean stom. cont. wt. (g)	0.853	4.204
Mean fish FL (cm)	28.4	32.1
Length range (cm)	6-59	7-64

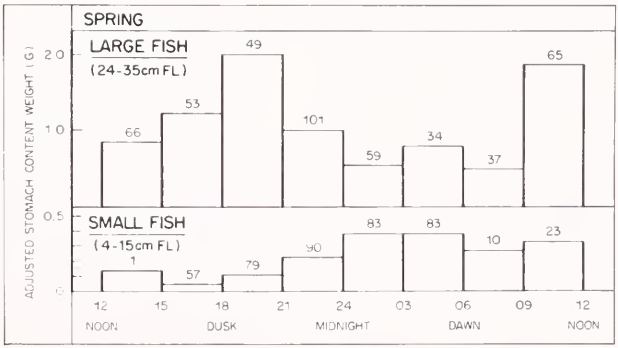

FIGURE 5.—Adjusted mean stomach content weight of large (24-35 cm FL) and small (4-15 cm FL) silver hake collected in springtime versus time of day. The number of fish sampled in each time period is given just above the histogram.

TABLE 5.—Composition of the diet of male silver hake in terms of percentage weight versus fish length. (+ indicates <0.1%.)

Prey	Length group (cm)															
	5-10		11-15		16-20		21-25		26-30		31-35		36-40		>41	
Polychaeta	—		—		—		0.3		+		0.3		—		—	
Crustacea	19.2		64.1		97.2		29.3		73.1		32.7		3.8		1.9	
Amphipoda	—		—		2.7		1.4		1.0		0.2		0.1		+	
Ampeliscidae		—		—		1.9		0.6		0.4		+		0.1		+
Oedicerotidae		—		—		—		—		0.1		0.1		+		—
Hyperiidae		—		—		0.8		0.6		0.4		0.1		—		—
Other Amphipoda		—		—				0.2		0.1		+		+		—
Decapoda	0.3		1.9		1.1		10.7		19.1		15.0		2.6		1.5	
Crangonidae		—		1.9		0.6		1.5		7.4		7.7		0.9		0.1
Pandalidae		—		—		—		8.3		9.8		5.7		1.7		—
Pasiphaeidae		—		—		—		—		—		—		—		—
Other Decapoda		0.3		—		0.5		0.9		1.9		1.6		—		1.4
Euphausiacea	—		50.3		92.7		14.2		41.4		15.9		+		—	
Mysidacea	11.3		11.9		—		—		10.4		0.8		0.2		0.4	
Cumacea	—		—		—		0.4		+		+		—		—	
Copepoda	—		—		0.7		+		—		—		—		—	
Other Crustacea	7.6		—		—		2.6		1.2		0.8		0.9		—	
Cephalopoda	—		—			—	4.4		0.2		8.3		2.5		—	
Loligo		—		—		—		—		—		8.1		—		—
Other Cephalopoda		—		—	+			4.4		0.2		0.2		2.5		—
Pisces	71.4		21.6			—	64.1		23.6		57.2		93.7		98.1	
Scomberesox saurus		—		—		—		—		—		—		—		—
Clupeidae		—		—		—		—		—		—		—		—
Merluccius bilinearis		—		—		—		10.0		5.0		7.7		70.0		66.2
Phycis chesteri		—		—		—		—		—		—		—		—
Ammodytes americanus		50.8		21.6		—		—		—		3.1		—		—
Scomber scombrus		—		—		—		—		—		9.2		—		—
Stenotomus chrysops		—		—		—		—		—		—		—		—
Peprilus triacanthus		—		—		+		—		—		8.0		—		—
Other Pisces		20.6		+	2.8			54.1		18.6		29.2		23.7		31.9
Miscellaneous	9.4		14.3				1.9		3.1		1.5		—		—	
No. examined	12		5		20		119		248		178		21		8	
No. empty	4		0		4		50		109		73		9		3	
Mean stom. cont. wt. (g)	0.030		0.435		0.414		0.400		0.456		1.215		3.565		7.282	
Mean fish FL (cm)	8.4		13.4		19.1		23.7		28.5		32.2		37.1		50.9	

TABLE 6.—Composition of the diet of female silver hake in terms of percentage weight versus fish length. (+ indicates <0.1%.)

Prey	Length group (cm)															
	5-10		11-15		16-20		21-25		26-30		31-35		36-40		>41	
Polychaeta	—		—		—		—		0.4		0.1		+		+	
Crustacea	8.7		100.0		75.2		27.9		39.9		13.0		2.0		0.2	
Amphipoda	0.3		—		0.3		1.8		1.3		0.8		+		+	
Ampeliscidae		—		—		—		0.7		0.5		0.2		+		—
Oedicerotidae		—		—		—		+		0.3		+		+		—
Hyperiidae		0.3		—		0.1		0.5		0.3		0.4		—		—
Other Amphipoda		—		—		0.2		0.6		0.2		0.2		+		+
Decapoda	—		95.4		7.2		21.1		20.3		5.9		1.4		0.1	
Crangonidae		—		95.4		1.8		6.6		5.1		1.9		0.2		+
Pandalidae		—		—		4.7		12.9		13.3		3.1		1.1		0.1
Pasiphaeidae		—		—		—		—		—		+		—		—
Other Decapoda		—		—		0.7		1.6		1.9		0.9		0.1		—
Euphausiacea	7.5		4.0		66.8		3.3		13.5		5.2		0.6		0.1	
Mysidacea	0.9		—		—		0.3		3.8		0.5		+		+	
Cumacea	—		—		—		0.1		+		+		—		—	
Copepoda	—		—		—		—		—		—		—		—	
Other Crustacea	—		0.6		0.9		1.3		1.0		0.6		+		+	
Cephalopoda	—		—		—		28.4		6.1		18.7		15.1		5.9	
Loligo		—		—		—		27.2		—		16.6		10.7		5.8
Other Cephalopoda		—		—		—		1.2		6.1		2.1		4.4		0.1
Pisces	81.9		—		22.0		42.9		51.8		66.7		82.7		93.6	
Scomberesox saurus		—		—		—		—		—		—		6.1		—
Clupeidae		—		—		—		—		—		5.4		3.8		2.8
Merluccius bilinearis		—		—		—		31.9		5.0		6.6		20.8		—
Phycis chesteri		—		—		—		—		—		—		—		—
Ammodytes americanus		81.9		—		—		—		0.1		3.2		0.5		2.7
Scomber scombrus		—		—		—		—		—		7.3		9.5		9.3
Stenotomus chrysops		—		—		—		—		1.6		—		—		3.7
Peprilus triacanthus		—		—		—		—		—		—		3.6		5.0
Other Pisces		—		—		22.0		11.0		45.1		44.2		38.4		70.1
Miscellaneous	9.4		—		2.8		0.8		1.8		1.5		0.2		0.3	
No. examined	9		3		22		113		202		259		126		103	
No. empty	2		0		3		45		83		120		54		47	
Mean stom. cont. wt. (g)	0.099		0.152		0.670		0.571		0.673		1.597		8.185		17.826	
Mean fish FL (cm)	8.0		12.0		18.5		23.4		28.0		32.9		37.7		46.0	

TABLE 7.—Geographic breakdown of the prey found in the stomachs of silver hake caught in the Northwest Atlantic during the years 1973-76. Data are expressed as a percentage weight. (+ indicates <0.1%).

Prey	Middle Atlantic	Southern New England	Georges Bank
Polychaeta	0.1	0.1	0.1
Crustacea	7.3	7.3	16.4
Amphipoda	0.5	0.2	0.4
Ampeliscidae	0.1	0.1	0.1
Oedicerotidae	0.2	+	0.1
Hyperiidae	0.1	0.1	0.1
Other Amphipoda	0.1	+	0.1
Decapoda	4.9	2 6	6.5
Crangonidae	2.4	1.0	1.3
Pandalidae	1.8	1.2	4.4
Pasiphaeidae	0.4	—	+
Other Decapoda	0.3	0.4	0.8
Euphausiacea	1.2	3.4	7.9
Mysidacea	0.3	0.7	1.2
Cumacea	—	0.1	+
Copepoda	+	+	+
Other Crustacea	0 4	0.3	0.4
Cephalopoda	4.3	13.7	6.7
Loligo	2.9	13.0	6.7
Other Cephalopoda	1.4	0.7	+
Pisces	87.5	78.4	76.4
Scomberesox saurus	—	—	6.1
Clupeidae	3.2	1.3	5.0
Merluccius bilinearis	20.8	7.9	0.4
Physis chesteri	—	—	0.8
Ammodytes americanus	1.7	0.4	4.8
Scomber scombrus	—	6.0	21.1
Stenotomus chrysops	—	4 1	—
Peprilus triacanthus	1.4	2.2	8.9
Other Pisces	60.4	56.5	29.3
Miscellaneous	0.8	0.5	0.4
No. of stomach examined	789	918	915
No. of empty stomachs	180	357	268
Mean stom. cont. wt. (g)	1.544	1 815	1.080
Mean fish FL (cm)	17.5	22.5	20.8
Length range (cm)	3-57	3-59	3-64

the majority of the identified fish prey. The stomachs of silver hake caught in Southern New England contain fairly high percentages of silver hake (7.9%), Atlantic mackerel (6.0%), and scup (4.1%). Silver hake caught on Georges Bank eat mostly Atlantic mackerel (21.1%), butterfish (8.9%), Atlantic saury (6.1%), herring (Clupeidae, 5.0%), and American sand lance (4.8%). Evidence of the cannibalistic nature of silver hake is seen in all three areas. In addition, silver hake taken as prey comprise the highest percentage of identified fish in both the Middle Atlantic and Southern New England (Table 7).

Crustaceans are most important in the diet of silver hake collected from Georges Bank (16.4%). Euphausiids (7.9%), decapods (mostly pandalid shrimp, 4.4%, and crangonid shrimp, 1.3%), and mysids (1.2%) account for the majority of crustacean prey consumed on Georges Bank. In the Middle Atlantic and Southern New England, Crustacea is of equal importance (7.3%) as a food. For Middle Atlantic fish, decapods (4.9%) and euphausiids (1.2%) make up the majority of crustacean prey identified in the stomachs. In Southern New England, euphausiids (3.4%) and decapods (2.6%) account for most of the Crustacea.

The Cephalopoda was the only other prey group recognized as an important food of silver hake. Fish in Southern New England eat the largest quantities of squid (13.7%). Silver hake sampled on Georges Bank and in the Middle Atlantic also take fairly large amounts of squid as prey (6.7% and 4.3%, respectively).

A comparison between the quantities of food in the stomachs of fish from each area revealed that Middle Atlantic silver hake have about two to three times more food in their stomachs (on the average) than fish from Southern New England or Georges Bank. Stomach content data for fish 24-35 cm FL from each area were adjusted for fish length; the adjusted mean stomach content weights were Middle Atlantic, 1.328 g; Southern New England, 0.593 g; and Georges Bank, 0.707 g. The quantity of food in the stomachs of Middle Atlantic silver hake is significantly different (with 95% confidence) from the quantity in the stomachs of fish from Southern New England ($F = 6.862$ exceeds $F_{0.05,\,1,21} = 4.32$). The adjusted mean stomach content weights of small (4-15 cm FL) silver hake from each area were Middle Atlantic, 0.149 g; Southern New England, 0.198 g; and Georges Bank, 0.214 g.

Yearly and Seasonal Differences

Percentages of various prey categories in the silver hake diet between years, seasons, and geographic areas indicate the stomach contents are quite variable (Table 8). For example, in the Middle Atlantic, the Crustacea portion of the diet of silver hake varies from 3.1% (spring 1973) to 70.0% (fall 1976). Similar variability can be seen in the percentages listed for most of the prey categories. Much of the observed variation is probably due to differences in predator lengths (note mean fish FL's given at the bottom of Table 8). Only one prey, the American sand lance, was noted as being unique in the diet of silver hake. American sand lance was only found in the stomachs of silver hake collected in the spring during 1975 and 1976. The largest percentage weights of American sand lance were derived from samples collected only during the spring of 1976 in all three areas. Another observation is that fish sampled in the spring tend to be larger (see mean lengths at bottom of Table 8) than those collected in the autumn.

The adjusted stomach content data for large and small silver hake from all areas and years combined indicate that about twice as much food is found in the stomachs during spring than in autumn. The adjust-

TABLE 8.—Annual and seasonal breakdown of the stomach contents for silver hake collected in the Middle Atlantic, Southern New England, and Georges Bank. Data are expressed as a percentage weight for fish collected during the spring (S) and autumn (F) of 1973-76. (+ indicates present but <0.1%.)

	1973		1974		1975		1976	
Prey	S	F	S	F	S	F	S	F
MIDDLE ATLANTIC								
Polychaeta	—	—	0.1	—	0.5	—	1.6	—
Crustacea	3.1	4.2	9.6	6.5	24.7	4.7	34.0	70.0
Amphipoda	+	0.4	1.2	1.2	1.3	2.7	2.1	15.2
Ampeliscidae	—	0.2	+	0.7	—	0.3	0.6	1.3
Oedicerotidae	—	+	1.1	—	0.4	—	0.9	—
Hyperiidae	—	0.1	—	0.5	+	2.1	—	12.1
Other Amphipoda	+	0.1	0.1	+	0.9	0.3	0.6	1.8
Decapoda	3.1	3.3	3.7	5.1	8.9	0.4	22.9	46.6
Crangonidae	1.4	0.5	2.0	4.4	5.9	0.3	11.1	25.8
Pandalidae	1.0	2.4	—	0.7	2.6	—	11.7	13.3
Pasiphaeidae	0.6	—	—	—	—	—	—	—
Other Decapoda	0.1	0.4	1.7	+	0.4	0.1	0.1	7.5
Euphausiacea	—	0.2	4.4	—	14.4	0.3	+	—
Mysidacea	—	+	—	—	—	—	5.4	—
Cumacea	—	+	+	+	0.1	—	+	—
Copepoda	—	—	+	+	—	+	—	—
Other Crustacea	+	0.3	0.3	0.2	+	1.3	3.6	8.2
Cephalopoda	—	14.9	9.7	—	25.2	—	6.3	—
Loligo	—	12.4	—	—	24.9	—	—	—
Other Cephalopoda	—	2.5	9.7	—	0.3	—	6.3	—
Pisces	96.5	80.9	79.5	93.0	46.6	93.7	54.8	5.2
Scomberesox saurus	—	—	—	—	—	—	—	—
Clupeidae	—	—	—	91.5	—	—	—	—
Merluccius bilinearis	23.3	49.0	—	—	4.0	—	—	—
Phycis chesteri	—	—	—	—	—	—	—	—
Ammodytes americanus	—	—	—	—	10.7	—	19.8	—
Scomber scombrus	—	—	—	—	—	—	—	—
Stenotomus chrysops	—	—	—	—	—	—	—	—
Peprilus triacanthus	—	—	—	—	24.4	—	—	—
Other Pisces	73.2	31.9	79.5	1.5	7.5	93.7	35.0	5.2
Miscellaneous	0.4	+	1.1	0.5	3.0	1.6	3.3	24.8
No. examined	39	144	193	54	67	91	111	93
No. empty	11	52	26	10	7	23	22	29
Mean stom. cont. wt. (g)	19.960	0.982	0.466	0.793	1.057	0.243	0.606	0.075
Mean fish FL (cm)	33.9	18.0	14.1	12.9	19.8	13.5	21.7	16.9
Length range (cm)	20-53	4-45	3-46	4-37	5-44	3-40	8-57	3-35
SOUTHERN NEW ENGLAND								
Polychaeta	0.1	—	+	—	+	+	0.2	+
Crustacea	2.8	12.5	3.3	46.1	7.9	17.0	19.8	2.2
Amphipoda	+	1.7	+	4.0	0.1	0.8	0.2	0.5
Ampeliscidae	—	1.6	+	1.5	0.1	0.2	+	+
Oedicerotidae	—	—	—	—	+	—	+	+
Hyperiidae	—	0.1	—	1.9	+	0.5	0.1	0.5
Other Amphipoda	+	+	+	0.6	+	0.1	0.1	+
Decapoda	1.8	8.4	0.1	13.7	6.9	9.7	5.5	1.2
Crangonidae	0.2	0.9	+	4.5	2.0	0.4	4.7	0.2
Pandalidae	0.9	7.3	—	7.0	1.8	9.1	0.8	1.0
Pasiphaeidae	—	—	—	—	—	—	—	—
Other Decapoda	0.7	0.2	0.1	2.2	3.1	0.2	—	+
Euphausiacea	0.5	0.9	3.2	23.5	0.8	4.9	9.9	+
Mysidacea	0.3	+	—	—	0.1	0.9	3.8	—
Cumacea	+	—	+	1.7	+	—	+	+
Copepoda	—	+	—	+	—	+	—	—
Other Crustacea	0.2	1.5	—	3.2	+	0.7	0.4	0.5
Cephalopoda	78.9	1.6	0.3	—	20.2	—	—	2.8
Loligo	78.2	—	—	—	20.2	—	—	—
Other Cephalopoda	0.7	1.6	0.3	—	—	—	—	2.8
Pisces	18.2	85.9	95.6	45.2	70.1	82.9	79.8	94.5
Scomberesox saurus	—	—	—	—	—	—	—	—
Clupeidae	—	—	—	—	—	31.8	—	—
Merluccius bilinearis	0.2	0.7	—	2.3	5.5	1.6	—	44.9
Phycis chesteri	—	—	—	—	—	—	—	—
Ammodytes americanus	—	—	—	—	1.6	—	1.8	—
Scomber scombrus	—	—	15.7	—	—	—	—	—
Stenotomus chrysops	—	—	—	—	—	—	—	24.7
Peprilus triacanthus	14.7	—	—	—	—	—	—	—
Other Pisces	3.3	85.2	79.9	42.9	63.0	49.5	78.0	24.9
Miscellaneous	+	+	0.8	8.7	1.8	0.1	0.2	0.5
No. examined	105	119	93	117	100	120	125	140
No. empty	33	86	40	38	41	31	43	45
Mean stom. cont. wt. (g)	2.406	0.401	6.902	0.107	0.952	0.581	2.181	1.970
Mean fish FL (cm)	15.9	27.5	31.2	16.8	24.4	18.1	23.0	22.9
Length range (cm)	6-47	4-49	9-59	4-37	6-55	4-55	3-53	4-54

TABLE 8.—*Continued.*

Prey	1973 S	1973 F	1974 S	1974 F	1975 S	1975 F	1976 S	1976 F
GEORGES BANK								
Polychaeta	—	—	—	—	+	+	+	—
Crustacea	70.8	15.0	41.8	18.2	10.9	5.9	18.7	6.0
Amphipoda	1.4	0.4	0.3	1.3	0.2	0.4	0.9	0.1
Ampeliscidae	0.1	0.3	+	0.7	—	0.2	—	0.1
Oedicerotidae	—	+	+	0.3	0.1	+	—	—
Hyperiidae	—	—	—	—	—	0.1	0.8	+
Other Amphipoda	1.3	0.1	0.3	0.3	0.1	0.1	0.1	+
Decapoda	60.7	13.9	2.5	12.6	1.0	3.2	2.8	4.5
Crangonidae	1.9	2.0	1.3	2.1	0.5	1.6	0.6	2.1
Pandalidae	44 5	11.6	—	8.3	—	1.1	2.0	2.2
Pasiphaeidae	—	—	0.1	—	—	—	—	—
Other Decapoda	14.3	0.3	1.1	2.2	0.5	0.5	0.2	0.2
Euphausiacea	2.3	0.2	31.2	2.6	9.4	0.5	14.8	+
Mysidacea	—	0.1	7.8	1.6	0.2	1.7	—	0.1
Cumacea	+	+	—	+	—	+	—	—
Copepoda	—	+	—	+	—	+	—	—
Other Crustacea	5.9	0.4	+	0.1	0.1	0.1	0.2	1.3
Cephalopoda	—	—	—	—	—	—	12.8	56.4
Loligo	—	—	—	—	—	—	12.8	56.2
Other Cephalopoda	—	—	—	—	—	—	—	0.2
Pisces	23.7	84.9	57.9	81.8	88.1	94.1	68.5	35.8
Scomberesox saurus	—	—	—	68.8	—	—	—	—
Clupeidae	—	—	—	—	—	39.2	—	—
Merluccius bilinearis	—	—	—	4.1	—	—	—	—
Phycis chesteri	—	—	—	—	3.2	—	—	—
Ammodytes americanus	—	—	—	—	—	—	31.6	—
Scomber scombrus	—	31.0	—	—	63.7	—	—	—
Stenotomus chrysops	—	—	—	—	—	—	—	—
Peprilus triacanthus	—	45.1	—	—	—	—	—	—
Other Pisces	23.7	8 8	57.9	8.9	21.2	54 9	36.9	35.8
Miscellaneous	5.5	0.1	0.3	+	1.0	+	—	1.8
No. examined	48	198	103	157	92	146	63	115
No. empty	24	39	39	27	18	39	34	48
Mean stom. cont. wt. (g)	0.340	1.029	0.996	0.577	2.629	0.906	2.478	0.767
Mean fish FL (cm)	31.4	16.6	24.2	16.0	24.5	18.1	29.7	22.3
Length range (cm)	27-42	4-54	8-49	4-40	11-54	4-48	10-64	3-55

ed mean stomach content weights are presented in Table 9 for each season, year, and geographic area. In almost every year, in all areas, the stomachs of similar-sized fish contain larger quantities of food in the spring than in the fall. Only two exceptions were noted to this trend (for which there is no ready explanation): Large fish collected on Georges Bank in 1973 and small fish collected on Georges Bank in 1974.

TABLE 9.—Annual and seasonal breakdown of the adjusted mean stomach content weight data of large (24-35 cm FL) and small (4-15 cm FL) silver hake gathered from three geographical areas in the Northwest Atlantic during 1973-76. (S = spring, F = autumn.)

Area	1973 S	1973 F	1974 S	1974 F	1975 S	1975 F	1976 S	1976 F	Averages S	Averages F
Middle Atlantic										
Large fish										
Adjusted weight (g)	5.545	1.081	0.995	0.325	2.203	0.912	0.936	0.149	2.420	0.617
Number in sample	26	68	44	9	26	29	38	43		
Small fish										
Adjusted weight (g)	—	0.108	0.180	0.096	0.148	0.142	0.207	0.155	0.178	0.131
Number in sample	—	61	136	33	31	45	47	42		
Southern New England										
Large fish										
Adjusted weight (g)	0.242	0.122	0.488	0.303	0.694	0.657	0.987	0.976	0.603	0.515
Number in sample	17	67	51	33	47	49	63	58		
Small fish										
Adjusted weight (g)	0.256	0.036	0.200	0.074	0.414	0.184	0.205	0.149	0.269	0.111
Number in sample	73	15	4	49	35	62	39	58		
Georges Bank										
Large fish										
Adjusted weight (g)	0.400	0.743	0.916	0.576	1.239	0 506	0.735	0.734	0.823	0.640
Number in sample	43	58	50	53	32	57	27	51		
Small fish										
Adjusted weight (g)	—	0.140	0.321	0.325	0.566	0.106	0.473	0.117	0.453	0.183
Number in sample	—	119	36	95	16	80	9	50		
Ave. large fish adj. wt.									1.282	0.591
Ave. small fish adj. wt.									0.300	0.142

Maturity Stage Versus Diet

Information on maturity was gathered in conjunction with food data for 759 adult silver hake (Table 10). Gonads were classified as 1) resting - gonad small in size and relatively translucent, 2) developing - gonad enlarged and either cream (males) or yellow-orange (females) colored, 3) ripe - gonad fills most of gut cavity, reproductive material either runs freely from an incision in the gonad or is extruded with pressure on abdomen of fish, 4) spent - gonad is flaccid, hemorrhaging is often evident.

TABLE 10.—Relationship between the adjusted stomach content weight and maturity stage of silver hake. Fish were caught on spring and autumn bottom trawl survey cruises conducted in the Northwest Atlantic from 1973 to 1976.

Stomach content data	Maturity stage:	Resting	Developing	Ripe	Spent
	Adj weight (g):	0.826	1.004	0.122	1.292
No. of fish examined		379	297	29	54
Mean fish FL (cm)		28 6	30.6	31.3	31.2
Length range (cm)		24-35	24-35	27-34	25-35

No particular prey type is found in the stomachs of fish in specific maturity stages; all mature silver hake eat mostly fish. However, the stomachs of spawning (ripe) silver hake contain an average of about nine times less food than the stomachs of fish otherwise classified (Table 10). During pre- and postspawning periods, stomachs contain the largest quantities of food (1.0 and 1.3 g, respectively).

Influence of Depth

Analysis of samples from silver hake caught at different bottom water depth ranges (27->365 m) revealed that the average length of fish, food type consumed, and quantity of food in the stomachs, varies with depth (Table 11). The majority (69.4%) of silver hake were caught at depths between 38 and 110 m. Considering only the depth ranges where more than 50 fish were sampled (i.e., 27-220 m, and representing 95.6% of all silver hake collected) the mean FL of fish increases with an increase in depth. Also, the percentage weight of euphausiids and squid in the stomachs tends to increase at deeper bottom depths, while the percentage weight of fish in the diet shows a corresponding decrease. The adjusted mean stomach content data for both small and large fish are given in Table 12. The data are from only those depth ranges from which more than 20 fish (within a size group) were collected. The adjusted stomach content weight of small silver hake steadily decreases from the 27-37 m depth range (0.3 g) to the 111-146 m depth range (0.1 g). The quantity of food found in stomachs of large fish is variable; it steadily decreases between the 27-37 m and 74-110 m depth ranges; increases at the 111-146 m range; and from 111-146 m to 257-293 m continues to decrease (Table 12). Overall, the trend is for fish sampled at deeper depths to have less food, on the average, in their stomachs. It should be mentioned here that silver hake are known to regurgitate part or all of their stomach contents when they are retrieved from deep water depths (pers. obs.). Although fish which show obvious signs of regurtitation (e.g., everted stomach) are not sampled on survey cruises, some fish may regurgitate and not be discernable from those which did not. This phenomenon, in part (other factors such as the decrease in abundance of typical prey of silver hake with an increase in depth or decrease in bottom water temperature may also be important in this regard, see Williams and Wigley 1977) could explain the decrease noted in stomach content weights with an increase in water depth.

DISCUSSION

The diet of silver hake consists almost exclusively of a combination of fish, crustaceans, and squid. The relative importance of each particular prey group as a food of silver hake is, for the most part, dependent on the size of the predator and/or the availability of the prey (Bigelow and Schroeder 1953; Jensen and Fritz 1960; Fritz 1962; Dexter 1969; Vinogradov 1972).

The composition of the diet of male and female silver hake is known to differ (Vinogradov 1972; Bowman 1975). The present investigation confirms earlier reports that females feed predominantly on fish and that males eat mostly crustaceans. In addition, it has been established that the stomachs of females contain larger quantities of food than the amounts in the stomachs of males of similar size. Since the rate of growth in fishes is directly related to their dietary intake, it is not surprising that females grow faster than males (Schaefer 1960).

Bowman and Bowman (1980) studied diurnal varia-

TABLE 11.—Breakdown by depth range of the stomach contents of silver hake caught at bottom water depths ranging from 27 to 365 m. Data expressed as a percentage weight. (+ indicates present but <0.1%).

Prey	Bottom depth range (m)									
	27-37	38-73	74-110	111-146	147-183	184-220	221-256	257-293	294-329	330-365
Polychaeta	0.4	+	+	—	—	0.1	—	—	—	—
Crustacea	14.1	6.6	6.1	7.1	18.5	37.1	21.8	8.3	4.3	34.0
Amphipoda	0.5	0.4	0.5	0.2	0.1	0.3	0.2	+	—	0.7
Ampeliscidae	0.1	0.1	0.1	0.2	+	0.3	—	—	—	—
Oedicerotidae	0.3	+	0.1	—	—	—	—	—	—	—
Hyperiidae	+	0.2	0.2	+	0.1	—	0.1	+	—	0.7
Other Amphipoda	0.1	0.1	0.1	+	—	+	0.1	+	—	—
Decapoda	8.2	4.3	4.3	1.5	0.3	7.8	0.5	0.6	—	10.7
Crangonidae	5.2	1.4	0.9	0.2	+	0.3	+	—	—	—
Pandalidae	1.8	2.5	2.8	1.0	—	5.8	—	—	—	—
Pasiphaeidae	1.0	—	—	—	—	—	—	0.1	—	—
Other Decapoda	0.2	0.4	0.6	0.3	0.3	1.7	0.5	0.5	—	10.7
Euphausiacea	3.8	0.7	1.0	5.2	16.1	29.0	20.1	5.9	3.5	22.6
Mysidacea	0.8	0.9	0.1	+	1.8	—	—	1.4	0.8	—
Cumacea	+	+	+	—	—	—	—	—	—	—
Copepoda	+	+	+	+	—	—	—	—	—	—
Other Crustacea	0.8	0.3	0.2	0.2	0.2	0.1	1.0	0.4	—	—
Cephalopoda	0.4	2.4	9.4	—	54.0	53.6	—	—	—	—
Loligo	—	2.0	7.4	—	53.7	—	—	—	—	—
Other Cephalopoda	0.4	0.4	2.0	—	0.3	53.6	—	—	—	—
Pisces	83.4	90.5	83.8	92.9	27.2	8.2	77.5	91.6	93.2	65.8
Scomberesox saurus	—	3.6	—	—	—	—	—	—	—	—
Clupeidae	—	1.3	4.2	—	12.8	—	—	—	—	—
Merluccius bilinearis	23.8	15.4	+	—	—	—	—	—	—	—
Physis chesteri	—	—	0.8	—	—	—	—	—	—	—
Ammodytes americanus	4.1	2.9	—	1.3	—	—	—	—	—	—
Scomber scombrus	—	5.8	23.4	—	—	—	—	—	—	—
Stenotomus chrysops	—	3.9	—	—	—	—	—	—	—	—
Peprilus triacanthus	—	1.0	9.9	—	9.2	—	—	—	—	—
Other Pisces	55.5	56.6	45.5	91.6	5.2	8.2	77.5	91.6	93.2	65.8
Miscellaneous	1.7	0.5	0.7	+	0.3	0.9	0.7	0.1	2.5	0.2
No. examined	330	1,136	752	172	120	93	50	45	9	15
No. empty	68	282	262	98	43	31	20	20	1	4
Mean stom. cont. wt. (g)	1.531	1.530	1.232	2.221	3.375	0.802	1.185	1.885	4.129	0.768
Mean fish FL (cm)	17.3	18.0	20.7	25.5	29.2	25.0	21.1	31.8	32.2	28.0
Length range (cm)	3-49	3-57	3-64	3-53	12-47	57-52	9-49	12-51	31-34	21-34

TABLE 12.—Adjusted mean stomach content data for large (24-35 cm FL) and small (4-15 cm FL) silver hake sampled within various ranges of bottom water depth. All samples were obtained during bottom trawl survey cruises and conducted in the Northwest Atlantic.

Bottom depth range (m)	Large fish (24-35 cm FL)		Small fish (4-15 cm FL)	
	Adjusted weight (g)	Number of fish	Adjusted weight (g)	Number of fish
27-37	1.240	85	0.252	190
38-73	1.020	384	0.183	600
74-110	0.612	295	0.136	334
111-146	1.260	93	0.116	25
147-183	0.946	94	—	—
184-220	0.296	44	—	—
257-293	0.082	25	—	—

tion in the feeding intensity of silver hake on Georges Bank in September 1978. They found that silver hake feed more intensively at night than during daylight. The findings of the present study are similar to those reported earlier (for the same size fish collected in autumn), but also indicate that an additional feeding period may occur around noon during springtime. No such pattern of feeding has been noted for adult silver hake in the past.

Differences in the composition and/or quantity of food in the stomachs of silver hake collected within various geographic areas have been observed previously by Schaefer (1960), Vinogradov (1972), and Langton and Bowman (1980). Two items are particularly noteworthy concerning the diet of silver hake in the different geographic areas studied here. The first is the large quantity of food in the stomachs of silver hake from the Middle Atlantic (on the average two or three times more than the quantities in the stomachs of Southern New England and Georges Bank fish). The second is the high percentage weight (20.8%) of silver hake in the diet of silver hake caught in the Middle Atlantic. Of interest is that Langton and Bowman (1980) also found that silver hake caught in the Middle Atlantic area (during the period 1969-72) are more cannibalistic than silver hake in other areas of the Northwest Atlantic.

Vinogradov (1972) concluded that the differences he observed in the feeding of silver hake in the Northwest Atlantic during 1965-67 were "due to variations from area to area in the species composition of the fish food and the rate of feeding." Vinogradov's mention of "the rate of feeding" referred to the variation in feeding intensity of silver hake throughout the year. He found silver hake feed most intensively in the spring-summer and autumn periods. During the summer (when silver hake spawn) and winter, he noted that the feeding rate diminishes. The data presented here, in conjunction with other published and unpublished data, tend to corroborate Vinogradov's conclusions. Silver hake caught in spring have twice as much food in their stomachs as those caught in fall (data from present study for 24-35 cm FL fish—1.3 g, spring; 0.6 g, fall). The stomachs of spawning silver hake contain small quantities of food (0.1 g) compared with fish with developing (1.0 g) or spent (1.3 g) gonads (data from present study). Fish >20 cm FL collected during late summer-early autumn have small quantities of food (mean stomach content weight of 0.2 g) in their stomachs (Bowman and Bowman 1980). The stomach contents of silver hake collected on Georges Bank during the winter (December-January) of 1976-77 were analyzed by Bowman and Langton (1978). They found the mean stomach content weight of fish 20 cm FL and larger to be 0.4 g. The stomachs of silver hake (all >29 cm FL) collected in February (late winter) of 1977 on Georges Bank, by American and Polish scientists aboard the Polish RV *Wieczno* (conducting research in conjunction with the Woods Hole Laboratory), contained an average of 0.1 g of food (unpublished data available from the author). The pattern of feeding intensity for silver hake throughout the year, based on the above information, is intensive feeding in the spring and early summer; curtailment of feeding in summer and early autumn (during spawning); resumption of feeding in the autumn, but to a lesser degree than in the spring; and finally a reduction in feeding throughout the winter. Somewhat similar feeding patterns have been established for other species of marine fish (Tyler 1971).

Grosslein et al. (1980) reported an increase in bottom trawl survey catches of American sand lance in 1976 in the Northwest Atlantic. The population upsurge of American sand lance combined with the high percentage weights of American sand lance found in silver hake stomach contents during 1976 is an indication of silver hake's opportunistic predatory behavior. Availability of prey is probably one of the most important factors in determining what types and how much food silver hake eat.

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ABUNDANCE AND VERTICAL DISTRIBUTION OF FISHES IN A COBBLE-BOTTOM KELP FOREST OFF SAN ONOFRE, CALIFORNIA

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ABSTRACT

Using visual belt transects on the bottom and vertically stratified belt transects taken with movie cameras in the water column, we assessed the species composition, vertical distribution, and standing stock of fishes in a forest of giant kelp and a nearby kelp-depauperate area off San Onofre, California. The volume of water-column "cinetransects" was calibrated for water clarity. Species such as garibaldi, blacksmith, and various rockfishes, which depend on high-relief rocky substrates, were rare or absent in these low-relief, cobble-bottom habitats. The species present in the kelp forest apparently did not depend on high-relief rock, at least in the presence of kelp. These species fell into three groups, based upon their vertical distributions: "canopy" species (kelp perch, giant kelpfish, and halfmoon), which occurred mainly in the upper water column; "cosmopolites" (kelp bass, white seaperch, and señorita), which occurred throughout the water column; and "bottom" species (California sheephead and various seaperches), which occurred mainly near the bottom. Despite the absence of reef-dependent species, estimated standing stocks of 388-653 kg/ha in the San Onofre kelp forest were as large or larger than estimates made by others in kelp forests located on higher relief bottoms. The kelp-forest areas at San Onofre also supported a larger standing stock of fishes (other than barred sand bass) than the adjacent area with little kelp. The relatively large standing stock of fishes in the kelp forest can be attributed to the presence of kelp and to the depth of the kelp forest. Located in relatively deep water (15 m), this kelp forest possessed an extensive midwater zone. The attraction of fish in moderate densities to the midwater zone of this kelp forest contributed substantially to overall biomass. We conclude that kelp per se can enhance the standing stock of fishes on a temperate reef, at least in areas of low bottom relief.

Rocky reef and giant kelp, *Macrocystis pyrifera*, habitats off the coast of southern California support a diverse and abundant assemblage of fishes (Limbaugh 1955; Quast 1968 a, b; Feder et al. 1974; Ebeling et al. 1980 a, b). Much of the richness of this ichthyofauna has been attributed to the rocky substrate; areas with a rugose, rocky bottom and little kelp seem to support more fish than areas with a flat bottom and dense kelp (Quast 1968 a, b; Ebeling et al. 1980a). However, kelp itself also provides a unique habitat for some fishes (Coyer 1979; Ebeling et al. 1980a) and a point of orientation in the water column for others (Quast 1968 a, b; Bray 1981). The kelp canopy may also serve as a nursery area for some species of fish (Miller and Geibel 1973; Feder et al. 1974; M. Carr[3] Unpubl. data).

Several approaches have been used to assess the influence of habitat on the abundance and composition of fish assemblages in nearshore kelp and rock habitats off California. Perhaps the best analytical approach is experimental, as employed by Miller and Geibel (1973), Bray (1981), and Carr (footnote 3) ; however, the comparative approach of Limbaugh (1955; also reported in Feder et al. 1974), Quast (1968 a, b), and Ebeling et al. (1980a) is also of value. Based on observations in a variety of areas, Limbaugh described the habits and habitats of many nearshore fishes. Quast and Ebeling et al. employed broad-scale quantitative sampling of fish assemblages in different areas. Quast's interpretation of data extended Limbaugh's natural history approach, and added to it the actual comparison of abundances in different habitats. Ebeling et al. (1980a) employed a multivariate analysis of habitat characteristics and relative abundances of species to define subassemblages of fishes, and also compared abundances in areas of different habitat characteristics.

In this paper we examine the abundance, vertical distribution, and species composition of noncryptic fishes in a forest of giant kelp near San Onofre, Calif. We also report the abundance and species composition of fishes in a nearby area with little kelp. This study, undertaken initially to predict the effects of a

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possible loss of kelp (Dean[4]) on the indigenous fish fauna, also allowed us to extend the comparative approach of Quast and Ebeling to assess two features of kelp-forest fish faunas and to further evaluate a sampling technique.

The portion of the kelp forest we examined was located in relatively deep water (15 m) and was anchored on a low-relief cobble bottom. Since it lacked a highly heterogeneous substrate, we were able, by comparison, to further evaluate the effects of kelp per se on nearshore fishes. Because the kelp forest was in deep water, we also had the opportunity to examine the vertical distribution of fishes in greater detail than other workers, by sampling four vertical strata, rather than the two strata (canopy and bottom) sampled by Quast (1968b) and Ebeling et al. (1980a, b).

Besides visual transects to sample fish on or near the bottom, we used underwater movies ("cinetransects") to estimate the abundance of fishes in the water column above the bottom. Alevizon and Brooks (1975) and Ebeling et al. (1980b) discussed the advantages and disadvantages of cinetransects, but provided only rough estimates of the area sampled in a cinetransect. In this paper we more carefully evaluate cinetransect volume, emphasizing the effect of underwater visibility on cinetransect width.

Our objectives in this paper are 1) to estimate cinetransect volume as a function of underwater visibility; 2) to examine the vertical distribution of fishes in a deep-water kelp forest; 3) to estimate the overall abundance and biomass of fishes, integrated over depth, in this kelp forest; and 4) to evaluate the importance of kelp to nearshore fishes, by comparing our data from the San Onofre kelp forest with that from an adjacent kelp-depauperate area and with other published data from kelp forests located on more rugose substrates.

MATERIALS AND METHODS

Study Areas

This study was conducted in and near the offshore portion of a giant kelp, *Macrocystis pyrifera*, forest near the San Onofre Nuclear Generating Station, between San Clemente and Oceanside, Calif. (Fig. 1).

San Onofre kelp (SOK) varied in areal extent from <5 to 95 ha during the mid- to late 1970's, and covered about 75 ha during the fall of 1979 (Dean footnote 4). SOK occupied a shallowly sloping, low-relief (<1 m) cobble and sand substrate between the depths of about 10 and 15 m. Two relatively permanent, offshore portions of SOK, and an area with little kelp located ≤100 m upcoast from SOK, served as our study areas. The upcoast (SOK-U) and downcoast (SOK-D) areas within SOK, and the kelp-depauperate area ("kelpless" cobble), were all about 15 m deep and 2-3 km from shore. Because of its depth, low relief, and periodic inundation by sand, the cobble substrate in all areas was relatively bare of understory algae and sessile invertebrates. However, some stands of the 1 m tall laminarian kelp *Pterygophora californica* were present, especially along the fringes of the *Macrocystis* forest and throughout the kelpless cobble area.

Sampling Methods

Our general sampling plan was to stratify fish censuses by depth and to replicate these samples over several dates. In the two kelp-forest areas, we censused each of three, equally spaced strata in the water column, plus a bottom stratum. Only the bottom stratum was censused at the kelp-depauperate area, since few kelp-associated fishes were observed above the bottom in this area. Sampling at each stratum was replicated hierarchically: A number of replicate transects were made within an area on a given sampling day, and counts from these transects were averaged. This was repeated on 4 or 5 d at each site. The daily averages at each stratum and area were themselves used as replicates that provided reasonably precise estimates of means per stratum and that allowed estimates of variability due to sampling error. Because of time and manpower constraints, the various study areas were usually sampled on different dates. All three water-column strata in a given area were sampled on the same day; the bottom stratum, however, was usually sampled on a different day.

All sampling took place from October through December 1979. This time of year offers the most consistently clear and calm water conditions. Since most migratory and transient species were excluded from analysis (see below), our fall study should reasonably characterize the general distribution and abundance of "resident", kelp-associated fishes at SOK. Within this period, sampling was generally limited to dates when horizontal visibility exceeded 3 m.

[4]T. A. Dean. 1980. The effects of San Onofre Nuclear Generating Station on the giant kelp, *Macrocystis pyrifera*. Annual report of the Kelp Ecology Project, January-December 1979, to the Marine Review Committee of the California Coastal Commission. Unpubl. rep., 189 p. Kelp Ecology Project, Marine Science Institute, University of California, Santa Barbara, CA 93106.

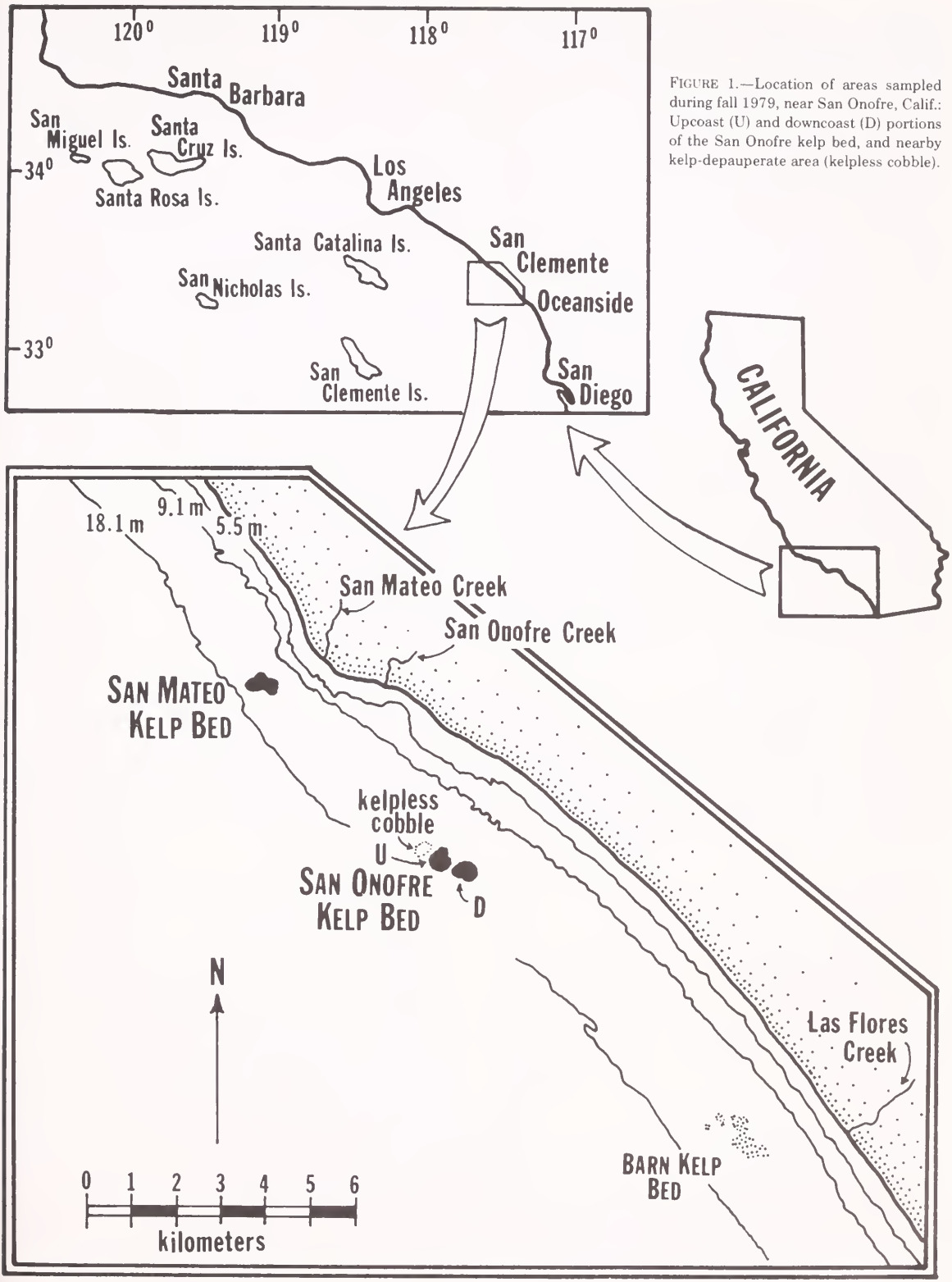

FIGURE 1.—Location of areas sampled during fall 1979, near San Onofre, Calif.: Upcoast (U) and downcoast (D) portions of the San Onofre kelp bed, and nearby kelp-depauperate area (kelpless cobble).

In each area, two permanently buoyed stations served as foci for sampling. At each station, we determined a range of suitable compass headings for transects. To assure complete coverage of the area, we divided each range of suitable headings into five equal subarcs and randomly chose transect headings from each subarc. Headings were selected separately for each sampling stratum. One transect per subarc was made on each sampling day for bottom sampling. In the water-column strata, where fish patchiness necessitated more samples, we made one transect in each subarc and added another transect from one of the subarcs (randomly chosen). Thus, five transects were usually made from each station per date on the bottom, and six at each station and depth stratum in the water column. Regardless of sampling method, transects began 7-10 m from the station hub. Transects were taken from both sampling stations on a sampling day. Data from the two stations at an area were pooled, since the abundances of major species were generally indistinguishable between stations in an area on a given date.

On the bottom, fish sampling was conducted visually in 75 m long strip transects. Divers (one per station) counted fish in bands estimated to be 3 m wide and 1.5 m high, while reeling out 75 m long lines along the predetermined compass headings. All noncryptic fishes within this band were identified and counted, with separate tallies kept for juvenile, subadult, and adult members of each species (Table 1). All subadult and adult *Macrocystis* plants >1 m tall (Dean footnote 4) were counted in the same 3 m wide band while reeling in the transect line on the return trip.

Transects in the water column at the two kelp-forest areas were made with underwater movie strips, using Elmo Super 311 Low Light[5] movie cameras (F/1.1), Giddings Cine-Mar housings, and Kodak Ektachrome 164 super-8 film cartridges. At 18 frames/s, the transects lasted about 3 min. Divers swam predetermined compass headings and photographed fish occurring in a 120° horizontal arc about the transect axis and 1.5 m above and below the diver's depth. The transect ended when the film cartridge was exhausted. Water-column transects were made in three depth strata: 3 m, 7.6 m, and 12 m (Table 2). Horizontal visibility was measured with each set of transects (at a depth on a sampling date), as the distance at which an olive-tan colored, 10 cm long float ("fish mimic") became indistinct. Films were later viewed in slow motion by at least two observers, at

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

TABLE 1.—Common and scientific names of fishes observed at the San Onofre kelp bed and adjacent kelpless cobble area during fall 1979 with the estimated weight of juveniles, subadults, and adults. Body weights for teleosts were estimated from average observed lengths, converted to weights using the length-weight regressions of Quast (1968a: Appendix B), after adjusting for the bias (underestimate) from the use of average body length to predict average body weight (see Pienaar and Ricker 1968). Weights of elasmobranchs were estimated from fishes trapped in the intakes of the San Onofre Nuclear Generating Station, Unit 1, during 1976-79.[1] Asterisks indicate species not included among kelp-bed "residents." Common names after Robins et al. (1980).

Family and species	Weight (g)		
	Juvenile	Subadult	Adult
Serranidae			
Paralabrax clathratus, kelp bass	7	200	1,050
Paralabrax nebulifer, barred sand bass	20	300	1,500
Embiotocidae			
Brachyistius frenatus, kelp perch	—	—	25
Embiotoca jacksoni, black perch	10	75	350
Phanerodon furcatus, white seaperch	10	50	175
Damalichthys vacca, pile perch	15	175	500
Rhacochilus toxotes, rubberlip seaperch	15	150	700
Hypsurus caryi, rainbow seaperch	10	60	150
Labridae			
Oxyjulis californica, señorita	0.5	5	55
Semicossyphus pulcher, California sheephead	50	250	875
Halichoeres semicinctus, rock wrasse	25	100	250
Girellidae			
Girella nigricans, opaleye	—	—	950
Scorpididae			
Medialuna californiensis, halfmoon	—	—	250
Pomacentridae			
Chromis punctipinnis, blacksmith	2	—	—
Hypsypops rubicundus, garibaldi	25	120	500
Clinidae			
Heterostichus rostratus, giant kelpfish	3	30	175
Cottidae			
Scorpaenichthys marmoratus, cabezon	—	—	1,500
Scorpaenidae			
Scorpaena guttata, California scorpionfish	—	—	550
Sebastes rastrelliger, grass rockfish[2]	—	—	400
Sebastes serranoides, olive rockfish[2]	4	175	—
Sebastes spp., juvenile rockfish[2]	1	—	—
Sciaenidae			
**Cheilotrema saturnum*, black croaker	—	—	225
Pristopomatidae			
**Xenistius californiensis*, salema	—	—	75
Atherinidae			
*silversides spp.	—	—	20
Carangidae			
**Trachurus symmetricus*, jack mackerel	—	115	—
Sphyraenidae			
**Sphyraena argentea*, Pacific barracuda	—	150	—
Carcharhinidae			
**Triakis semifasciata*, leopard shark	—	—	2,000
Rhinobatidae			
**Platyrhinoides triseriata*, thornback	—	—	240
Myliobatidae			
**Myliobatis californica*, bat ray	—	—	6,700
Torpedinidae			
**Torpedo californica*, Pacific electric ray	—	—	9,450

[1]E. DeMartini and R. Larson. 1980. Predicted effects of the operations of San Onofre Nuclear Generating Station Units 1, 2, and 3 on the fish fauna of the San Onofre region. Report submitted to the Marine Review Committee of the California Coastal Commission. Unpubl. rep., 27 p. Marine Science Institute, University of California, Santa Barbara, CA 93106.

[2]Members of the genus *Sebastes* will be grouped under "rockfish spp." in subsequent tables

TABLE 2.—Bathymetric sampling strata at the San Onofre kelp bed. Weighting factors (W_h) are shown for the above-bottom strata and for the above-bottom versus bottom strata.

Sampling depth (m)	Depth Range represented (m)	Extent of range (m)	W_h (above-bottom only)	W_h (all strata)
3	0-5.3	5.3	0.3926	
7.6	5.3-9.8	4.5	0.3333	[1]0.9
12	9.8-13.5	3.7	0.2741	
15 (bottom)	13.5-15.0	1.5	—	0.1
	0-15		1.0	1.0

[1]Weighting factor for above-bottom strata combined

which time fish that were distinguishable on film were identified, counted, and assigned to maturity classes as above.

Transect Volume

The volume of visual bottom transects was considered to be fixed, and the volume of water-column cinetransects to be dependent on underwater visibility. The volume of bottom transects was fixed at 75 m × 3 m × 1.5 m = 337.5 m^3, since the length of transects was measured, and the height and width of transects were fixed at values less than horizontal visibility. Cinetransect length was taken as the average distance covered in simulated, 3-min cinetransects swum by three divers over a metered line. Each diver swam two simulations against the current, and two with the current. The cross-sectional area of a cinetransect was treated as an ellipse with a minor (vertical) axis of 1.5 m, the distance above and below the diver that fish were photographed. The major axis of the ellipse was a function of camera range, the distance at which fish could be distinguished on film. The particular function was cos 30° × camera range, since divers photographed fish within a 120° arc (60° on each side of the transect axis) (Fig. 2). Thus, the volume of cinetransects at a given depth on a given day was calculated as

$$V = 1.5\,\pi\,L\,(\cos 30^\circ \times CR),$$

where V was cinetransect volume in cubic meters; 1.5, the minor axis of the ellipse; L, the cinetransect length as determined above; and CR, the camera range at that depth on that day. Camera range itself was estimated as a function of the horizontal visibility at a depth on a sampling date.

The relationship between camera range and horizontal visibility was estimated empirically under different conditions. The main "other condition" that we evaluated was the orientation of the camera to the sun. In trials run at different visibilities, two fish of similar appearance (usually a kelp perch, *Brachyistius frenatus*, and a white seaperch, *Phanerodon furcatus*) were held on a spear by one diver and photographed with our usual equipment by another diver at distances decremented from the limits of horizontal visibility (measured as described above). At each visibility, trials were run with the camera facing into the sun and with the camera facing away from the sun. Two observers viewed the film from each trial and determined camera range as the greatest distance at which the two fish could be distinguished on film. The criteria for distinguishability were the same as those used in evaluating whether or not to count a fish when we viewed regular cinetransects.

Data for camera range versus horizontal visibility were fit to several asymptotic functions. The fitting

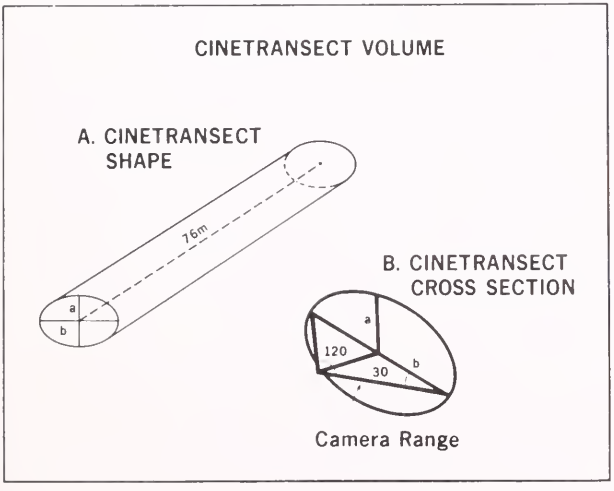

FIGURE 2.—A. Estimated shape of area sampled in underwater transects taken with motion pictures (cinetransects). The length of 76 m was estimated from simulated transects. B. Elliptical cross section of a cinetransect, with minor axis (a) of 1.5 m and major axis (b) calculated from camera range when divers surveyed a 120° horizontal arc about the central axis of the transect.

routine was BMDP program P3R, nonlinear regression (Dixon and Brown 1979). The function with the smallest residual mean square was selected to represent the relation between camera range and horizontal visibility, and was employed in estimating camera range at a depth on a sampling date.

Data Analysis

We reduced data into two general forms: densities (number or biomass per unit volume) in different strata, and abundances integrated throughout the entire water column. The first was used to examine the vertical distribution of individual species or of the entire assemblage and to compare the relative abundances of species in a stratum. The second was used to estimate the overall abundance of the assemblage and to compare the overall abundances of different species. In both cases, the final point and interval estimates were based on the means and variances, over dates, of daily means.

The daily estimate of density (per 1,000 m^3) for each species in a depth stratum was estimated as the mean number or biomass per transect on that day, times the ratio (1,000/transect volume), where transect volume was estimated as above. Biomass of a species on a given transect was estimated by counts of individuals in different maturity classes, converted to wet weights by the key in Table 1.

Our estimate of a species' density in a depth stratum was calculated as the mean of the daily density estimates in that stratum. Similar estimates were made for the sum of all "resident" teleosts. Excluded from the analysis of total fish density and abundance were elasmobranchs and certain teleosts (silversides, jack mackerel, Pacific barracuda, black croaker, and salema) that were rare at SOK, are seasonal visitors to kelp beds, or are not primarily associated with rock reefs and kelp forests (Feder et al. 1974). Species such as white seaperch and barred sand bass often occur in other habitats, but were included in our analysis because they may have at least a marginal association with kelp-rock habitats and were frequently encountered and abundant in our samples.

By weighting the average density of a species (or the assemblage) in a stratum by the volume of water represented by samples in that stratum, we were able to obtain estimates of abundance integrated from surface to bottom (Snedecor and Cochran 1980:444). The sampling day was an integral component of our analysis, but only the above-bottom strata were sampled on the same day at a given site. To obtain accurate estimates of variance for integrated abundances, then, we assembled our integrated estimates in two stages. We first estimated stratified mean density for the above-bottom strata on each day and averaged these values over days. We also computed mean density (over days) in the bottom stratum. Secondly, we computed stratified mean density (and its standard error) for the above-bottom and bottom strata, using the means and variances calculated above. The stratified mean density estimates for the entire water column were then scaled to represent abundances over 100 m^2 of bottom.

Samples in each stratum were assumed to represent a range of depths extending to the midpoints between strata, with the 3 m stratum also extending to the surface (Table 2). Weighting factors for the strata were determined from the relative extents of the depth ranges represented. Among the above-bottom strata, relative weighting factors were the vertical ranges of these strata divided by 13.5 m. For the bottom versus above-bottom strata the depth ranges were divided by 15 m.

Daily estimates of stratified mean density in the above-bottom strata were calculated as

$$D_{wc} = \sum_h W_h D_h,$$

where D_{wc} was the estimate of stratified mean density in the 3 m, 7.6 m, and 12 m strata; W_h, the weighting factor; and D_h, the mean density on that day in stratum h (Snedecor and Cochran 1980). The mean ($\bar{D}_{wc}$) and variance (S^2_{wc}) of these daily estimates were then computed. The mean ($\bar{D}_b$) and variance (S^2_b) of estimated daily densities on the bottom were also calculated.

Stratified mean abundance throughout the entire water column was estimated as

$$\bar{A}_{st} = \left(\frac{1{,}500}{1{,}000} \right) \sum_h W_h D_h,$$

where $\bar{A}_{st}$ was the stratified mean estimate of integrated abundance over 100 m^2 of bottom, W_h was the weighting factor, and $\bar{D}_h$ was the mean density in either the above-bottom strata ($\bar{D}_{wc}$) or in the bottom stratum ($\bar{D}_b$). The term in the summation is the estimate of stratified mean density (per 1,000 m^3) over all strata, and the ratio (1,500/1,000) converts this value to abundance over 100 m^2 of bottom.

The standard error of $\bar{A}_{st}$ was calculated as

$$S_{\bar{A}_{st}} = \sqrt{\left(\frac{1{,}500}{1{,}000} \right)^2 \sum_h W_h^2 S_h^2 / n_h},$$

where S^2_h was the variance of daily density estimates in either the above-bottom (S^2_{wc}) or bottom (S^2_b)

strata; W_h, the weighting factor; and n_h, the number of days sampled in stratum h. The portion of the formula included in the summation is the usual estimate of variance for stratified means (Snedecor and Cochran 1980), and the root of this sum is the standard error of mean density (per 1,000 m^3) throughout the water column. Multiplying by $(1{,}500/1{,}000)^2$ adjusts the standard error for the larger volume of water in the column over 100 m^2.

Estimates of integrated abundance at the kelp-depauperate site were obtained by converting mean density on the bottom to mean density over 100 m^2.

Arithmetic means (of untransformed data) were used for all estimates of density and abundance. Geometric means (obtained by back-transforming the means of log-transformed data) underestimate absolute densities in a manner proportional to their variances. Adjustments for this underestimation (Elliott 1971) are usually based on the assumption of log-normal distributions, and we could not make such an assumption. However, some statistical comparisons were made with log-transformed data to avoid the problem of heterogeneous variances. These were comparisons of mean numbers and biomass on the bottom, where varying transect volume did not confound the calculation of variance. Other comparisons, however, were made with untransformed data. These included tests for differences in numbers or biomass in the above-bottom strata and in the entire water column. When all three areas were compared, a one-way ANOVA was used if variances were not heterogeneous. T-tests for unequal variances (Bailey 1959) were used for pairwise comparisons of areas when variances were unequal.

RESULTS

Cinetransect Calibration

We estimated cinetransect length to be about 76 m. Six down-current trials averaged 78.3 m in length (standard error (SE) = 1.5 m, range = 74-82 m), 6 upcurrent trials averaged 72.8 m in length (SE = 2.3 m, range = 67-82 m), and the overall average was 75.6 m (SE = 1.5 m).

Camera range was an asymptotic function of horizontal visibility, with little increase in camera range at visibilities beyond 7-9 m (Fig. 3). Camera range was appreciably lower when the camera was facing the sun than vice versa, particularly at greater visibilities. This was reflected in each of the curves fit (Table 3). Since divers did not record whether actual transects faced into or away from the sun, we used the curve fit to all camera range-horizontal visibility values to calibrate cinetransect volume. The logistic equation provided, by slight margin, the best fit to

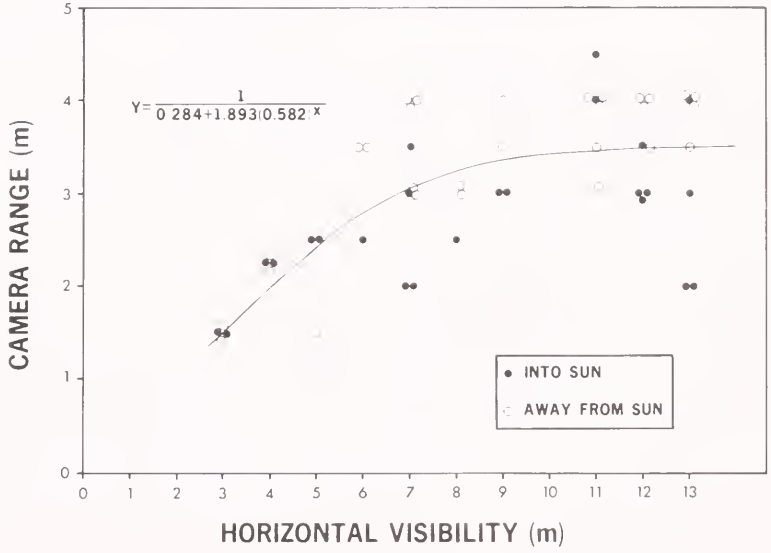

FIGURE 3.—Relation of camera range (the distance at which fish could be distinguished on film) and horizontal visibility. Points are observations of maximum camera range at different visibilities with the camera facing into and away from the sun. The equation and line show the logistic function fit to these points.

these data (Table 3) and was the one employed in calculating cinetransect volume.

Distribution and Abundance of Fishes

Five sets of bottom transects were made in each study area. Water-column samples were taken on five dates at SOK-U and on four at SOK-D. Transect number and visibility at depth on each date are shown in Table 4.

Of the 28 species recorded in this study, 19 were "resident" teleosts. Of these, 13 species were recorded on more than two transects in the two kelp-forest areas (Table 5). These 13 common species could be assigned to bathymetric categories, based on their vertical patterns of frequency of occurrence (Table 5) and density (Tables 6, 7) within SOK.

Kelp perch, halfmoon, and giant kelpfish were most common in the upper strata and are designated "canopy" species. While halfmoon and giant kelpfish were observed in all strata, all three species were most abundant in the 3 m stratum. Only halfmoon reached moderate abundances at 7.6 m in the SOK-D area (Tables 5, 6, 7).

Señorita, white seaperch, and kelp bass were common throughout the water column (Tables 5, 6, 7) and are designated "cosmopolites". These three species were among the most common and abundant fishes in all strata. The white seaperch was the most cosmopolitan of the three in 1979, its density and frequency of occurrence on transects varying little with depth. The señorita was the most abundant species in nearly all strata. The kelp bass was also abundant at all depths. Its numerical density varied little among the water-column strata, but was generally greater on the bottom. Its biomass was greater in the lower strata (Tables 6, 7). Young kelp bass concentrated in the upper water column (Table 8), contributing to the relatively low biomass per fish for kelp bass in the 3 and 7.6 m strata. Our data indicate

TABLE 3.—Functions fit to camera range (Y) versus horizontal visibility (X) relationship, and the best fit parameters as determined by BMDP program P3R (Dixon and Brown 1979). Also noted are the asymptotes calculated for each equation and data set, and the residual mean squares. Into = trials made with the camera facing into the sun; Away = trials made with the camera facing away from the sun; All = curves fit to all data. P_1, P_2, and P_3 are arbitrary symbols for the parameters of each function; there is no implied correspondence between the numbered parameters of different functions.

Function name and formula	Set of trials	P_1	P_2^2	P_3	Asymptote (m)	Residual mean square
Logistic	All	0.284	1.89	0.582	3.52	0.369
$Y = 1/(P_1 + F_3^Y)$	Away	0.259	2.63	0.560	3.86	0.250
	Into	0.317	1.20	0.618	3.15	0.355
Gompertz	All	1.27	−3.19	0.647	3.56	0.370
$Y = e^{(P_1 + P_2 P_3^X)}$	Away	1.37	−3.88	0.648	3.94	0.255
	Into	1.15	−2.35	0.656	3.16	0.354
Von Bertalanffy	All	3.60	0.334	1.43	3.60	0.372
$Y = P_1 (1 - e^{P_2 (X - P_3)})$	Away	4.03	0.301	1.62	4.03	0.261
	Into	3.17	0.361	1.07	3.17	0.353
Michaelis-Menton	All	4.21	1.92	2.03	4.21	0.377
$Y = \frac{P_1 (X - P_2)}{P_3 + X - P_2}$	Away	4.94	1.91	2.79	4.94	0.269
	Into	3.51	2.01	1.28	3.51	0.354
Beverton-Holt	All	0.194	1.06	—	5.15	0.388
$Y = 1/(P_1 + P_2/X)$	Away	0.158	1.17	—	6.33	0.284
	Into	0.241	0.92	—	4.15	0.352

TABLE 4.—Sampling dates, number of transects, and visibilities measured during fall 1979 sampling in two areas within the kelp bed at San Onofre (SOK-U and SOK-D) and in a nearby cobble-bottom area with little kelp (Cobble). Horizontal visibility (vis.) measured in meters

	SOK-U								SOK-D								Cobble	
	3 m		7.6 m		12 m		Bottom		3 m		7.6 m		12 m		Bottom		Bottom	
Date	*n*	vis.	*n*	vis.	*n*	vis	*n*	vis	*n*	vis.	*n*	vis.	*n*	vis.	*n*	vis.	*n*	vis.
10 Oct.							10	2.95										
15 Oct.															9	2.14		
17 Oct.							9	2.89									7	3.00
22 Oct.							10	2.75							9	3.42		
24 Oct.																	10	2.60
26 Oct.									11	14.00	12	8.50	11	3.50				
31 Oct.							10	3.85									10	5.00
7 Nov.															10	3.90		
12 Nov.	12	7.30	12	5.10	12	4.75												
14 Nov																	10	5.50
16 Nov.															10	4.50	10	4.85
21 Nov.							10	8.75										
26 Nov.									12	10.25	12	7.00	12	4.00				
28 Nov.															10	4.00		
30 Nov	12	12.55	12	7.05	12	3.15												
5 Dec.									12	16.00	12	13.75	12	7.25				
7 Dec.	12	10.50	12	5.85	12	5.10												
10 Dec.									12	8.25	12	7.80	12	6.90				
12 Dec.	12	9.45	12	6.95	12	8.50												
19 Dec.	13	10.50	12	8.50	12	5.25												
Total	61		60		60		49		47		48		47		48		47	
Mean		10.06		6.69		5.35		4.24		12.13		9.26		5.41		3.59		4.19

that the upper kelp canopy serves as a nursery for young-of-the-year kelp bass, and these cryptic fish were probably much more abundant there than shown by our counts. We examined vertical segregation of size classes only for kelp bass. This is because our 1979 data were too few to evaluate vertical segregation by size that has since been noted for two other species (señorita and blacksmith) in several

TABLE 5.—Percent of transects on which species were observed during fall 1979, in two portions of a kelp forest near San Onofre, Calif. (SOK-U and SOK-D) and in a nearby kelpless cobble area (Cobble). Species' ranks are shown in parentheses. Number of transects is noted in the column heading.

	SOK-U				SOK-D				Cobble
Species	3 m n=61	7.6 m n=60	12 m n=60	Bottom n=49	3 m n=47	7.6 m n=48	12 m n=47	Bottom n=48	Bottom n=47
kelp bass	52(3)	50(3)	60(1.5)	61(2.5)	74(2)	77(2)	81(1)	81(2)	26(4.5)
barred sand bass		2(10)	8(4.5)	59(4)			9(8)	58(5)	53(1)
kelp perch	59(2)	13(4)	2(13)		49(3)	10(6.5)	9(8)		
black perch			8(4.5)	41(5)			9(8)	65(3)	26(4.5)
white seaperch	41(4)	58(2)	60(1.5)	39(6.5)	40(4)	56(3)	62(3)	44(7.5)	15(8)
pile perch		2(10)	3(10)	20(9)	4(9)		17(5)	42(9)	11(9)
rubberlip seaperch			3(10)	16(10)				19(10)	4(12.5)
rainbow seaperch				39(6.5)				44(7.5)	19(6 5)
señorita	93(1)	87(1)	58(3)	61(2.5)	96(1)	94(1)	66(2)	63(4)	43(2)
California sheephead			5(7.5)	58(1)	2(10.5)	19(5)	36(4)	90(1)	36(3)
rock wrasse				29(8)		2(9.5)	4(10)	46(6)	6(10.5)
opaleye	3(8)								2(15)
halfmoon	16(6.5)	7(6)	2(13)	2(14)	36(5)	38(4)	11(6)	4(12.5)	19(6.5)
blacksmith		2(10)					2(11.5)		
garibaldi								4(12.5)	
giant kelpfish	24(5)	8(5)	7(6)	3(11)	21(6)	10(6.5)		4(12.5)	
cabezon				2(14)				2(16.5)	
California scorpionfish								2(16.5)	4(12.5)
rockfish spp.			3(10)	2(14)					6(10.5)
black croaker								2(16.5)	
salema								4(12.5)	
silversides	16(6.5)				19(7)				
jack mackerel	2(9.5)	3(7.5)	5(7 5)		17(8)	8(8)	2(11.5)		
Pacific barracuda					2(10.5)	2(9.5)			
leopard shark				2(14)					
thornback									2(15)
bat ray				2(14)				2(16.5)	
Pacific electric ray	2(9.5)	3(7.5)	2(13)						2(15)

TABLE 6.—Mean numerical and biomass densities (per 1,000 m³) of fishes observed in n daily samples per depth stratum at the SOK-U area in the San Onofre kelp bed during fall 1979. Values are the grand means (±1 standard error) of the daily means (adjusted for transect volume) over transects taken each sampling day.

	SOK-U							
	Numerical density (no./1,000 m³)				Biomass density (kg/1,000 m³)			
	3 m (n=5)	7.6 m (n=5)	12 m (n=5)	Bottom (n=5)	3 m (n=5)	7.6 m (n=5)	12 m (n=5)	Bottom (n=5)
Species	$\bar{x}$ SE	$\bar{x}$ SE	$\bar{x}$ SE	$\bar{x}$ SE	$\bar{x}$ SE	$\bar{x}$ SE	$\bar{x}$ SE	$\bar{x}$ SE
kelp bass	1.57 0.87	2.67 1.19	2.48 0.93	4.76 1.20	0.091 0.071	0.416 0.171	0.664 0.270	1.372 0.372
barred sand bass	0	0.02 0.02	0.13 0.04	3.30 0.70	0	0.024 0.024	0.173 0.046	4.434 0.930
kelp perch	1.39 0.26	0.23 0.13	0.02 0.02	0	0.035 0.007	0.006 0.003	neg.	0
black perch	0	0	0.12 0.07	2.25 0.65	0	0	0.046 0.028	0.717 0.209
white seaperch	1.91 1.21	3.16 1.20	2.33 0.86	3.07 0.59	0.319 0.210	0.491 0.209	0.287 0.105	0.376 0.108
pile perch	0	0.02 0.02	0.08 0.05	0.66 0.11	0	0.009 0.009	0.039 0.025	0.263 0.079
rubberlip seaperch	0	0	0.04 0.03	1.08 0 35	0	0	0.028 0.017	0.634 0.265
rainbow seaperch	0	0	0	2.02 0.92	0	0	0	0.167 0.068
señorita	26.95 6.53	24.45 5.78	4.66 2.22	14 16 5.95	0.950 0.223	1.103 0.225	0.241 0.110	0.566 0.237
California sheephead	0	0	0.13 0.06	4.87 1.16	0	0	0.058 0.040	1.561 0.338
rock wrasse	0	0	0	1 20 1.24	0	0	0	0.237 0.022
opaleye	0.03 0.03	0	0	0	0.033 0.033	0	0	0
halfmoon	0.27 0.20	0.08 0.05	0.02 0.02	0.06 0.06	0.068 0 050	0.020 0.012	0.006 0.006	0.015 0.015
blacksmith	0	002 0.02	0	0	0	neg	0	0
garibaldi	0	0	0	0	0	0	0	0
giant kelpfish	0.35 0.08	0.09 0.04	0.08 0.04	0.18 0.12	0.018 0.007	0 004 0.003	0.015 0.008	0.014 0.012
cabezon	0	0	0	0.06 0.06	0	0	0	0.089 0.089
Calif. scorpionfish	0	0	0	0	0	0	0	0
rockfish spp.	0	0	0.04 0.02	0.06 0.06	0	0	0.003 0.003	0.024 0.024
black croaker	0	0	0	0	0	0	0	0
salema	0	0	0	0	0	0	0	0
silversides	4 21 1.54	0	0	0	0.092 0.029	0	0	0
jack mackerel	0.09 0.90	8.77 8.74	0.50 0.36	0	0.010 0.010	1.008 1.005	0.057 0.041	0
Pacific barracuda	0	0	0	0	0	0	0	0
leopard shark	0	0	0	0.06 0.06	0	0	0	0.119 0.119
thornback	0	0	0	0	0	0	0	0
bat ray	0	0	0	0.06 0.06	0	0	0	0.397 0.397
Pacific electric ray	0.01 0.01	0.03 0.02	0.02 0.02	0	0.136 0 136	0.320 0.196	0.154 0.154	0

TABLE 7.—Mean numerical and biomass densities (per 1,000 m^3) of fishes observed in n daily samples per depth stratum at the SOK-D area in the San Onofre kelp bed during fall 1979. Values are the grand means (±1 standard error) of the daily means (adjusted for transect volume) over transects taken each sampling day.

	SOK-D											
	Numerical density (no./1,000 m^3)								Biomass density (kg/1,000 m^3)			
	3 m (n=4)		7.6 m (n=4)		12 m (n=4)		Bottom (n=5)		3 m (n=4)		7.6 m (n=4)		12 m (n=4)		Bottom (n=5)	
Species	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
kelp bass	4.23	0.63	4.61	1.09	4.84	1.07	12.87	3.95	0.726	0.162	1.101	0.440	1.621	0.672	2.363	0.675
barred sand bass	0		0		0.12	0.02	3.14	0.29	0		0		0.178	0.029	3.446	0.577
kelp perch	0.83	0.20	0.19	0.09	0.11	0.08	0		0.021	0.005	0.005	0.002	0.003	0.002	0	
black perch	0		0		0.18	0.11	4.77	0.63	0		0		0.040	0.017	1.401	0.089
white seaperch	3.50	2.38	4.15	1.52	4.83	0.94	3.64	1.48	0.582	0.407	0.681	0.269	0.693	0.180	0.399	0.137
pile perch	0.04	0.04	0		0.23	0.13	1.74	0.18	0.013	0.013	0		0.105	0.068	0.682	0.056
rubberlip seaperch	0		0		0		0.64	0.24	0		0		0		0.447	0.165
rainbow seaperch	0		0		0		2.49	0.71	0		0		0		0.238	0.053
señorita	19.46	2.82	21.04	3.57	5.68	1.82	13.31	7.77	0.569	0.078	1.039	0.158	0.312	0.100	0.435	0.205
California sheephead	0.02	0.02	0.60	0.23	1.52	0.42	13.66	1.29	0.017	0.017	0.181	0.119	0.770	0.386	4.990	0.322
rock wrasse	0		0.02	0.02	0.06	0.03	1.86	0.49	0		0.005	0.005	0.028	0.004	0.405	0.110
opaleye	0		0		0		0		0		0		0		0	
halfmoon	1.09	0.44	2.92	1.83	0.35	0.19	0.12	0.12	0.237	0.110	0.730	0.457	0.087	0.047	0.030	0.030
blacksmith	0		0		0.03	0.04	0		0		0		neg.		0	
garibaldi	0		0		0		0.12	0.07	0		0		0		0.014	0.009
giant kelpfish	0.28	0.06	0.10	0.02	0		0.12	0.07	0.024	0.007	0.008	0.004	0		0.012	0.010
cabezon	0		0		0		0.07	0.06	0		0		0		0.099	0.099
Calif. scorpionfish	0		0		0		0.06	0.06	0		0		0		0.033	0.033
rockfish spp.	0		0		0		0		0		0		0		0	
black croaker	0		0		0		11.85	11.85	0		0		0		2.667	2.667
salema	0		0		0		8.89	5.93	0		0		0		0.667	0.444
silversides	5.99	3.96	0		0		0		0.120	0.079	0		0		0	
jack mackerel	20.96	9.05	19.34	17.69	3.32	3.32	0		2.410	1.040	2.224	2.035	0.381	0.381	0	
Pacific barracuda	0.13	0.13	0.61	0.61	0		0		0.019	0.019	0.092	0.092	0		0	
leopard shark	0		0		0		0		0		0		0		0	
thornback	0		0		0		0		0		0		0		0	
bat ray	0		0		0		0.12	0.12	0		0		0		0.794	0.794
Pacific electric ray	0		0		0		0		0		0		0		0	

TABLE 8.—Mean numerical densities (per 1,000 m^3) of young-of-the-year (yoy), all juveniles (including yoy), subadult, and adult kelp bass in n daily samples per depth stratum at SOK-U and SOK-D during fall 1979. Grand means calculated as in Tables 6 and 7.

	Numerical density (no./1,000 m^3)							
	3 m (n = 5)		7.6 m (n = 5)		12 m (n = 5)		Bottom (n = 5)	
SOK-U	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
yoy	0.65	0.20	0.36	0.12	0.10	0.05	0.24	0.24
all juvs.	1.23	0.62	0.85	0.34	0.90	0.38	1.36	0.76
subadults	0.32	0.25	1.76	0.94	1.18	0.52	2.59	0.69
adults	0.02	0.01	0.05	0.04	0.40	0.24	0.80	0.26
	3 m (n = 4)		7.6 m (n = 4)		12 m (n = 4)		Bottom (n = 5)	
SOK-D	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
yoy	0.88	0.42	0.33	0.13	0.20	0.09	0.12	0.12
all juvs.	1.50	0.62	1.24	0.19	1.37	0.50	5.21	3.26
subadults	2.52	0.98	2.88	0.87	2.39	0.84	6.72	3.05
adults	0.20	0.12	0.49	0.28	1.08	0.49	0.94	0.18

kelp beds off northern San Diego County (DeMartini et al.[6]).

Seven of the 13 common species were most abundant near the bottom (Tables 5, 6, 7). Rainbow seaperch and rock wrasse rarely, if ever, strayed above the bottom. Black perch and rubberlip seaperch were recorded occasionally at 12 m, but were much more abundant on the bottom. Pile perch were seen, at one site or the other, in all strata, but were most abundant on the bottom and at 12 m. Barred sand bass also concentrated on the bottom and, to a lesser degree, at 12 m. California sheephead were observed as shallow as 3 m at SOK-D, but no shallower than 12 m at SOK-U.

Species composition and relative abundance in each stratum reflected the distributional patterns of the species (Tables 9, 10). The three cosmopolitan species were among the three to five most abundant species in every stratum, particularly above the bottom. At 3 and 7.6 m, they made up 89-99% of total numerical density. The remaining fish in these strata were mainly upper water-column species, with a few of the more errant bottom species (such as California sheephead and pile perch) entering at 7.6 m. The three cosmopolites again dominated the assemblage at 12 m, forming 86-94% of fish numbers. A few individuals of canopy species were present at 12 m, however, and a greater number of bottom species were observed. The bottom stratum contained the greatest number of recorded species, and individuals were distributed more evenly among these species. The cosmopolites were still among the most abundant species on the bottom, but several of the bottom-zone species (such as California sheephead, black perch, and barred sand bass) were also abun-

[6]E. DeMartini, F. Koehrn, D. Roberts, R. Fountain, and K. Plummer. Variations in the abundances of fishes within and between stands of giant kelp (*Macrocystis pyrifera*) during successive years. Manuscr. in prep. Marine Science Institute, University of California, Santa Barbara, CA 93106.

TABLE 9.—Percent contribution of species to total numerical and biomass density at the SOK-U area of the San Onofre kelp bed during fall 1979. Percentages are given by stratum and for abundance integrated throughout the water column. Only those species contributing 1% or more are listed. Stratum values are based on data in Tables 6 and 7; integrated abundances on Table 11.

3 m		7.6 m		12 m		Bottom		Integrated	
Species	%	Species	%	Species	%	Species	%	Species	%
SOK-U Numbers									
señorita	83.0	señorita	79.5	señorita	46.0	señorita	37.5	señorita	72.0
white seaperch	5.9	white seaperch	10.3	kelp bass	24.5	Calif. sheephead	12.9	white seaperch	9.3
kelp bass	4.8	kelp bass	8.7	white seaperch	23.0	kelp bass	12.6	kelp bass	9.1
kelp perch	4.3			barred sand bass	1.3	barred sand bass	8.7	kelp perch	2.1
giant kelpfish	1.1			Calif. sheephead	1.3	white seaperch	8.1	Calif. sheephead	2.0
				black perch	1.2	black perch	6.0	barred sand bass	1.4
						rainbow seaperch	5.4		
						rock wrasse	3.2		
						rubberlip seaperch	2.9		
						pile perch	1.7		
SOK-U Biomass									
señorita	62.7	señorita	53.2	kelp bass	42.6	barred sand bass	42.4	señorita	30.2
white seaperch	21.1	white seaperch	23.7	white seaperch	18.4	Calif. sheephead	14.9	barred sand bass	19.1
kelp bass	6.0	kelp bass	20.1	señorita	15.4	kelp bass	13.1	kelp bass	17.7
halfmoon	4.5	barred sand bass	1.2	barred sand bass	11.1	black perch	6.8	white seaperch	14.2
kelp perch	2.3	halfmoon	1.0	Calif. sheephead	3.7	rubberlip seaperch	6.1	Calif. sheephead	6.6
opal	2.2			black perch	2.9	señorita	5.4	black perch	3.2
giant kelpfish	1.2			pile perch	2.5	white seaperch	3.6	rubberlip seaperch	2.7
				rubberlip seaperch	1.8	pile perch	2.5	pile perch	1.5
				giant kelpfish	1.0	rock wrasse	2.3	halfmoon	1.2
						rainbow seaperch	1.6		

TABLE 10.—Percent contribution of species to total numerical and biomass density at the SOK-D area of the San Onofre kelp bed during fall 1979. Percentages are given by stratum and for abundance integrated throughout the water column. Only those species contributing 1% or more are listed. Stratum values are based on data in Tables 6 and 7; integrated abundances on Table 11.

3 m		7.6 m		12 m		Bottom		Integrated	
Species	%	Species	%	Species	%	Species	%	Species	%
SOK-D Numbers									
señorita	66.1	señorita	62.6	señorita	31.6	Calif. sheephead	23.3	señorita	51.7
kelp bass	14.4	kelp bass	13.7	kelp bass	27.0	señorita	22.7	kelp bass	17.4
white seaperch	11.9	white seaperch	12.3	white seaperch	27.0	kelp bass	22.0	white seaperch	13.1
halfmoon	3.7	halfmoon	8.7	Calif. sheephead	8.5	black perch	8.1	Calif. sheephead	6.3
kelp perch	2.8	Calif. sheephead	1.8	halfmoon	1.9	white seaperch	6.2	halfmoon	4.4
				pile perch	1.3	barred sand bass	5.4	black perch	1.7
				black perch	1.0	rainbow seaperch	4.2	kelp perch	1.2
						rock wrasse	3.2	barred sand bass	1.1
						pile perch	3.0		
						rubberlip seaperch	1.1		
SOK-D Biomass									
kelp bass	32.6	kelp bass	29.4	kelp bass	42.2	Calif. sheephead	33.3	kelp bass	28.2
white seaperch	26.2	señorita	27.7	Calif. sheephead	20.1	barred sand bass	23.0	Calif. sheephead	17.2
señorita	25.6	halfmoon	19.5	white seaperch	18.1	kelp bass	15.8	señorita	14.5
halfmoon	12.3	white seaperch	18.2	señorita	8.1	black perch	9.3	white seaperch	14.3
giant kelpfish	1.1	Calif. sheephead	4.8	barred sand bass	4.6	pile perch	4.5	barred sand bass	8.9
				pile perch	2.7	rubberlip seaperch	3.0	halfmoon	7.8
				halfmoon	2.3	señorita	2.9	black perch	3.4
				black perch	1.0	rock wrasse	2.7	pile perch	2.3
						white seaperch	2.7	rock wrasse	1.1
						rainbow seaperch	1.6	rubberlip seaperch	1.0

dant. The gradual change in species composition that occurred between the water-column strata became more abrupt at the bottom.

The vertical profile of total numerical density reflected changes in the abundance of the most numerous species, señorita, and the increase in species number on the bottom. Numerical density was about the same at 3 and 7.6 m, dropped at 12 m, and peaked on the bottom (Fig. 4). Small differences in species composition at 3 and 7.6 m led to only small differences in the abundances of noncosmopolites, and the cosmopolites (particularly señorita) had similar densities in these strata (Tables 6, 7). Despite increased abundances of bottom species at 12 m, the loss of upper water-column species and the decline in abundance of señorita led to low overall numerical densities in this stratum (Tables 6, 7). Señorita became more abundant again in the bottom stratum, kelp bass reached peak density, and the bottom species became abundant (Tables 6, 7), leading to high numerical densities on the bottom (Fig. 4).

Biomass density did not differ among the water-column strata, but reached an exaggerated peak on the bottom (Fig. 5). At 12 m, the increase in size of kelp bass, and the addition of large-bodied species like California sheephead, barred sand bass, and

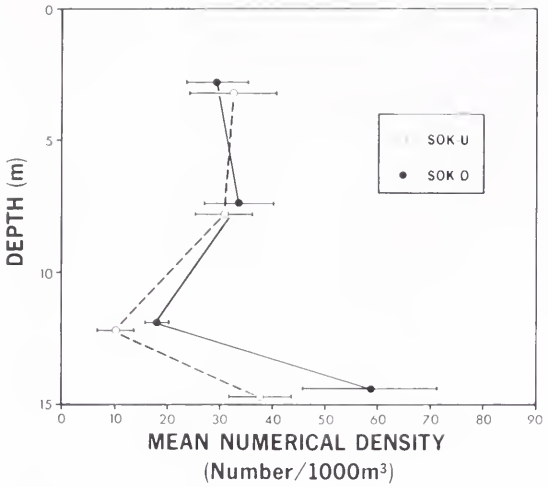

FIGURE 4.—Vertical distribution of the numerical densities of all resident teleosts in two areas within the San Onofre kelp bed during fall 1979. Points are mean densities over sampling dates at each site and stratum, and bars represent one standard error of the mean.

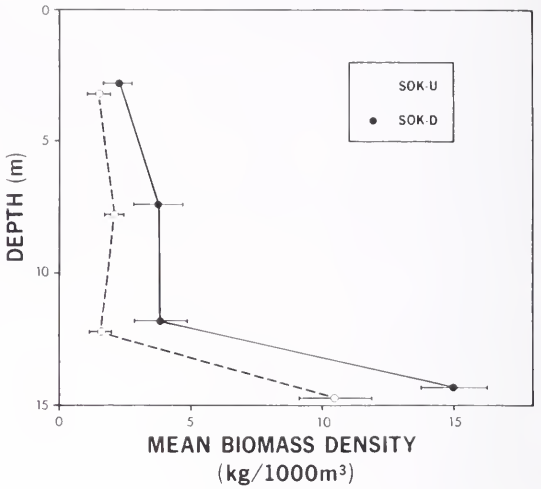

FIGURE 5.—Vertical distributions of the biomass density of all resident teleosts in two areas within the San Onofre kelp forest during fall 1979. Points are mean densities over sampling dates at each site and stratum, and bars represent one standard error of the mean.

various embiotocids compensated for the decline in abundance of señorita (Tables 6, 7). The higher numerical densities of these large fishes on the bottom contributed most to the peak biomass densities in this stratum.

Weighting densities for the size of stratum, we estimated that on average about 40 and 46 fish occurred over 100 m² at SOK-U and SOK-D, respectively, with corresponding biomass values of 3.9 and 6.5 kg/100 m² (Table 11). About 66% (SOK-D) to 77% (SOK-U) of all individuals occurred in the upper two strata, 9% (SOK-U) to 14% (SOK-D) at 12 m, and 14% (SOK-U) to 19% (SOK-D) on the bottom. The small vertical extent of the bottom stratum diminished its contribution to the abundance of fish integrated over the entire water column. About 44-45% of fish biomass occurred in the two upper strata, 15% (SOK-U) to 22% (SOK-D) occurred at 12 m, and 34% (SOK-D) to 40% (SOK-U) on the bottom. Thus much of biomass was near the bottom, but because of

TABLE 11.—Abundance of resident teleosts, based on densities integrated through the water column over 100 m² of bottom. The standing stock in numbers and biomass is given for each of two areas (SOK-U and SOK-D) within the San Onofre kelp bed, and for an adjacent area of cobble bottom with little kelp (Cobble), for samples taken in fall 1979.

	Numbers per 100 m²						Biomass (kg) per 100 m²					
	SOK-U		SOK-D		Cobble		SOK-U		SOK-D		Cobble	
Species	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
kelp bass	3.66	1.02	8.04	0 80	0.25	0 14	0.67	0.15	1.83	0.41	0.12	0.04
barred sand bass	0.55	0.11	0.52	0.04	1.16	0.37	0.74	0.14	0.58	0.09	1.69	0.55
kelp perch	0.85	0.20	0.57	0 05	0		0.02	0.01	0.01	0.01	0	
black perch	0.38	0.10	0.78	0 10	0.54	0.32	0.13	0.03	0.23	0.02	0.19	0.11
white seaperch	3.76	1.43	6.05	1.54	0 46	0.31	0.55	0.24	0.93	0.30	0.07	0.06
pile perch	0.14	0.03	0.37	0.07	0 05	0.02	0.06	0.02	0.15	0.03	0.02	0.01
rubberlip seaperch	0.18	0.05	0.10	0.04	0 03	0.02	0.11	0.04	0.07	0.02	0.02	0.01
rainbow seaperch	0.30	0 14	0.37	0.11	0 01	0.12	0.03	0.01	0.04	0.01	0 01	0.01
señorita	28.86	4 63	23 88	2.06	2 16	0.77	1.17	0.21	0.95	0.05	0.06	0 04
Calif. sheephead	0.78	0.18	2.89	0.30	0 61	0 20	0.26	0.05	1.12	0.17	0.18	0.06
rock wrasse	0.18	0.04	0.31	0.08	0.03	0.01	0.04	0.01	0.07	0.02	0.01	0.01
opaleye	0.02	0.02	0		0.01	0.01	0.02	0.02	0		0.01	0.01
halfmoon	0.20	0 13	2.04	1.03	0 11	0.05	0.05	0.03	0 51	0.26	0.03	0.01
blacksmith	0.01	0.01	0.01	0.04	0		neg.		neg.		0	
garibaldi	0		0.02	0.01	0		0		neg.		0	
giant kelpfish	0.28	0.07	0 21	0.04	0		0.02	0.01	0.02	0.01	0	
cabezon	0.02	0.01	0.01	0.01	0		0.01	0.01	0.02	0.02	0	
Calif. scorpionfish	0		0.01	0.01	0.02	0.01	0		neg		0.01	0.01
rockfish spp.	0.02	0.01	0		0.04	0.03	0.01	0.01	0		0.01	0.01
All residents	40.4	6.0	46.2	4 1	5.6	0.94	3.9	0.5	6.5	0.7	2.4	0.6

their more extensive bathymetric ranges, the low biomass-density upper strata still contributed nearly one-half of total biomass.

The most abundant species at SOK were the cosmopolites (Tables 9, 10, 11). Señorita, kelp bass, and white seaperch comprised 82 and 90% of all individuals in the kelp forests at SOK-D and SOK-U, respectively. These species also contributed strongly to overall integrated biomass, although large species like California sheephead, barred sand bass, and halfmoon were also important. As a result, the distribution of biomass among species was more even than the distribution of numbers (Tables 9, 10, 11).

Two relatively large fishes were more abundant at SOK-D than SOK-U during fall of 1979, contributing to the differences (see below) in our estimates of total biomass at each site (Table 11). The integrated abundance of kelp bass was significantly higher, or nearly so, at SOK-D (Numbers: $t = 3.37$, df $= 7$, $0.01 < P < 0.02$; Biomass: $t = 2.65$, df $= 4$, $0.05 < P < 0.1$). California sheephead were also more abundant at SOK-D, as tested with log-transformed bottom data (Numbers: $t = 4.81$, df $= 6$, $P < 0.01$; Biomass: $t = 3.35$, df $= 5$, $0.02 < P < 0.05$) and with integrated abundances (Numbers: $t = 6.03$, df $= 5$, $P < 0.01$; Biomass: $t = 4.92$, df $= 4$, $P < 0.01$). Halfmoon seemed to be more abundant at SOK-D, but the difference was not significant (Numbers: $t = 1.78$, df $= 3$, $P > 0.1$; Biomass: $t = 1.78$, df $= 3$, $P > 0.1$).

At the kelpless cobble site, most fish were bottom species and cosmopolites (Tables 5, 11). While barred sand bass, black perch, and California sheephead were fairly abundant in this area, the average abundances of other species were less than in the kelp-bed areas. The integrated numerical abundance of all fishes was significantly lower in the kelpless cobble area (cobble vs. SOK-U: $t = 5.71$, df $= 4$, $P < 0.01$; cobble vs. SOK-D: $t = 9.42$, df $= 3$, $P < 0.01$; SOK-U vs. SOK-D: $t = 0.79$, df $= 7$, $P > 0.4$). A one-way ANOVA of log-transformed counts on the bottom showed significant differences among the three areas ($F_{2,12} = 9.42$, $P < 0.01$), but an a priori comparison of SOK-U and SOK-D versus the cobble area was not significant ($F_{1,12} = 1.207$, $P > 0.25$). Thus, the lower overall numerical abundance at the kelpless cobble area was due largely to the presence of fish above the bottom at SOK. The integrated total biomass of fish did not differ significantly among the three areas ($F_{2,11} = 0.25$, $P > 0.75$), even though the point estimate of 2.4 kg/100 m² at the cobble area was lower than both values at SOK. However, barred sand bass made up over 70% of fish biomass in the cobble area, so most other species were much less abundant there.

We estimated the density of *Macrocystis* plants >1 m tall to be 7.51 ± 0.71 (1 SE) plants/100 m² at the "kelpless" cobble area, 23.11 ± 1.47 plants/100 m² at SOK-U, and 30.18 ± 1.69 plants/100 m² at SOK-D. Thus, some kelp was present at the cobble area, but the density of subadult-adult plants there was 25-32% of density in our kelp-bed areas.

DISCUSSION

Sampling

Regardless of water clarity, our camera and film were unable to resolve fish beyond 3-4 m; this set an upper limit of just over 1,000 m³ to cinetransect volume. Alevizon and Brooks (1975) noted that in very clear, shallow waters, fish seemed difficult to distinguish on film beyond 5 m. Ebeling et al. (1980b) found camera range to be 3-3.5 m at horizontal visibilities of 4 and 15 m, and concluded that there was essentially no relation between camera range and horizontal visibility. Our data show this to be true at visibilities >7-9 m. The fixed focal length of the camera, shallow depth of field at maximum aperture, and quality of film account for the limited camera range, as discussed by Ebeling et al. (1980b). However, our data show that camera range decreases when visibility decreases to values that approach maximum camera range. Corrections for visibility are common in terrestrial line transects, whether the area of a given transect is taken as fixed throughout or as variable (Caughley 1977; Burnham et al. 1980). We regarded the volume of a given cinetransect to be fixed, its width determined by visibility.

The relatively low upper limit to camera range may help to make cinetransects in the water column more accurate than visual censuses. Searching efficiency would likely be poorer for broad visual transects made to the limits of visibility. Furthermore, it is difficult to judge arbitrary smaller distances in open water, unless they are only a meter or two on either side of the diver. Cinetransects provide an almost automatic upper limit to transect width, and this limit is wide enough (about 3 m to either side in moderately clear water) that a substantial volume of water is censused.

We have not verified the exact volume sampled in each of our cinetransects, nor are we able to compare densities measured in cinetransects with actual densities (Brock 1982), since the latter have not been measured by any method. To our knowledge, only Keast and Harker (1977) have actually marked the outside boundaries of visual underwater transects. However, Terry and Stephens (1976) and Stephens

and Zerba (1981) utilized two divers, swimming parallel, unmarked courses and counting fish between each other, to sample rocky-reef fishes. Perhaps such a method could be used to evaluate densities estimated in cinetransects.

Species Composition, Distribution, and Abundance

The species observed in the San Onofre kelp forest were a subset of the species found in other nearshore areas of hard substrate and vegetation off southern California. Many reef-dependent fishes that are very common in other kelp forests were either rare or unrecorded at San Onofre. Species such as blacksmith and opaleye (Ebeling and Bray 1976; Hobson and Chess 1976), garibaldi (Clarke 1970), painted greenling (DeMartini and Anderson 1979), and some species of *Sebastes* (Larson 1980) depend on rugose reefs for shelter or spawning sites. Some turf-grazing and otherwise bottom-feeding species of embiotocids also appeared to be less abundant at San Onofre than in other areas. Our estimates of 14-37 kg/ha of pile perch, 38-78 kg/ha of black perch, and 10-18 kg/ha of rubberlip seaperch were mostly smaller than the estimates of Ebeling et al. (1980b) off Santa Barbara and Santa Cruz Island. The rarity and low abundance of all these species markedly alters the character of the fish assemblage at San Onofre.

The abundant species at San Onofre kelp forest either are less dependent on rock reefs (at least, if kelp is present) or associate preferentially with low-relief substrates. The former group might include the canopy species, the cosmopolitan kelp bass and señorita, and perhaps the epibenthic California sheephead. The latter group might include barred sand bass and white seaperch. These two species (and perhaps señorita) were more common at San Onofre than others (Ebeling et al. 1980a, b) have reported in kelp forest anchored on high-relief substrates. Barred sand bass occurred in over half of the bottom transects at SOK, but in no more than 12% of bottom transects near Santa Barbara (Ebeling et al. 1980a). We found white seaperch in 40-60% of our transects, while Ebeling et al. (1980a) saw them on 7-42% of all transects (but 20-42% of "sandy margin" transects). Both of these species have been reported as associating with sand or the sand-rock interface (Quast 1968a; Feder et al. 1974; Ebeling et al. 1980a). Moreover, barred sand bass have a warmwater affinity (Frey 1971) and on average should be more abundant farther south in the Southern California Bight. The abundance of white seaperch at SOK may be unusually high during the fall. At this time, white seaperch appear to use the SOK habitat for mating as well as feeding. While some individuals of white seaperch are found in kelp forests all year, much of their populations in kelp beds off northern San Diego County move offshore after fall (authors' observations).

The vertical distributions of species present at the San Onofre kelp bed were similar to patterns described in other kelp forests. Kelp perch, giant kelpfish, and, to a lesser extent, halfmoon have been recognized as water-column and canopy species (Quast 1968a; Feder et al. 1974; Bray and Ebeling 1975; Ebeling and Bray 1976; Hobson and Chess 1976; Coyer 1979; Ebeling et al. 1980a, b). Kelp bass and white seaperch have been described as members of a vertical "commuter" group of fishes in kelp forests near Santa Barbara (Ebeling et al. 1980a). The term "cosmopolite" better describes the habits of these two fishes. Señorita also fell into Ebeling et al.'s "canopy" group, but its occurrence throughout the water column was recognized by Hobson (1971), Ebeling and Bray (1975), Bernstein and Jung (1979), and others. We feel that it too should be considered a cosmopolite. Pile perch and rubberlip seaperch were also assigned to the commuter group of Ebeling et al. (1980a) and did appear above the bottom at San Onofre. However, the dense midwater aggregations of these species observed elsewhere were not present at San Onofre. Perhaps the relatively low density of these species at San Onofre was responsible for the absence of these aggregations. On the other hand, our fairly frequent observation of California sheephead well above the bottom is apparently new. Quast (1968a), in fact, noted that sheephead seem "reluctant" to leave the bottom. Barred sand bass, black perch, rainbow seaperch, and rock wrasse occurred almost exclusively on the bottom, and have been generally recognized as bottom dwellers.

Our estimates of vertically integrated standing stock were surprisingly high. Most estimates of fish biomass on tropical and temperate reefs fall into the range of a few to several hundred kg/ha (Brock 1954; Bardach 1959; Randall 1963; Quast 1968b; Talbot and Goldman 1972; Miller and Geibel 1973; Jones and Chase 1975; Russell 1977). It is encouraging that our estimates of 3.88-6.53 kg/100 m^2 (388-653 kg/ha) fell within this range. Furthermore, our density estimates for fall 1979 are generally similar to subsequent estimates made for canopy and bottom strata during the fall periods of 1980 and 1981 (E. DeMartini[7] Unpubl. data). In particular, the densities of resi-

[7]E. DeMartini, Marine Science Institute, University of California, Santa Barbara, CA 93106.

dent species (kelp bass and California sheephead) that contributed most to biomass estimates for fall 1979 were not consistently larger or smaller, if different at all, at SOK during fall 1980 and 1981. Hence we feel that our estimates for fall 1979 are typical for SOK during this season. Furthermore, while species such as kelp bass and sheephead were most abundant at SOK-D during fall 1979, this was not always true in 1980 and 1981; the site of greater abundance switched between SOK-U and SOK-D for many species over the period of 1979-81 (DeMartini et al. footnote 6). Thus we also conclude that apparent differences between SOK-U and SOK-D during fall 1979, although perhaps statistically real, are not meaningful for our general characterization of standing stock at SOK. For this reason, we have provided data for the areas separately as brackets for our estimates of conditions in the San Onofre kelp bed in general, and do not specifically attribute the greater abundance of fishes at SOK-D to greater numerical density of giant kelp plants >1 m tall.

The surprising aspect of our standing-stock estimates is that they are as large or larger than those of Quast (1968b) in nearshore areas of greater bottom relief. Subtracting elasmobranchs, "nonresident" teleosts, and cryptic bottom species, his estimates of standing stock at two sites near San Diego were about 366 kg/ha for Del Mar and 299 kg/ha for Bathtub Rock. Thus, even though our areas at San Onofre lacked many individuals of such great contributors to biomass at Quast's sites as opaleye, blacksmith, kelp rockfish, and garibaldi, our bracketed values of biomass were of the same order to nearly twice Quast's estimates. Below, we examine three possible reasons for this perceived disparity: Bias due to sampling methods, bias due to the times and places sampled, and the possibility that there really was a relatively large standing stock of fishes at San Onofre.

Our sampling methods may have led to overestimates, or Quast's (1968b) to underestimates, of standing stock. Quast's quantitative collection at Del Mar lacked a wall net, so some fish may have escaped. Although he used transect densities for three of the abundant species in his corrected estimates, his transect method of counting fish to the limits of visibility may have led to reduced searching efficiency (as discussed above). It is less likely that we counted fish in a larger volume than we think. We may have inflated our estimates of integrated abundance by sampling the bottom stratum on different days than the water-column strata, so that the same individuals could have figured into average density in more than one stratum as distributions changed from day to day. Such errors would have been most serious in the cosmopolitan species, and perhaps in large bottom species (like California sheephead) that also occurred in the water column. However, even in our 3 m stratum, the average numbers of señorita and white seaperch per transect (uncorrected for visibility) were greater than similar averages obtained by Ebeling et al. (1980a, b) in cinetransects off Santa Barbara, implying that these species really were abundant during the fall at San Onofre. For kelp bass, the average standing stock above the bottom was 48 ± 13 (SE) kg/ha at SOK-U and 148 ± 40 at SOK-D. These values are large fractions of our total respective estimates of about 69 and 183 kg/ha. Similarly, our estimates of sheephead biomass on the bottom alone were 23 ± 5 kg/ha at SOK-U and 75 ± 5 kg/ha at SOK-D, compared with our total estimates of about 26 and 112 kg/ha at the respective areas. We conclude that, while sampling problems may have contributed some bias to both our estimates and those of Quast's, much of the difference between Quast's estimates and ours is real, and fish really were relatively more abundant in the areas we sampled at SOK during the fall.

Our selection of sampling times and places could have led to estimates that are somewhat unrepresentative of conditions in general at San Onofre. Seasonal factors might be involved for some of our "resident" species. Dense concentrations of some fishes (notably white seaperch) may be atypically high at SOK and perhaps other kelp beds during the fall, when these areas are used for breeding. Many species of fish can be found in kelp beds all year, but their abundances might nevertheless fluctuate greatly as individuals move among areas within kelp beds, between different kelp beds, and perhaps between different nearshore habitats. We feel that our samples accurately characterize the standing stock of fishes at San Onofre kelp in the fall, but cannot extend our observations to other seasons.

Horizontal patchiness in the distribution of fish may also have affected our estimates. Our kelp-forest sampling areas were near the offshore edge of a large area of surface canopy, and fish often were quite dense at the actual edge of the kelp forest. Limbaugh (1955), Quast (1968a), Feder et al. (1974), Hobson and Chess (1976), Bray (1981), and others have discussed this "edge effect". Although many of our transects did not (by chance) sample the edge of the bed, the averages we calculated nonetheless may have overestimated the density of some species throughout the entire bed. However, our estimates of fish density at the particular study areas should be relatively unbiased. Quast's (1968b) Del Mar collec-

tion was also made at the edge of a kelp forest, so comparison with our areas is warranted.

The comparatively large standing stock of fishes at SOK in part reflects the nature of the kelp forest off San Onofre. This kelp forest was located in relatively deep (15 m) water, and was of moderate (0.1 adult plant/m^2; Dean footnote 4) kelp density, with a surface canopy. Both of Quast's (1968b) sites were located in relatively shallow (7.6-10.7 m) water. Furthermore, Quast's Bathtub Rock site lacked a surface kelp canopy. A substantial part of the fish biomass we observed at San Onofre was in the extensive canopy and midwater zones. Nearly half of the biomass occurred in the upper two strata at each site, and about one-quarter occurred in the midwater (7.6 m) stratum alone. The contribution of the upper water column to overall standing stock is also illustrated by the relative importanceof the cosmopolitan species. Ranging throughout the water column, kelp bass, white seaperch, and señorita comprised about 60% of total biomass at the San Onofre kelp bed. The relative contribution of water-column species to overall standing stock would be lower in kelp forests anchored on high-relief rock, because reef-dependent species would be more abundant than at San Onofre. However, the presence of an extensive bathymetric zone from the canopy into midwaters provided space, forage, and orientation for a substantial standing stock of fishes in the San Onofre kelp bed. The lack of such an extensive midwater zone may have limited the abundance of canopy and cosmopolitan species at Bathtub Rock and Del Mar, accounting, in part, for the relatively low estimates of standing stock in these areas.

Our study, then, suggests that kelp per se can enhance the potential standing stock of fishes in an area. Our kelp-forest areas lacked a high-relief bottom and the species of fish that depend on it. The remaining fish were those that either tolerate or are not influenced by a cobble bottom, and those that depend intimately on kelp. Yet the standing stock of fishes at the San Onofre kelp bed was substantial. The reduced numerical abundance of fishes and smaller biomass (excluding barred sand bass) in our kelp-depauperate area further indicates the importance of kelp at San Onofre. Experimental manipulation of kelp density is probably the best test of the influence of kelp on fish abundance (Miller and Geibel 1973; Bray 1981; M. Carr footnote 3). We also recognize that large-scale oceanographic factors may strongly affect survivorship of planktonic larvae and the subsequent abundance of juvenile and adult fishes (Stephens and Zerba 1981; Parrish et al. 1981). However, our comparisons indicate that giant kelp, even in only moderate density, was necessary for the existence of a large standing stock of diverse fishes in cobble-bottom areas. We conclude that, while rock reefs enhance the fish fuana of an area whether or not there is kelp, the presence of kelp in an area of low-relief bottom also augments the abundance of juvenile and adult fish on a local scale. Kelp may also contribute strongly to the standing stock of fish in areas of high-relief bottom, but no one to date has adequately evaluated this hypothesis. We predict that the densities of canopy species and cosmopolites like kelp bass and señorita will also prove to be related to the density of giant kelp on high-relief bottoms.

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THE INVERTEBRATE ASSEMBLAGE ASSOCIATED WITH THE GIANT KELP, *MACROCYSTIS PYRIFERA*, AT SANTA CATALINA ISLAND, CALIFORNIA: A GENERAL DESCRIPTION WITH EMPHASIS ON AMPHIPODS, COPEPODS, MYSIDS, AND SHRIMPS[1]

JAMES A. COYER[2]

ABSTRACT

The motile invertebrate assemblage associated with the giant kelp, *Macrocystis pyrifera*, fronds was examined monthly from June 1975 through December 1976, at Santa Catalina Island, California. Replicate samples were collected from each of three vertical zones (canopy [C], middle [M], bottom [B]).

The number of species collected from all zones was 114 and ranged from 51 to 75 for any given month. Amphipods, copepods, mysids, and shrimps comprised the majority of invertebrate abundance (86 [C], 92 [M], 93% [B]) and biomass (90 [C], 89 [M], 86% [B]). Gammarid amphipods dominated the assemblage in numbers (34 [C], 60 [M], 51% [B]), biomass (34 [C], 68 [M], 67% [B]), and number of species (20).

The assemblage displayed three patterns of vertical stratification within the *Macrocystis* forest: 1) The mean number of species progressively decreased from the bottom to the canopy (several species displayed zone preferences); 2) more individuals and a greater total biomass were present in the lower zones than in the canopy; and 3) the mean lengths of gammarids, mysids, and shrimps were significantly larger and proportionately greater numbers of large individuals were present in the canopy than in either of the lower zones.

Subtidal forests of giant kelp have long attracted the interest of biologists, beginning with Darwin's (1860: 240) description of the organisms associated with the giant kelp forests off Tierra del Fuego. Since the advent of scuba techniques in the mid-1950's, several studies have examined in detail the attached and/or motile species of invertebrates associated with surfaces of the giant kelp, *Macrocystis pyrifera* (Limbaugh 1955; Clarke 1971; Ghelardi 1971; Jones 1971; Wing and Clendenning 1971; Miller and Geibel 1973; Lowry et al. 1974; Bernstein and Jung 1979; Yoshioka 1982 a, b). Few, however, have attempted a long-term and comprehensive examination of the entire assemblage of small and motile invertebrates found with the giant kelp. The assemblage is important for several reasons, notably as the major source of food for most fishes residing within the kelp forests (see fish diet studies by Quast 1968; Hobson 1971; Bray and Ebeling 1975; Hobson and Chess 1976).

The present report examines the composition, patterns of vertical stratification, and seasonal dynamics of the small and motile invertebrate assemblage associated with the fronds of *M. pyrifera*. A general overview of the assemblage and a detailed examination of the amphipods, copepods, mysids, and shrimps are presented.

STUDY AREA

The study area was Habitat Reef, located in Big Fisherman Cove, Santa Catalina Island, Calif. (lat. 33°28'N, long. 118°29'W). Habitat Reef is a fingerlike extension of bedrock ranging in depth from 2 to 18 m and is bounded on the three outer margins by an expansive area of shelly debris substrate. The western and northern sides of the reef slope sharply to a depth of 20-25 m, whereas the eastern edge slopes gradually to a shallower area ranging from 8 to 19 m. Water temperatures at Habitat Reef ranged from 13.6° to 21.2°C during the study, warmest during July through September and coolest from December to February.

The algal community of the shoreward portion (<3 m depth) of Habitat Reef was dominated by *Phyllospadix torreyi*, *Eisenia arborea*, *Cystoseira neglecta*, and *Sargassum muticum* (seasonally). The outermost portion (>3 m depth) was dominated by *Macrocystis* and the understory algae in this area was sparse, although small patches of *Dictyopteris zonarioides* and *C. neglecta* were present in some areas.

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MATERIALS AND METHODS

Zonation and Kelp Density

The kelp forest at Habitat Reef was divided into three vertical zones: Canopy (C), middle (M), and bottom (B). The canopy extended from the water surface to a depth of 1 m, the bottom ranged from just above the kelp holdfasts to 2 m above the substrate, and the middle included the area between the canopy and the bottom. Holdfasts were not examined. Kelp density was measured by randomly establishing 25 circular 1 m^2 plots within the study area during November 1975 and October and December 1976. The number of enclosed plants and the number of fronds/plant were determined.

Sampling Procedure

Samples were collected monthly from plants in the central portion of the kelp forest (7-9 m depth) during tidal heights ranging from +1.0 to +1.3 m mean lower low water. From June through September 1975, three replicate samples were collected from each zone; from October 1975 through December 1976, five replicates were collected. Only one sample was collected from any plant, and this sample consisted of the entire plant portion within the desired zone. The middle and bottom zones were collected by carefully severing the upper portions and allowing them to drift away. Disturbance to the lower zones during this procedure was negligible. Similar amounts of kelp were collected from each zone throughout the study (n = 19; $\overline{kg}$ = 2.5[C] 2.1[M], 2.3 [B]).

The kelp-associated invertebrates were collected by scuba divers maneuvering a plankton net (1 m diameter, 3 m long, 0.33 mm mesh) over the desired portion of the plant. This procedure captured most motile invertebrates on the kelp, as well as within the surrounding water column (1 m diameter). The enclosed sample was placed in a large container filled with warm freshwater (providing a thermal and salinity shock), vigorously agitated, and removed. The remaining water was filtered through a 0.25 mm sieve and the residue preserved. Thus, the term "invertebrate" in this investigation refers to all motile individuals larger than 0.33 mm (excluding protozoans, cnidarians, and nematodes).

The efficiency of the agitation-freshwater method was tested by placing the processed kelp into another container of warm freshwater and allowing it to stand for 4 h. Subsequent agitation and filtering indicated that 96% of all motile invertebrates in each zone were removed by the initial agitation-freshwater treatment.

Organisms were identified to species (except for some juveniles). The wet weight of kelp from each sample was measured, and abundances of all taxa were expressed as the number of individuals per kilogram (wet weight) of kelp. The somewhat unconventional normalization of species abundance to unit biomass was selected for three reasons. First, structural complexity within the kelp forest habitat is created by interdigitating kelp blades and stipes and is a function (in part) of both kelp surface area and biomass. Many kelp-associated species, particularly the swarming mysids, may respond primarily to structural complexity of the habitat when seeking shelter and/or food. Secondly, biomass is much easier and faster to measure than is surface area (conversion ratios of kelp wet weight to surface area [both sides of blades + stipes] and kelp dry weight to wet weight are presented in Table 1). Thirdly, unit biomass will facilitate comparisons with invertebrate associations of other species of marine algae for which it is difficult to compute a unit area (i.e., bushy reds and browns).

TABLE 1.—Ratios of kelp wet weight (kg) to kelp surface area (m^2) and dry weight (kg) to wet weight (kg).

	Wet weight/area			Dry weight/Wet weight		
Zone	$\bar{x}$	SD	n	$\bar{x}$	SD	n
Canopy	0.21	0.002	10	0.16	0.010	6
Middle	0.19	0.002	10	0.15	0.025	6
Bottom	0.42	0.040	10	0.13	0.042	6

Determination of Invertebrate Lengths and Biomass

Growth series within the principal taxa were established. Individuals (n = 30-94) were measured to the nearest 0.04 mm, using a dissecting microscope and occular micrometer, blotted dry, and weighed using an analytical balance to determine length-weight relationships. Smaller and/or minor taxa (copepods, ostracods, caprellids, molluscs, etc.) were assigned constant weights based on the mean weight of 20 individuals.

Vertical patterns of size-stratification were examined by measuring the lengths of principal taxa within each zone for each quarter from January 1975 through October 1976. Single samples were collected in January and April 1975; subsequent samples were replicated (3 or 5). For shrimps and mysids, all (January through July 1975) or up to 75 individuals of each major species were measured

from each replicate of each zone; for gammarid amphipods, at least 50 individuals (comprising all species) were measured from one randomly selected replicate of each zone. Replicates were pooled and size-frequency distributions were determined for each taxon within each of the zones. The non-parametric Kolmogorov-Smirnov (K-S) two-sample test (one-tailed) was used to test whether the values from one distribution were stochastically larger than the values from another distribution (Siegel 1956).

The mean weight of an individual within a major taxon (shrimps, mysids, gammarids) was determined from the mean length and the appropriate length-weight formula. The mean weight then was multiplied by the mean monthly abundance of the taxon to determine the taxon biomass. Quarterly length measurements were applied to the month preceding and following the measuring month (i.e., April measurements were assigned to March and May) for biomass measurements. Monthly abundance values of the smaller taxa were multiplied by the assigned weight to estimate the biomass.

RESULTS

Kelp Density

Macrocystis density at Habitat Reef was high (4.7 plants/m^2) from November 1975 through August 1976 (Table 2). In late September 1976, density and canopy cover were reduced (1.5/m^2) and continued to decline over the next 4 mo.

TABLE 2.—*Macrocystis* density and the number of fronds/plant (± width of 95% C.I./2) at Habitat Reef. Sample size in parentheses.

Date	Density/m^2	No. of fronds/plant
Nov. 1975	4.7±2.3 (25)	3.4±1.0 (118)
Oct. 1976	1.5±0.7 (29)	6.7±1.6 (46)
Dec. 1976	0.7±0.3 (25)	4.7±2.6 (17)

General Taxonomic Composition of the Invertebrate Assemblage

The invertebrate assemblage associated with the fronds of *Macrocystis* was composed primarily of amphipods, copepods, mysids, and shrimps (Tables 3, 4). Mysids and shrimps were among the largest

TABLE 4.—Mean abundance ($\overline{no}$./kg kelp ± width of 95% C.I./2) for the major invertebrate taxa within each zone. Parenthetical values are the mean length and weight ($\overline{mm}$, $\overline{mg}$) of each taxon; an asterisk indicates that a constant length and weight was used for all zones. All values are averaged over the entire 19-mo study.

Taxon	Canopy	Middle	Bottom
Gammarid amphipods	882.4 ± 267.0 (2.8,0.6)	4,123.0 ± 890.2 (1.8,0.4)	3,117.8 ± 715.3 (2.0,0.4)
Copepods	1,128.0 ± 370.2	1,977.0 ± 540.8 *(0.8,0.1)	2,453.1 ± 441.0
Ostracods	188.2 ± 76.7	108.8 ± 51.1 *(0.9,0.1)	65.7 ± 30.0
Echinoids (juv.)	13.9 ± 25.5	260.5 ± 375.4 *(0.5,0.1)	83.0 ± 119.2
Mysids	91.4 ± 57.8 (6.2,3.5)	151.8 ± 38.9 (4.7,1.3)	108.0 ± 50.5 (4.4,1.2)
Molluscs ("shelled")	14.8 ± 9.0	98.0 ± 21.8 *(1.3,0.7)	168.4 ± 44.9
Caridean shrimps	136.5 ± 48.4 (7.1,3.8)	65.2 ± 28.4 (6.0,2.7)	51.4 ± 16.0 (5.4,2.3)
Platyhelminthes	31.7 ± 17.1	36.8 ± 16.2 *(−,3.8)	34.0 ± 17.0
Cladocerans	72.2 ± 93.4	9.2 ± 5.1 *(0.7,0.1)	9.3 ± 6.9
Polychaetes	8.8 ± 11.3	28.0 ± 8.0 *(3.3,0.5)	17.4 ± 7.2
Cypris (barnacle) larvae	13.4 ± 16.6	24.0 ± 22.1 *(0.7,0.1)	14.3 ± 9.4
Molluscs (nudibranchs)	10.9 ± 11.3	13.4 ± 11.8 *(1.3,1.1)	8.1 ± 7.5
Sphaeromatid isopods	0.1 ± 0.1	0.2 ± 0.1 *(2.4,1.1)	19.7 ± 23.0
Caprellid amphipods	4.1 ± 2.0	2.7 ± 1.0 *(6.9,0.8)	1.8 ± 1.3
Idoteid isopods	3.1 ± 3.2	0.1 ± 0.1 *(7.2,4.0)	0.1 ± <0.1
Asteroids (juv.)	0.2 ± 0.1	1.1 ± 1.3 *(2.7,2.0)	0.6 ± 0.8
Jaeropsid isopods	0.1 ± 0.1	0.2 ± 0.3 *(2.3,0.3)	1.4 ± 0.9
Cumaceans	0 —	0.2 ± 0.2 —	0.3 ± 0.3
Brachyurans (zoea)	0 —	0 — —	0.1 ± <0.1
Ophiuroids (juv.)	0 —	<0.1 ± <0.1 —	<0.1 ± <0.1
Tanaids	0 —	<0.1 ± 0.1 —	0.1 ± 0.1

TABLE 3.—The mean (± width of 95% C.I./2) monthly abundance ($\overline{no}$. organisms/kg kelp) and biomass ($\overline{mg}$ organisms/kg kelp) for each major invertebrate group associated with the giant kelp. Data are averaged over the entire 19-mo study; proportions of total numbers or biomass (all species) are presented in parentheses.

Zone	Gammarids	Copepods	Mysids	Shrimps	Total
Canopy					
Numbers	882 ± 267 (33.9)	1,128 ± 370 (43.4)	91 ± 58 (3.5)	136 ± 48 (5.2)	2,599 ± 580
Biomass	589 ± 236 (33.8)	56 ± 18 (3.2)	336 ± 255 (19.3)	583 ± 300 (33.4)	1,743 ± 765
Middle					
Numbers	4,123 ± 890 (59.8)	1,977 ± 541 (28.7)	152 ± 39 (2.2)	65 ± 28 (0.9)	6,900 ± 1,382
Biomass	1,634 ± 359 (68.4)	99 ± 27 (4.1)	218 ± 68 (9.1)	174 ± 71 (7.3)	2,387 ± 493
Bottom					
Numbers	3,118 ± 715 (50.8)	2,453 ± 441 (39.9)	108 ± 51 (1.7)	51 ± 16 (0.8)	6,153 ± 937
Biomass	1,388 ± 337 (67.4)	123 ± 22 (6.0)	143 ± 83 (6.9)	116 ± 37 (5.6)	2,061 ± 454

species present, copepods among the smallest (Table 4).

The number of species collected from all zones totaled 114, but ranged from 51 to 75 for any given month (Fig 1). When ranked by the mean monthly abundance, 7 species were dominant (>100/kg), 23 were common (10-100/kg), 24 were uncommon (1-10/kg), and 60 were rare (<1/kg). Crustaceans and gastropods had the greatest species representation with 63 and 36 species present, respectively. The 10 most abundant species within the canopy and bottom and 9 of the top 10 species in the middle were crustaceans; of the 14 crustacean species represented, 6 were gammarid amphipods and 4 were harpacticoid copepods (Table 5).

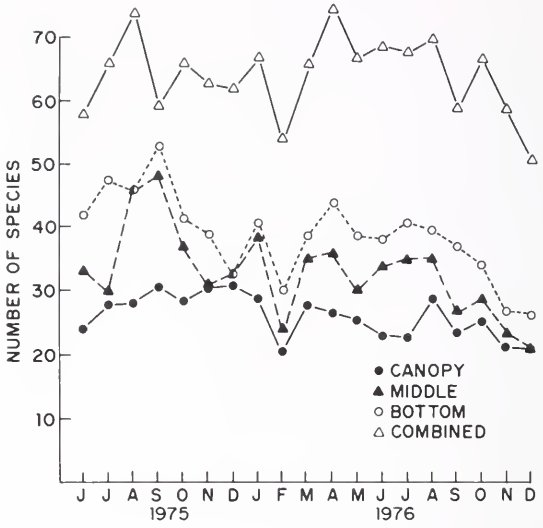

FIGURE 1.—The number of invertebrate species present in each of the vertical zones. Many species are present in more than one zone. Grand means (± width of 95% C.I./2): 26.7 ± 1.6 (C), 33.0 ± 3.3 (M), 38.9 ± 3.2 (B).

Vertical Patterns of Distribution, Abundance, and Sizes

Invertebrate numbers and biomass ($\overline{no.}$/kg kelp, $\overline{mg}$/kg kelp) were greatest in the middle (6,900, 2,387) and bottom (6,143, 2,061) zones, lowest in the canopy (2,599, 1,743; Table 3). Similarly, the number of species was always lowest in the canopy, intermediate in the middle, and highest in the bottom (Student's t-test, $P < 0.05$; Fig. 1).

Gammarid amphipods were the most important taxon associated with *Macrocystis*, dominating the invertebrate assemblage within each zone in terms of numbers (34-60%) and biomass (34-68%; Table 3). Twenty species were collected with fewer species present in the canopy (11) than in the middle (16) or bottom (18).

Collectively, *Microjassa litotes*, *Gitanopsis vilordes*, and *Aoroides columbiae* comprised 83% by number of all gammarids in the canopy, 92% of those in the middle, and 70% of the gammarids in the bottom. The most abundant gammarid in the canopy was *G. vilordes* (53.0%); *M. litotes* was most abundant in the middle (49.0%) and bottom (33.8%; Table 6, Fig. 2). Among the other gammarids present, *Ampithoe plea* and *Hyale frequens* were much more common in the canopy than in the lower zones, whereas *Batea transversa* and *Pontogeneia rostrata* were abundant in the bottom zone and uncommon in the canopy (Table 6).

Numerically, copepods formed a major portion of the invertebrate assemblage (29-43%), but contributed very little to the total biomass (3-6%; Tables 3, 4). Although numerous in all zones, copepods were more abundant in the middle and bottom (Table 3, Fig. 2). Most (88% by number) in the middle zone consisted of *Porcellidium viridae*, *Porcellidium* sp. A, and *Tisbe* sp. In the canopy and bottom zones, *P. viridae*, *Tisbe* sp., and *Scutellidium lamellipes* accounted for 89 and 92%, respectively.

Mysids and shrimps were minor numerical components of the assemblage (2-3 and 1-5%, respectively), but formed major proportions of the invertebrate biomass (7-19, 6-33%; Tables 3, 4). Each of the three

TABLE 5.—The ten most abundant invertebrate species in each zone. Abundances are mean monthly values for the 19-mo study (C = copepod, G = gammarid amphipod, M = mysid, O = ostracod, S = shrimp, E = echinoid [urchin]).

Canopy	$\overline{No.}$/kg kelp	Middle	$\overline{No.}$/kg kelp	Bottom	$\overline{No.}$/kg kelp
Porcellidium viridae (C)	557	*Microjassa litotes* (G)	2,018	*Porcellidium viridae* (C)	1,768
Gitanopsis vilordes (G)	466	*Gitanopsis vilordes* (G)	1,551	*Microjassa litotes* (G)	1,054
Tisbe spp. (C)	303	*Porcellidium viridae* (C)	1,106	*Gitanopsis vilordes* (G)	778
Macrocyprina pacifica (O)	165	*Aoroides columbiae* (G)	600	*Pontogeneia rostrata* (G)	397
Aoroides columbiae (G)	164	*Tisbe* spp. (C)	358	*Tisbe* spp. (C)	374
Scutellidium lamellipes (C)	144	*Porcellidium* sp. A (C)	270	*Aoroides columbiae* (G)	350
Hippolyte clarki (S)	137	*Strongylocentrotus* sp. (E)	260	*Batea transversa* (G)	342
Microjassa litotes (G)	103	*Siriella pacifica* (M)	148	*Scutellidium lamellipes* (C)	163
Ampithoe plea (G)	91	*Scutellidium lamellipes* (C)	137	*Porcellidium* sp. A (C)	113
Acanthomysis sculpta (M)	74	*Macrocyprina pacifica* (O)	88	*Siriella pacifica* (M)	99

TABLE 6.—The ten most abundant gammarid amphipods in each zone. Abundances are mean monthly values for the 19-mo study.

Canopy	$\overline{No.}$/kg kelp	Middle	$\overline{No.}$/kg kelp	Bottom	$\overline{No.}$/kg kelp
Gitanopsis vilordes	466	*Microjassa litotes*	2,018	*Microjassa litotes*	1,054
Aoroides columbiae	164	*Gitanopsis vilordes*	1,183	*Gitanopsis vilordes*	778
Microjassa litotes	103	*Aoroides columbiae*	600	*Pontogeneia rostrata*	435
Ampithoe plea	91	*Batea transversa*	82	*Aoroides columbiae*	350
Hyale frequens	24	*Pontogeneia rostrata*	40	*Batea transversa*	342
Batea transversa	2	*Ampithoe plea*	37	*Ampithoe plea*	147
Pontogeneia rostrata	1	*Pleustes platypa*	5	*Pleustes platypa*	12
Pleustes platypa	1	*Erichthonius brasiliensis*	1	*Erichthonius brasiliensis*	8
Erichthonius brasiliensis	1	*Pleusirus secorrus*	1	*Amphilochus* sp.	2

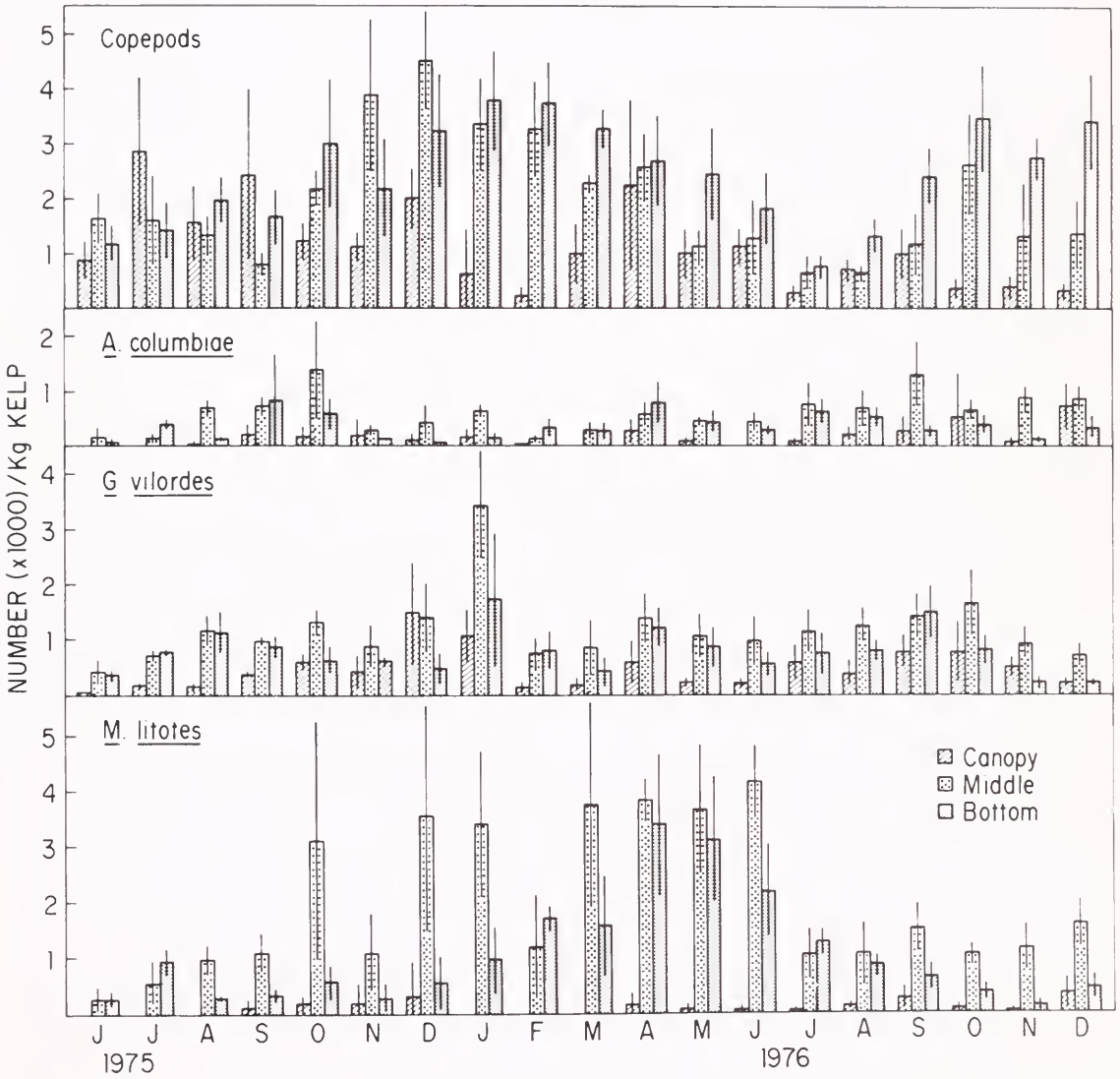

FIGURE 2.—Monthly abundances (mean and 95% C.I.) of copepods (all species) and the gammarid amphipods (*Aoroides columbiae*, *Gitanopsis vilordes*, *Microjassa litotes*) in each vertical zone. Each value represents the mean of three (July-September 1975) or five (October 1975-December 1976) replicate samples.

mysid species present differed in their patterns of vertical distribution. *Acanthomysis sculpta* essentially was confined to the canopy ($\overline{no.}$/kg ± width of 95% C.I./2 = 73.6 ± 56.4 [C], 4.0 ± 2.2 [M], 7.7 ± 5.2 [B]), and accounted for 80.5% (by number) of all mysids in the zone, whereas *S. pacifica* was less abundant in the canopy (17.8 ± 6.3 [C], 147.6 ± 39.1 [M], 99.2 ± 46.9 [B]), but was dominant in the middle (97.2%) and bottom (92.2%). An unidentified erythropinid rarely was encountered and, when present, found only in the lower zones (0 [C], 0.2 ± 0.2 [M], 0.7 ± 0.5 [B]). Nearly all (99.9%) of the shrimps associated with the kelp fronds were *Hippolyte clarki*, and this species was most abundant in the canopy (Table 3, Fig. 3).

Throughout most of the study, gammarid sizes were largest in the canopy, intermediate in the bottom, and smallest in the middle (K-S test; C-M, C-B, M-B: $P < 0.01$; Table 4, Fig. 4). Mysids and shrimps also were largest in the canopy, but were smallest in the bottom (K-S test; C-M, C-B, M-B: $P < 0.001$; Table 4, Fig. 4). Among the mysids, *S. pacifica* was more slender (mm, $\overline{mg}$ = 6.5, 2.9 [C], 4.7, 1.2 [M], 4.5, 1.2 [B]) than *A. sculpta* (6.2, 3.7 [C], 4.2, 1.7 [M], 3.1, 1.1 [B]). Combined size distributions of the four major taxa for the 19-mo study (weighted according to mean monthly abundance) revealed proportionately greater numbers of large individuals present in the canopy than in either the middle or the bottom (K-S test; C-M, C-B: $P < 0.001$; M-B: ns; Fig. 5)

Seasonal Patterns of Species, Abundances, and Sizes

No seasonal patterns were apparent for total number of invertebrates in the canopy; however, total biomass increased dramatically (from 1,696 to 6,315 g/kg kelp) during winter 1975-76 (Fig. 6). In the lower zones, both numbers and biomass were highest during winter 1975-76 and the following spring (Fig. 6).

Seasonal patterns of abundance for the major species were evident only for the shrimp *H. clarki*, which displayed maximum abundance during both winters of the study (Fig. 3). The canopy mysid, *A. sculpta*, was abundant (113.2-395.5/kg kelp) during winter 1975 and early spring 1976, but was uncommon (6.5/kg kelp) during the following winter (Fig. 3). Single monthly samples collected in winter 1974-75 also indicated high numbers (79.2-169.8/kg kelp) of the canopy mysid. Seasonal patterns were not evident for the three most common gammarids (Fig. 2). As a group, copepods were most abundant during winter and early spring in the lower zones, but no seasonal pattern was apparent (Fig. 2).

Seasonal variations in the sizes of gammarids, mysids, and shrimps were frequently observed (Fig. 4). Gammarid sizes were largest during winter and spring in the canopy (2.76-3.85 mm), but no seasonal patterns were present in the lower zones. Carapace lengths of *S. pacifica* were largest during winter in the canopy (1.68-1.89 mm) and middle (1.24-1.45 mm) with 1976 measurements greater than 1975. Smallest sizes were present during summer in both the canopy (1.28-1.39 mm) and middle (0.92-1.22 mm). No seasonal patterns were present in the bottom. The shrimp *H. clarki* was largest in the canopy during winter-spring of both years (1.55-2.08 mm) and during spring 1975 and winter 1976 in the middle (1.56-1.64 mm) and bottom (1.36-1.43 mm). Smallest shrimps were present during fall in all three zones (1.30-1.42 mm [C]; 1.01-1.17 mm [M]; 1.02-1.03 mm [B]). No pattern was observed for *A. sculpta*.

DISCUSSION

Kelp Density

Elevated temperatures and/or low nutrients may have caused the Habitat Reef kelp forest to decline in late 1976. Kelp forests in southern California deteriorate when the water temperature exceeds 20°C for substantial periods (North 1971), and high temperatures often are associated with low nutrients (Jackson 1977). Significantly, temperatures at Habitat Reef did not reach 20°C in 1975, but exceeded 20°C from mid-June to November 1976. During the second half of 1976, other areas of southern California also experienced warm water and corresponding declines in *Macrocystis* standing crop (Southern California Edison Co. 1978[3]).

Preference of *Macrocystis* as a Habitat

Few of the 114 species associated with *Macrocystis* fronds at Habitat Reef were restricted to the frond habitat. Most were present, and many were more abundant in *Macrocystis* holdfasts, understory algae, or other habitats within or adjacent to Habitat Reef (Hobson and Chess 1976; Hammer and Zimmerman 1979). A few, however, such as the gammarid *M. litotes*, the shrimp *H. clarki*, and both species of mysids, were more abundant in the *Macrocystis* fronds than in other habitats.

[3]Southern California Edison Company. 1978. Annual operating report, San Onofre Nuclear Generating Station, Vol. IV. Biological, sedimentological, and oceanographic data analyses. Southern California Edison Co., Rosemead, CA 91770, 300 p.

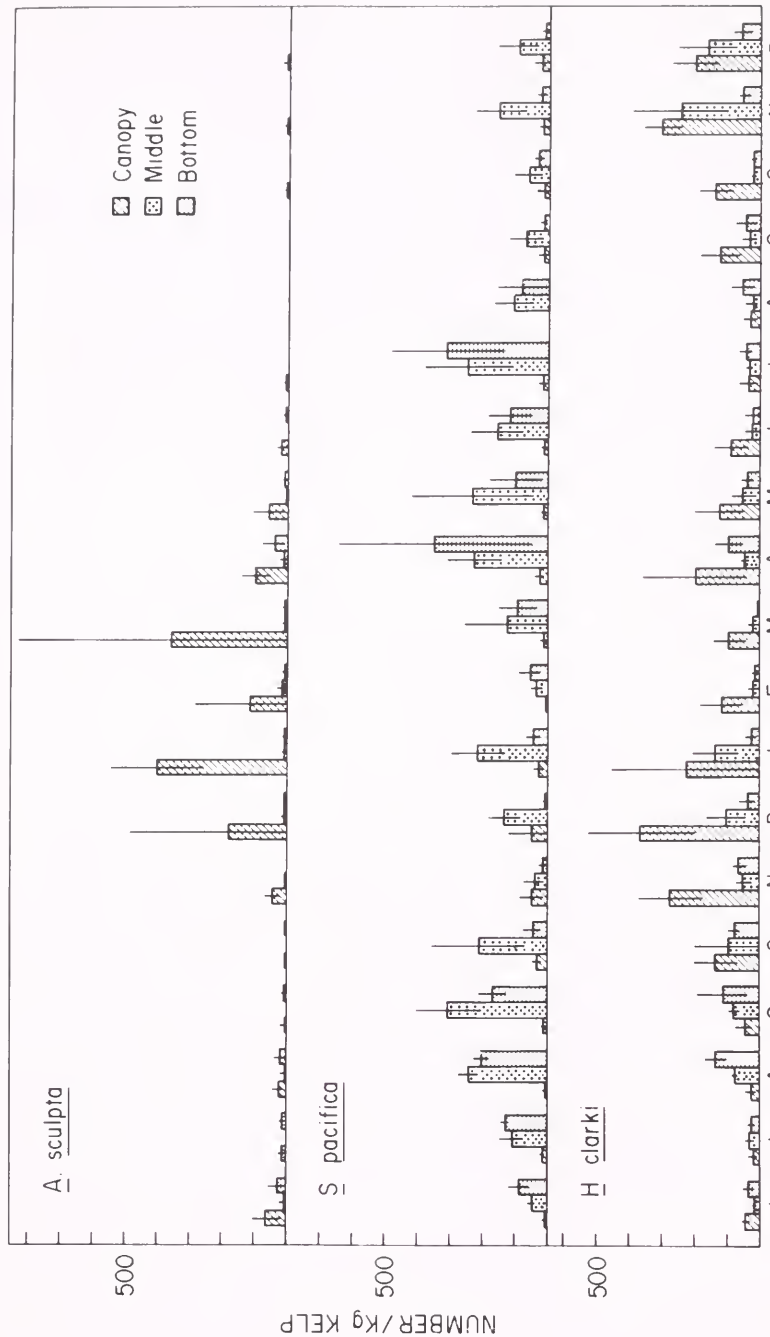

FIGURE 3.—Monthly abundances (mean and 95% C.I.) of the mysids (*Acanthomysis sculpta*, *Siriella pacifica*) and the shrimp (*Hippolyte clarki*) in each vertical zone. Each value represents the mean of three (July-September 1975) or five (October 1975-December 1976) replicate samples.

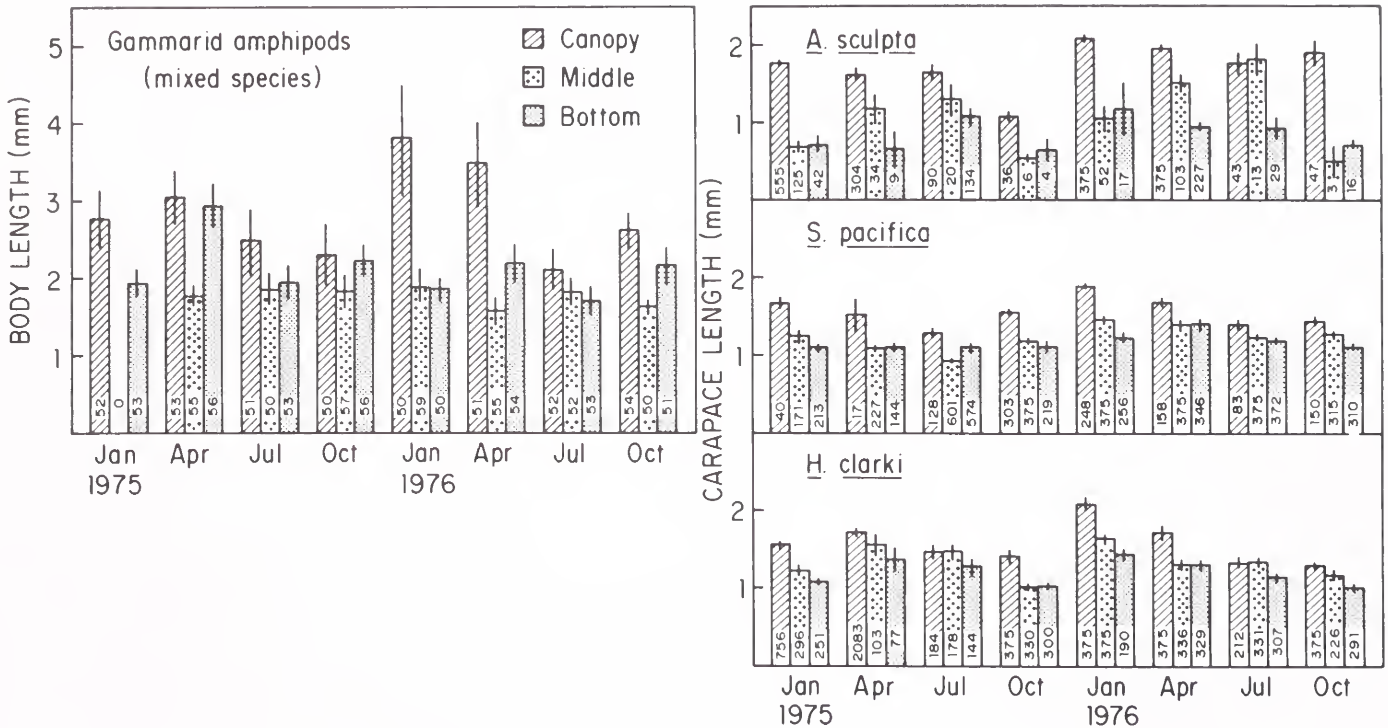

FIGURE 4.—Mean sizes (mean and 95% C.I.) of gammarid amphipods (all species), mysids (*Acanthomysis sculpta*, *Siriella pacifica*), and shrimps (*Hippolyte clarki*) within each vertical zone. Values from January and April 1975 for gammarids, mysids, and shrimps are from a single sample. Subsequent values for mysids and shrimps represent pooled subsamples from either three (July 1975) or five (October 1975-October 1976) replicate samples; subsequent gammarid values are from one randomly selected replicate. In all cases, the total number of individuals measured is noted within the columns.

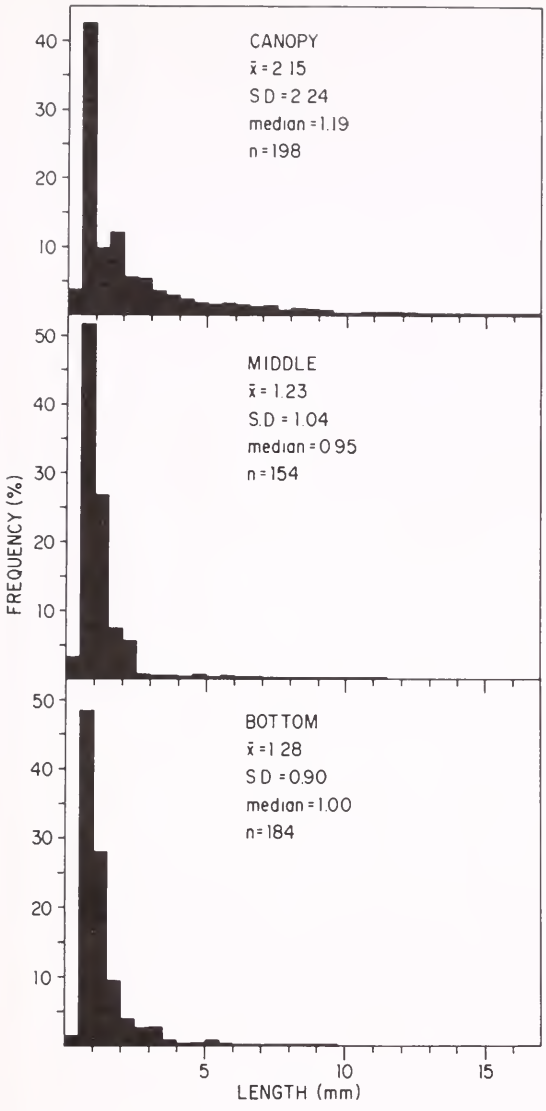

FIGURE 5.—Combined size-frequency distributions of copepods, gammarid amphipods, mysids, and shrimps measured quarterly from July 1975 through October 1976 for each of the three vertical zones. Copepods were measured during 1 mo only because of their small size and variability. After normalization (%), the distributions of each taxon were weighted according to mean monthly abundance to create the combined distributions. The numbers of each taxon measured before weighting are (C, M, B): copepods (54, 54, 55), gammarids (308, 323, 317), mysids (2,037, 2,625, 2,500), and shrimps (1,896, 1,776, 1,561). Statistics determined after weighting are displayed in the figure.

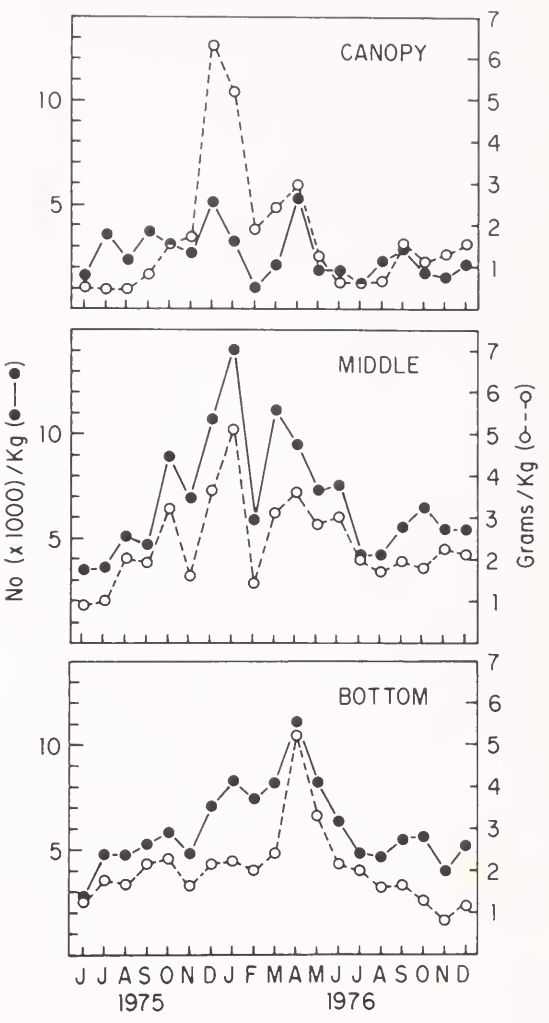

FIGURE 6.—Monthly variation in numbers and biomass of all invertebrate taxa (combined) within each vertical zone. Each monthly value for the canopy, middle, and bottom represents a mean of three (June-September 1975) or five (October 1975-December 1976) replicate samples.

Mysids are remarkably specific in habitat preferences. Clarke (1971) found 12-14 species of mysids cooccurring in the kelp forests off San Diego and Baja California, but only *A. sculpta* and *S. pacifica* were associated with the kelp fronds. Similar patterns were observed at Habitat Reef, as both *A. sculpta* and *S. pacifica* were present in large numbers within the kelp fronds, but were rarely observed in *Macrocystis* holdfasts or other algal habitats within or near Habitat Reef (Hammer and Zimmerman 1979). Hobson and Chess (1976) found a few individuals of *A. sculpta* in the water column at night, but most remained closely associated with the kelp which was utilized as food. In contrast, *S. pacifica* migrated from kelp fronds into the surrounding open water at night to capture small plankton (Hobson and Chess 1976).

Vertical Patterns of Species, Abundances, and Sizes

Several of the commonly occurring species within the Habitat Reef kelp forest were far more abundant in the canopy than in the lower zones. *Ampithoe plea*, *Hyale frequens*, *Acanthomysis sculpta*, and *Hippolyte clarki* all displayed this type of distribution, and other investigators have noted the canopy preferences of these species. Limbaugh (1955) described a large canopy-dwelling amphipod (*Ampithoe* sp.) that formed a tube by rolling and "stitching" the edge of a *Macrocystis* blade. Several investigators working in kelp forests off San Diego and at Habitat Reef have noted the canopy occurrence of *Acanthomysis sculpta* (Limbaugh 1955; Clutter 1967; Clarke 1971; Hobson and Chess 1976) and *H. clarki* (Hobson and Chess 1976). Lowry (unpubl., cited in Lowry et al. 1974) observed large numbers of *H. californiensis*, a close relative of *H. clarki*, in the canopy of kelp forests off central California.

The canopy contained larger gammarids, mysids, and shrimps as well as proportionately greater numbers of large individuals of these groups than in either of the lower zones. Size-selective predation by fishes frequently has been documented to be a major factor in structuring aquatic communities (Brooks and Dodson 1965; Archibald 1975; Vince et al. 1976; Macan 1977; Nelson 1979) and may account for the size distributions of invertebrates observed at Habitat Reef. The interdigitating fronds of the canopy greatly increase the structural complexity in this zone and may offer more spatial refuge for motile invertebrates than provided by the middle and bottom zones. As increased structural complexity has been demonstrated to decrease effectiveness of prey capture by fishes, particularly larger prey (Vince et al. 1976; Brock 1979; Coen et al. 1981; Heck and Thoman 1981; Savino and Stein 1982), the canopy complexity may discourage extensive foraging by fishes.

Relatively few fishes forage within the kelp canopies off southern California. The most abundant fish is the kelp perch, *Brachyistius frenatus*, a small diurnal species that forages preferentially in the canopy and preys extensively on small gammarids and copepods (Hobson 1971; Bray and Ebeling 1975; Hobson and Chess 1976). Other fishes are observed in the kelp canopy, but the large-mouthed species are much less abundant than the kelp perch and forage more often in other areas of the kelp forest, and the small-mouthed species capture small planktonic prey or utilize small invertebrates attached directly to the kelp surfaces (Bray and Ebeling 1975; Hobson and Chess 1976; Bernstein and Jung 1979). Consequently, predation pressure on larger individuals of motile prey in the canopy may be reduced relative to the lower zones, resulting in a proportionately greater abundance of larger individuals. For example, the mysid *S. pacifica* was much more abundant in the lower zones than in the canopy, yet the largest individuals consistently were present in the canopy.

Alternate hypotheses may explain the size stratification of some species. Intraspecific behavioral interactions may confine certain size classes to specific zones, as demonstrated experimentally for an amphipod (Van Dolah 1978). Larger individuals may be more abundant in the canopy simply in response to the presence of preferred food types and/or sizes, although this hypothesis has not been examined.

The size distribution of invertebrates in the lower zones resembled the size distribution of insects in temperate terrestrial forests (Schoener 1971), in that both areas supported large numbers of small, and few large, individuals. The size distribution in the canopy, however, was somewhat similar to the insect size distribution of tropical terrestrial forests where there are proportionately greater numbers of large insects (Schoener and Janzen 1968; Schoener 1971). The presence of larger insects in the tropical forests effectively expands the food size dimension relative to the temperate forests (assuming equal abundance). The expansion has been hypothesized to account for some of the increased diversity of bird species in the tropics, as much of this increase is due to the addition of insectivorous birds adapted to capture large insects (Schoener 1971).

In contrast to the tropical forests, the higher proportion of large prey items in the Habitat Reef kelp canopy apparently did not attract additional species of fish predators. Nevertheless, it may be useful to examine the size distributions of important prey items in other kelp forests to determine whether a relationship exists between prey size distributions and fish species diversity.

Seasonal Patterns of Species, Abundances, and Sizes

The kelp-associated invertebrates as a group did not exhibit seasonal cycles. Numbers and biomass generally were highest during winter 1975, with the marked increase in biomass due primarily to increased abundances of the relatively large canopy mysid *A. sculpta* and shrimp *H. clarki*. Gammarid amphipods, particularly *M. litotes*, were largely re-

sponsible for the increased abundances in the lower zones during this period.

Fluctuations in the population size of several species may have been associated with changes in kelp biomass, particularly the general decline of kelp biomass beginning in fall 1976. The canopy mysid probably attains its greatest population size during winter; however, the canopy was markedly reduced in area by winter 1976-77 and the mysid was rare. Copepods and gammarids displayed decreased canopy abundances during late 1976, and in the lower zones, abundances of the gammarid *M. litotes* began to decline as kelp biomass was reduced. As the canopy mysid and *M. litotes* were major components of the general invertebrate peak observed during winter 1975-76, their reduced abundances in late 1976 undoubtedly were a major reason for the absence of a general invertebrate peak in late 1976.

Reduction in kelp biomass, however, did not affect *H. clarki*. Even though the shrimp was most numerous in the canopy, its abundance in the reduced canopy of late 1976 was similar to levels recorded in the larger canopy of late 1975.

Although the amount of kelp biomass ultimately must determine the abundance and occurrence of kelp-associated invertebrates, the importance of proximal factors remains to be determined. Proximal factors may be particularly important in many areas of southern California, where the kelp forests are characterized by relatively long-term cycles of loss and renewal (Rosenthal et al. 1974). In such conditions of relative biomass constancy, abundances of some species may not be correlated with seasonal changes (i.e., temperature, day length, nutrients, etc.). Additional research is necessary to determine the importance of proximal factors such as kelp quality (healthy vs. decomposing), inter- and intraspecific competition for space and food, and predation by fishes and/or motile invertebrates, in determining the abundance and occurrence of kelp-associated invertebrates.

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SPRING AND SUMMER PREY OF CALIFORNIA SEA LIONS, *ZALOPHUS CALIFORNIANUS*, AT SAN MIGUEL ISLAND, CALIFORNIA, 1978-79.

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ABSTRACT

During the late spring and summer of 1978 and 1979, 224 scats were collected from rookeries of the California sea lion, *Zalophus californianus*, at San Miguel Island for the purpose of identifying prey species. A total of 2,629 otoliths and 2,061 cephalopod beaks were recovered. The frequency of occurrence for the four most commonly identified prey species was 48.7% Pacific whiting, *Merluccius productus*; 46.7% market squid, *Loligo opalescens*; 35.9% rockfish, *Sebastes* spp.; and 20.0% northern anchovy, *Engraulis mordax*. Seasonal variability in the frequency of occurrence of these four prey species from late spring to summer indicates that California sea lions feed opportunistically on seasonally abundant schooling fishes and squids. Five species of fish (California smoothtongue, *Bathylagus stilbius*; northern lampfish, *Stenobrachius leucopsarus*; chub mackerel, *Scomber japonicus*; medusafish, *Icichthys lockingtoni*; sablefish, *Anoplopoma fimbria*) and one cephalopod (two-spotted octopus, *Octopus bimaculatus*) were identified as previously unreported prey of the California sea lion.

The California sea lion, *Zalophus californianus*, is the most abundant pinniped inhabiting the coastal waters off California (Le Boeuf and Bonnell 1980). During the summer most California sea lions are on or near their breeding sites which are located on islands south of Point Conception, along the coast of southern California, Baja California, and into the Gulf of California. After the breeding season in the summer, a portion of the subadult and adult male sea lion populations migrates north of Point Conception as far as British Columbia, while the rest of the population remains off the coasts of southern California and Baja California, Mexico (Peterson and Bartholomew 1967). Numerous studies of the food of migrant male California sea lions have been conducted in the areas north of their traditional breeding islands (Briggs and Davis 1972; Jameson and Kenyon 1977; Morejohn et al. 1978; Bowlby 1981; Everitt et al. 1981; Jones 1981; Ainley et al. 1982; Bailey and Ainley 1982), while comparatively little information has been reported on the feeding behavior of sea lions in areas off the coast of California south of Point Conception (Rutter et al. 1904; Scheffer and Neff 1948; Fiscus and Baines 1966). From the information presented in all of these studies, it has been suggested that California sea lions feed opportunistically on a variety of prey species (Antonelis and Fiscus 1980) and that "switch feeding" is probably an important component of their feeding behavior (Bailey and Ainley 1982). However, since most of the information on sea lion feeding behavior is based on observations north of their breeding islands, additional information from within their breeding range would allow us to determine if similar feeding characteristics can be expected in other geographical areas.

Studies conducted before 1970 usually obtained stomach contents for feeding information by killing sea lions, while most post-1970 feeding studies have used nonlethal techniques including examination of scats and oral rejecta (spewings) and direct behavioral observations. Another method was the examination of gastrointestinal tracts from animals found dead. In this study, prey-species classification is based on the identification of fish otoliths and cephalopod beaks found in scats collected during the spring and summer for two consecutive years on the California sea lion rookeries of San Miguel Island, Calif. In addition to the identification of prey, we calculated the percent frequency of occurrence of each prey, compared annual and seasonal differences in prey selection, and estimated the lengths and weights of the most frequently occurring prey species.

MATERIALS AND METHODS

Scats were collected from areas utilized exclusively

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by California sea lions on the west end of San Miguel Island, Calif., during spring (2-3 May 1978; 2 and 16 May 1979) and summer (3-4 August 1978; 30-31 July 1979). During both sample periods, scats were collected from areas where mostly females and juveniles of both sexes occurred and relatively few (<12% of the total animals censused) adult and subadult males were present. In order to document the occurrence of prey species which were consumed at or close to the time of collections, only recent scats, which showed no obvious signs of desiccation, were collected. Each scat was placed in a plastic bag, where it was later soaked in water or a solution of about 1 part liquid detergent to 100 parts water for about 24 h. Each bag was shaken occasionally to facilitate emulsification of the digested organic material, and then rinsed with water through three nested sieves with screen mesh sizes of 3.35 mm, 2.00 mm, and 1.00 mm from top to bottom. After most of the soft digested organic material was washed away, fish otoliths and cephalopod beaks were removed and stored in a solution of 70% ethanol. Prey totals were determined by using the higher number of left or right otoliths and upper or lower squid beaks. The otoliths were identified by the late J. Fitch, California Department of Fish and Game, Long Beach, Calif., the octopus beaks by E. Hochberg, Santa Barbara Museum of Natural History, Santa Barbara, Calif., and the squid beaks by the second author.

The data for each of the four major prey species were summarized by a three-way (2×2×2) contingency table and tested for independence of occurrence by season, year, and both season and year (Fienberg 1977).

Length measurements of these otoliths and squid beaks were used to estimate the body lengths or ages of the most frequently occurring prey species. Although many otoliths and beaks of all sizes were recovered from the scats in good condition, some were not measured because they were broken or showed obvious signs of damage from digestion. We assumed that damage to the otoliths and squid beaks collected in this study was not dependent on size. Lengths of northern anchovy, *Engraulis mordax*, were estimated from a regression equation of fish lengths on otolith lengths (Spratt 1975). Length information for rockfish, *Sebastes* spp., was obtained from previously reported data (Phillips 1964) for specimens (bocaccio, *Sebastes paucispinis*) of the same age as most of the rockfish reported in this study. Bocaccio was chosen as the representative rockfish because it has been reported as the most abundant rockfish in the waters near San Miguel Island (Best and Oliphant 1965). The regression equation used to estimate the length of Pacific whiting, *Merluccius productus*, was derived in this study from specimens collected off the coast of southern California by the National Marine Fisheries Service (NMFS). The Pacific whiting otoliths and the corresponding length information were provided by K. Bailey of the NMFS Northwest and Alaska Fisheries Center, Seattle, Wash. Market squid, *Loligo opalescens*, lengths were estimated from a regression equation of dorsal mantle length on upper hood length of the beak. Upper hood measurements were chosen for the estimation of squid lengths because they were reported as having the highest correlation to dorsal mantle length (Kashiwada et al. 1979).

In order to detect changes in the diet which would reflect apparent yearly changes in the age and size composition of a specific prey-species population, we compared the lengths of otoliths for 1978 and 1979 using the Wilcoxon rank sum test (Hollander and Wolfe 1973).

Weight estimates of the most frequently occurring prey species were obtained by using the prey length estimate (described above) in regression equations of length and weight measurements or by obtaining weight data from fish which were the same age as those identified in the scats (Phillips 1964; Fields 1965; Dark 1975; Pacific Fishery Management Council 1978). The total estimated weight for each of the four major prey species was obtained by multiplying the weight of the average-sized prey by the number of individuals represented in the scat collection. Differences between these estimates could not be statistically analyzed because the raw data for the growth curves of each species were not available.

The names of fishes follow Fitch and Lavenberg (1968) and Robins (1980), and those of cephalopods follow Fields (1965) and Young (1972).

RESULTS

We collected 224 California sea lion scats on San Miguel Island during the spring and summer of 1978 and 1979. From 195 (87%) of those scats, we recovered 2,629 otoliths and 2,061 cephalopod beaks. Twenty-nine (13%) scats did not contain otoliths or cephalopod beaks. The prey species identified in the scats are shown in Table 1 by their percentage of occurrence. The four most frequently occurring prey in scats containing otoliths and/or cephalopod beaks were Pacific whiting (48.7%), market squid (46.7%), juvenile rockfish from the *Sebastes paucispinis-goodei-jordani* complex

TABLE 1.—Percentage occurrence of all prey species identified from 195 California sea lion scats collected on San Miguel Island, Calif., spring and summer, 1978-79.

Prey		Occurrence	
Scientific name	Common name	No.	%
Merluccius productus	Pacific whiting	95	48.7
Loligo opalescens	market squid	91	46.7
Sebastes spp.	rockfish (juvenile)	70	35.9
Engraulis mordax	northern anchovy	39	20.0
Octopus rubescens	red octopus[1]	19	9.7
Trachurus symmetricus	jack mackerel	9	4.6
Onychoteuthis borealijaponicus	nail squid	9	4.6
Gonatidae (other than *Gonatus* sp.)	squid	8	4.1
Scomber japonicus[2]	chub mackerel	7	3.6
Peprilus simillimus	Pacific pompano	5	2.5
Symbolophorus californiensis	California lantern-fish	5	2.5
Gonatus sp.	squid	2	1.0
Microstomus pacificus	Dover sole	2	1.0
Bathylagus stilbius[2]	California smooth-tongue	2	1.0
Seriphus politus	queenfish	2	1.0
Zalembius rosaceus	pink surf perch	1	0.5
Anoplopoma fimbria[2]	sablefish	1	0.5
Porichthys notatus	plainfin midshipman	1	0.5
Icichthys lockingtoni[2]	medusafish	1	0.5
Stenobrachius leucopsarus[2]	northern lampfish	1	0.5
Octopus bimaculatus[2]	two-spotted octopus	1	0.5

[1]Pelagic life stage
[2]Not previously reported as prey of the California sea lion.

(35.9%)[2], and northern anchovy (20.0%). All other prey species occurred in <10.0% of the scats.

Relative length and weight estimates of the four major prey species and the information used to calculate these estimates are shown in Figure 1 and Table 2, respectively. The length and weight information for rockfish is from data reported by Philips (1964) for one of the three species (*S. paucispinis*) represented in this study.

Measurements of otoliths from Pacific whiting and northern anchovy provided sufficient information to compare changes in the size and age of each prey group from 1978 to 1979. For Pacific whiting the lengths of otoliths were significantly greater ($W^* = 5.82, P < 0.0001$) in 1979 ($\bar{x} = 7.71$ mm, $n = 90$) than in 1978 ($\bar{x} = 6.71$ mm, $n = 132$). From these otolith measurements, we estimated the mean length of Pacific whiting at 156 mm in 1978 and 176 mm in 1979. All of the Pacific whiting otoliths were obtained from 1- and 2-yr-old fish. The occurrence of 1-yr-old fish in the sea lion diet was estimated at 98.5% in 1978 and 70% in 1979. For northern anchovy, the lengths of otoliths were significantly greater ($W^* = 4.36, P < 0.0001$) in 1978 ($\bar{x} = 3.58$ mm, $n = 19$) than in 1979 ($\bar{x} = 3.01$ mm, $n = 75$). For these otolith measurements we estimated the mean length of northern anchovy at 111 mm in 1978 and 92 mm in 1979. Although all age classes of northern anchovy were recovered from the scats, there was a notable change in the percent occurrence of yearling fish from 1978 (42%) to 1979 (81%).

The percentage of occurrence in the four major prey species is shown for the spring and summer of 1978 and 1979 in Figure 2. From the three-way contingency table analysis, it was determined that Pacific whiting occurred significantly more frequently in 1978 than in 1979 ($P < 0.01$), and there was a greater percentage of occurrence in spring than in summer ($P < 0.01$). For rockfish, there was no significant difference in occurrence between years; however, there was a greater percentage of occurrence in the summer than in spring ($P < 0.01$). The percentage occurrence of northern anchovy was not significantly different between season, but there was a significantly greater occurrence in 1979 than in 1978 ($P < 0.01$). The relative proportion of occurrence for the two seasons for each year was significantly different ($P < 0.01$) for Pacific whiting, rockfish, and northern anchovy. Tests of significance could not be done for market squid because of the strong three-way interaction between occurrence, season, and year. It is apparent, however, that the percent occurrence of market squid did increase from spring to summer during both years of the study (Fig. 2).

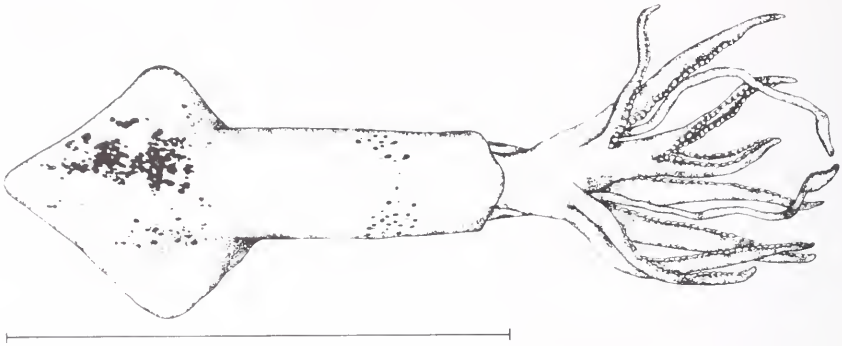
[2]About 95% of the juvenile rockfish were yearlings and were included in this three-species complex because their otoliths are too similar to differentiate.

TABLE 2.—Information used in estimating the length of the four major prey species identified from the scats of California sea lions, on San Miguel Island, Calif., 1978-79.

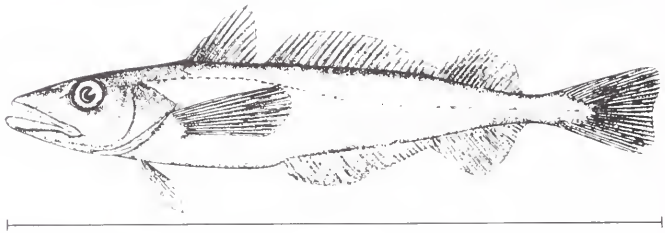
Prey species	Regression equation	n	R^2	Y	X	Reference
Market squid	$Y = 0.243 + 0.0481X$	60	0.974	upper hood length (mm)	dorsal mantle length (mm)	Kashiwada et al. 1979
Pacific whiting	$Y = 26.2 + 19.38X$	84	0.977	fork length (mm)	otolith length (mm)	This study
Juvenile rockfish[1]	([1])	155		([1])	([1])	Phillips 1964
Northern anchovy	$Y = -8.4946 + 33.216X$	677	0.774	standard length (mm)	otolith length (mm)	Spratt 1975

[1]Length measurements are from yearling bocaccio, *Sebastes paucispinis*.

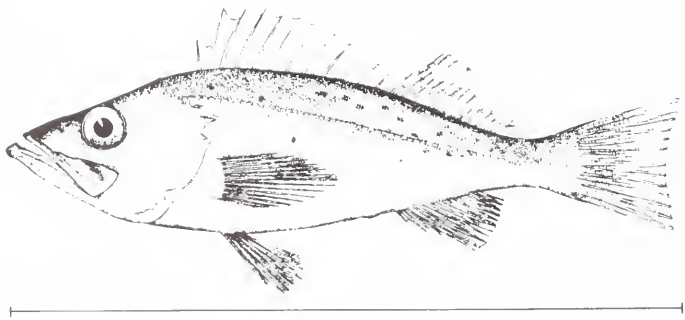
MARKET SQUID
$\bar{x}$ = 127 mm (Weight = 47.0 g)
SD = 17 mm
Range = 62–185 mm
n = 76



PACIFIC WHITING
$\bar{x}$ = 166 mm (Weight = 42.6 g)
SD = 60 mm
Range = 89–261 mm
n = 222



BOCACCIO (Rockfish)
$\bar{x}$ = 171 mm (Weight = 45.4 g)
SD = 22 mm
Range = 129–227 mm
n = 155



NORTHERN ANCHOVY
$\bar{x}$ = 95 mm (Weight = 10.8 g)
SD = 8 mm
Range = 55–141 mm
n = 94

FIGURE 1.—Relative length and weight estimates of the four major prey species identified in California sea lion scats collected on San Miguel Island, Calif., spring and summer, 1978-79. Methods used to calculate these estimates are shown in Table 2.

The number of prey species occurring in individual scats changed from spring to summer. For combined years, the percentages of scats containing single or multiple prey are shown in Figure 3. In the spring, the percentage of singly occurring prey species in scats was 59.7%; in the summer the percentage dropped to 34.6%. Scats containing more than one prey increased from 17 species combinations occurring in 40.3% of the scats in the spring to 23 in 65.4% during the summer.

The percentages of the total estimated weight of the four major prey species for spring and summer are

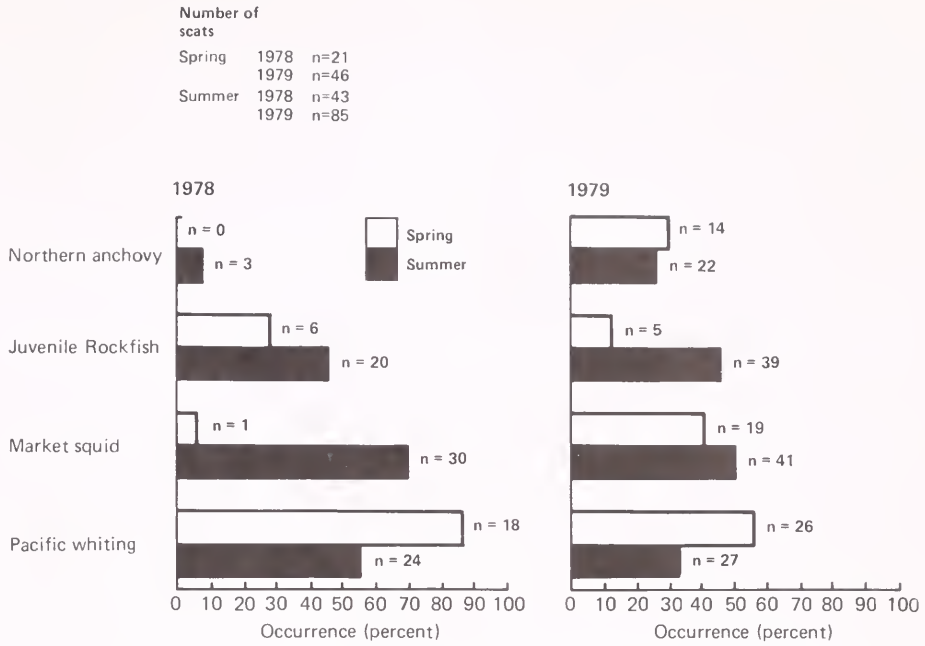


FIGURE 2.—Spring and summer occurrence (percentage) of the four major prey species identified in California sea lions scats collected on San Miguel Island, Calif., 1978-79.

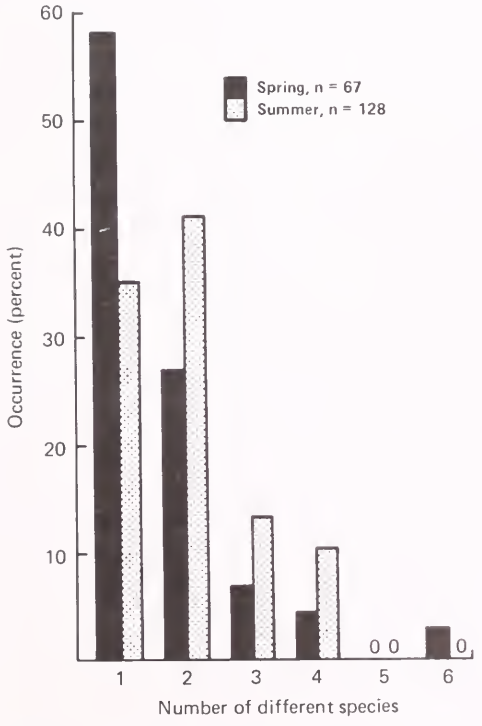


FIGURE 3.—Occurrence of single and multiple prey species in individual sea lion scats collected on San Miguel Island, Calif., 1978-79.

shown in Figure 4. The seasonal changes in the percent of weight for Pacific whiting showed a decrease from spring to summer in 1978 and 1979, while an increase occurred from spring to summer for market squid in 1978 and rockfish in 1979. There was relatively little change in the percentage of weight between the two seasons for market squid in 1979 and rockfish in 1978. The northern anchovy also showed little difference between the two seasons during both years. Additionally, the results from this analysis show that market squid made the greatest contribution to the total estimated weight of prey in the summer of 1978 (71.2%) and for both spring (53.9%) and summer (48.7%) of 1979, while Pacific whiting made the greatest contribution to the total estimated weight only in the spring of 1978 (87.3%).

DISCUSSION

Pacific whiting, market squid, juvenile rockfish, and northern anchovy were the four most important prey of California sea lions at San Miguel Island during the spring and summer of 1978 and 1979. These four prey species have also been reported as common prey of California sea lions in areas north of Point Conception (Morejohn et al. 1978; Everitt et al. 1981; Jones 1981; Ainley et al. 1982) and exemplify

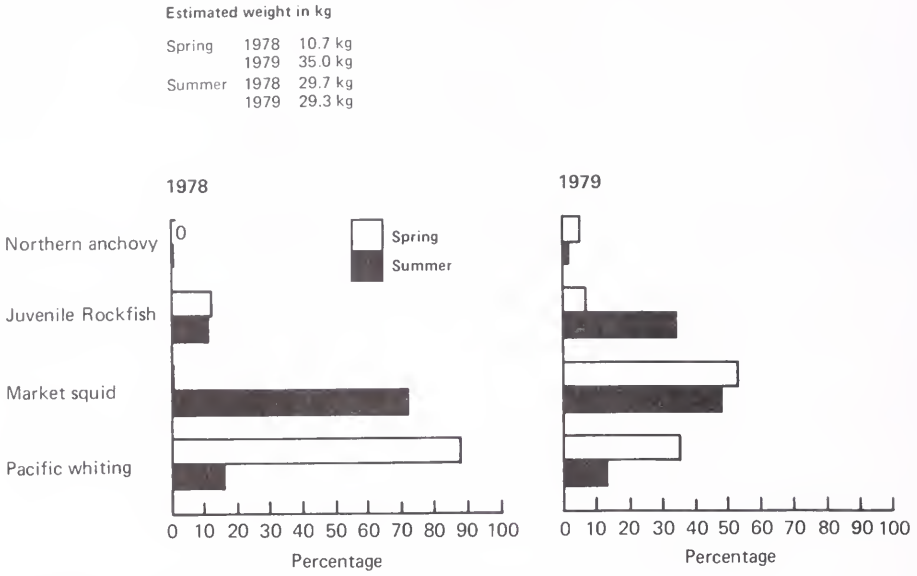


FIGURE 4.—Percentages of the total estimated weight for the four major prey species in spring and summer, 1978-79.

the type of large, dense schooling prey which are commonly fed upon by many of the pinnipeds in the coastal waters off California (Antonelis and Fiscus 1980). Furthermore, the variety of food items reported in this and other studies (Jameson and Kenyon 1977; Morejohn et al. 1978; Bowlby 1981; Jones 1981; Ainley et al. 1982) indicates that California sea lions are capable of foraging on a wide range of fish and cephalopods.

The range in the average length estimates of the four major prey species (95-171 mm) does not exhibit a great diversity in size, and may reflect a size preference for sea lions feeding in the waters near San Miguel Island. Both Pacific whiting and rockfish attain a much larger size as adults (Phillips 1964; Dark 1974), while the length estimates of northern anchovy and market squid are within the size range of juveniles and adults (Fields 1965; Spratt 1975).

As more information is obtained on the prey and the foraging behavior of California sea lions, researchers will attempt to evaluate the biomass of each prey species consumed (Bailey and Ainley 1982). These types of studies require information on the variations in the diet of California sea lions throughout their range. For this reason, we compare the estimated length data of market squid and Pacific whiting from this study with similar information reported in areas north of Point Conception. The estimated lengths were similar for market squid which were preyed upon by California sea lions in Monterey Bay, Calif. (Morejohn et al. 1978) and in the waters near San Miguel, with mean values of 130 mm (Morejohn et al. 1978, estimated from figure 27) and 127 mm, respectively. California sea lions foraged on all age classes of market squid in both areas. For Pacific whiting, however, differences between the northern and southern range of the California sea lion were apparent, with estimated length averages ranging from 250 to 360 mm at Southeast Farallon Island, Calif. (Bailey and Ainley 1982) compared with an average of 166 mm at San Miguel Island. Primarily 1- and 2-yr-old fish were preyed upon near San Miguel, while 2- and 3-yr-old fish were reported as prey at Southeast Farallon.

From these comparisons, we assume that squid of all sizes and age classes will be preyed upon by California sea lions, in both their breeding and nonbreeding ranges. For Pacific whiting, however, there are apparent differences in the size and age classes consumed by California sea lions in the two areas. These differences could be related to three possible factors: 1) There could be differential feeding according to various age and/or sex classes of sea lions which occur in the two areas. When present, there are mostly subadult and adult males at Southeast Farallon Island, and at San Miguel Island there are comparatively fewer subadult and adult males and many more females and juveniles of both sexes (Peterson and Bartholomew 1967; Le Bouef and Bonnell 1980; Ainley et al. 1982). 2) Differences

between the two areas may be an artifact of the different methods used for estimating fish length. 3) What appears most probable to us, is the differential geographical distribution of Pacific whiting according to age. Generally, the younger fish occur in the southern portion of their range, and, although there is some overlap in age groups, the age and size of the fish increase in a northward direction (Bailey et al. 1982).

In cases where sufficient life history information is available, seasonal or annual changes in the occurrence of the four major prey (Fig. 2) can be related to known changes in the prey's relative abundance and availability to California sea lions. During both years of this study, the decrease in the occurrence of Pacific whiting in the scats from spring to summer appears to reflect known changes in the migration pattern of the species when adults and a portion of the juvenile population migrate toward shore and north of Point Conception (T. Dark[3]). For market squid and juvenile rockfish, however, the movement patterns off the coast of California are conspicuously different than Pacific whiting. Generally, market squid increase in abundance in shallow waters (5-50 m depth) near the northern California Channel Islands in late spring, and peak numbers occur in the early summer during spawning (S.Kato[4]). Inspection of the unpublished data from the 1970-75 commercial catches of market squid within 30 nmi of Point Bennett, San Miguel Island, also indicated that peak abundance occurs during the summer months.[5] Similarly, in spring through summer, juvenile rockfish (*S. paucispinis* and *S. jordani*) from the three-species complex identified in this study begin to move into more shallow waters (5-50 m depth) as they complete the pelagic stage of their life cycles (E. Hobson[6]). In these three instances, seasonal changes in the relative availability of Pacific whiting, market squid, and juvenile rockfish are reflected in the frequency of their occurrence in sea lion scats. A similar relationship was also suggested by Bailey and Ainley (1982), when they observed a seasonal change in the prey consumed by California sea lions near the Farallon Islands.

Although the percentage of occurrence of northern anchovy in the scats showed no significant seasonal changes from spring to summer, the annual occurrence of otoliths from northern anchovies in the sea lion scats was significantly greater in 1979 than in 1978. Their low numbers in the 1978 scats could be related to a decline in the northern anchovy population resulting from poor recruitment of the 1974-77 year classes (Mais 1981). In 1978, however, the year-class recruitment was strong (Mais 1981), and the increased abundance appears to be reflected in an increased percentage of occurrence in the 1979 collection. This explanation is corroborated by our comparison of the northern anchovy otoliths collected during the 2 years, where we found that the 1979 scats contained significantly smaller fish which were mostly (81%) yearlings from the 1978 year class.

Differences in the annual occurrence of Pacific whiting and market squid were also noted in this study. For market squid, there was no fishery information available during the time of this study which would provide us with a possible explanation for these differences. With Pacific whiting, however, the decrease in occurrence in the scats from 1978 to 1979 appears to be related to exceptionally high recruitment of the 1977 year class which was followed by an average, or possibly somewhat less-than-average, recruitment in 1978 (T. Dark footnote 3). This information is corroborated by a comparison of the Pacific whiting otoliths collected during the 2 years of our study. In 1978, sea lions preyed upon significantly smaller fish which were mostly (98.5%) yearlings from the 1977 year class.

Our analysis of the frequency occurrence of prey species per individual scat (Fig. 3) suggests that California sea lions commonly feed on single prey species during the spring and feed more frequently on multiple prey species in the summer. This shift from single to multiple occurrence of prey species in scats could reflect a decrease in the overall availability of the potential prey species in the summer which may necessitate foraging on a greater variety of food items for survival (Morse 1980). Alternatively, numerous potential prey species may become more available (Morse 1980) during the summer; thus, California sea lions could forage opportunistically on a greater variety of schooling fishes or squids which concentrate in a comparatively small area of high productivity.

There are, however, a variety of factors which could affect prey-species availability. Seasonal migration, diel vertical migration, variability in schooling behavior, or physiological changes associated with spawning (Moyle and Cech 1982) are probably some of the more important factors related to prey selec-

[3]T. Dark, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112, pers. commun. 1982.

[4]S. Kato, Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920, pers. commun. 1981.

[5]Data provided by E. Knaggs, Calif. Dep. Fish and Game, Long Beach, Calif., 1982.

[6]E. Hobson, Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920, pers. commun. 1981.

tion and preference of California sea lions which necessitate additional research.

Unfortunately, virtually no information has been reported on the digestive rates or retention time of the prey species' hard parts in California sea lions. Therefore, it is presently impossible to ascertain how many meals, or portions thereof, are represented in a single scat. There is some evidence, however, from feeding studies (Pitcher 1980) of harbor seals, *Phoca vitulina*, and (Miller 1978) northern fur seals, *Callorhinus ursinus*, which indicates that cephalopod beaks are not readily passed through the intestinal tract and are regurgitated. This would result in an underrepresentation of cephalopod beak percentage-of-occurrence data from scats as suggested by Morejohn et al. (1978). Furthermore, the possible occurrence and identification of hard parts of secondary prey (from the stomach of the prey of the marine mammal) could bias the results of scat or stomach analysis (Perrin et al. 1973).

Additional information on the feeding habits of California sea lions can also be obtained from the weight estimates of the four major prey species identified in this study. The 1978 and 1979 percentages of total weight estimates (Fig. 4) for each major species showed seasonal changes that are similar to the analysis of percentage of occurrence (Fig. 2), although there are a few exceptions. In 1979 the market squid weight estimate showed a slight decrease, instead of an increase, from spring to summer, however, of more importance, is its relationship to Pacific whiting. The estimated weight of market squid from the scats clearly exceeded the relative weight of Pacific whiting and other prey species consumed during the spring and summer of 1979. These results suggest market squid may be a more important food item than was predicted from the analysis of their percent of occurrence. The importance of the squid in the diet of the California sea lion during the summer months near the northern California Channel Islands was also documented by Rutter et al. (1904), when they found that 84.6% ($n = 13$) of the animals examined had squid in their stomachs.

Bailey and Ainley (1982) estimated the spring and summer percent (weight) of Pacific whiting in the California sea lion diet in the southern region to be within a range of 50 to 90%. Yet our estimates fell below 40% in the spring of 1979 and below 20% in the summer of both 1978 and 1979, and only one instance (spring 1978) did our estimates fall within the range suggested by Bailey and Ainley (1982). Since Bailey and Ainley (1982) based their estimates on data from California sea lions in the northern region, we assume our estimates more accurately represent the percent (weight) of Pacific whiting in the diet of California sea lions south of Point Conception, and we recommend that additional feeding studies of California sea lions be conducted throughout their range.

The percentage of estimated weight results also suggests that Pacific whiting was preyed upon more heavily in the spring of 1978 than in the spring of 1979. This is consistent with the exceptionally high recruitment of the 1977 year class of Pacific whiting (discussed above) which was available as yearlings to California sea lions in 1978.

Although these weight (biomass) estimates are only approximate measurements, they appear instructive when used in conjunction with percentage-of-occurrence data. Unfortunately, there is some uncertainty as to the accuracy of using estimates of weight to estimate consumption. Our ability to make consumption estimates awaits the resolution of several questions: 1) What proportion of a given meal is represented in a single scat? 2) Are there differential digestive rates of fish and squid? 3) Do sea lions of different ages and sexes digest food differently?

The results of this study suggest that the California sea lions found on San Miguel Island feed opportunistically on prey species of changing availability, and we agree with Bailey and Ainley (1982) that they are behaviorally flexible enough to switch from one major prey species to another, both seasonally and annually. This type of flexibility in foraging appears to be adaptive and may be a major factor contributing to the success of the California sea lion population off the coasts of California and Baja California.

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LARVAL DEVELOPMENT OF THE SCUP, *STENOTOMUS CHRYSOPS* (PISCES: SPARIDAE)[1]

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ABSTRACT

Larval scup, *Stenotomus chrysops* (Linnaeus 1766), were reared from eggs hatched in an aquarium. Measurements of morphological features for 88 specimens from 2.0 to 16.9 mm SL indicate that growth is gradual and continual with no well-defined changes in relative body proportions. Twenty-four myomeres are present in larvae, agreeing with published reports of vertebrae numbers in adult scup. Ossification begins first in the skulls of 6.1 mm SL larvae, and by 7.0 mm SL the vertebrae, neural spines, and fin rays are beginning to ossify. Ossification is nearly complete in 18.7 mm SL juveniles. Three preopercular spines are present in 4.1 mm SL specimens; the numbers of spines increase and by 16.9 mm SL the preopercular margin is serrate. Median fin development occurs at 4.1 mm SL, all fins are present in 8.8 mm SL larvae, and a full complement of rays are observed by 12.8 mm SL. Larvae are completely scaled by 13.0 mm SL.

Scup, *Stenotomus chrysops* (Linnaeus 1766), the only common sparid in southern New England waters, is a popular sport and commercial fish in spring and summer. Their range is from South Carolina to Sable Island, Nova Scotia, although they are uncommon north of Cape Cod (Breder 1948; Bigelow and Schroeder 1953; Leim and Scott 1966). Scup move inshore in schools in early April in the Chesapeake Bay area and in May north to Cape Cod. Most scup spend the summer in bays or within 8-10 km of the coast where they spawn from May to August with a peak in June in Narragansett Bay (Perlmutter 1939; Bigelow and Schroeder 1953; Wheatland 1956; Herman 1963). In late October scup begin to move offshore to depths of 40-100 m. Commercial catches between January and April indicate that many scup winter off Virginia and North Carolina (Neville and Talbot 1964; Smith and Norcross 1968).

Despite the commercial importance and abundance of this species, only one description of the eggs and larvae exists (Kuntz and Radcliffe 1917). This description, which has been paraphrased several times, and the accompanying illustrations, which have been reprinted several times, provide no information on osteological development nor do they present meristic and morphometric data. Consequently we undertook to rear larvae from laboratory-spawned eggs to provide specimens for a more complete description which would be useful for identification of wild larvae.

METHODS

Adult fish captured by trawl in Narragansett Bay, R.I., were held in a 58 m^3 aquarium until they spawned naturally. Fertilized eggs were collected from the aquarium with plankton nets and incubated in 40 l aquaria at 18° and 21°C in 31‰ salinity. The postincubation series for this study was reared at 18°C. After hatching, the larvae and juveniles were fed zooplankton and brine shrimp nauplii. Larvae were removed regularly for our studies and preserved in 4% buffered Formalin[4] and Formalin with Ionol added as a color preservative. Specimens up to 19.5 mm standard length (SL) are included in this description, but scup were reared to >40 mm in some of our experiments. Eighty-eight larvae from 2.0 to 16.9 mm SL were measured with an ocular micrometer. The data were pooled for all fish of the same SL, and all measurements converted into percentages of SL and summarized in Table 1. The following measurements were made:

Total length (TL): Tip of snout to end of caudal fin or finfold.

Standard length (SL): Tip of snout to end of notochord in larvae prior to and during notochord flexure; tip of snout to base of hypural plate once it is formed. All references to length or size in the text refer to SL unless otherwise noted.

Postanal length: Anus to end of notochord measured along midline of body.

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

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TABLE 1.—Summary of nine morphological features of specimens of *Stenotomus chrysops* as shown by their percentages of standard length.

SL (mm)	TL (mm)	SL:TL	Postanal length: SL	Preanal length: SL	Head length: SL	Snout length: SL	Prepectoral length: SL	Prepelvic length: SL	Eye diam SL	Body depth: SL
2.0	2.1	95.2	45.0	40.0	10.0	2.5	—	—	7.5	30.0
2.1	2.3	91.3	46.7	40.5	11.0	3.8	—	—	7.7	29.0
2.2	2.4	91.7	46.6	42.7	12.5	3.4	—	—	7.6	26.0
2.3	2.5	92.0	43.5	38.0	10.9	4.3	—	—	7.6	25.0
2.6	2.8	92.9	42.3	36.5	17.3	3.8	19.2	—	7.5	24.0
2.7	2.9	93.1	41.0	36.6	18.2	5.4	21.5	—	7.7	21.0
2.8	3.0	93.3	40.8	36.0	18.6	5.5	20.8	—	6.2	24.0
2.9	3.1	93.5	41.4	36.6	18.5	4.1	21.6	—	6.9	20.7
3.0	3.2	93.8	42.8	37.8	17.8	5.0	21.1	—	7.6	22.4
3.2	3.4	94.1	43.8	37.5	18.8	4.7	21.9	—	8.1	22.6
3.4	3.6	94.4	42.6	38.2	19.1	5.1	23.5	—	8.1	22.6
3.5	3.7	94.6	41.4	37.1	18.1	4.3	22.4	—	8.8	28.1
3.6	3.8	94.7	40.7	37.0	18.5	5.6	21.8	—	8.8	20.6
3.7	3.9	94.9	41.9	37.2	18.9	5.4	21.6	—	8.8	22.9
3.9	4.1	95.1	43.6	38.5	17.9	5.1	20.5	—	8.1	28.4
4.1	4.3	95.3	43.9	39.0	17.1	4.9	22.0	—	8.3	24.4
4.3	4.6	93.5	46.5	41.9	20.9	4.7	22.1	—	8.2	29.5
4.6	4.9	93.9	45.7	41.3	21.2	4.9	23.9	—	8.2	29.5
4.8	5.1	94.1	45.7	41.7	20.8	6.3	25.0	—	8.9	30.0
4.9	5.2	94.2	44.9	40.8	21.9	5.6	25.5	—	8.7	30.4
5.4	5.6	96.4	51.9	48.1	22.2	5.6	25.0	—	9.5	23.8
5.5	5.9	93.2	51.9	46.7	23.9	7.3	27.6	—	10.9	38.2
5.6	6.2	90.3	48.2	44.6	23.2	5.4	26.8	—	9.5	22.4
6.1	6.9	88.4	53.0	48.1	25.1	7.7	30.1	—	9.8	29.5
6.4	7.4	86.5	56.3	50.0	25.0	9.4	29.7	—	10.0	25.8
6.6	6.6	86.8	54.5	50.0	25.8	7.6	31.8	—	9.8	30.3
7.1	8.0	88.8	54.9	50.7	25.4	7.0	31.0	—	9.9	21.1
7.9	9.2	85.9	53.2	49.4	24.7	7.6	29.7	—	9.5	25.3
8.5	10.3	82.5	57.1	52.9	25.3	7.1	28.8	35.3	9.4	27.1
9.2	10.9	84.4	55.4	51.1	26.1	7.6	29.3	38.0	9.2	27.2
9.9	11.8	83.9	54.5	50.5	24.2	9.1	32.3	33.3	9.1	27.3
10.0	12.0	83.3	58.5	52.5	27.5	9.0	30.5	37.0	9.5	26.0
12.0	14.5	82.8	56.7	50.8	25.8	9.2	30.0	35.8	9.2	26.7
12.6	15.4	81.8	55.6	50.0	26.2	8.7	31.0	34.1	8.7	25.4
13.1	15.6	84.0	56.5	51.9	28.2	8.4	32.1	35.9	10.7	30.5
13.5	16.3	82.8	56.3	52.6	21.5	8.1	30.4	34.1	8.9	29.6
14.6	17.0	85.9	54.8	50.0	25.3	8.9	32.2	35.6	9.6	26.0
14.9	17.1	87.1	54.4	48.3	25.5	8.1	30.9	34.2	8.7	26.8
15.9	18.8	84.6	59.1	54.7	25.2	8.2	31.4	38.4	7.5	32.7
16.9	20.6	82.0	62.1	59.2	30.2	11.2	35.5	42.6	10.7	33.7

[1]Notochord flexion

Preanal length: Tip of snout to anus measured along midline of body.

Head length: Tip of snout to posterior margin of otic capsules in young larvae; tip of snout to cleithrum once it is apparent.

Eye diameter: Horizontal distance between anterior and posterior edges of orbit.

Snout length: Tip of snout to anterior margin of eye.

Body depth: Vertical height of body at pectoral axis.

Prepectoral length: Tip of snout to axil of pectoral fin, or its anlage, measured along midline of body.

Prepelvic length: Tip of snout to axil of pelvic fins, measured along midline of body.

Meristics: Fin rays and spines were counted as they became apparent. Myomeres (total, precaudal, and caudal) were counted. Seventeen specimens were cleared and stained by Hollister's method (Hollister 1934) to determine the ossification sequence of developing skeletal elements to verify counts of bony structures.

DESCRIPTION

Eggs

The scup egg is spherical, buoyant, and transparent. The shell is unsculptured and the yolk unsegmented. It has one gold-colored oil globule that is posterior in the yolk sac and bears black pigment. The yolk is about 78% and the oil globule about 21% of the egg diameter. The average diameter of the 97 eggs we measured was 0.93 mm (range 0.81-1.00 mm). They hatched in 70-75 h at 18°C and in 44-54 h at 21°C. These measurements and the incubation time are similar to those found by others for this species (Kuntz and Radcliffe 1917; Perlmutter 1939; Bigelow and Schroeder 1953; Wheatland 1956).

Larvae

Newly hatched larvae average 2.0 mm SL. The eyes are not pigmented and the mouth is not functional. The head is bent slightly over the elliptical yolk sac. Yolk sac and oil globule are absorbed and gut differentiation occurs between 48 and 72 h after hatching at 18°C. During this period the eyes become pigmented, the mouth functional, and the larvae begin to feed. Larvae ranging in size from 2.0 to 18.7 mm are shown in Figure 1.

Yolk Absorption and Gut Differentiation

At hatching the gut is a tube with a constriction at its posterior end that extends to the ventral edge of the finfold, but by 48 h (2.7 mm) a foregut and hindgut

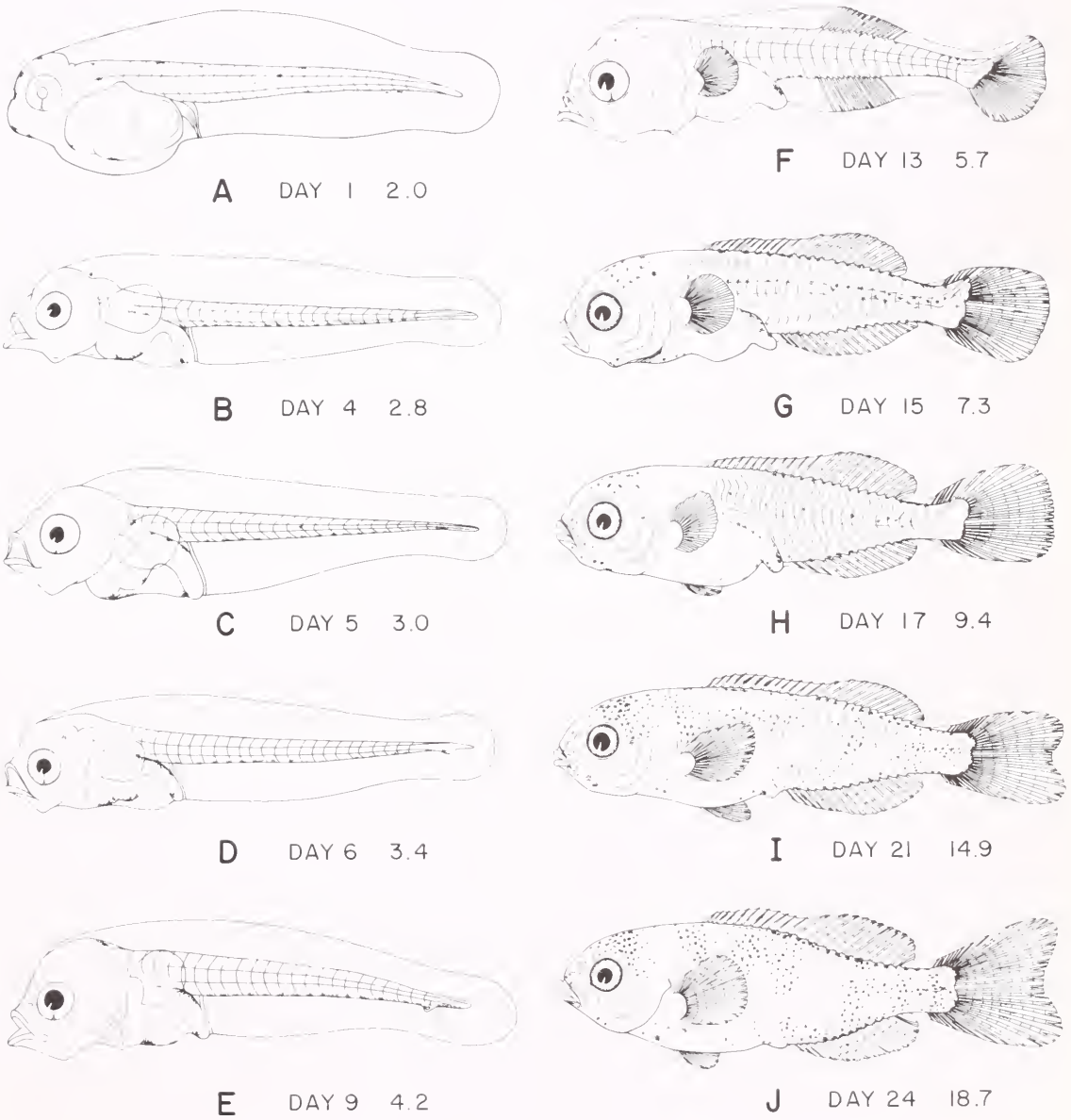

FIGURE 1.—Development of *Stenotomus chrysops*. Lengths (SL) are in millimeters.

can be distinguished. The hindgut appears to be muscular and remains a tube until between day 7 and day 9 (ca. 4.0 mm), when a well-defined stomach becomes apparent and the hindgut is relatively shorter.

Total Length and Standard Length

Larval growth appears to be gradual and continuous with no well-defined changes in relative body proportions. Apparent slight changes which are noticeable after notochord flexion relate to a change in measurement from an SL which is actually notochord length to one which is a true SL.

Postanal Length

Postanal length remains about 45% from 2.0 to 4.9 mm SL, when notochord flexion is occurring. A gradual increase to 62.1% in juveniles longer than 16.9 mm SL is concurrent with development of vertebrae and overall growth of the larvae.

Preanal Length

Preanal length increases relative to SL from 36.0% at 2.0 mm to 41.9% at 4.9 mm to >59% for juveniles longer than 16.9 mm. The lengthening of the body cavity during growth accounts for the increase in preanal length.

Head Length

Head length increases relative to SL from an average of 11.1% (10-12.5%) in newly hatched larvae (2.0-2.3 mm) to 17.3% in 2.6 mm larvae, then gradually increases to 30.2% in the largest juvenile specimen. In very young larvae the otic capsules are the reference structure for head measurements. However, once the cleithrum develops it is used as the reference structure for subsequent head measurements and an increase in head length percentage is observed.

Eye Diameter

The ratio of eye diameter to SL in our series is 6.2-10.9% of SL. It averages 7.5% SL in 2.0-3.0 mm larvae, and 8.5% SL (range 8.1-8.9%) in 3.2-4.9 mm larvae. In larvae >4.9 mm the average is 9.5% of SL (range 7.5-10.9%). Variation in individuals of the same size is considerable.

Snout Length

As with eye diameter, there is considerable variation among individuals of the same size. At hatching the snout length is 2.5% of SL, but this increases gradually to 9.4% of SL at 15.9 mm and 11.2% of SL in the juveniles.

Body Depth

Body depth ranges from 25 to 30% in newly hatched larvae, but once the yolk is absorbed it decreases to between 21 and 24.4% of SL (with one exception) up to 3.9 mm, and then increases to 22.4 to 33.7% of SL.

Prepectoral Length

Anlagen are present at hatching. Initially prepectoral length is about 19.2% of SL. This increases gradually during the larval and postlarval period to 35.5% of SL in the juvenile.

Prepelvic Length

Pelvic fin buds do not appear until the larvae are 8.0-8.5 mm long. Prepelvic to SL ratio is about 35.6% (range 33.3-38.4%) for larvae from 8.5 to 15.9 mm SL, but increases to 42.6% of SL in the juvenile.

MERISTICS

Scup, being typical of most perciform fish, have 24 myomeres. This agrees with Miller and Jorgenson's (1973) vertebrae numbers for adult fish.

FIN DEVELOPMENT

At hatching a finfold extends from the top of the head to the visceral sac interrupted only by the anus. There are no fin rays. A remnant of this persists between the anus and the first anal fin ray in a larva 9.1 mm long. Fin sequence development is given in Table 2.

Anlagen of the pectoral fins are present in most, if not all, hatchlings. These are low buds at first, but by the time the larvae are about 2.5 mm these fins have bases and blades. By removing pectoral fins from one side of some of our larvae and flattening them out, we could see 13 rays in one 4.9 mm larva and 10 rays in a 5.7 mm larva. Aside from these two, however, we could not see pectoral fin rays, even on cleared and

TABLE 2.—Summary of fin development sequence in larvae of *Stenotomus chrysops*.

Fin	Notochord or standard length (mm)			
	Buds first appear	Rays first appear	Full complement of rays	Number of rays in fully developed fin
Dorsal		5.5-6.0	10.8	XII + 12
Caudal			10.4-10.8	32-34
Principal		4.3	5.3	Dorsal 9
				Ventral 8
Secondary		5.3		Dorsal 7-8
				Ventral 8-9
Anal		5.5-6.0	10.8	III + 11
Pelvic	5.7	8.8-10.0	12.8-13.2	I + 5
Pectoral	2.3	2.9-3.0	10.4-10.8	16

stained specimens until the larvae were about 8.0 mm, when the larvae had nearly the full complement of 15-16 pectoral rays.

An anlage of the caudal base can be seen in larvae as small as 3.4 mm. Some of the principal caudal rays are detectable in the finfold of larvae as small as 4.3 mm, and are the first rays of any fins to appear. Notochord flexion in our series begins at 4.7 mm. By 5.3 mm all of the principal caudal rays are present as are some of the secondary ones. Flexion is complete at about 8.0 mm and the caudal fin begins to fork at about 10 mm. Full complements of caudal rays (9-10+9+8+8-10) are present in larvae 14 mm or longer. Secondary rays develop in a posterior to anterior direction.

The soft-ray parts of the median fins first develop beginning at 5.3 mm in our series. Anal and dorsal rays develop together. In both fins, the central soft rays develop first. The development of anterior and posterior rays follows rapidly so that when the larvae in our series are >6.0 mm, full complements of 11-12 soft rays are present in these fins. Development of the spiny rays in these fins is from posterior to anterior and follows the soft-ray development. An exception is the posteriormost spiny rays in both fins that appear first as soft rays.

The last fins to appear are the pelvics. Anlagen are first seen in our series in some larvae at 5.7 mm. Other larvae are >7.0 mm long before these anlagen are visible. Development thereafter is from the distal edge medially. Full arrays of 1 spine and 5 soft rays are present in larvae 8.5 mm or longer.

Adult scup have six pairs of branchiostegals. Five pairs of these are present in a 4.2 mm larva of our series. They were visible in all of our series that were 5.0 mm or larger. The sixth pair, the median one, is not visible in some of our larvae even at 16.5 mm. The first five pairs usually appear simultaneously, but the sixth appears later.

PIGMENT

Although scup have chromatophores other than melanophores, these faded rapidly after preservation in Formalin. This account is confined to melanophore pigmentation (Fig. 1). Pigmentation other than that by melanophores is extensive on embryos and early larvae and is described and illustrated by Kuntz and Radcliffe (1917).

Head Region

Newly hatched scup have unpigmented eyes. Two rows of stellate melanophores, one on either side, extend from the snout back over the eyes and continue as part of a lateral series on the trunk. At a length of about 2.5 mm there is a hiatus in this series that extends from mideye level to over the visceral sac.

At 4.0-5.0 mm length, the pattern that will culminate in that of the juvenile has begun to appear. There are few, usually no, melanophores on the dorsal and lateral parts of the head anterior to the middle of the eyes. However, there are several prominent melanophores on the posterior midbrain and several on the hindbrain. Ventrally there is usually no pigment on the head. A few of our specimens have one or two small melanophores.

Development beyond this stage consists of a gradual increase of pigment on the dorsal and dorsolateral parts of the head. Most of it occurs above mideye level. A few melanophores appear on the snout and below the eye. There is a prominent melanophore, sometimes accompanied by one or two small ones as well, at the articulation of the lower jaw with the quadrate bone.

Between the head and the trunk pigmentation in the occipital region there is a gap in the dorsal pigment with relatively little pigment in it . This gap is part of the barred pattern of the juvenile.

Trunk and Tail Region

At hatching there are two dorsal rows of stellate melanophores extending from the head to beyond myomere 20. They appear to be between myomeres on the myosepta. Occasionally these rows are interrupted by "missing" melanophores. When this is so, the melanophore is usally lower down on the side of the body. A few, usually three or four, melanophores occur at various places on the anterior part of the yolk sac, and there are one or two on the oil globule. Some specimens have widely spaced melanophores on the ventral margin of the tail.

This pattern persists until the larvae are about 2.5 mm long with a gradual increase in the number of melanophores along the ventral margin of the tail. The melanophores on the yolk sac and oil globule disappear with the exception of one or two on the midventral line of the anterior part of the yolk sac.

In larvae 4.0-5.0 mm long, most of the pigment is on the peritoneum dorsal to the viscera and along the midventral line. Anteriorly there is a melanophore at the cleithral symphysis and posterior to it a large one midventrally on the anterior belly and a smaller one on the posterior belly. There is a prominent melanophore on the hindgut just anterior to the anus. Posterior to this there is a melanophore on most of the anal pterygiophores; this pattern is continued externally on the ventral myosepta. Dorsally there are several melanophores on the posterior pterygiophores of the dorsal fin. There are usually a few scattered spots on the finfold and, on some specimens, a few on the sides.

The peritoneal pigment becomes denser and more prominent in 9-10 mm larvae, however, it is often obscured because of the opacity of the thickening body musculature in preserved specimens. The hindgut is nearly covered by large melanophores. The melanophores on the midventral line are still present, usually accompanied by two or three smaller ones. The melanophore just posterior to the anus is still present, but less prominent.

The trunk and tail pigment is more extensive at 9-10 mm. There are many more pigment spots along the sides, but these are still widely spaced, especially anteriorly. There is pigment along the bases of the dorsal and anal fins that continues posterior to them to the procurrent caudal rays. A line of melanophores runs dorsoventrally at about the juncture of the caudal fin rays and caudal bones. Internally there are melanophores near the bases of the haemal and neural arches. These become increasingly obscure as the body musculature thickens.

Pigment development beyond this size is characterized by the development of the barred pattern of the juvenile accompanied by a general increase in pigment everywhere, especially above the midlateral line.

OSSIFICATION

A total of 17 fish were stained with Alizarin Red to determine where ossification began and the sequence in which the bones ossified. A summary of osteological development is presented in Table 3.

There is no dye uptake in 5.2 or 6.0 mm larvae, although the cartilaginous skeleton is easily distinguished. Cartilaginous hypural plates are present in larvae undergoing notochord flexure (5.4-5.6 mm). The first ossification occurs in skulls of 6.1 mm larvae. The premaxillary, maxillary, dentary, articular, and quadrate bones associated with the jaws, the preoperculum, hyomandibular, branchiostegal rays, and cleithrum showed varying degrees of dye uptake. There is no ossification posterior to the cleithrum.

By 7.0 mm more ossification of the skull occurs, notably the pterygoid, metapterygoid, opercular series, supracleithrum, and frontal bones. The circumorbitals, as well as the parasphenoid and the scapula, show the beginning of dye uptake. Ossification has begun in the first 10 vertebrae, the neural spines of the first 4 vertebrae, and the pectoral and caudal fin rays.

In 9.3 mm specimens the skull is further developed; teeth are visible and the lachrymal, dermethmoid, nasal, prefrontal, and urohyal bones show varying degrees of ossification. The postcleithrum is well developed and the radials, scapula, and coracoid are ossifying. The entire vertebral column is ossified with the exception of the ultral centrum and penultimate vertebrae. Both haemal and neural spines are ossified. The pleural ribs, and the dorsal and anal fin rays are beginning to ossify; hypural plates and caudal fin rays are partially ossified.

By 10.8 mm the distal vertebrae (caudal complex) have ossified and scales are present. The pelvic fin supports and rays show some dye uptake. Pterygiophores are present as cartilage. All the dorsal and anal fin rays and spines have ossified.

Skull development and ossification of most of the bones of the skull is complete by 14.5 mm. The radials and scapula which were just beginning to ossify in the 10.8 mm fish are now complete. Pelvic fin supports are complete. The pleural ribs are

TABLE 3.—Summary of osteological development in laboratory reared larvae of *Stenotomus chrysops*.

	Notochord or standard length (mm)		
	First appearance in cartilage	First evidence of ossification (stain uptake)	All ossifying
Cartilaginous skeleton	5.2		
Hypural plates	5.4	9.3	14.5
Vertebrae and neural spines		7.0	10.8
Pectoral girdle	7.0	10.8	14.5
Pectoral and caudal fin rays		7.0	9.3
Haemal spines		9.3	9.3
Pleural ribs		9.3	14.5
Dorsal and anal fin rays		9.3	10.0
Caudal complex		10.8	10.8
Pelvic fin supports		10.8	14.5
Pelvic girdle		10.8	18.7

stained as are the pterygiophores. The hypural plates are all present and completely ossified; a few dorsal plates are still partially cartilaginous.

By the time scup are 18-19 mm long, they are juveniles. Ossification continues in the skull with the bones being joined at suture points; the pelvic girdle is complete. The pterygiophores and ribs have completed ossification.

PREOPERCULAR SPINES

Figure 2 shows the development of preopercular spines. We saw them first on a 4.1 mm specimen, which has three spines on the preopercular margin. Thereafter their number increases until there are so many on a 16.9 mm specimen that the margin is serrate. Specimens larger than about 25 mm have nearly smooth preopercular margins.

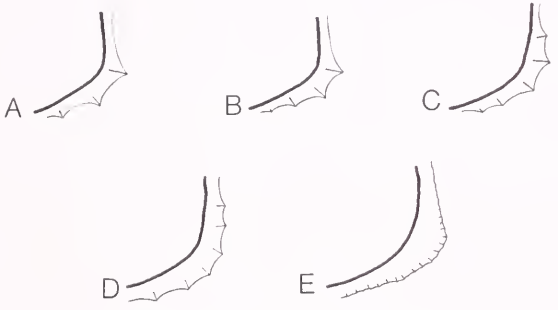

FIGURE 2.—Development of the preopercular spines of *Stenotomus chrysops*. Standard lengths in millimeters of the specimens are A) 4.1, B) 5.6, C) 8.3, D) 9.8, and E) 16.9.

SCALES

The first scales are seen between 9.9 and 10.8 mm. At 12.3-13.0 mm the larvae are completely scaled.

COMPARISONS

The geographical extent of spawning of *S. chrysops* is not known. The authors can find no record of it spawning south of the New York Bight. At least one other species of *Stenotomus*, *S. caprinus* (Bean 1882), occurs in the western North Atlantic. According to Geohagen and Chittenden (1982), the major population of this species is in the northern Gulf of Mexico and it occurs only rarely along the east coast to North Carolina. A third nominal species, *S. aculeatus* (Valenciennes 1830), said to replace *S. chrysops* south of Cape Hatteras, is of doubtful validity. Birdsong and Musik (in 1977 reprint of Hildebrand and Schroeder 1928) placed *S. aculeatus* in the synonomy of *S. chrysops*; Robins et al. (1980) did not list *S. aculeatus*. Dahlberg (1975) mentioned young stages of *S. chrysops* with crossbars (i.e., juveniles) in his account of Georgia coastal fishes, although it is not clear whether he had taken such specimens in his collections.

This issue is further complicated by lack of information about the northern extent of spawning of other sparid fishes. If their spawning ranges overlap with that of *S. chrysops*, then the younger larvae of some species will probably be confused with scup larvae, at least until the dorsal, anal, and pectoral fin rays can be counted. Except for the reference to juvenile scup on the Georgia coast by Dahlberg, the authors can find no references to such an overlap.

We have seen larval scup in collections misidentified as *Scomber scombrus*, the Atlantic mackerel, from which they can be separated at all stages by the numbers of myomeres (24 in scup and 31 in mackerel). We have also seen larval gerreid fishes misidentified as scup. Among other characters, scup differ from gerreid fishes in lacking the long premaxillary spines that extend up between the eyes in gerreids.

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DESCRIPTION OF EGGS, LARVAE, AND EARLY JUVENILES OF GULF MENHADEN, *BREVOORTIA PATRONUS*, AND COMPARISONS WITH ATLANTIC MENHADEN, *B. TYRANNUS*, AND YELLOWFIN MENHADEN, *B. SMITHI*[1]

WILLIAM F. HETTLER[2]

ABSTRACT

Morphometric, meristic, and pigmentation descriptions of laboratory-reared gulf menhaden, *Brevoortia patronus*, and Atlantic menhaden, *B. tyrannus*, indicate that larvae of these species can be distinguished from each other by the number of myomeres and vertebrae; that Atlantic menhaden can be distinguished from yellowfin menhaden, *B. smithi*, by the number of myomeres and vertebrae, by pigmentation, and by morphometrics; and that gulf menhaden can be separated from yellowfin menhaden by pigmentation and morphometrics. Unlike yellowfin menhaden, gulf and Atlantic menhaden lacked paired melanophores along the dorsal midline forward of the dorsal fin and along the ventral midline between the paired fins. Compared with yellowfin menhaden larvae of equal lengths, gulf menhaden had less body depth, shorter heads and snouts, smaller eyes, and longer prepelvic and predorsal distances. Gulf menhaden eggs averaged 1.29 mm in total diameter, 0.95 mm in yolk diameter, and 0.20 mm in oil droplet diameter. Twelve-hour-old larvae had a snout-notochord tip length of 3.3 mm. Their growth rate averaged 0.30 mm/day through 90 days of rearing at 20°C. On specimens 6-17 mm the mean number of myomeres was 44.6; on specimens >15 mm the mean number of vertebrae was 45.3. Postdorsal-preanal myomeres decreased from 5.3 to 1.8 as the dorsal fin grew and the gut shortened during development. Transformation from larva to juvenile in laboratory-reared gulf menhaden was completed at a smaller size than reported for field-caught fish (25 vs. 28 mm SL).

Eggs and larvae of gulf menhaden, *Brevoortia patronus* Goode, have not been described, even though this species is the most economically important clupeid in the United States. The gulf menhaden purse seine fishery landed an average of 660,368 t annually from 1977 to 1981, making it the largest fishery in the United States (U.S. National Marine Fisheries Service 1982). Gulf menhaden, one of three species of *Brevoortia* in the Gulf of Mexico, are found from Florida Bay to the Gulf of Campeche, Mexico. They spawn in the northern gulf at least as far offshore as the 80 m isobath between mid-October and late March, with a peak in December (Christmas and Waller 1975[3]); juveniles are estuarine dependent. Yellowfin menhaden, *B. smithi*, and finescale menhaden, *B. gunteri*, co-occur with gulf menhaden, but contribute <1% to the landings. The Atlantic menhaden, *B. tyrannus*, which supports a large purse seine fishery along the U.S. Atlantic coast, is a large-scaled cognate of the gulf menhaden, but does not occur in the Gulf of Mexico (Hildebrand 1963). Distribution of yellowfin menhaden is continuous around Florida to as far north as North Carolina.

Menhaden larvae superfically resemble the larvae of other clupeids with which they co-occur and can be distinguished from them (Houde and Fore 1973; Houde and Swanson 1975), but current descriptions (Suttkus 1956; Houde and Fore 1973; Houde and Swanson 1975; Jones et al. 1978) are not adequate to separate sympatric *Brevoortia* larvae. Eggs, larvae, and juveniles of yellowfin menhaden have been described (Houde and Swanson 1975), whereas the early development of finescale menhaden has not. Gulf and yellowfin menhaden hybrids in the eastern Gulf of Mexico (Hettler 1968; Turner 1969; Dahlberg 1970) further complicate separation by species. Although gulf and Atlantic menhaden larvae cannot be confused in ichthyoplankton collections because of their allopatric separation by the Florida Peninsula, Atlantic and yellowfin menhaden larvae may be confused in collections from the east coast of Florida, where both species are known to spawn during the winter (Dahlberg 1970).

In this paper, I describe the eggs, larvae, and early

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[3]Christmas, J. Y., and R.S. Waller. 1975. Location and time of menhaden spawning in the Gulf of Mexico. Unpubl. manuscr., 20 p. Gulf Coast Research Laboratory, Ocean Springs, MS 39564.

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juveniles of gulf menhaden spawned and reared in the laboratory using morphometrics, meristics, and pigmentation features, and I compare gulf menhaden larvae with yellowfin menhaden larvae described by Houde and Swanson (1975). Morphometric and meristic data on laboratory-spawned and reared Atlantic menhaden are also presented to supplement the composite description of this species by Jones et al. (1978) and to aid in the separation of Atlantic menhaden and yellowfin menhaden larvae. Characters for separating *Brevoortia* from other clupeids are reviewed.

METHODS

Gulf menhaden were collected as mature adults in September 1981 near Gulf Breeze, Fla., tranported to the Beaufort Laboratory, and induced to spawn with human chorionic gonadotropin (HCG) and carp pituitary (Hettler 1983). Spawnings that occurred in November 1981 and February 1982 provided a developmental series of eggs, larvae, and juveniles up to 90 d old, reared at a temperature of 20° ± 2°C and a salinity of 30‰. One hundred eggs, preserved during the early embryo stage, and 100 live eggs were measured.

Atlantic menhaden were captured as juveniles in September 1978 near Beaufort, N.C., and reared to sexual maturity in the laboratory for 19 mo. They were induced to spawn in April 1980, and the larvae were reared at temperatures that began at 15°C and increased to 25°C during development (Hettler 1981). This spawning resulted in a developmental series of larvae and juveniles up to 130 d old.

All specimens were preserved in 2% buffered formaldehyde in seawater before being measured. The following morphometic measurements were taken with an ocular micrometer in a dissecting microscope on 123 gulf menhaden and 196 Atlantic menhaden.

Standard length (SL)—tip of snout to tip of notochord before and during notchord flexion; in postflexion larvae, tip of snout to posterior margin of hypural bones. All references to length in this paper are standard length unless otherwise stated.

Preanus length—tip of snout to posterior end of anus, measured along midline.

Predorsal length—tip of snout to anterior edge of dorsal fin base, measured along midline.

Prepelvic length—tip of snout to anterior insertion of pelvic fin, measured along midline.

Body depth—vertical depth at symphysis of the cleithra, exclusive of the finfold.

Dorsal and anal fin base lengths—distance from anterior to posterior edges of fin base; in larvae with incomplete fins, distance from origin of first ray to the insertion of the last ray.

Head length—tip of snout to posterior margin of otic capsules in yolk-sac larvae; tip of snout to opercular margin in older larvae and juveniles.

Snout length—tip of snout to anterior margin of eye.

Eye diameter—horizontal distance between anterior and posterior edges of fleshy orbit.

Myomeres were counted on semidry specimens (not completely immersed) up to 17 mm with transmitted unpolarized light by adjusting the microscope mirror to give maximum contrast between myosepta and myomeres. Myomeres were classified as follows:

Total myomeres—all myomeres between the most anterior myoseptum and the most posterior myoseptum.

Preanal myomeres—number anterior to the myomere in which the anterior ray of the anal fin is inserted or to the myomere in contact with the downward curve of the dorsal margin of the anus in larvae without anal fin rays.

Postanal myomeres—number posterior to the anterior insertion of the anal fin.

Predorsal myomeres—number anterior to the myomere containing the origin of the first dorsal fin ray.

Postdorsal-preanal myomeres—number between the myomere connected to the last dorsal fin ray and the most posterior preanal myomere.

Following morphometric measurements on all specimens and myomere counts on specimens with visible myomeres, the pigment pattern was recorded and specimens of gulf menhaden were illustrated with a camera lucida. Atlantic menhaden were not illustrated as the figures in Jones et al. (1978) are adequate.

Specimens were then used for counts of fin rays, pterygiophores, predorsal bones, vertebrae, and scutes. Specimens were transferred to 95% ethanol, stained with alcian blue for cartilage, cleared with trypsin, stained with alizarin red S for bone, and stored in 100% glycerin[4].

[4]Taylor, W. R., and G. C. Van Dyke. 1978. Staining and clearing small vertebrates for bone and cartilage study. Unpubl. manuscr., 19 p. National Museum of Natural History, Washington, DC 20560.

DESCRIPTION

Embryos

Gulf menhaden eggs were spherical, and had an unsculptured chorion, a faintly segmented yolk, and a single oil droplet. Living eggs were buoyant in salinities >26‰. Twenty-seven percent had both an outer and inner chorionic membrane. This has not been reported in wild-caught *Brevoortia* eggs. This inner chorion was not an artifact of preservation, since live eggs also contained a double chorion, but may have been a result of induced ovulation by HCG and carp pituitary. Dimensions of preserved and live eggs were the same as maximum sizes given by Houde and Fore (1973) for gulf menhaden eggs taken in plankton collections (Table 1). At its widest point the perivitelline space was 24-28% of the egg diameter. Eggs produced during December 1982 by another spawning group of gulf menhaden were smaller than gulf menhaden eggs produced the year before; total diameter was 1.18-1.22 mm; the yolk diameter was 0.66-0.79 mm; the oil droplet was 0.16 mm. The adults producing these eggs were smaller (17.8 cm mean length, 90 g mean weight) than the spawners that produced the larger eggs (20 cm, 135 g) (Table 1). Small adult size may be responsible for the small eggs as well as the reduced fecundity. Only a few hundred fertilized eggs were collected from the December 1982 group of 20 fish.

TABLE 1.—Mean diameter (mm) of gulf menhaden, *Brevoortia patronus*, eggs. Numbers in parentheses are equal to one standard deviation of the mean.

Eggs	*N*	Total diameter	Inner chorion diameter (if present)	Yolk diameter (along axis)	Oil droplet diameter
Preserved	100	1.29 (0.04)	1.23 (0.04)	0.95 (0.05)	0.20 (0.02)
Live	100	1.30 (0.05)	1.25 (0.03)	0.97 (0.04)	0.19 (0.01)

Advanced embryos had 30-40 small melanophores on each side along the dorsal surface from the posterior end of the head to the notochord tip (Fig. 1A).

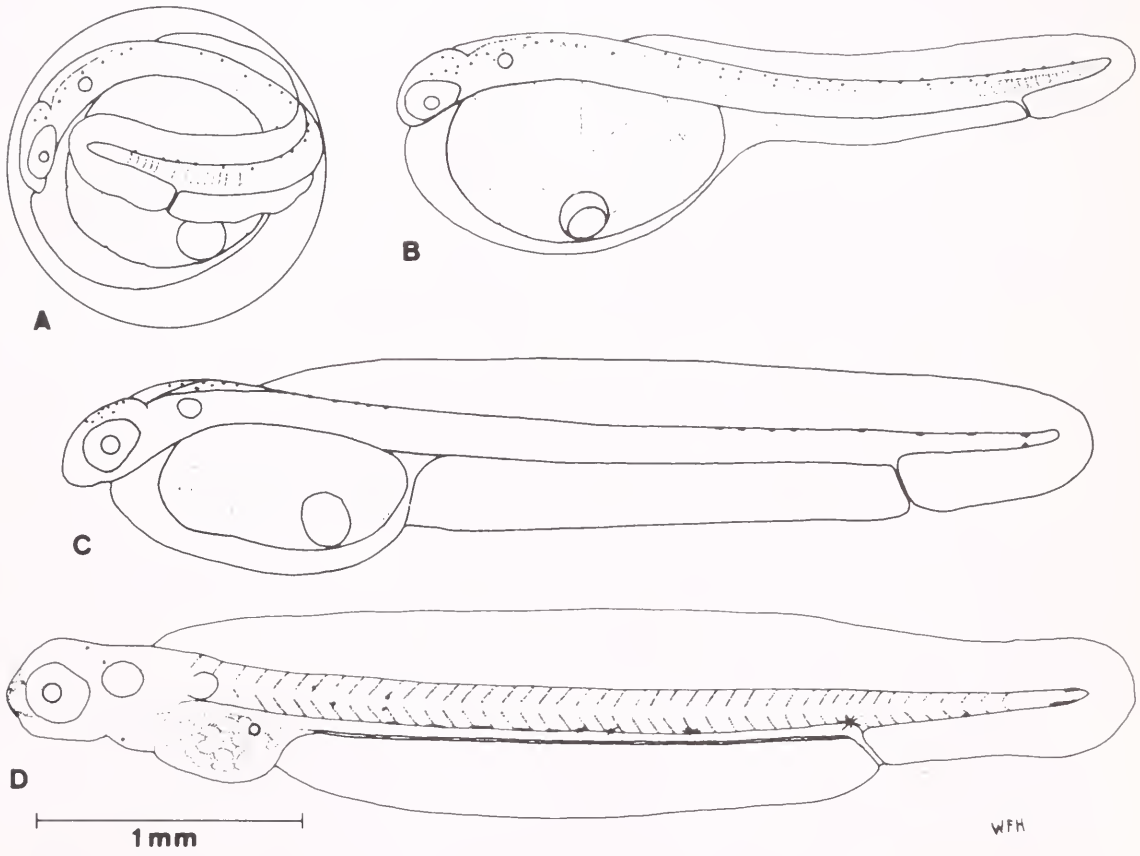

FIGURE 1.—Early stages of *Brevoortia patronus*. A. Embryo 40 h after fertilization. B. 2.6 mm larva, 5 min after hatching. C. 3.5 mm larva, 1 d after hatching. D. 3.9 mm larva, 2 d after hatching.

About 15-20 myomeres were visible in the caudal region. The yolk was faintly segmented into irregular globules. Eggs hatched in 40-42 h at a water temperature of 19°-20°C.

Atlantic menhaden eggs spawned in the laboratory were larger than gulf menhaden eggs in total diameter (1.54-1.64 mm) but similar in yolk diameter (0.82-0.95 mm) and oil droplet diameter (0.20-0.23).

Larvae

Growth

Gulf menhaden larvae were 2.6-3.0 mm SL immediately after hatching (Fig. 1B), but within 6 h had a mean length of 3.3 mm. The yolk and oil droplet were absorbed, the eyes were pigmented, and the mouth was functional at a length of 4.5 mm, 4 d after hatching. The growth rate of larvae at 20° ± 2°C averaged 0.30 ± 0.03 mm/d through 90 d of rearing (Fig. 2). Yellowfin menhaden reared for 32 d at 20°C grew 0.36 mm/d (Hettler 1970). Yellowfin menhaden reared at 26°C grew 0.45 mm/d until the 20th day (Houde and Swanson 1975).

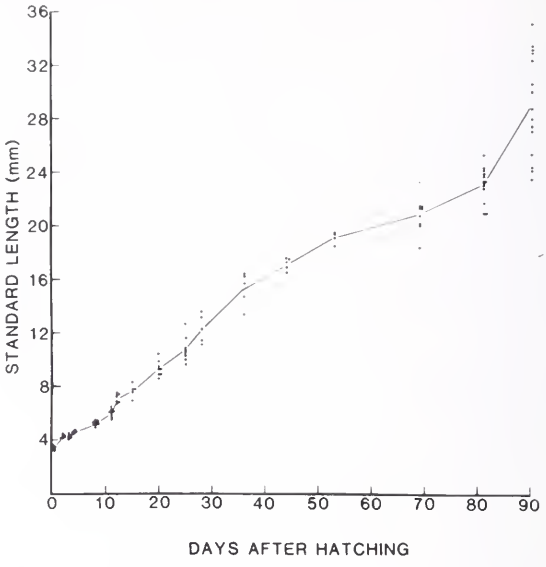

FIGURE 2.—Growth of laboratory-reared larvae of *Brevoortia patronus*. Lines connect means of each age group.

Body Proportions

For 123 gulf menhaden, 3.1-34.9 mm, body depth, head length, prepelvic length, dorsal fin base length, anal fin base length, snout length, and eye diameter all increased relative to standard length as larvae grew, while preanus length and predorsal length decreased (Table 2). The decrease in predorsal length resulted from the forward movement of the dorsal fin, and the decrease in preanus length reflected the transformation from an elongate clupeiform larva shape to the laterally flattened fusiform shape of the juvenile. Transformation from the larval to the juvenile form in gulf menhaden began at about 19 mm (Fig. 3C) and was completed at about 25 mm. Atlantic menhaden larvae completed transformation at about 27 mm.

TABLE 2.—Proportions of head and body parts of gulf menhaden, *Brevoortia patronus*, expressed as a percent of standard length. Characters were not developed at lengths marked with a dash.

Length class (mm, SL)	Number of specimens	Preanus length	Predorsal length	Prepelvic length	Body depth	Dorsal fin base length	Anal fin base length	Head length	Snout length	Eye diameter
3.0-3.9	6	84.0	—	—	—	—	—	14.1	2.3	5.2
4.0-4.9	19	80.2	—	—	9.7	—	—	13.5	1.7	5.4
5.0-5.9	12	81.4	—	—	9.6	—	—	15.8	3.0	5.2
6.0-6.9	8	82.4	69.3	—	8.4	4.4	—	15.5	3.1	5.0
7.0-7.9	7	83.0	70.2	—	8.2	5.0	—	15.4	2.9	4.9
8.0-8.9	4	83.2	67.6	—	7.9	8.2	—	15.5	3.1	4.8
9.0-9.9	5	83.9	65.8	—	8.3	10.0	3.8	16.2	3.6	5.0
10.0-10.9	6	85.5	65.6	—	8.3	11.5	4.9	16.9	3.7	5.0
11.0-11.9	3	85.5	65.2	—	8.9	13.2	5.6	17.7	3.9	5.2
12.0-12.9	2	83.1	63.0	—	8.6	13.3	6.0	16.9	3.6	4.8
13.0-13.9	3	84.2	62.8	—	9.9	15.1	6.8	17.8	3.7	4.9
14.0-14.9	1	81.0	62.0	41.5	10.0	14.5	7.5	17.0	3.5	5.0
15.0-15.9	1	82.2	61.2	—	10.7	15.4	7.5	18.2	3.7	5.1
16.0-16.9	4	79.8	60.8	44.2	10.8	15.3	9.4	18.9	4.0	5.5
17.0-17.9	3	79.0	61.0	44.3	12.4	14.8	11.0	19.4	4.1	5.5
18.0-18.9	2	76.0	57.0	47.6	18.1	16.8	12.3	24.1	5.0	7.3
19.0-19.9	4	76.2	56.4	46.9	17.8	16.6	12.8	24.0	5.1	6.8
20.0-21.9	8	71.4	51.8	50.0	25.8	18.6	16.0	28.1	6.0	8.1
22.0-23.9	8	70.2	48.6	49.2	28.0	18.4	15.7	28.9	6.1	8.4
24.0-25.9	6	70.7	47.9	49.6	29.1	19.3	16.0	29.3	6.6	8.5
26.0-27.9	3	70.6	44.7	50.0	31.6	19.2	17.0	29.7	6.9	8.6
28.0-29.9	1	70.2	43.5	49.4	30.1	20.1	16.4	27.7	6.4	7.7
30.0-34.9	7	72.7	47.7	51.3	36.0	19.4	17.1	31.5	7.2	7.8

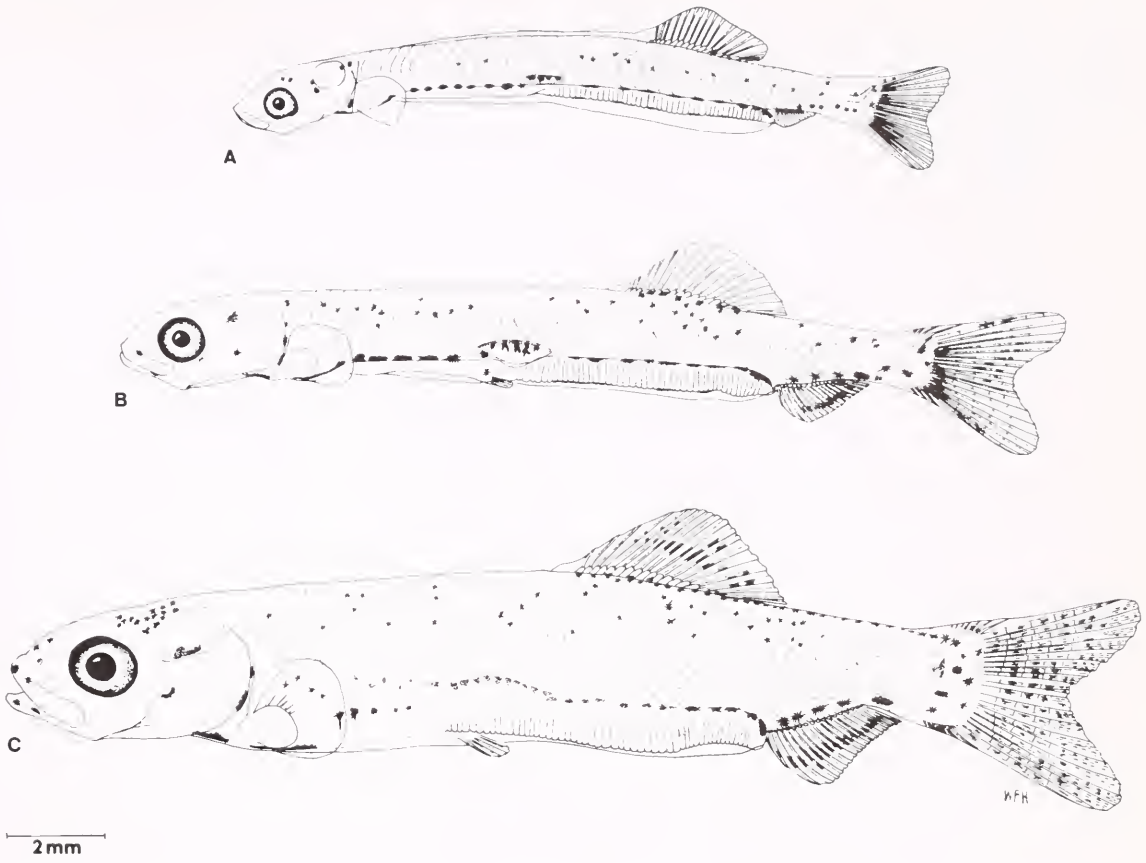

FIGURE 3.—Larval *Brevoortia patronus*: (A) 13.0 mm (28 d after hatching). (B) 16.5 mm (44 d after hatching). (C) 18.9 mm (53 d after hatching).

Gulf menhaden larvae and Atlantic menhaden larvae could not be separated morphometrically (Table 3, Fig. 4), but both could be separated from yellowfin menhaden larvae between 10 and 20 mm (Houde and Swanson 1975) by body depth, prepelvic length, and head length. Snout length and eye diameter may be useful to distinguish 15-25 mm specimens; snouts $\geq 7\%$ of SL and eye diameter $\geq 9\%$ of SL probably identify yellowfin menhaden.

Myomeres

The total number of myomeres could be counted only on specimens under 17 mm in length. Although the preanal myomeres could be easily counted on larger specimens, the last few postanal myomeres on the peduncle became indistinguishable. The number of myomeres (mean = 44.6) did not change significantly with length in gulf menhaden and corresponds with the number of adult vertebrae (44-46; mean = 44.7 not counting the hypural bones) reported by Dahlberg (1970). Radiographs of 20 adult gulf menhaden spawners used in my study showed that all fish had either 45 or 46 vertebrae (counting hypurals), with a mean of 45.6. During development the dorsal and anal fins moved in relation to the myomeres (Table 4). The anterior end of the dorsal fin moved from myomere 30 forward to myomere 23, numbered from head to tail. The posterior end of the dorsal fin remained fixed at myomere 32. The anus and the anterior end of the anal fin moved forward from myomere 37 to myomere 34. The postdorsal-preanal myomere count of 2 or 3 is diagnostic for *Brevoortia* at lengths >14 mm. Atlantic menhaden larvae 6-16 mm SL had a mean of 47.2 myomeres, with about two more predorsal myomeres and one more postanal myomere than gulf menhaden. Myomere number and distribution for gulf menhaden and yellowfin menhaden (Houde and Swanson 1975) were so similar that neither were useful for

TABLE 3.—Proportions of head and body parts of Atlantic menhaden, *Brevoortia tyrannus*, expressed as a percent of standard length. Characters were not developed at lengths marked with a dash.

Length class (mm, SL)	Number of specimens	Preanus length	Predorsal length	Prepelvic length	Body depth	Dorsal fin base length	Anal fin base length	Head length	Snout length	Eye diameter
3.0-3.9	4	85.4	—	—	—	—	—	14.5	1.9	6.7
4.0-4.9	10	82.8	—	—	8.3	—	—	12.0	1.9	5.4
5.0-5.9	15	81.0	—	—	8.4	—	—	12.1	2.2	5.0
6.0-6.9	7	81.4	—	—	8.4	—	—	13.3	2.5	4.8
7.0-7.9	18	82.3	71.0	—	8.0	2.6	—	13.7	2.6	4.8
8.0-8.9	12	82.7	69.6	—	7.9	4.3	—	13.9	2.6	4.8
9.0-9.9	13	82.8	67.3	—	8.3	6.5	2.4	15.0	3.0	5.2
10.0-10.9	13	85.6	66.9	—	8.6	9.5	4.2	16.4	3.4	5.3
11.0-11.9	8	85.9	66.4	—	8.7	10.1	5.0	16.6	3.5	5.4
12.0-12.9	10	84.7	64.6	—	9.1	11.5	5.5	17.6	3.7	5.6
13.0-13.9	10	83.2	63.6	—	9.4	13.0	6.7	18.2	4.0	6.0
14.0-14.9	7	82.9	62.7	45.8	9.8	13.6	7.1	18.3	4.0	6.2
15.0-15.9	7	81.7	61.9	45.3	10.0	14.0	7.8	18.3	4.0	6.2
16.0-16.9	9	80.8	62.5	45.5	11.4	14.0	8.8	20.2	4.1	6.8
17.0-17.9	8	79.9	60.2	47.6	12.8	15.2	10.0	22.9	4.5	7.3
18.0-18.9	6	77.9	58.6	47.0	14.2	15.7	10.6	23.2	4.4	7.4
19.0-19.9	9	76.9	57.3	48.0	16.1	16.0	11.8	23.8	4.6	7.8
20.0-21.9	7	74.2	53.8	48.6	19.8	17.1	14.2	27.2	4.8	8.0
22.0-23.9	3	73.4	50.4	50.9	24.7	17.7	16.1	29.8	5.5	8.0
24.0-25.9	2	72.7	51.4	51.3	25.4	17.6	15.9	31.0	5.7	7.6
26.0-27.9	3	74.7	49.6	52.8	29.1	19.6	18.0	31.1	7.0	8.3
28.0-29.9	1	72.6	48.9	51.5	29.0	17.3	16.3	31.3	6.8	7.8
30.0-34.9	4	75.4	49.6	52.4	32.6	20.0	15.6	33.0	8.2	8.8
35.0-39.9	3	76.0	49.9	53.2	36.5	20.4	16.6	33.6	7.6	7.8
40.0-49.9	4	74.9	49.6	52.2	33.5	20.5	17.1	32.2	7.6	8.3
60.0-69.9	3	74.8	48.9	52.2	33.4	19.5	16.8	32.4	7.0	5.3

TABLE 4.—Number of myomeres relative to dorsal fin and anal locations on gulf menhaden, *Brevoortia patronus*, larvae.

Length class (mm, SL)	Preanal			Postanal			Predorsal			Postdorsal-Preanal		
	N	Range	Mean	*N*	Range	Mean	*N*	Range	Mean	*N*	Range	Mean
<6.0	4	36-37	36.7	4	9	8.0	—	—	—	—	—	—
6.1-8.0	16	36-37	36.7	3	7-9	7.7	9	28-30	28.9	9	4-6	5.3
8.1-10.0	9	35-38	36.3	9	8-10	8.6	9	26-28	27.3	9	3-5	4.4
10.1-12.0	10	33-37	35.4	10	8-10	9.1	10	23-27	25.2	10	3-4	3.3
12.1-14.0	4	33-35	34.0	4	8-10	9.5	4	23-25	23.7	4	2-3	2.2
14.1-17.0	4	32-33	32.5	—	—	—	4	22-23	22.2	5	1-2	1.8

separating small larvae of these species. Yellowfin menhaden had a mean of 45.7, about one less predorsal myomere, and about one to two more postanal myomeres than gulf menhaden. Atlantic menhaden had about two more preanal myomeres and about one more postanal myomere than gulf menhaden at each size class (Table 5).

Meristics

In gulf menhaden the caudal and dorsal fins were the first fins to initiate development and the pectoral fins were the last fins to complete development, even though they were the first fins to form as nonrayed buds (Table 6, Fig. 1C). Two specimens had an extra principal ray in both the upper and lower group of caudal rays. Vertebrae centra did not first stain with alcian blue as did other bony structures. At 13 mm, vertebrae first stained with alizarin red S, with the staining reaction progressing from the middle of the column towards each end as length increased. The neural and haemel spines initially stained blue, beginning at each end of the column and progressing towards the middle. The mean number of vertebrae,

TABLE 5.—Number of myomeres relative to dorsal fin and anal locations on Atlantic menhaden larvae, *Brevoortia tyrannus*. Myomeres on specimens <6 mm could not be accurately counted.

Length class (mm, SL)	Preanal			Postanal			Predorsal			Postdorsal-Preanal		
	N	Range	Mean	*N*	Range	Mean	*N*	Range	Mean	*N*	Range	Mean
6.1-8.0	13	38-40	38.7	13	8-10	9.0	10	30-31	30.7	10	5-6	5.7
8.1-10.0	16	37-40	38.4	16	8-11	9.9	16	27-30	29.0	10	4-6	5.2
10.1-12.0	16	36-37	36.1	16	10-11	10.8	16	25-28	26.2	16	3-5	4.0
12.1-14.0	14	35-37	35.6	10	10-11	10.7	14	24-26	25.1	14	3-4	3.2
14.1-16.0	2	35-36	35.5	—	—	—	2	24-25	24.5	3	3	3.0

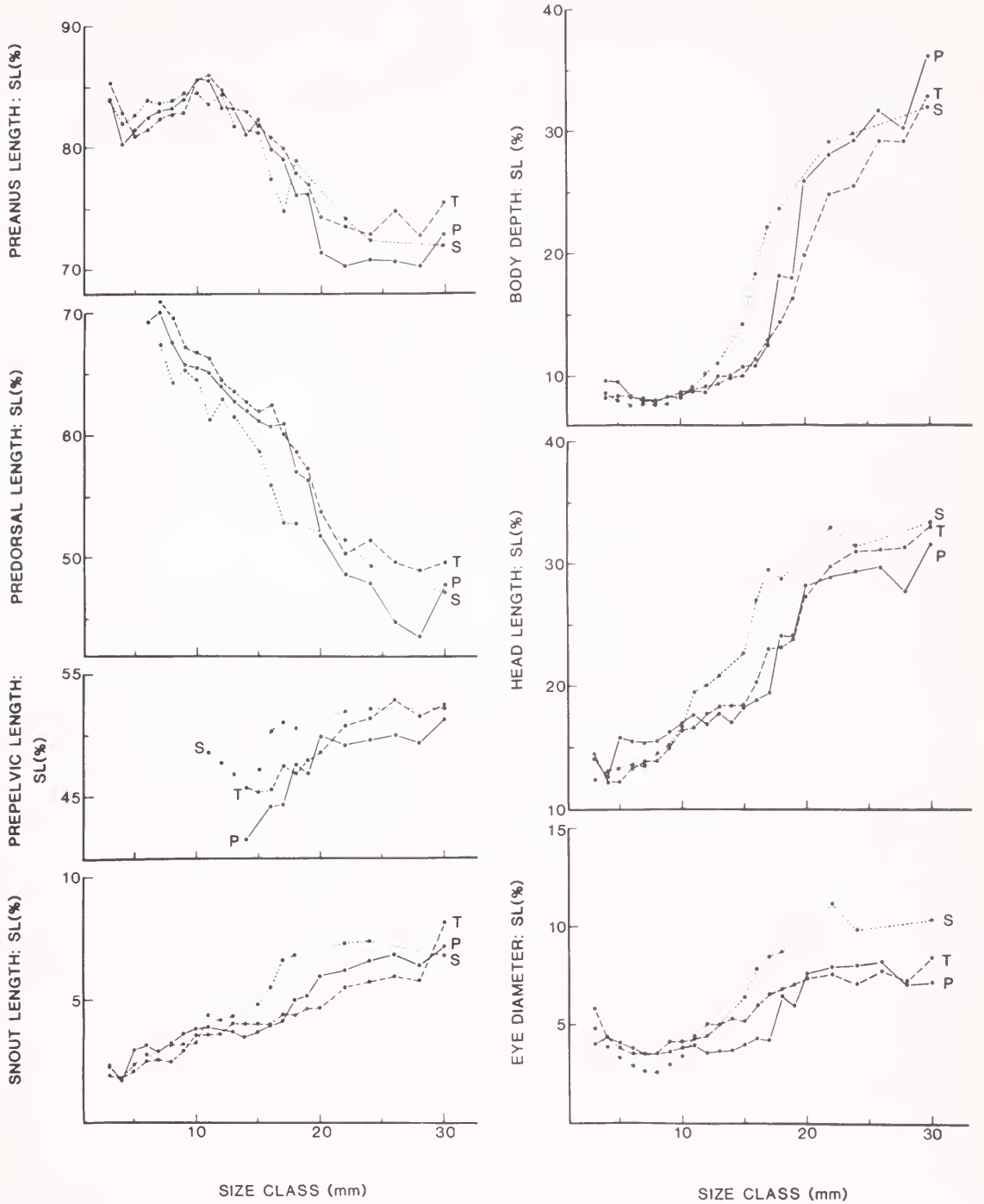

FIGURE 4.—Morphometric comparisons as a percentage of standard length of laboratory-reared *Brevoortia patronus* (P), *B. tyrannus* (T), and *B. smithi* (S). Yellowfin menhaden data from Houde and Swanson (1975).

TABLE 6.—Meristics in gulf menhaden, *Brevoortia patronus*, (35 specimens) and in Atlantic menhaden, *B. tyrannus*, (34 specimens).

Meristic	Size (mm SL) when first stained		Size (mm SL) when all are stained		Number in full complement	
	B. patronus	*B. tyrannus*	*B. patronus*	*B. tyrannus*	*B. patronus*	*B. tyrannus*
Caudal fin rays						
Principal	8	9	9	12	10-11 (dorsal)	10 (dorsal)
	16	13	18	20	9-10 (ventral)	9 (ventral)
Procurrent					8-9 (dorsal)	7-8 (dorsal)
					7-8 (ventral)	6-7 (ventral)
Dorsal fin						
Pterygiophores	8	8	16	16	19-21	18-19
Rays	8	9	19	17	21-23	20-22
Anal fin						
Pterygiophores	9	10	16	15	17-20	17-20
Rays	10	12	17	15	18-22	19-21
Pelvin fin rays	16	15	18	18	7	7
Pectoral fin rays	18	18	21	21	13-15	15-17
Predorsal bones	19	17	21	21	9-11	10-12
Vertebrae	13	14	16	15	45-46	48-49
Ventral scutes	21	21	31	27	29-31	32-33

including the hypural bones, was 45.3 counted in 21 specimens longer than 16 mm SL. The first bones to stain with alizarin red S were the dentaries, the maxillaries, and the cleithra which occurred in 9 mm specimens.

Only vertebrae and ventral scute counts were useful in separating gulf menhaden and Atlantic menhaden; other meristics overlapped (Table 6). Yellowfin menhaden larvae could not be separated from the two large-scaled menhaden by meristics, with the possible exception of Atlantic menhaden that had 47-48 vertebrae and yellowfin menhaden that had 45-47 (including the hypural bones) (Dahlberg 1970).

Pigmentation

Pigmentation of gulf menhaden larvae (Figs. 1, 3, 5, 6) was similar, but not identical, to the pigmentation described for yellowfin menhaden (Houde and Swanson 1975) and Atlantic menhaden (Jones et al. 1978). Gulf menhaden up to 8 mm had 1 melanophore on the dorsal side of the notochord tip and 1 or 2 melanophores on the ventral side of the notochord tip, which is diagnostic for the genus *Brevoortia* (Figs. 1C, D, 5A). Lateral pigmentation, although found on the trunk of specimens as small as 4.9 mm, was not found on all small specimens. At 10 mm, all specimens had 5-20 melanophores scattered the length of the trunk. Larvae 4-5 mm had 10-20 tiny melanophores on top of the head. One 7.8 mm larva had a single stellate melanophore on top of the head behind the eyes. One single medial melanophore, which enlarged into additional melanophores as larvae grew, was present along the isthmus (ventral midline forward of the cleithrum) on 6 mm and larger larvae. On 8-20 mm larvae, 1 or more melanophores occurred along the

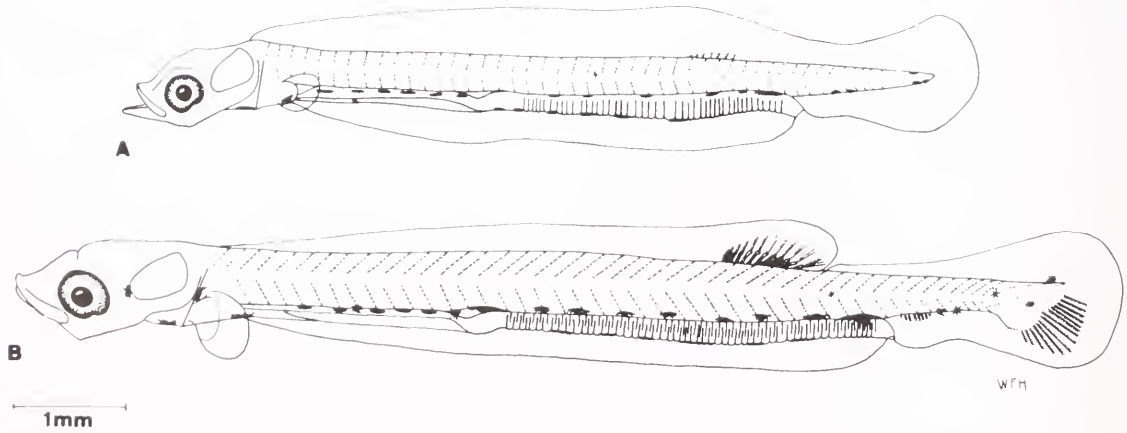

FIGURE 5.—Larval *Brevoortia patronus*: (A) 7.2 mm (12 d after hatching). (B) 9.2 mm (20 d after hatching).

FIGURE 6.—Juvenile *Brevoortia patronus* 33.8 mm (90 d after hatching).

cleithrum axis on each side. Along the surface, lateral and parallel with the dorsal surface of the foregut, there were usually 6-10, but sometimes up to 20, rectangular melanophores on each side. These paired melanophores were positioned anteriad to 2 or 3 stellate melanophores covering the dorsal surface of the gas bladder. A series of 10-18 medial, unpaired melanophores occurred between the trunk musculature and the dorsal surface of the gut. This series merged into 1-3 stellate melanophores projecting ventrally over the end of the gut towards the anus. A medial string of nearly continuous, thin melanophores traced the junction of the finfold along the ventral surface of the hindgut. Dorsal to the base of the anal fin 2 or more melanophores were always present in larvae >5 mm. The caudal fin was pigmented by 10 mm, whereas the medial fins, lower jaw tip, snout, and nape acquired pigment by 18 mm (Fig. 3C). Pigment was absent on the surface lateral to the ventral portion of the foregut between the distal end of the pectoral fin rays and the pelvic fin. Melanophores were present on specimens >17 mm along the base of the dorsal fin and along the dorsal midline between the dorsal and caudal fins. Paired melanophores were absent between the head and dorsal fin. For pigment descriptions of gulf menhaden larvae and juveniles >19 mm, see Suttkus (1956).

Other Structures

By 4.5 mm, the dentaries, maxillaries, branchial arches, cleithra, and hypurals were stained with alcian blue, but the first bones to accept alizarin red S stain, and thus indicate ossification, were the cleithra in 8.5 mm specimens. Flexion of the notochord upward to initiate caudal fin development began at 7 mm. Ossification of the hypural bones began at 10 mm and was completed at 15 mm. Eight maxillary teeth and three dentary teeth on each side were observed on 10 mm larvae. Fourteen teeth on each maxillary and three teeth on each dentary were still visible on 25 mm juveniles. In the oral cavity of 16-24 mm larvae, one or two teeth projected downward from each endopterygoid bone and one or two teeth projected upward from the second basibranchial cartilage. These teeth were absent in fully transformed juveniles. Scales were first visible along the dorsolateral margin of the caudal peduncle and along the midline on each side of the trunk at the beginning of transformation, which occurred at 19 mm.

COMPARISON AMONG *BREVOORTIA* AND WITH OTHER CLUPEIDS

Of the *Brevoortia* species, eggs and larvae of gulf menhaden were the most difficult to distinguish from yellowfin menhaden. Gulf menhaden had 44-46 myomeres, whereas yellowfin menhaden had 45-47 (Houde and Swanson 1975). Morphometrics may be useful to distinguish 10-25 mm specimens of gulf menhaden from yellowfin menhaden. At equal lengths, gulf menhaden had less body depth, a shorter head length, a longer prepelvic distance, a longer predorsal distance, a shorter snout, and a smaller eye. Yellowfin menhaden >17 mm had paired melanophores between the head and the dorsal fin (Houde and Swanson 1975), whereas gulf menhaden did not. Wild specimens of yellowfin menhaden from southern Florida also had a double row of melanophores along the ventral midline between the pectoral and pelvic fins, but neither laboratory-

reared gulf menhaden or wild specimens of gulf menhaden collected from four locations along the northern Gulf of Mexico had ventral midline pigment. Gulf menhaden had more dorsal fin rays, but both species had an equal number of anal rays. Fertilized eggs of the two species had the same diameter, but gulf menhaden had a larger oil droplet (0.20 vs. 0.15 mm) than yellowfin menhaden. No description of finescale menhaden larvae exists, but presumably they have 42-43 myomeres, based on the number of vertebrae reported for this species (Dahlberg 1970). Although gulf menhaden larvae are geographically separated from Atlantic menhaden larvae, they can be separated by counting myomeres or vertabrae; gulf menhaden, 44-46; and Atlantic menhaden, 47-48. Atlantic menhaden and yellowfin menhaden had nearly equal dorsal and anal fin ray numbers, but Atlantic menhaden had one to four more myomeres and lacked dorsal and ventral midline paired melanophores anterior to the dorsal and pelvic fins. Mophometric differences between Atlantic menhaden and yellowfin menhaden are similar to differences between gulf menhaden and yellowfin menhaden.

There are some differences in egg and larval meristics and morphology data between my study and the literature, which may be due to differences between laboratory-reared and wild specimens. Houde and Fore (1973) reported that gulf menhaden had 45-48 myomeres (vs. 44-46 that I found for gulf menhaden), 20-23 anal rays (vs. 19-21), 17-21 dorsal rays (vs. 20-22), and reported that pelvic fins in northern gulf specimens were not developed until 20 mm (vs. 18 mm). They also reported that gulf menhaden eggs had a diameter of 1.04-1.30 mm (vs. 1.18-1.34 mm), an oil droplet of 0.08-0.20 mm (vs. 0.16-0.22 mm), and a wide perivitelline space of about 33% (vs. 24-28%). Jones et al (1978) reported that Atlantic menhaden egg diameter was 1.30-1.95 mm (vs. 1.54-1.64 mm that I found for Atlantic menhaden), that yolk diameter was 0.90-1.20 (vs. 0.82-.095 mm), and that the oil droplet diameter was 0.11-0.17 (vs. 0.20-0.23). For Atlantic menhaden larvae of unspecified lengths they reported 16-18 dorsal rays (vs. 20-22), 18-20 anal rays (vs. 19-21), and a body depth:standard length ratio of about 0.05 at 23 mm total length (vs. about 0.20 I found at the same length); however, the body depth ratio is undoubtedly a typographical error.

Laboratory-reared gulf menhaden and Atlantic menhaden both appeared to transform into juveniles at a smaller size than wild fish. Morphometric data and photographs of specimens of gulf menhaden from Louisiana indicated that the juvenile form was not reached until about 30 mm SL (Suttkus 1956). Lewis et al. (1972) indicated that Atlantic menhaden from North Carolina did not complete "prejuvenile" growth until about 33 mm SL. Houde and Swanson (1975) suggested that tank-reared yellowfin menhaden transformed at smaller sizes than did wild fish, and I concur.

Characters useful for separating eggs and larvae of *Brevoortia* from other clupeids have been identified (Houde and Fore 1973; Richards et al. 1974; Houde and Swanson 1975; Powles 1977). *Sardinella* and *Opisthonema* have about the same total myomere counts as *Brevoortia*, but usually have 6-9 post-dorsal-preanal myomeres. *Etrumeus* has the same or more total myomeres than *Brevoortia*, but about 10 fewer anal rays. The smaller larvae of *Sardinella*, *Opisthonema*, and *Etrumeus* have no pigment on the dorsal side of the notochord tip, whereas *Brevoortia*, *Harengula*, and *Jenkinsia* have this pigment. However, *Jenkinsia* and *Harengula* have 42 or fewer myomeres. The spawning seasons of all these genera overlap with the spawning season of *Brevoortia* species (Houde and Fore 1973; Powles 1977; Jones et al. 1978). Larvae of *Dorosoma* and *Alosa* are not normally found in marine waters with *Brevoortia*.

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DISTRIBUTION OF ICHTHYOPLANKTON OFF SAN ONOFRE, CALIFORNIA, AND METHODS FOR SAMPLING VERY SHALLOW COASTAL WATERS

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AND WILLIAM WATSON[1]

ABSTRACT

Spatial abundance patterns of inshore marine fish larvae, together with day-night and ontogenetic changes in these patterns, were investigated at a single site off the southern California coast using neustonic, midwater, and epibenthic samplers. Fifteen of the nineteen most abundant taxa showed statistically significant abundance patterns: Five taxa were principally in the inshore (<2 km from shore) epibenthos, one in the inshore neuston, two in the neuston and midwater less than about 5 km from shore, three to midwater 2-5 km from shore, and four in midwater offshore of about 3.5 km. Abundance patterns for the three most common taxa, *Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*, shifted toward shore and toward the bottom with increasing larval size. Comparison of *E. mordax* egg and larval abundances indicated a large excess of larvae over eggs nearshore. Only two taxa showed statistically significant day-night pattern changes; both were lower in the water column during the day.

The existence of inshore abundance maxima implies significant survival value in occupying the nearshore zone. The shallow waters of the southern California coast may represent a nursery area comparable in importance to the estuarine nurseries of the Atlantic coast of North America.

Through the pioneering California Cooperative Oceanic Fish Investigation (CalCOFI) work of the late E. H. Ahlstrom and co-workers (Ahlstrom 1959, 1965), ichthyoplankton of the Southern California Bight are generally well known. However, the CalCOFI effort was concentrated on species found principally offshore of the 100 m isobath, and the larvae of most inshore fishes are rare or missing in the published CalCOFI data. Recent studies of ichthyoplankton in the Southern California Bight inshore of the 100 m isobath (Brewer et al. 1981; Gruber et al. 1982; Brewer and Smith 1982) have indicated that many of these larvae are found in the relatively shallow waters.

In this paper we present methods for sampling quantitatively the entire water column in shallow waters (6-75 m) and describe the spatial abundance patterns of the most commonly occurring larval fishes. Of particular interest was the distribution of larvae in the onshore-offshore vertical plane. Ontogenetic pattern changes were investigated for three abundant species: *Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*.

The study was done off San Onofre, Calif., (Fig. 1) from September 1977 to September 1979. Unit 1 of the San Onofre Nuclear Generating Station, a 500-megawatt plant located 1.5 km northwest of the sampling area, was operating continuously throughout the course of the study. However, this plant has been shown to have only very localized effects which have not interfered measurably with the results reported herein (Marine Review Committee 1979[3]; Bartlet et al. 1981[4]). This study was completed prior to the beginning of operation of Units 2 and 3 of the San Onofre Nuclear Generating Station.

Our sampling methodology resulted from a preliminary study in which we found that a combination of sampling gear was necessary to estimate nearshore larval abundance. The chief purpose of this paper is to present these sampling methods. Results are shown which verify the effectiveness of these methods and further suggest some peculiarities of the nearshore habitat.

[1]Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Suite 110, Encinitas, CA 92024.
[2]Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Suite 110, Encinitas, Calif.; present address: Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, CA 90007.

[3]Marine Review Committee. 1979. Interim report of the Marine Review Committee to the California Coastal Commission. Part 1: General summary of findings, predictions, and recommendations concerning the cooling system of the San Onofre Nuclear Generating Station. *In* Marine Review Committee Document 79-02, p. 1-20. Marine Review Committee of the California Coastal Commission, 631 Howard Street, San Francisco, CA 94105.

[4]Barnett, A. M., P. D. Sertic, and S. D. Watts. 1981. Final report: Ichthyoplankton preoperational monitoring program. Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Encinitas, CA 92024, 8 p.

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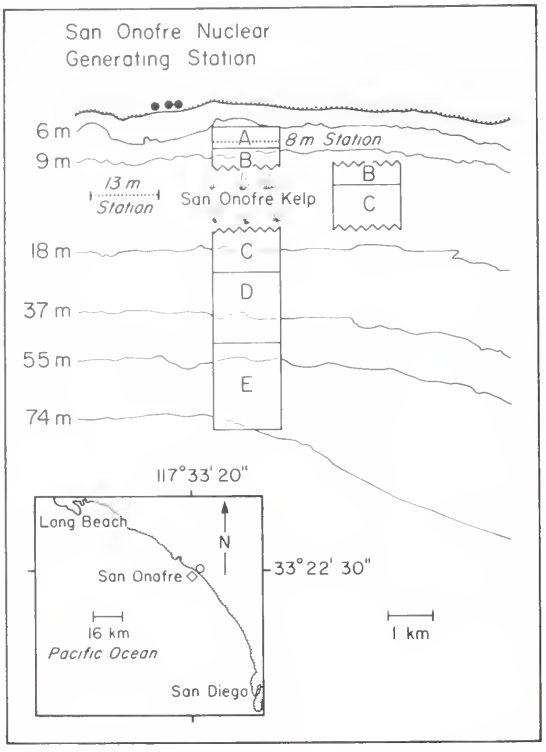

FIGURE 1.—Chart of the sampling area and its position off the southern California coast. The one- and two-dimensional pattern analyses were based on samples taken at a randomly selected isobath in each of the five sampling blocks (A-E) on each sampling date. The study of daily vertical migration was based on samples taken along the 8 and 13 m isobaths (dotted lines).

METHODS

Preliminary Study

In shallow depths, interfaces at the sea surface and seabed comprise a substantial portion of the water column. In addition, concentration of a species at either interface would necessitate sampling the epibenthic and neustonic layers as well as the midwater column to obtain quantitative abundance estimates.

Neustonic, midwater, and epibenthic samplers were used in a preliminary study[5] between September and November 1977, to verify their effectiveness and to select mesh size, net design, standard sample size, and sampling time for the ensuing full-scale program. The results of this brief study indicated that

1. Filtration efficiency was at least 85% for all nets and lengths of tow.
2. Samples of 400 m^3 were adequate to attain asymptotes of numbers of taxa per tow. A sampled volume of 400m^3 from the epibenthos was the maximum that could be handled economically.
3. The 12 most abundant larval fish taxa were neither randomly nor evenly distributed with respect to the three vertical strata. Half the taxa were principally epibenthic, while 25% were neustonic and 25% were most abundant in midwater.
4. Only one of these taxa showed a daily vertical migration; *Paraclinus integripinnis*, not a top-ranking species in the ensuing study, tended to descend from midwater to the epibenthic layer at night.
5. Size of individuals and apparent abundance of most taxa increased at night, probably because of visual avoidance during the day.
6. Nitex netting of 0.333 mm mesh retained more fish eggs and smaller anchovy larvae than did 0.505 mm mesh.

From the preliminary results, it was clear that the bongo net alone would undersample significant fractions of many larval populations. Since our goal was to estimate the density and distribution of nearshore ichthyoplankton, we decided to use all three types of gear with 0.333 mm mesh and to filter a target volume of 400 m^3.

Sampling Gear

A bongo net was selected for sampling the midwaters, as recommended by Smith and Richardson (1977). An opening-closing 71 cm Brown-McGowan bongo net (total mouth area = 0.79 m^2) was used. A General Oceanics[6] (GO) flowmeter was mounted in the starboard frame. The bongo net, as conventionally used, is placed on the wire some distance above a weight and towed astern. The geometry of this arrangement and the circular net mouths make the gear ill-suited for sampling the plankton in the neustonic and epibenthic strata near the sea surface and seabed, respectively. Therefore, specially designed samplers, described below, were used to sample these layers.

We chose the brown manta net (Brown and Cheng

[5]Barnett, A. M., J. M. Leis, and P. D. Sertic. 1978. Report to the Marine Review Committee on the preliminary ichthyoplankton studies. Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Encinitas, CA 92024.

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

1981) as our neustonic sampler. This net had an 88 cm wide mouth and fished to a depth of 16 cm. Fiberglass-covered styrofoam floats kept the top of the net out of water, and a 3 m spar and asymmetrical bridle kept the gear outboard of the bow wave. A weight suspended from the end of the wire held the bridle well below the surface, out of the path of the net. The sampler was launched and recovered off the quarter by means of a tag line. Both a Tsurumi-Seiki (TSK) flowmeter and a GO flowmeter were mounted in the mouth of the net. The GO meter served as a back-up for the TSK, which sometimes fouled with kelp and eelgrass.

The Auriga net,[7] used to sample the epibenthic layer, consisted of a rectangular net frame (0.5 m high $\times$ 2 m wide) attached to a chassis equipped with a pair of side-mounted, 2 m diameter wheels. The device rolled on the bottom so that the mouth of the net was 10 cm (original design) or 17 cm (later versions) above the bottom of the wheels. A series of 12 cm diameter plastic rollers below the mouth of the net helped prevent the sampler from digging into the bottom and presumably minimized escapement below the net. Both GO and TSK flowmeters were mounted within the mouth of the Auriga net. The Auriga net was towed off the stern. Divers have observed (M. Sowby[8]) that the mouth of the Auriga assumes a horizontal attitude when the wheels are off the bottom. We therefore believe that contamination of the epibenthic samples by midwater plankton was minimal during launch and recovery, when the main component of (relative) water movement was across, rather than through, the mouth. Any contamination that did occur should have been a function of depth, which was always $<20\%$ of the length of an epibenthic tow (this potential source of error has been ignored in the density calculations).

Although serious clogging was not apparent in the preliminary study, denser plankton concentrations at other times of the year might clog the nets before 400 m^3 of water could be filtered. Clogging would be most serious for oblique bongo tows, because it would result in undersampling of the upper part of the water column. In anticipation of this possibility, the area of mesh in all nets was increased according to the criteria suggested by Smith et al. (1968, equation 5) in order to sample 500 m^3 (bongo), 400 m^3 (Auriga), and 200 m^3 (Manta) for "green" coastal waters. The filtering ratios (R = mesh pore area/net mouth area) of bongo, Auriga, and Manta nets were increased to 7.8, 6.6, and 10.7, respectively, by adding mesh cylinders ahead of the conical portions of the nets. External flowmeters were not used in the subsequent surveys, but tows were carefully timed. Internal flowmeter readings were checked upon recovery, and samples were repeated if the readings differed by more than 20% from expected values.

Except for the limited study of daily vertical migration, all sampling was done at night. The deck lights were always off during the neuston tows. All samplers were launched, towed, and recovered with the vessel underway at about 1 m/s. For bongo tows, wire was paid out (scope about 2:1) until the weight, located 1.5 below the center of the net frame, bumped the bottom. Then the nets were opened, and a stepped oblique tow was made consisting of 18 30-s steps. The Auriga sampler was towed with a scope of 3:1 and recovered after 6.5 min on the bottom. With the small-mouthed Manta net, the volume of 400 m^3 was achieved by towing two nets simultaneously, off port and starboard, for 20 min (about 1.4 km).

Samples were preserved in 5-10% seawater-Formalin.

Sampling Locations and Frequency

Since we eventually wanted to assess the effects of a power plant cooling system, it was necessary to concentrate much of our sampling effort within the depth contours encompassing the cooling structures. At the same time, in order to estimate the abundance of nearshore species, we needed to sample far enough from shore to delimit their centers of abundance. We decided upon a stratified random sampling design (Snedecor and Cochran 1967) wherein, on each sampling date, the neustonic, midwater, and epibenthic layers were sampled along a randomly chosen depth contour in each of five blocks (Figs. 1, 2). The five blocks were defined by depth contours: A) 6-9 m, corresponding to cooling water intake locations; B) 9-12 m and C) 12-22 m, both corresponding to future diffuser discharge locations; D) 22-45 m, corresponding to a faunal break between inshore and coastal zooplankton assemblages (Barnett and Sertic[9]); and E) 45-75 m, chosen a priori as the likely offshore limit of most nearshore larval fishes.

The sampling transect thus consisted of 15 strata: Three depth layers in each of five blocks (Fig. 2). To

[7]Marine Biological Consultants, Inc., 947 Newhall Street, Costa Mesa, CA 92627.

[8]M. L. Sowby, Marine Biological Consultants, Inc., 947 Newhall Street, Costa Mesa, CA 92627, pers. commun. 1979.

[9]Barnett, A. M., and P. D. Sertic. 1979. Spatial and temporal patterns of temperature, nutrients, seston, chlorophyll-a and plankton off San Onofre from August 1976 - September 1978, and the relationships of these patterns to the SONGS cooling system. *In* Marine Review Committee Document 79-01, p. vii through 9-89. Marine Review Committee of the California Coastal Commission, 631 Howard Street, San Francisco, CA 94105.

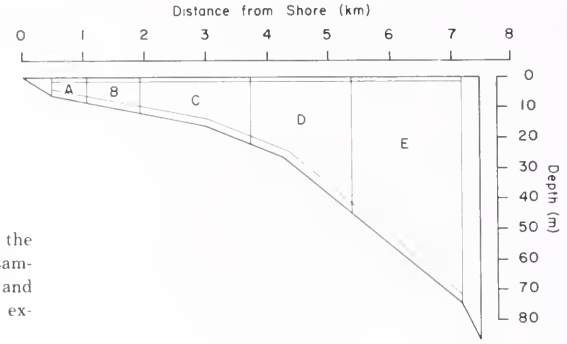

FIGURE 2.—Diagrammatic profile of the study transect showing the 15 strata sampled off San Onofre, Calif. Neustonic and epibenthic layers are vertically exaggerated.

avoid the San Onofre kelp bed, some of the tows in the B and C blocks were offset by about 1 km. Wilcoxon signed rank tests of samples taken from B block and B offset (Fig. 1) showed no significant differences in species abundances ($P > 0.05$) between the main block and the offset which could not be related to the inshore-offshore patterns discussed below.

The transect was sampled monthly in January and February 1978, fortnightly from March through August 1978, and again monthly through September 1979. During each of these 28 sampling periods, the five blocks were surveyed once each night for 1-3 nights, giving a total of 57 sampling dates for the 21-mo study.

As noted above, we chose a standard sampled volume of 400 m^3 based on the preliminary study. This volume was large enough to assure a representation of all abundant species throughout the year. Volume was used as the sampling unit, although an argument based on the scale of patchiness could be made for length of tow (i.e., 400 m in each water layer) as the criterion, rather than volume filtered (P. Smith[10]). Most tows were at least 400 m long.

Laboratory Procedures

Samples were sorted for fish eggs and larvae under dissecting microscopes at 10× magnification. The choice of 400 m^3 as the sampled volume was made at a time of year when ichthyoplankton abundance was low (Walker et al.[11]); consequently the samples from other times of year were larger than necessary to represent the nearshore assemblage. Samples with large plankton volumes were subsampled, using a Folsom plankton splitter before sorting. The size of the subsample was set to include at least 100 non-engraulid larvae (the mean number of larvae counted per subsample was 277, of which 62.8% was *E. mordax*). This fraction was usually one-fourth and was seldom smaller than one-eighth. Eggs were sorted from 1%, 5%, or 10% (to get at least 100 eggs) of the residue of the fraction sorted for larvae. Sorting efficiency was maintained above 90%.

Some epibenthic samples contained so much sand and detritus that it was necessary to clean them before sorting, using a flotation technique adapted from Ladell (1936). After removal of large fish and debris, such a sample was mixed with a 40% $MgSO_4$ solution (specific gravity = 1.2) in a large separator fashioned from a 19 l (5-gal) plastic carboy with the bottom cut off and the neck fitted with a rubber hose and ball valve. Most detritus sank, while plankton floated to the top. The heavy material was drained off and processed once or twice more to ensure separation of the plankton. Checks of the heavy residue of three such samples showed that more than 99% of the larvae were separated by flotation.

All larvae were identified to the lowest taxonomic category currently possible. Eggs were identified as *Engraulis mordax* or "other". In some larval categories (e.g., Atherinidae, Goby Type A), our ability to discriminate among species or larval types (sensu Richardson and Pearcy 1977) improved as the study progressed. However, not all of the old collections were reprocessed. When mixed taxa showed seasonal and spatial coherence, they were retained for the analyses presented here.

Pattern Analysis

All counts of eggs and larvae were standardized to number/400m^3. Thus the standardized numbers

[10]P. E. Smith, La Jolla Laboratory, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, pers. commun. 1979.

[11]Walker, H. J., A. M. Barnett, and P. D. Sertic. 1980. Seasonal patterns and abundance of larval fishes in the nearshore Southern California Bight off San Onofre, California. Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Encinitas, CA 92024.

were roughly the same as the actual numbers of eggs and larvae caught, a desirable situation for analysis with transformed data (Murphy and Clutter 1972). These values were transformed by $\log (X + 1)$ before analysis for offshore and vertical pattern. The results were back-transformed, resulting in geometric means with asymmetric confidence bounds, and presented as number/100m^3.

To describe the cross-shelf abundance patterns of ichthyoplankton, a procedure was adopted involving Hotelling's T^2 test and a series of *a posteriori* t-tests (Morrison 1976) to divide the 15 strata into groups. These parametric methods allowed us to detect significant differences in mean abundance among components of a pattern and to determine confidence bounds on the means.

Hotelling's T^2 test was selected over an analysis of variance (ANOVA) because the covariance structures in the data tended not to meet the assumptions of standard ANOVA models (i.e., errors were not independent; the abundances of neighbor strata were likely to be correlated). The T^2-test allows this correlation by using the sample covariance matrix, rather than (as in ANOVA) assuming a specified covariance pattern (Winer 1971; Morrison 1976).

With a significant T^2 test result obtained ($P \leq 0.05$), *a posteriori* multiple t-tests were used to separate strata into groups having significantly different abundances. The strata were contrasted in a series of t-tests using the Bonferroni statistic, $t(0.05)_{k,s}$ *where* k = potential number of contrasts, s = number of sampling periods − 1, and 0.05 = overall type I (α) error. The value of k was set as the number of all possible contrasts among m strata plus 5, for further tests employing combinations of the initial strata: i.e., $k = \frac{(m)(m-1)}{2} + 5$. Bonferroni t-values were taken from Myers (1972, table A-12).

After the initial series of t-tests of all possible comparisons, strata found not to differ significantly were pooled into initial groups. The time-averaged abundance of each stratum was used to calculate the initial groups' mean abundance

$$Z_j = \sum_{i=1}^{n} Z_i/n$$

where Z_j is the initial group mean, n is the number of strata in the initial group, and Z_j are the means of individual strata. Further t-tests (the total of all tests $\leq k$) were made to contrast the resulting initial groups. If more than one final grouping was possible, the final set of groups selected was that which maximized the t-statistic.

Both the Hotelling T^2 and the t-test assume normally distributed data. Excessive zero values in a data set violate this assumption in a way that cannot be corrected by transformations. The methods used here were robust with respect to zero values in zooplankton data (Barnett et al.[12]); nevertheless, some sampling dates for 12 of the 19 ichthyoplankton taxa analyzed were deleted in one of two ways in order to reduce the number of zero observations. The preferred method, useful for eight seasonally abundant taxa, was to eliminate from analysis all consecutive samples taken when the annual abundance cycle was lowest. In these cases, the number of survey dates was ≤ 57 (Fig. 3), and means and confidence bounds presented (Table 1) apply to the "season of abundance". The second method, used for four sporadically abundant taxa, was to include only those

[12]Barnett, A. M., A. E. Jahn, and P. D. Sertic. 1980. Long term average spatial patterns of zooplankton off San Onofre and their relationship to the SONGS cooling system, MEC01380994. Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Encinitas, CA 92024.

TABLE 1.—Geometric mean abundance (no./100m^3) with 96% confidence bounds (C.B.) for the 15 larval fish taxa showing statistically significant cross-shelf patterns off San Onofre, Calif. Groups of strata which differ significantly in mean abundance are ranked from highest to lowest. Refer to Figure 3 for locations of these groups.

Mean abundance:	Highest											Lowest
Strata groups:	1			2			3			4		
95% C.B.:	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper
Gibbonsia sp. A	0.15	0.35	0.66	0.00	0.01	0.03						
Seriphus politus	5.47	22.71	91.93	1.15	2.67	5.85	0.19	0.67	1.66	0.07	0.24	0.50
Gobiesox rhesodon	0.81	2.07	4.84	0.13	0.32	0.60	0.00	0.02	0.05			
Goby Type A	1.09	2.70	6.28	0.35	0.88	1.88	0.09	0.28	0.56	0.01	0.04	0.07
Genyonemus lineatus	8.36	37.21	162.71	0.84	2.65	7.46	0.17	0.68	1.78	0.04	0.23	0.57
Atherinidae	9.71	23.11	54.54	1.37	4.17	11.83	0.27	0.66	1.32	0.00	0.05	0.11
Hypsopsetta guttulata	0.06	0.27	0.63	0.01	0.03	0.08						
Hypsoblennius spp.	0.44	1.03	2.13	0.03	0.09	0.17						
Engraulis mordax	44.03	88.49	177.60	21.78	47.81	104.56	8.41	19.58	45.19	1.67	3.93	8.86
Paralichthys californicus	0.66	1.81	4.40	0.15	0.38	0.75	0.04	0.12	0.23			
Pleuronichthys verticalis	0.04	0.13	0.24	0.00	0.02	0.05						
Citharichthys spp.	0.06	0.20	0.40	0.00	0.03	0.07						
Sebastes spp.	0.42	1.28	3.22	0.07	0.30	0.69	0.00	0.03	0.07			
Stenobrachius leucopsarus	0.24	0.83	2.14	0.01	0.05	0.11						

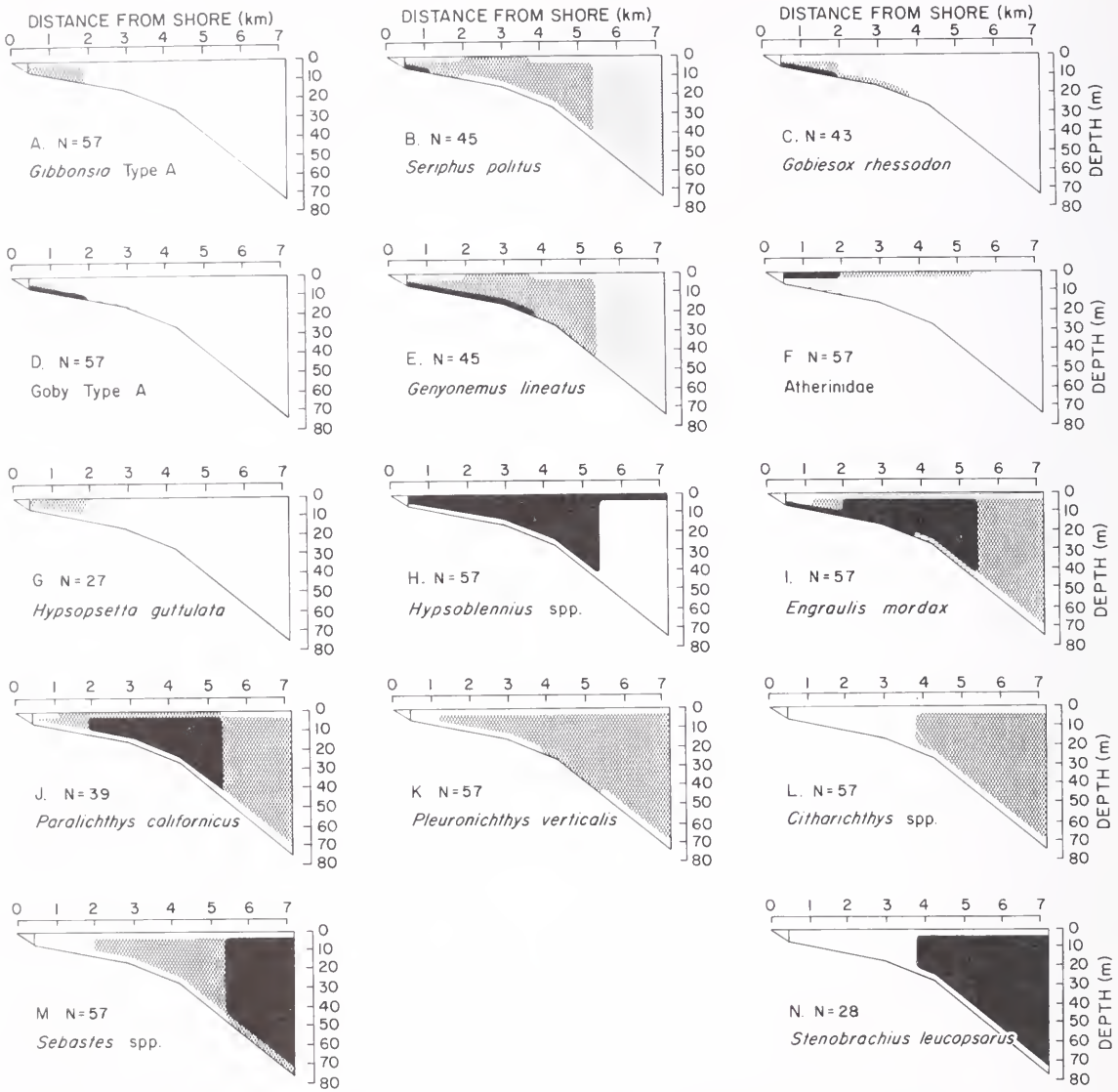

FIGURE 3.—Cross-shelf abundance patterns for the 14 most common larval fish taxa off San Onofre, Calif. Shading indicates relative abundance in groups of strata differing significantly in mean abundance. Heavier shading indicates higher abundance; the darkest shading (black) is used for centers of abundance with larval densities >3 individuals/400 m^3 (0.75/100 m^3). N = Numbers of surveys used in analysis. Geometric mean abundances with 95% confidence bounds for each of these groups are given in Table 1.

dates when a taxon was present. The latter method was used only to obtain cross-shelf patterns; in these cases, mean abundances in the various parts of the pattern are relative numbers, and confidence bounds were not calculated (Table 1).

All testing was done on the basis of abundance alone, without regard to the strata being grouped. Final groupings of strata are shown in diagrams of the cross-shelf transect (Fig. 3). Occasionally, non-abutting strata were members of the same statistical group. These are depicted as being physically connected when such an interpretation is reasonable. In all cases, shading is used to indicate groups of strata which differ significantly.

RESULTS

Cross-Shelf Patterns

The 19 larval taxa analyzed were those which rank-

ed among the 10 most abundant in any of the 5 sampling blocks. Fourteen taxa showed significant differences among the strata which were resolved into spatial patterns (Table 1, Fig. 3). Taxa with centers of abundance nearest shore tended to be concentrated in either the epibenthic or the neustonic layer. Of the five epibenthic taxa, four (*Gibbonsia* Type A, *Scriphus politus*, *Gobiesox rhessodon*, and Goby Type A [consisting of *Ilypus gilberti* and *Quietula y-cauda*]; Fig. 3A-D) had centers of abundance within 2 km of shore. The fifth, *Genyonemus lineatus*, was most abundant out to about 4 km (Fig. 3E). Atherinidae (Fig. 3F) were neustonic and most abundant within 2 km of shore. *Hypsopsetta guttulata* (Fig. 3G) was abundant in the neustonic and midwater layers out to 2 km. It had the most nearshore pattern of any midwater taxon. *Hypsoblennius* spp. were concentrated in the neustonic and midwater layers out to about 5 km and in the neustonic layer beyond 5 km from shore (Fig. 3H).

The remaining six taxa with discernible patterns were all most concentrated in midwater. The centers of abundance of *Engraulis mordax* and *Paralichthys californicus* (Fig. 3I, J) extended from 2 to ~5 km from shore, while those of *Pleuronichthys verticalis*, *Citharichthys* spp., *Sebastes* spp., and *Stenobrachius leucopsarus* appeared to extend seaward of the sampling area (Fig. 3K-N).

Five taxa (*Chromis punctipinnis*, *Paralabrax* spp., *Parophrys vetulus*, *Peprilus simillimus*, and *Pleuronichthys ritteri*) were not shown to have patterns by this analysis.

Vertical Migration

Because the basic study plan called for nighttime sampling, the patterns described would pertain to nighttime distributions. The preliminary study found little evidence of daily vertical migration; nevertheless, we conducted a further small study of vertical migration to test whether the vertical component of the patterns remained the same during daylight hours. The study was conducted at two inshore locations (Fig. 1). A description of the vertical study is given in the Appendix.

There was no indication of vertical migration at the 8 m station, but at the 13 m station two taxa, *Hypsoblennius* spp. and *Paralichthys californicus*, showed significant ($P < 0.05$) vertical shifts downward in the water column during the day (Fig. 4). The low probability (0.055) of the F value for *Gobiesox rhessodon* (App. Table 2), though higher than the customary rejection level of 0.05, suggests a daily change in vertical distribution. The data indicate this species may, like *Paraclinus integripinnis* in the preliminary study, tend to migrate or settle from midwater into the epibenthic layer at night.

Onshore-Offshore Abundance

The analysis of cross-shelf pattern assumes that larvae are uniformly distributed throughout each mid water stratum, an assumption that becomes increasingly untenable with depth of stratum. Layering of ichthyoplankton within the midwater zone will cause an apparent decrease in density in the seaward blocks, as more of the volume used in the density calculations comes from deeper waters where a species may be rare. To eliminate bias in the cross-shelf patterns due to inclusion of noncontributing depths in the density calculations, one-dimensional abundances were calculated based on the estimated number of larvae under a unit (100 m^2) of sea surface in each offshore block

$$N = \sum_{i=1}^{3} n_i d_i$$

where n = larvae/100 m^3 in stratum i and d = vertical thickness of stratum i in meters (0.16 m, neustonic; 0.50 m, epibenthic; depth of water column −1 m, midwater).

The one-dimensional patterns, which emphasize numbers of larvae (Table 2), provide a useful comparison to the two-dimensional patterns which emphasize larval density (Table 1, Fig. 3). All epibenthic and neustonic taxa had similar onshore-offshore centers of abundance as determined by both methods. This was expected, since their cross-shelf abundance patterns were essentially one-dimensional. *Gibbonsia* Type A, *Seriphus politus*, *Gobiesox rhessodon*, Goby Type A, and Atherinidae, all with abundance centers within 2 km of shore in the two-dimensional analysis (Fig. 3), likewise had one-dimensional maxima shoreward of 2 km. With the exception of *S. politus*, these taxa were less than half as abundant beyond 2 km. *Genyonemus lineatus*, most concentrated in the epibenthic layer within about 4 km of shore, had a one-dimensional maximum at 2-4 km but remained abundant (>½ maximum) out to ~5 km.

Of the eight midwater taxa, only two had one-dimensional patterns which differed from their two-dimensional patterns *Engraulis mordax* appeared more abundant farther offshore in one dimension (cf. Table 2 and Fig. 3I). The steady increase in abundance of *E. mordax* with distance from shore is at odds with its two-dimensional pattern (Fig. 3I) and

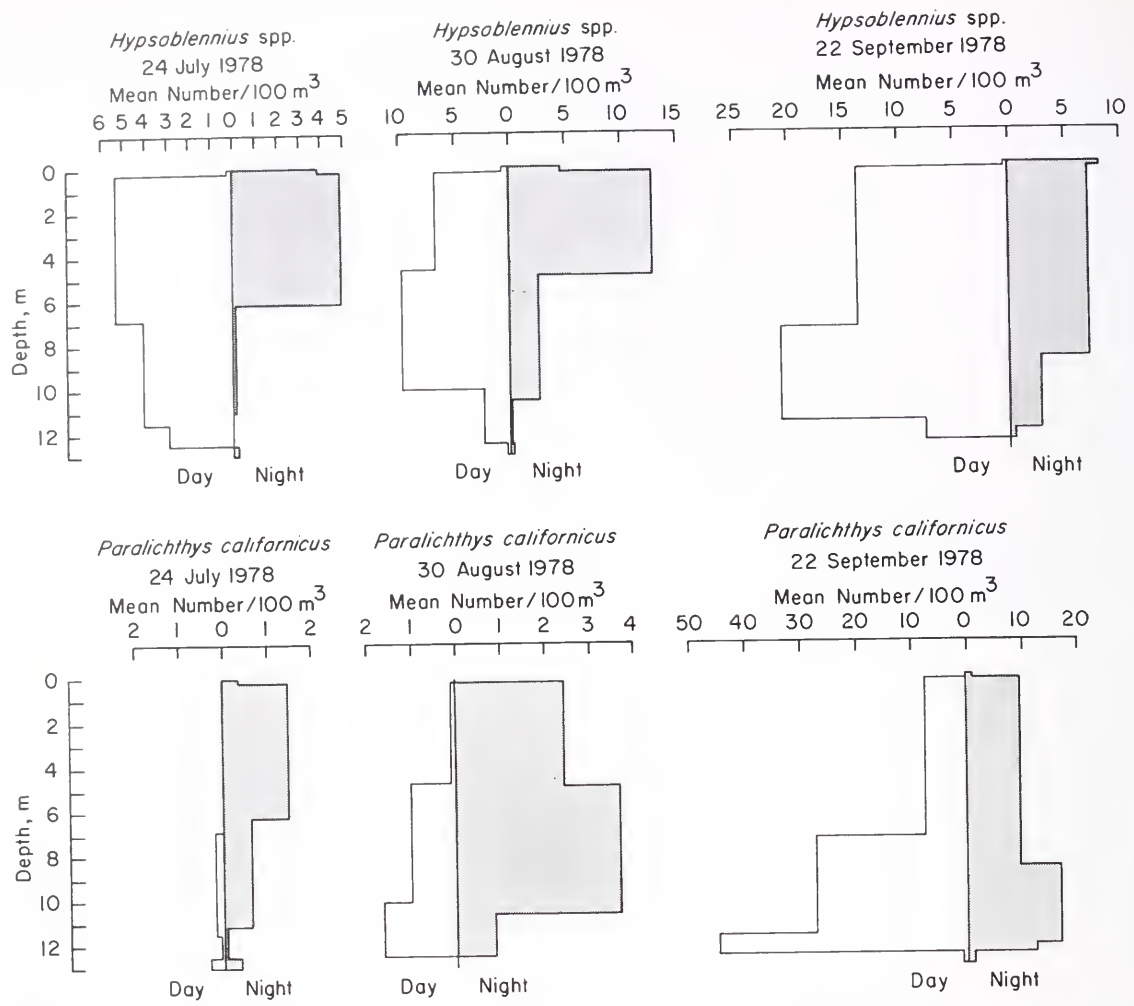

FIGURE 4.—Average vertical abundance profiles of *Hypsoblennius* spp. and *Paralichthys californicus* during the study of daily vertical migration off San Onofre, Calif. The depth ranges of the five sampling strata are the averages (based on four to six profiles) for each sampling period. Note that the horizontal (abundance) scale varies.

TABLE 2.—Numbers of larvae under 100 m² of sea surface in the five sampling blocks, averaged over 57 cruises, off San Onofre, Calif.

Sampling block Offshore limits (km):	A 0.5-1.1	B 1.1-1.9	C 1.9-3.7	D 3.7-5.4	E 5.4-7.2
Gibbonsia Type A	6.4	10.3	1.5	0.3	1.1
Seriphus politus	273.9	103.9	217.9	118.9	93.7
Gobiesox rhessodon	4.6	12.1	5.3	1.1	3.0
Goby Type A	24.5	17.5	3.5	2.9	1.1
Genyonemus lineatus	132.7	312.4	623.3	566.5	221.1
Atherinidae	35.7	28.1	11.7	8.9	4.9
Hypsopsetta guttulata	3.1	3.2	3.9	0.6	0.7
Hypsoblennius spp.	27.5	26.9	48.1	63.0	36.9
Engraulis mordax	970.0	1,833.4	6,454.4	9,250.2	10,263.5
Paralichthys californicus	4.3	11.4	90.0	103.2	42.4
Pleuronichthys verticalis	0.4	2.3	13.4	36.4	11.7
Pleuronichthys ritteri	<0.1	0.2	5.6	30.9	13.9
Citharichthys spp.	2.9	3.5	9.9	17.9	31.0-
Sebastes spp.	<0.1	<0.1	18.2	77.7	518.6
Stenobrachius leucopsarus	0.1	0.4	4.4	29.1	106.1
Chromis punctipinnis	0	0	0.8	6.6	53.3
Paralabrax spp.	0.1	0.8	34.3	97.8	84.1
Parophrys vetulus	0.5	0.3	0.1	7.3	33.6
Peprilus simillimus	2.0	4.1	3.6	10.0	17.4

indicates that this species must be vertically stratified beyond the 45 m contour. This agrees with the findings of Ahlstrom (1959) in which the majority of *E. mordax* larvae occurred above 50 m. In contrast, *Pleuronichthys verticalis* peaked in abundance at 4-5 km rather than extending offshore as in the two-dimensional analysis (cf. Table 2 and Fig. 3K). This result may have occurred because the tests used in the two-dimensional analyses failed to distinguish between offshore blocks due to the small number (27) of non-zero observations for this species.

Four of the five taxa lacking statistically significant two-dimensional patterns (*Chromis punctipinnis*, *Paralabrax* spp., *Parophrys vetulus*, *Peprilus simillimus*) appeared to be most abundant beyond 4-5 km when considered in one dimension (Table 2). The fifth, *Pleuronichthys ritteri*, peaked in abundance at 4-5 km from shore.

Ontogenetic Pattern Changes

Larvae of the three most abundant species were divided into size groups, which were analyzed separately for spatial pattern. To prevent temporal bias in the patterns, only 1978 data were used since they covered a full year. Larvae of two sciaenids, *Genyonemus lineatus* and *Seriphus politus*, were each divided into groups corresponding to developmental stages. Preflexion larvae, with straight notochords and no hypural development, were analyzed separately from more fully developed, and presumably more mobile, flexion and postflexion larvae. Hypural development was found to begin at 3.8 mm for *G. lineatus* and at 4.1 mm for *S. politus*. Similarly, *Engraulis mordax* larvae were divided into early and late developmental stages, but this was done on the basis of size alone and did not correspond to flexion of the notochord. Early preflexion larvae (<6 mm), termed "early stage", were analyzed separately from other larvae, termed "late stage". One hundred larvae or all specimens, whichever was less, were measured for each species in each collection. When only the first 100 larvae were measured, the proportions of the various size classes were applied to the total.

To examine the ratio of older to younger larvae, the total number in each sampling block (Fig. 1) was calculated, using a longshore dimension of 1 m, i.e., number in block,

$$N_b = N \cdot L,$$

where N is number under 100 m^2 of sea surface in the block, and L is the onshore-offshore extent of the block in hundreds of meters.

The patterns of all three species were more nearshore and epibenthic for older larvae (Table 3, Fig. 5). The ratio of older to younger larvae was about 1:2 for all three species (transect totals, Table 4). This ratio increased in the shoreward blocks for *G. lineatus* and *S. politus*, reaching maxima in blocks A and B. The ratio of older to younger *E. mordax* larvae was maximum in blocks C and D. The remarkable aspect of the *E. mordax* data is that there were far too few eggs in the nearshore zone to account for the numbers of larvae. The ratio of total *E. mordax* larvae to eggs was about 28:1. The median size of the larvae was about 6 mm, corresponding to an average age of roughly 10 d (Methot and Kramer 1979). Zweifel and Lasker (1976) found a time to hatching of 2.5 d (at about 16°C). The ratio of 10-d-old larvae to eggs thus has an upper limit of the order 4:1 in the absence of mortality, implying at least a sevenfold excess of larvae in these nearshore samples. The minimum diameter of *E. mordax* eggs during the months of maximum egg abundance is about twice the mesh opening of the plankton nets used, so that sampling deficiencies for these immobile objects should be negligible.

TABLE 3.—Geometric mean abundance (no.100m^3) with 95% confidence bounds (C.B.) for younger and older age groups of larvae of *Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*, showing statistically significant cross-shelf patterns off San Onofre, Calif. Groups of strata which differ significantly in mean abundance are ranked from highest to lowest. Refer to Figure 5 for locations of these groups.

Mean abundance:	Highest											Lowest
Strata groups:	1			2			3			4		
95% C.B.:	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper
Engraulis mordax												
early stage larvae	2.33	13.21	70.06	0.52	3.31	16.24	0.22	1.10	3.63			
late stage larvae	23.43	62.42	165.65	5.53	14.34	36.60	0.92	2.99	8.72			
Genyonemus lineatus												
Preflexion stage larvae	1.55	7.42	32.40	0.73	3.15	11.52	0.33	1.11	2.93	0.04	0.26	0.64
flexion and postflexion stage larvae	7.46	30.88	125.51	0.53	1.56	3.97	0.10	0.62	1.90	0.02	0.08	0.14
Seriphus politus												
preflexion stage larvae	0.58	1.37	2.90	0.15	0.49	1.12	0.04	0.16	0.33			
flexion and postflexion stage larvae	4.31	20.64	95.57	0.50	1.90	5.86	0	0.10	0.22			

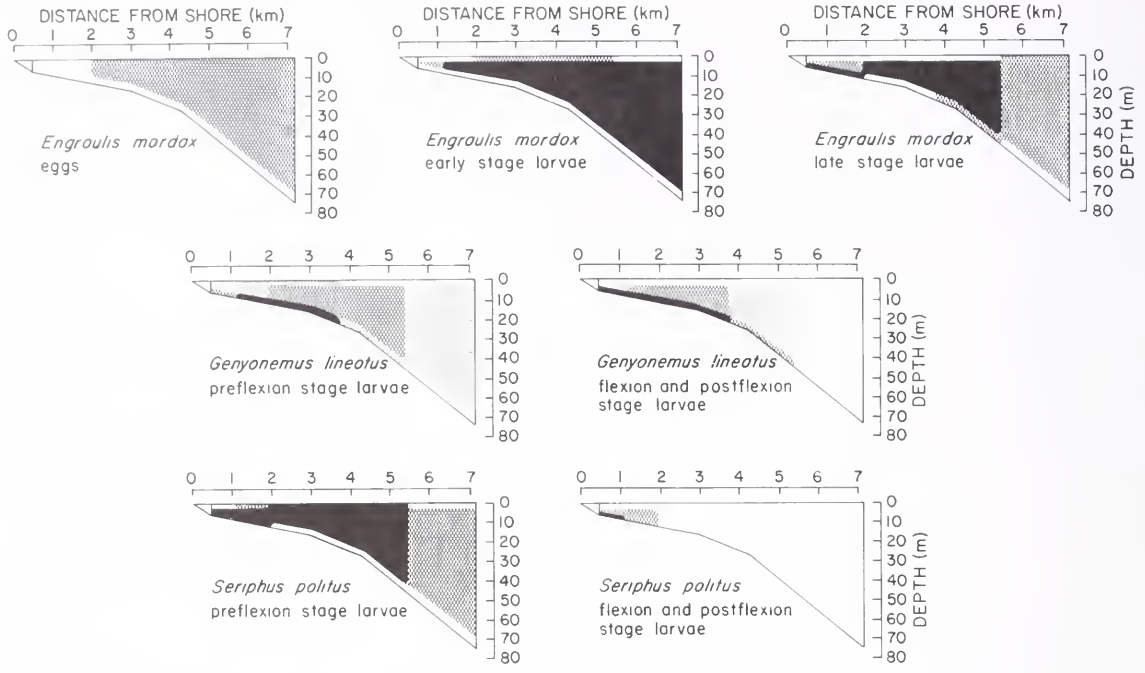

FIGURE 5.—Changes with development stage in the cross-shelf abundance patterns of *Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus* off San Onofre, Calif. Shading indicates relative abundance in groups of strata differing significantly in mean abundance. Heavier shading indicates higher abundance; the darkest shading (black) is reserved for densities >3 individuals/400 m^3 (0.75/100 m^3). Geometric mean abundance and 95% confidence bounds for each group are given in Table 3.

TABLE 4.—Early life stages of *Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*, for 1978 off San Onofre, Calif. See Figure 1 for description of sampling blocks.

Species	Sampling block (avg. no./m of coastline)					Total average no.
	A	B	C	D	E	
Engraulis mordax						
eggs	3,100	25,334	85,372	75,238	95,782	284,826
larvae <6 mm	85,302	363,002	1,387,638	1,770,549	1,770,939	5,377,430
larvae >6 mm	42,970	86,977	816,941	1,164,417	607,805	2,719,110
Genyonemus lineatus						
preflexion larvae	463	688	7,440	9,290	3,724	21,605
flexion and post-flexion larvae	464	2,969	4,198	2,699	107	10,437
Seriphus politus						
preflexion larvae	592	490	4,200	2,137	2,103	9,522
flexion and post-flexion larvae	2,214	809	779	197	96	4,095

DISCUSSION

The methods we have employed for sampling very shallow inshore waters, though not without shortcomings, have proven satisfactory in that they clearly emphasize the degree to which many larval fishes are concentrated in different layers, especially near bottom. Any quantitative sampling of nearshore fish larvae over soft bottom (at least) in the Southern California Bight must clearly include the epibenthic layer. However, our method of doing so may leave room for improvement. The Auriga net probably does not sample the 17 cm immediately above the substrate, unless the rollers induce an avoidance response such that larvae swim upward and into the mouth. Moreover, we have not determined the thickness of the epibenthic microhabitat or whether it is the same for all species. The sharpness of some abundance patterns suggests this layer may be no more than 1 m thick (the bongo net tows began about 1 m above the bottom), but small errors in this determination, and failure to sample obliquely from the

top of the range of the epibenthic gear, could make large differences (by a factor of 2) in the abundance estimates of some taxa.

Other studies from the Southern California Bight have shown cross-shelf patterns similar to those which we describe. For example, Gruber et al. (1982; sampling neuston and midwater) and Brewer et al. (1981; sampling the entire water column) both showed vertical and cross-shelf changes in species composition. In both studies, atherinid larvae were principally neustonic. Brewer et al. (1982) took 69% of all larvae on their surveys from the epibenthic stratum. Both studies showed that clinids, most gobiids, sciaenids, and atherinids were most prevalent nearer shore. Such inshore-offshore patterns have also been shown further north along the west coast (Pearcy and Meyers 1974; Richardson and Pearcy 1977).

Icanberry et al. (1978) conducted a distributional study of ichthyoplankton above the epibenthic stratum at two nearshore stations off Diablo Canyon, about 100 km northwest of the Southern California Bight. Though there is taxonomic overlap between their study and ours, their sampling was too nearshore to delimit the offshore extent of any species in our study. Published data on widely (offshore) ranging species are contained in the CalCOFI atlas series (Kramer and Ahlstrom 1968; Ahlstrom 1969, 1972; Ahlstrom and Moser 1975) and complement some of the offshore patterns reported here.

Engraulis mordax, one of these widely ranging species, spawns principally offshore (Richardson 1981; Brewer and Smith 1982). The number of excess *E. mordax* larvae (over those which can be accounted for by eggs) in the nearshore zone must come from outside the sampling area, and these larvae must begin moving shoreward at an early age. Richardson (1981) suggested that currents might be a mechanism through which larvae of the northern subpopulation of *E. mordax* are redistributed. We presently cannot identify a mechanism for the redistribution off San Onofre. However, if one assumes it involves some behavioral response to environmental cues, it is worth considering just how far a larval anchovy might swim. Hunter (1972) estimated cruising speed on the order of one-half body length/s. At this speed, a 6 mm larva would swim about 250 m/d, far enough to move several kilometers along an environmental gradient during the larval period. Any behavior allowing larvae to remain in the nearshore zone (e.g., orientation toward the bottom), once encountered, could help explain their observed concentration.

The increased concentration of older larvae of *E. mordax*, *Genyonemus lineatus*, and *Seriphus politus* nearshore and near the bottom is reminiscent of the invasion and retention of larval and postlarval fishes in estuaries and tidal creeks of the Atlantic coast (cf. Chao and Musick 1977; Weinstein et al. 1980). Older larvae of *Paralichthys californicus*, although too rare for statistical analysis, also appeared more concentrated nearshore than did the younger larvae. Whatever the mechanisms for such ontogenetic redistribution, they must be at least partly behavioral. Weinstein et al. (1980) found vertical movements in response to tides, whereby postlarvae became more concentrated near the bottom during ebb flows, thus taking advantage of the slower seaward current in the boundary layer. In the Southern California Bight the mean nearshore flow is alongshore, with relatively weak cross-shelf components (Hendricks 1977; Reitzel 1979[13]; Parrish et al. 1981; Winant and Bratkovich 1981). The major source of cross-shelf water motion is internal waves of tidal frequency (Winant and Olson 1976) which propagate toward shore. For these waves to propagate, the water column must be stratified. It is notable that larval *S. politus*, which displayed the most intense ontogenetic redistribution, is most abundant during late summer-early fall (Walker et al. footnote 11), the season of maximum thermal stratification in the Bight (Cairns and Nelson 1970). Thus it may be that *S. politus* and other semiplanktonic organisms of the shallow shelf waters take advantage of internal tides in somewhat the same way that the estuarine fauna use the surface tide to regulate position. It is conceivable that due to dissipation of energy, seaward motions in the boundary layer are slower than shoreward motions.

A similar internal wave mechanism for shoreward migration has been suggested by Norris (1963). He hypothesized that postlarval *Girella nigricans* might swim ahead of the cold waters of the incoming internal wave fronts, thus producing the observed early shoreward migration of that species.

Brewer and Smith (1982) estimated that the numbers of *E. mordax* larvae spawned in the nearshore waters were approximately proportional to the area the nearshore waters represented in the total waters inhabited by the central subpopulation. They concluded that the nearshore region off southern

[13]Reitzel, J. 1979. Physical/chemical oceanography. *In* Interim report of the Marine Review Committee to the California Coastal Commission. Part II: Appendix of technical evidence in support of the general summary. MRC Document 79-02(II), p. 6-23. Marine Review Committee of the California Coastal Commission, 631 Howard Street, San Francisco, CA 94105.

California was not a preferred habitat for adult spawning during 1978-80. Our ratios of *E. mordax* eggs to early larvae support this conclusion.

On the other hand, larval survivorship may be enhanced in these nearshore waters. Hjort (1914), Lasker (1975), and Brewer and Smith (1982) pointed out that the number of eggs and larvae surviving to recruitment may vary independently of spawning stock size. Brewer and Smith (1982) indicated that the shallow coastal region's importance as a nurseryground for *E. mordax* is not yet clear. Their preliminary length-frequency data show relatively high numbers of large size classes nearshore, which are rare further offshore. Our preliminary length-frequency data corroborate this. The onshore ontogenetic shift of these larvae is a conspicuous and persistent feature of our data set (fig. 5). Thus nearshore environmental conditions may enhance growth or survivorship or both for *E. mordax* larvae as well as for other larvae with typically inshore patterns.

The larval taxa discussed in this paper represent some 12% of the types identified in the course of this study. Less common taxa were omitted for statistical reasons, but inspection of the data suggests that the patterns of abundance shown here are typical. Larvae of many species found in our study are most abundant in shallow water within a few kilometers from shore. Laroche and Holton (1979), noting the inshore abundance of 0-age *Parophrys vetulus* off the Oregon coast, suggested a nusery function for those open, nearshore areas. Concentration of juvenile fishes well inshore of adult depth ranges is also well known along the southern California coast (Limbaugh 1961; Feder et al. 1974).

Whether such patterns result from behavioral mechanisms leading to nearshore concentration, from differential onshore-offshore mortality, or simply from random movements away from very localized spawning sites, their evolution and maintenance imply significant value in occupying nearshore waters. Eppley et al. (1978) found higher concentrations of phytoplankton inshore of the 50-100 m depth contours, and Lasker (1975, 1978) showed that nearshore abundance of suitable-sized phytoplankton can be an important determinant of year-class strength in *E. mordax*. Gruber et al. (1982) noted that Pacific sardine, *Sardinops caeruleus*, once spawned over wide areas of the California Current region, but the reduced stock now concentrates its spawning effort nearshore. They suggested the productive nearshore zone may be especially important to recovering fish stocks, a situation which might apply to northern anchovy at some future date.

Pearcy and Myers (1974) noted that a number of studies found estuaries of northern California and Oregon to be important nurseries. However, estuaries in the Southern California Bight, as along much of the Pacific coast of North America, are small and far between. Enhanced productivity in the shallow waters of the open coast seems to provide a nursery area for many Southern California fishes analogous to the estuarine nurseries of other regions.

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APPENDIX 1

On 24 July, 30 August, and 22 September 1978, vertically stratified samples were taken at one station along the 8 m isobath and at another along the 13 m isobath. A sample set, or profile, consisting of five strata was sampled at each station: Neustonic, three midwater strata, and the epibenthic layer (the midwater strata were chosen with regard to the depths of power plant cooling structures). At the 8 m station, the midwater strata were 1) the lower 3 m of the water column, 2) 3 m above the bottom, and 3) the water column above stratum 2. At the 13 m station, the lower midwater stratum was the lower 2 m of the water column, while the upper two depended on the vertical thermal structure. When a thermocline was present, as during the September cruise and intermittently during the August cruise, the middle stratum extended from 2 m above the bottom to the base of the thermocline, and the upper stratum from the top of the thermocline to just below the surface. In the absence of a well-defined thermocline, the water column above 2 m from the bottom was divided into two equal parts. Sample sets were replicated four to six times in the day and again at night, resulting in 325 samples in the vertical migration study.

Data from the two stations were analyzed separately, since all sampling depths (except the neustonic layer) differed between stations. No analysis was done of the effects of the thermocline, since its extreme movements with respect to the vertical scale of interest would require a more intensive sampling program. In this analysis nominal sampling depths were treated as constants.

Because of patchy distributions of ichthyoplankton and movements of the thermocline (August and September), inherent variability was expected among the sets of profiles taken on a given date. In order to separate this variability from variability due to sampling date (cruise), time of day, and "error", we analyzed the data in a repeated-measures type analysis of variance design (App. Table 1). In this design, the depth effect was contained within the fixed-effect time of day and the random-effect cruise. The questions addressed were 1) whether there was a depth effect, i.e., significant differences among strata, within cruise × time-of-day blocks, and 2) if a depth effect did exist, whether there was a significant depth × time-of-day interaction. This interaction, interpreted (when significant) as daily vertical migration, was evaluated as the F-ratio of the depth × time of day to the depth × time of day × cruise mean square errors. When the three-way term was insignificant (in this case, $P > 0.75$), the error sums of squares and the three-way sum of squares were pooled, and this pooled term was used as the denominator in the F-ratio (Sokal and Rohlf 1969: 266).

The 10 most frequently occurring taxa were analyzed (App. Table 2). (A high frequency of occurrence was important to keep cell variances relatively homogeneous.) To reduce the effect of day-night differences in apparent abundance (most likely from visual net avoidance), we reduced each profile to a set of differences, or Δ's between adjacent strata, e.g.

$$\Delta_1 = \text{(abundance at depth 1)} - \text{(abundance at depth 2)}.$$

Abundance was expressed as $\log_{10}(X + 1)$, where X = larvae/100m^3. Any daily change in the relative abundance in two strata would thus be manifest in a change in sign and/or magnitude of the corresponding Δ.

APPENDIX TABLE 1.—ANOVA model applied in the analysis of daily vertical migration. The last two terms can form the error estimate (ε) in Appendix Table 2.

$$Y_{ijkm} = \mu + C_i + T_j + P_{m(ij)} + D_k + CT_{(ij)} + CD_{(ik)} + TD_{(jk)} + DP_{(m(ij)k)} + CTD_{(ijk)} + \varepsilon_{ijkm}$$

where	Y_{ijkm}	=	Density
	μ	=	Mean effect
	C_i	=	Sampling date (cruise) effect
	T_j	=	Time-of-day effect (day-night)
	$P_{m(ij)}$	=	Depth profile within cruise and time-of-day
	D_k	=	Depth effect
	$CT_{(ij)}$	=	Interaction, cruise × day-night period
	$CD_{(ik)}$	=	Interaction, cruise × depth
	$TD_{(jk)}$	=	Interaction, day-night period × depth
	$DP_{(m(ij)k)}$	=	Depth k for profile m within cruise and time-of-day
	$CTD_{(ijk)}$	=	Interaction, cruise × day-night period × depth
	ε_{ijkm}	=	Residual error

APPENDIX TABLE 2.—*F*-table for the 10 most frequently occurring larval fish taxa off San Onofre, Calif.: repeated-measures ANOVA. *D* = depth, *TD* = day-night period X depth, *CTD* = cruise X day/night period X depth. When the *CTD* mean square error (MSE) was insignificant ($P > 0.75$), the *CTD* and Error (ε) sums of squares were pooled. The *TD* interaction term, when significant ($^{*}P \leq 0.05$; $^{**}P < 0.01$), is interpreted as daily vertical migration. Frequency refers to the number of samples in which a taxon occurred out of 325 total samples. Results are presented for the 13 m station only.

Taxa	Freq	Source	df	MSE	*F*	*P*
Engraulis mordax	251	*D*	3	0.79065	4 101	0.010
		TD	3	0.18989	0.335	0.801
		CTD	6	0.56687	2.940	0 013
		ε	69	0.19281		
Seriphus politus	232	*D*	3	1.72110	8 943	<0.001**
		TD	3	0 06644	0.045	0.986
		CTD	6	1 46510	7 613	0.000
		ε	69	0.19246		
Hypsoblennius spp.	206	*D*	3	3.93932	19 586	<0.001
		TD	3	2.37801	12.344	0.000**
		CTD	6	0 09508	0.473	0.826
		ε	69	0.20113		
Genyonemus lineatus[1]	148	*D*	3	1.56249	11.853	<0.001
		TD	3	0.82790	5 377	0.100
		CTD	3	0.15403	1.168	0.332
		ε	45	0.13183		
Cheilotrema saturnum	144	*D*	3	1.15593	13.838	<0.001
		TD	3	0.03663	0 145	0.929
		CTD	6	0.25185	3 015	0.011
		ε	69	0.08353		
Menticirrhus undulatus	125	*D*	3	2 52228	31.968	<0.001
		TD	3	0 03333	0.294	0.829
		CTD	6	0 11325	1 435	0.214
		ε	69	0.07890		
Paralabrax spp.	122	*D*	3	1.86818	15.383	<0.001
		TD	3	0.60921	1.802	0.247
		CTD	6	0.33768	2 781	0.018
		ε	69	0.12144		
Paralichthys californicus	119	*D*	3	2 97375	15 609	<0.001
		TD	3	0.76462	4.873	0.047*
		CTD	6	0.15653	0 822	0.557
		ε	69	0.19051		
Gibbonsia Type A	114	*D*	3	1 25337	25 265	<0.001
		TD	3	0.20486	1.742	0.258
		CTD	6	0.11763	2.371	0.039
		ε	69	0.04961		
Gobiesox rhessodon	113	*D*	3	3 52655	103.984	<0.001
		TD	3	0 17248	4 528	0.055
		CTD	6	0.03806	1 122	0 359
		ε	69	0.03391		

[1]The analysis of *G. lineatus* differed from those of other taxa. At the 13m station, the 24 July cruise was eliminated because the extremely low abundance of *G. lineatus* on that date caused the variance to be unacceptbly heterogeneous (by inspection).

RING DEPOSITION IN THE OTOLITHS OF LARVAL PACIFIC HERRING, *CLUPEA HARENGUS PALLASI*

MICHAEL D. MCGURK[1]

ABSTRACT

The first normal ring in the sagittae of Pacific herring, *Clupea harengus pallasi*, larvae is deposited at the age of complete yolk absorption. The rates of deposition of subsequent rings in four groups of larvae that were fed daily ranged from 0.12 to 0.96 rings per day, and only two of the four groups had a daily pattern. Larvae that were starved from hatch deposited one normal ring on day 6 posthatch, but all ring deposition stopped thereafter. The starvation of subgroups of larvae after 7 days of feeding and after 25 days of feeding produced deposition rates that were not significantly different from those of the parent feeding groups. The average rates of normal ring deposition were positively correlated with the average rates of growth in length. Daily ring deposition in herring larvae <20 mm long occurs in populations with an average growth rate equal to or higher than 0.36 mm per day.

Rings or increments in the otoliths of fishes have been used to age wild larvae of several species (Ralston 1976; Kendall and Gordon 1978; Methot and Kramer 1979; Townsend and Graham 1981; Lough et al. 1982; Victor 1982). This method has two assumptions: 1) The first ring is deposited at a fixed age in each species, and 2) the rate of ring deposition is constant at 1 ring/d. Evidence from studies of ring deposition in enclosure-reared larvae of the Atlantic herring, *Clupea harengus harengus*, (Geffen 1982; Lough et al. 1982); northern anchovy, *Engraulis mordax*, (Brothers et al. 1976); and English sole, *Parophrys vetulus*, (Laroche et al. 1982) indicates that these two assumptions may not be true in first-feeding larvae that are starving or growing slowly. The deposition of subsequent rings may be significantly <1 ring/d. This paper reports that the first ring is deposited at a fixed age in herring larvae and that this age is coincidental with the age at complete yolk absorption. It also confirms that the subsequent rate of deposition is not always daily but that it is positively correlated with the rate of growth in body length.

MATERIALS AND METHODS

Experimental Groups

The batch experiments reported here were part of a research program on culturing Pacific herring larvae. Several different container sizes, temperatures, and prey types were employed (Table 1). Six groups of Pacific herring larvae were reared from the egg: Four were fed daily from hatch, one was starved from hatch, and one was terminated 3 d after hatch before food was offered. Two additional starving groups were formed from subgroups that were removed from feeding tanks after 7 d of feeding and after 25 d of feeding and then starved to death.

TABLE 1.—The experimental groups of Pacific herring larvae and their rearing conditions.

Group	Tank volume (l)	Rearing Temperature (°C)	Feeding treatment	Food organisms
1980A	50	12.1	fed from day 2	*Artemia*
1980B	50	12.1	starved from day 7	none
1980C	50	12.1	starved from hatch	none
1980D	50	7	starved from hatch	none
1981A	1,000	8-9	fed from hatch	*Artemia*, plankton
1981B	2,000	9-10	fed from hatch	plankton
1982A	25	8-9	fed from hatch	*Artemia*
1982B	25	8-9	starved from day 30	none

Rearing Conditions

Three groups, 1980A, 1980C, and 1980D, were raised from eggs in 50 l circular aquaria in April-June 1980. The eggs were laid on the walls of a holding tank by adult herring that had been captured in the Strait of Georgia by personnel of the Pacific Biological Station, Nanaimo, B.C. Therefore, the eggs came from the lower east coast stock (Taylor 1964). After 14 d incubation at 7°C, the eggs were hatched and the larvae of 1980A and 1980C were transferred to the rearing aquaria. The mean (±1 SD) temperature of these tanks during the rearing period was 12.1° ± 0.9°C. The 1980A group was fed from hatch to the

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end of the experiment, and the 1980C group was starved from hatch to death. The 1980D group was reared at 7°C for 3 d, before it was accidentally destroyed. A fourth group, 1980B, was formed from a 1980A subsample and was placed in its own 50 l aquarium after 7 d of feeding and then starved for 5 d.

Two groups, 1981A and 1981B, were reared in April-May of 1981 at the Bamfield Marine Station, Bamfield, B.C. The eggs came from spawn laid on *Fucus* spp. in the intertidal zone of Toquart Bay, Barkley Sound, B.C. Therefore, the eggs came from the lower west coast stock. The first population, 1981A, was raised in a 1,000 l circular, flow-through aquarium. The water temperature rose gradually from 8° to 9°C over the rearing period. Food was added daily. Group 1981B was reared in a culture chamber suspended in Bamfield Inlet. The chamber, a 2,000 l circular tank (Marliave 1981), floated at the surface of the Inlet. Wild plankton was swept through louvres on one side of the chamber by tidal currents and was trapped in the chamber where it served as food for the larvae. During the first 3 wk , no herring larvae was in the plankton from the Bamfield Inlet, so the tank population was not contaminated with wild herring. The surface water temperature of the Inlet over the rearing season was 9°-10°C.

One group, 1982A, was reared from eggs in the laboratory at the Bamfield Marine Station, April-May 1982. The group grew in a 25 l rectangular aquaria cooled to 8°-9°C. The eggs came from spawn laid on eelgrass, *Zostera marinus*, in the intertidal zone at the head of Bamfield Inlet and, therefore, came from the lower west coast stock. The fish were fed from hatch to age 30 d, and then the survivors were moved to another tank of the same size where they were starved for 8 d. This subgroup was named 1982B.

The lighting for all the laboratory groups was fluorescent and was on a 10-h light: 14-h dark cycle. This cycle was cued to the natural photoperiod with light sensors. Water in all of the tanks, except 1981A and 1981B, was gently aerated with an airstone, and about one-third of the volume was replaced daily with fresh seawater. Dead organisms and feces were daily siphoned off the floor in all tanks, except 1981B which did not accumulate wastes because its floor, drilled with over 1,000 small holes, was self-cleaning.

Hatching

All larvae in any single group were hatched within 24 h of each other. In 1980, hatching was stimulated by scraping the eggs off the wall of a holding tank. In 1981 and 1982, hatching was stimulated by exposing late-stage eggs to air for 15 min. The exposure caused an explosive hatch when the eggs were returned to seawater. The egg masses were removed from the tanks <24 h after hatching began.

Food

Food for three of the four fed populations consisted of freshly hatched *Artemia* nauplii. One of the feeding groups, 1981B, fed exclusively on wild plankton swept into the chamber by tidal currents. Another group, 1981A, was raised on a diet of *Artemia* nauplii supplemented with wild plankton captured with a plankton net from the surface of Bamfield Inlet. In all feeding groups, food was first supplied either at hatch or before the second day after hatch, the day when Pacific herring larvae first begin to exhibit feeding behavior. Both the *Artemia* nauplii and the wild zooplankters were attracted to the overhead light, and they tended to cluster in a patch at the surface of the water. Enough food organisms were added each day to the feeding groups to maintain the patches at all times so that the larvae of these groups had the opportunity to feed at will at any time. It is not known whether the 1981B larvae in the culture chamber had a similar opportunity, but the relatively high growth rate of this group indicates that food was abundant.

Absence of food organisms in the water of starving groups was ensured by filtering seawater through a layer of glass wool before it was added to a tank. Samples of filtered water were examined under a microscope to verify the absence of food organisms.

Samples

Samples of 10-18 larvae were taken from each of the groups at intervals of 2-20 d. In 1980 the fish were frozen at −10°C, and in 1981 and 1982 they were preserved in 37% isopropyl alcohol. The standard length was measured from the tip of the snout to the end of the notochord with the vernier scale of a compound microscope. Some of the larvae were measured live before preservation, stored individually, and then measured again 1-6 mo later. Freezing caused a mean (±1 SD) percent shrinkage of 6.3 ± 3.5 ($n = 26$), and isopropyl alcohol caused a mean (±1 SD) percent shrinkage of 0.04 ± 3.2 ($n = 97$) which was not significantly different from 0% shrinkage ($t = 0.0124$, $df = 96$, $P > 0.9$). An examination of the individual percent shrinkages showed no trend with live standard length. Frozen lengths were corrected to live lengths by multiplying by the factor

1.063. Alcohol-preserved lengths did not require correction.

Ring Counting

After extraction from the skull the sagittae were placed on a glass slide under immersion oil; their diameters were measured with an ocular micrometer. Sagittae are slightly flattened spheroids in young larvae and tend to become more oval in shape as the fish grows. The diameter measured was always the longest axis of the otolith. The sagittae were photographed at 400-1,000×, the developed film was projected on a screen, and the rings were counted. A single ring consisted of a dark band and an adjacent light band. All rings, no matter how faint, were counted in order to avoid observer bias towards a daily ring pattern. Two classes of rings were observed: 1) A group of 1-5 thin, faint rings clustered about the nucleus surrounded by 2) wider, darker rings that composed the majority of the rings in most larvae. In some sagittae the second class of rings were separated from the first by a distinct ring which may have been a check deposited in response to the exhaustion of the yolk. The two classes could not always be clearly distinguished, particularly in slow-growing fish. The first class corresponds to Geffen's (1982) "yolk sac" rings and the second to her "normal" or "regular" rings. In this paper the first class will be unnamed for two reasons: 1) Most of the rings were found in the larvae that had completely absorbed their yolk, so they were not exclusively yolk-sac rings, and 2) it has not been established that the two classes of rings are fundamentally different from each other, so the introduction of new terminology is premature. Geffen (1982) defined a "first heavy ring" that was found between the outer margin of the nucleus and the first normal ring. This term has not been used because the first normal ring was not always distinguishable from subsequent normal rings on the basis of width or darkness.

Each sagitta was counted three times, and the mean of the three counts was taken as the final count of that sagitta. The ring count of a fish was the mean of the final counts of its two sagittae. The mean (±1 SD) difference in final counts between sagittae from the same fish was 1.3 ± 1.4 which was not significantly different from zero ($t = 0.9028$, df = 148, $0.4 > P > 0.2$). The sagittae of 21 large larvae (live length range = 14-29 mm, age range = 20-54 d posthatch) selected at random from several groups were photographed and then fixed to a glass slide with cyanoacrylate glue and ground to the midplane with metallic lapping paper. They were rephotographed and recounted. The mean (±1 SD) difference was 1.1 ± 2.0 which was not significantly different from zero ($t = 0.5273$, df = 20, $0.5 > P > 0.9$). Inspection of the data revealed no trend of the difference with age or with the ring count of the nonground sagittae.

Data Analysis

The average rates of ring deposition and of growth in length were calculated as the slopes of linear predictive regressions of mean ring number and mean length on age posthatch. The homogeneity of the variances of the means of a group was tested with Bartlett's test (Sokal and Rohlf 1969), and, if they were found to be heterogenous, each mean was weighted with its sample size divided by its variance. *T*-tests were used to test the significance of differences between the slope of a regression of mean ring number on age and 1 ring/d and 0 ring/d. *F*-tests were used in covariance analyses to test for significant differences between two slopes.

RESULTS

Growth in live standard length was positive in all groups except 1980C and 1980B, in which the starving larvae shrank (Fig. 1). There are indications that growth was curvilinear, especially in 1980A and 1981B where the growth rates between the two last sampling dates in each group were much less than the previous growth rates. However, linear growth was assumed for the purpose of obtaining average growth rates to compare with the average ring deposition rates (Table 2). Growth rate was highest in the 2,000 l culture chamber and lowest in the 25 l aquarium, and there was a positive but nonsignificant correlation between growth rate and container size in the four fed groups ($n = 4$, $r = 0.90$, $0.05 > P > 0.10$).

Thin, faint rings of the first class were found in the otoliths of most of the 1980 fish that were <14 mm long, but were not found in the otoliths of any 1981 and 1982 fish (Fig. 2). These rings may have been deposited at any time between the late embryo and the postyolk-sac stage. The only sample of otoliths

TABLE 2.—Linear regressions of mean standard length on age in 7 groups of Pacific herring larvae.

Group	*y*-intercept (mm)	Slope (mm/d)	SE of slope	*r*	No. of means	*n*	df
1980A	10.4	0.180	0.030	0.97	4	36	1,2
1980B	13.1	−0.004	0.019	0.19	3	20	1,1
1980C	11.2	−0.107	0.031	0.90	5	50	1,3
1981A	8.2	0.231	0.011	0.99	6	57	1,4
1981B	8.4	0.290	0.049	0.96	5	60	1,3
1982A	10.6	0.090	0.047	0.89	3	38	1,1
1982B	11.4	0.100	0.035	0.89	4	39	1,2

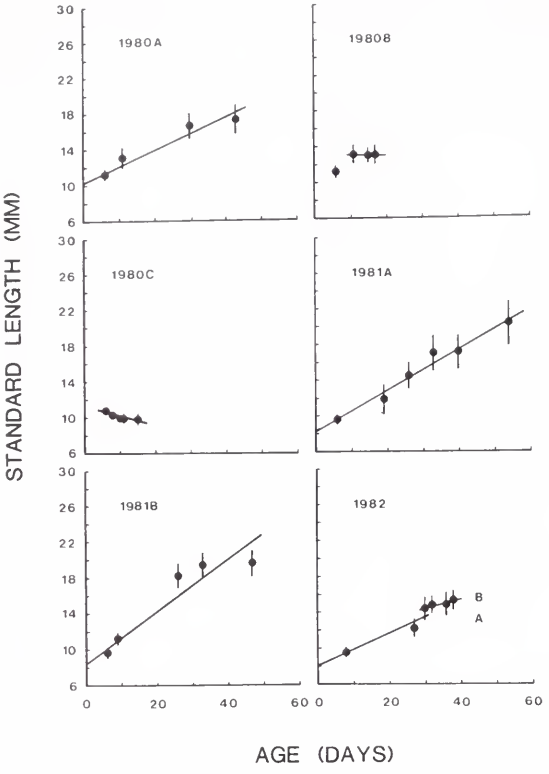

FIGURE 1.—Mean (±1 SD) live standard length at age posthatch for seven groups of Pacific herring larvae. See Table 2 for the regression equations.

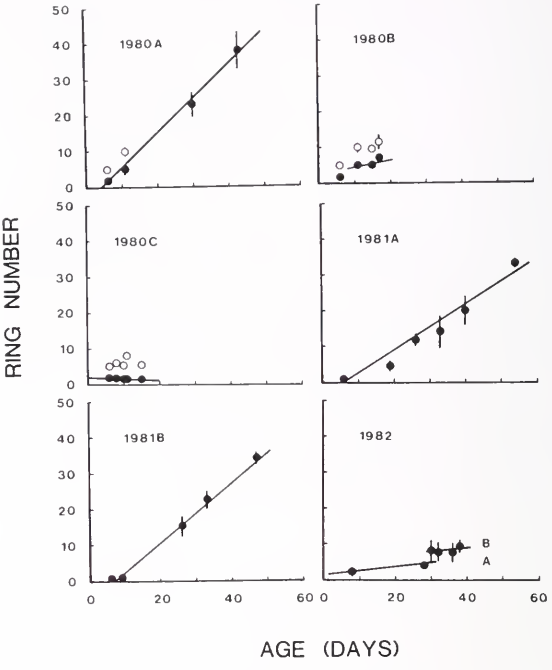

FIGURE 2.—Mean (±1 SD) ring count at age posthatch for seven groups of Pacific herring larvae. Open circles are total rings and closed circles are normal rings only. See Table 3 for the regression equations.

from yolk-sac larvae was a single sample from 1980D that had a mean (±1 SD) ring count of 5.2 ± 0.8 (n = 9) on day 1 posthatch. The rings were not observed in older, larger larvae; they may have been present but obscured by overburden over the nucleus. This phenomenon has been observed in the otoliths of larval largemouth bass, *Micropterus salmoides*, (Miller and Storck 1982). A group of 7-8 "prolarval rings" that were clustered about the nucleus at swim-up were visible for only 10-15 d afterward, because the nucleus became more opaque with age.

The first normal ring was deposited in all groups including 1980C by day 6 posthatch, the day after complete yolk absorption. This agrees well with the age at first increment of 4.5 (range = 0-9 d) found for Atlantic herring by Lough et al. (1982) and with the age of 6 d found for the same species by Geffen (1982). This indicates that herring larvae of both species do have a fixed age at first increment deposition and that it coincides with the age at complete yolk absorption.

Rates of subsequent ring deposition for the four fed groups were not all daily, and they ranged from 0.12 to 0.96 rings/d (Table 3); only two groups, 1980A and 1981B, had rates that were not significantly different from 1 ring/d ($t = 0.5772$, df = 3, $0.5 > P > 0.9$ and $t = 2.0142$, df = 4, $0.10 > P > 0.20$, respectively). The 1981A group had a rate that was significantly <1 ring/d ($t = 6.3465$, df = 5, $0.01 > P > 0.001$) but also significantly > 0 ($t = 10.8062$, df = 5, $P < 0.001$) and the 1982A group had a rate that was significantly <1 ring/d ($t = 10.0228$, df = 2, $0.01 > P > 0.001$) and not significantly >0 ($t = 1.3667$, df = 2, $0.20 > P > 0.40$).

The rate of ring deposition in 1980C, the group that was starved from hatch, was −0.05 ring/d, which was

TABLE 3.—Linear regressions of mean normal ring number on age in 7 groups of Pacific herring larvae.

Group	y-intercept (mm)	Slope (ring/d)	SE of slope	r	No. of means	n	df
1980A	−4 12	0 96	0.06	0.99	4	36	1,2
1980B	2.06	0.23	0 28	0 63	3	20	1,1
1980C	2.12	−0.05	0 02	0.83	5	50	1,3
1981A	−9.31	0 63	0.05	0.99	6	57	1,4
1981B	−5.60	0.83	0.08	0.99	5	60	1,3
1982A	1.45	0 12	0.08	0.83	3	38	1,1
1982B	4 90	0 10	0.11	0.53	4	39	1,2

not significantly different from 0 ($t = 2.2831$, df = 4, $0.10 > P > 0.20$). This indicates that the starvation of first-feeding larvae stopped ring production. The 1980B group had a rate which was not significantly different from one of 1 ring/d ($t = 2.3397$, df = 2, $0.10 > P > 0.20$) and not significantly different from a rate of 0 ($t = 0.6989$, df = 2, $0.50 > P > 0.90$) or from the rate of its parent feeding group, 1980A ($F = 5.9185$, df = 1.3, $0.25 > P > 0.50$). One reason for these results is that the 1980B group had only three data points for the regression, and the standard error of the slope was therefore relatively high: 122% of the value of the slope (Table 3). I conclude that starvation for 5 d after a feeding period of 6-7 d has no effect on the rate of ring deposition. The 1982B group had a ring depoistion rate that was not significantly different from 0 ($t = 0.7843$, df = 3, $0.40 > P > 0.50$) and which was not significantly different from the rate of its parent feeding group, 1982A ($F = 0.1352$, df = 1, 3, $P > 0.75$). I conclude that starvation for 8 d after a feeding period of about 25 d has no effect on the rate of ring deposition, at least not in 25 l enclosures.

The average ring deposition rates were significantly positively correlated with the average growth rates ($n = 7, r = 0.83, 0.01 > P > 0.05$) (Fig. 3). The regression of ring rate on growth rate was:

$$\text{Ring rate} = 0.14 + 2.40\ (\text{growth rate}).$$

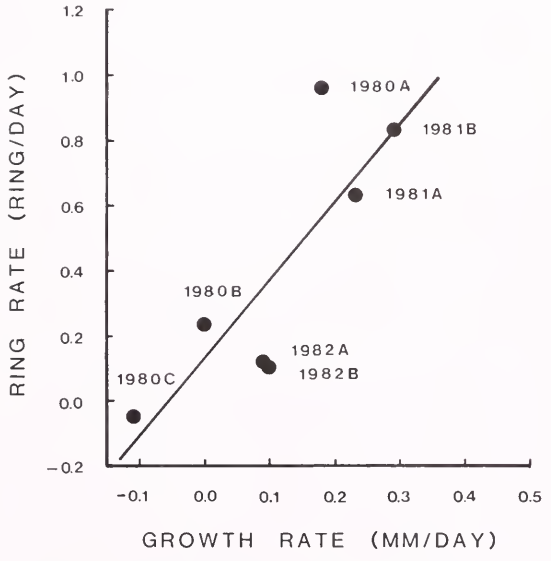

FIGURE 3.—Relationship between the average ring deposition rates and the average growth rates of seven groups of Pacific herring larvae. See text for regression equation.

The residuals of this regression were not correlated with container size, and there was no obvious relationship with prey type. However, there was a significiant positive correlation between the residuals and the mean rearing temperature ($n = 7, r = 0.83, 0.01 > P > 0.02$). The midpoints of the temperature range were used as an estimate of the mean temperature (Table 1). A regression of ring deposition rate on growth rate and temperature increase the multiple r to 0.99:

$$\text{Ring rate} = -1.39 + 3.36\ (\text{growth rate}) + 0.14\ (\text{temperature}).$$

These results confirm the correlation between ring deposition rate and growth rate found for Atlantic herring larvae by Geffen (1982), who interpreted the relationship as being curvilinear and linearized it by transforming both variables with logarithms. In order to compare the two sets of data the relationship between ring deposition rate and growth rate was assumed to be linear. A covariance analysis of the slopes of the two linear regressions indicated that there was no significant difference between them at the 0.05 probability level. Data from this study and from Geffen's were pooled and a single linear regression was calculated ($n = 12, r = 0.85, P < 0.001$):

$$\text{Ring rate} = 0.17 + 2.12\ (\text{growth rate}).$$

The influence of temperature on ring deposition rate could not be compared between the two data sets because the rearing temperature for Geffen's fish was not constant over the rearing period.

Plots of fish length on otolith diameter for the seven populations were curvilinear, and the rate of growth of fish length decreased with increasing otolith diameter. Transforming otolith diameter with logarithms best linearized the data, transforming both variable with logarithms produced lower correlation coefficients in all groups. Thus length was regressed on log (otolith diameter) (Table 4, Fig. 4). An analysis of covariance that included all seven groups indicated that the slopes of the regressions were significantly different from each other at the 0.05 probability level. Inspection of the slopes and their standard errors indicated that the fed groups and 1980B had slopes of a similar value and that 1980C and 1982B had slopes of a similar value but that they were much lower than those of the fed groups. The two groups were subjected to separate covariance analyses, and in each group the slopes were found to be not significantly different from each other at the 0.05 probability level. The

TABLE 4.—Linear regressions of fish length on log (otolith diameter).

Group	y-intercept (mm)	Slope (mm/μm)	SE of slope	r	n	df
1980A	−5 76	11.57	0.49	0.97	36	1,34
1980B	−4 54	10 77	3.17	0.73	12	1,10
1980C	2 73	4.40	2.10	0.28	52	1,50
1981A	−7 50	13.36	0 43	0.97	57	1,55
1981B	−5.50	12 14	0 46	0.96	60	1,58
1982A	−7 24	12.73	1 45	0.83	38	1,36
1982B	4.82	5.94	1 65	0.59	27	1,25

Lough et al. (1982); they have also been described in the otoliths of larval turbot, *Scopthalmus maximus*, (Geffen 1982) and Arcto-Norwegian cod, *Gadus morhua*, (Gjøsaeter and Tilseth 1982). Increments have also been found inside the nucleus in Atlantic herring (Lough et al. 1982), in three species of the genus *Lepomis*, and in the Mozambique mouthbreeder, *Tilapia mossambica*, (Taubert and Coble

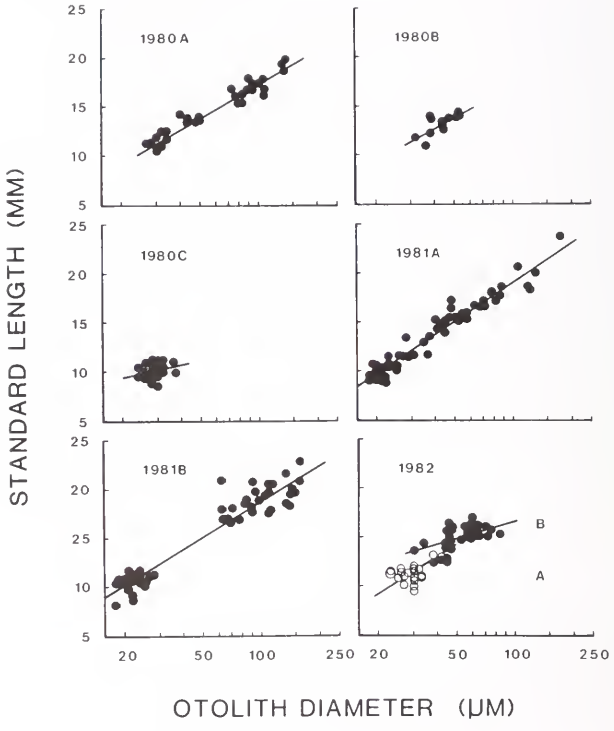

FIGURE 4.—Relationship of fish length to log (otolith diameter) for seven groups of Pacific herring larvae. Open circles in 1982 are 1982A and solid circles are 1982B. See Table 4 for the regression equations.

slope of the 1980B group was not significantly different from either the feeding groups or the starving groups because of its high standard error. The four fed groups were pooled to give a single regression ($n = 191, r = 0.95, P < 0.001$):

$$\text{Fish length} = 30.90 + 12.49 \log (\text{otolith diameter}).$$

The three starved groups could not be pooled because of the different growth and feeding histories of each group.

DISCUSSION

The first class of thin rings was found in the otoliths of Atlantic herring larvae by Geffen (1982) and by Lough et al. (1982); they have also been described in the otoliths of larval turbot, *Scopthalmus maximus*, (Geffen 1982) and Arcto-Norwegian cod, *Gadus morhua*, (Gjøsaeter and Tilseth 1982). Increments have also been found inside the nucleus in Atlantic herring (Lough et al. 1982), in three species of the genus *Lepomis*, and in the Mozambique mouthbreeder, *Tilapia mossambica*, (Taubert and Coble 1977). In at least one species of fish, the mummichog, *Fundulus heteroclitus*, these nonregular rings are regular daily rings that are deposited before hatching (Radtke and Dean 1982). The relationship between the number of nonregular rings, the age and size of the fish, and rearing conditions can only be determined with more experimental work, particularly on the sagittae of embryo and yolk-sac herring.

Presence of the thin rings in the 1980 fish and their absence in the 1981-82 fish was not the result of genetic differences between the eggs of the lower east coast stock and the eggs of the lower west coast stock. The sagittae of many small (length range = 9-20 mm) wild herring larvae captured from Bamfield Inlet in 1981 and 1982 were found to have several thin, faint rings around the nucleus (McGurk unpubl. data). It seems more reasonable to hypothesize that

the difference arose from factors that have already been reported to affect the rate of deposition of normal rings. These factors include temperature (Taubert and Coble 1977; Marshall and Parker 1982), short-term temperature fluctuations (Brothers 1978), and feeding activity (Uchiyama and Struhsaker 1981; Neilson and Geen 1982). Lough et al. (1982) suggested that the first class of thin rings were related to the inability of first-feeding larvae to meet their metabolic energy demands during the transition from yolk to exogenous food. This argument implies that the 1980 herring larvae were less able to capture sufficient food during first feeding than the 1981-82 larvae. However, this hypothesis does not explain the presence of the faint rings in the 1980C larvae that were starved from hatch.

Results of this study confirm the observations of Geffen (1982) that the rate of normal ring production is not always daily in young herring larvae and that it is positively correlated with the rate of growth in body size. The correlation means that normal rings cannot be used with confidence to age wild herring larvae less than about 20 mm long, unless the average growth rate of the population is known to be higher than about 0.36 mm/d (calculated from the regression of ring deposition rate on growth rate for Pacific herring only). Growth of larval fishes is influenced by several factors: temperature (Kramer and Zweifel 1970), food density (Haegele and Outram 1978), and container size (Theilacker 1980). The tendency for larger containers to support higher growth rates in the four fed groups of this study may explain why only two of the four had a daily ring pattern. The correlation implies that, if the rate of growth is slowed or stopped by starvation after a period of feeding, then the rate of ring deposition should also slow or stop. The two experimental groups that were treated in this manner did not produce rings at rates that were significantly different from those of their parent feeding groups. This suggests that a starvation period >5-8 d is necessary in order to demonstrate a statistically significant effect. Larger rearing containers are also recommended to produce greater contrast in growth rates between feeding and starving fishes.

Container size, temperature, or prey size may possibly have additional effects on the rate of ring deposition apart from that which is explained by growth rate. Temperature does explain some of the residual variance of the ring deposition rate-growth rate regression. However, published evidence on effect of constant temperature on ring deposition does not support the hypothesis that higher temperatures produce more increments. For example, Neilson and Geen (1982) found no difference between the number of increments produced by juvenile chinook salmon, *Oncorhynchus tshawytscha*, reared at 5.2°C and at 11.0°C. The effects of such environmental factors as light, temperature, and prey type on the ring pattern of herring sagittae can only be determined with a well-controlled experimental study.

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FISHES, FISH ASSEMBLAGES, AND THEIR SEASONAL MOVEMENTS IN THE LOWER BAY OF FUNDY AND PASSAMAQUODDY BAY, CANADA

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ABSTRACT

Five fish assemblages, dominated by pleuronectids, cottids, gadids, clupeids, and rajids, were identified from collections taken during a 5-year survey in the lower Bay of Fundy region, Canada. Individual assemblages occurred in each of estuarine, beach, pelagic, and offshore hard- and soft-bottom habitats. Species and/or age-class components within assemblages varied seasonally but, in general, each assemblage was distinct. There was a progressive seaward displacement of these assemblages from shallow, inshore to deeper, offshore habitats in winter followed by a reversal during summer. Yearly changes in species occurrence and abundance during the study period were predominantly attributable to variation in ocean climate. Long-term changes in abundance of two commercial species at one of the sampling sites, since a similar study there in 1965, appear related to population fluctuations in the Bay of Fundy and the Gulf of Maine. The beach habitat apparently served as a major nursery area for juvenile gadids, pleuronectids, and clupeids.

Although the fish fauna of the Bay of Fundy-Gulf of Maine system is well documented (Bigelow and Schroeder 1953; Leim and Scott 1966), few studies have examined long-term spatial and temporal changes or interrelationship among the fish assemblages. Previous studies in this region were concerned with the biology and seasonal movements of a single species (McCracken 1959, 1963; McKenzie and Tibbo 1961; Wise 1962) or the occurrence and composition of communities at a single site (Bigelow and Schroeder 1939; Tyler 1971).

Moore (1977) and Quinn (1980) have emphasized the need for long-term research to establish baseline information and estimates of natural variability for fisheries assessments and pollution impact studies. This is particularly true for inshore regions because of their importance as nurseries and feeding grounds (Warfel and Merriman 1944; Rauck and Zijlstra 1978). The increasing interest in trophic relationships among entire communities of fishes is further reason to document movement, abundance, and co-existence of fishes potentially utilizing the same food resource (Richards 1963; Keast 1970; Tyler 1972; Steiner 1976; Hacunda 1981).

Long-term changes in fish assemblages have been attributed to overexploitation of one or more of the species within the assemblage (Brown et al. 1973; Burd 1978; Sherman et al. 1981) and climatic variations (Dow 1964; Sutcliffe et al. 1977). However, it is usually difficult to separate natural fluctuations from those caused by imbalance in competitive and predator-prey relationships due to exploitation (Cushing 1980; Daan 1980; Sissenwine et al. 1982). With the view in mind of assessing these long-term changes to properly assign cause and effect, repetitive, in-depth studies of well-known or type localities are needed.

This study examines spatial and temporal variation in fish diveristy and abundance over a 5-yr period at two offshore stations within Passamaquoddy Bay, one offshore station in the Bay of Fundy, and at inshore and beach stations in Passamaquoddy Bay. One offshore station was the same station sampled by Tyler (1971) during 1965-66, allowing documentation of changes that have occurred over the intervening 10-15 yr.

METHODS

Three offshore stations in the Bay of Fundy (B) and in Passamaquoddy Bay (A, C) (Fig. 1) were sampled

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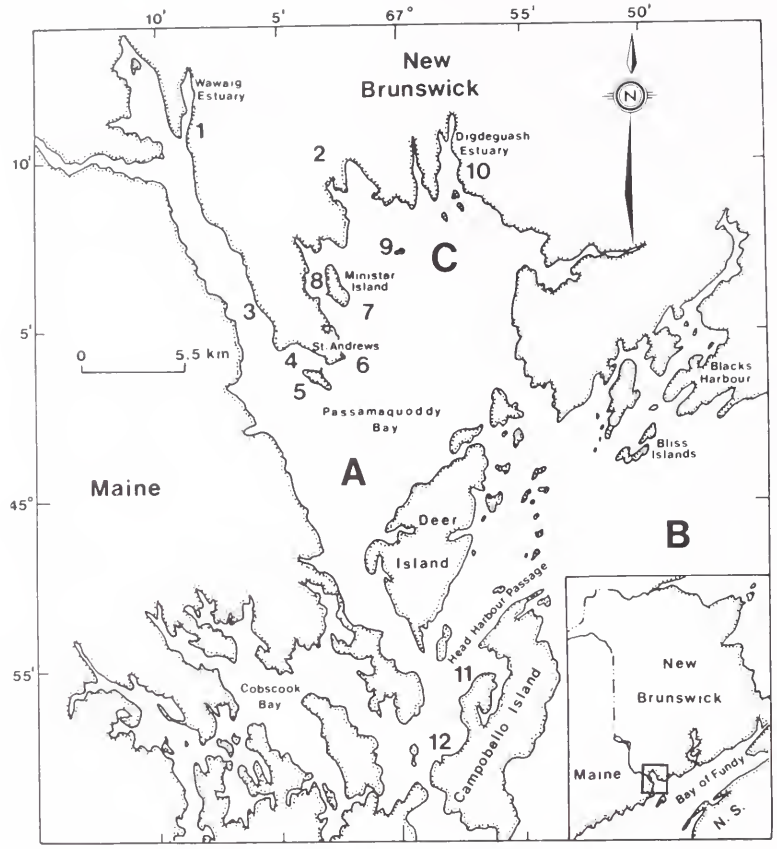

FIGURE 1.—Passamaquoddy Bay and the adjacent Bay of Fundy indicating sampling stations occupied during the study.

at approximately monthly intervals over a 5-yr period, 1976-81 (Table 1). Station A was the same site sampled by Tyler (1971) during 1965-66. Fish were collected using a ¾-35 shrimp trawl (3.8 cm stretch mesh nylon; 15.5 m foot rope), similar to the ¾-35 Yankee trawl used by Tyler (1971), towed by the 150-hp, 14 m stern trawler, Fisheries and Oceans' RV *Pandalus II*. Tows at each station were along a 1.6 km transect at about 4 km/h. Stations A and B were sampled once per trip between 1976 and 1979, and station C was sampled sporadically. From 1979 to 1981, tows at stations A and B were replicated and station C was sampled regularly. Captured fishes were identified to species, and adults and juveniles were categorized by size and enumerated separately. During the final year of collecting, fork length of all fishes was recorded to the nearest centimeter and otoliths were collected from Atlantic cod, ocean pout, American plaice, winter flounder, and witch flounder for age determination. Atlantic cod otoliths were sectioned for aging, other species were aged using the whole otolith. Results reported are the empirical length at age.

Between June and September 1976, 12 estuarine, intertidal, and inshore marine stations were sampled within Passamaquoddy Bay and Head Harbour Passage (Fig. 1). In addition, station 3 was sampled monthly during the period May 1976-November 1977, station 8 was sampled at approximately weekly intervals from May to September 1981, and stations 1 and 10 were sampled in December 1980 (Table 1). Fish were collected using a 9 m, 1.3 cm mesh beach seine, a 3.7 m shrimp trawl with a 3 mm cod end towed behind a 5 m Boston whaler, or bottom-set gill nets with stretched mesh sizes ranging from 7.6 to 17.8 cm. Standard fishing efforts employed with each gear type were shore seine hauls of 5 min during the 2-h period before and after low water, trawl tows of 10 min, and overnight gill net sets of 16 h.

Temperature, salinity, and substrate type were

TABLE 1.—Physical and chemical characteristics and sampling history of stations in the Bay of Fundy and Passamaquoddy Bay. Gear: ST = shrimp trawl; S = seine; GN = gill net. Bottom type: M = mud; Sa = sand; Rk = gravel or rock.

Station	Gear	Maximum depth (m)	Bottom type	Sampling temp. range (C)	Sampling salinity range (‰)	Collection period	Sampling trips
A	ST	80	M-Rk	0-15	29.5-32.5	1976-81	39
B	ST	80	M	1-12	31.0-32.5	1976-81	37
C	ST	20	M	0-15	—	1978-81	15
1	S	1.5	M-Rk	14.5-20.0	22.1-26.0	06-08/76, 12/80	3
2	S	1.5	M-Rk	15.5-22.5	26.0-29.5	05-08/76	4
3	S	1.5	Sa-Rk	0.0-16.0	21.0-30.0	05/76-11/77	16
4a	S	1.5	Rk	12.5	29.0	06, 07/76	2
4b	ST	7.5	Rk	12.5	—	07/76	1
5a	S	1.5	Sa	14.5	30.0	07, 08/76	2
5b	GN	33	Sa-M	—	—	08/76	1
6	S	1.5	Sa-M	14.0	28.0-30.0	08-09/76	2
7	GN	30	M	13.5	28.0	06/76	1
8a	S	1.5	M-Sa	11.0-18.5	28.7-30.7	06, 07/76	2
						05-09/81	23
8b	ST	12	Rk-Sa	—	—	06, 07/76	2
9	S	1.5	Sa	14.0	29.5	06,08/76	2
10	GN	3	M-Rk	13.0	28.0	06, 09/76, 12/80	3
11	S	1.5	M	—	—	07/76	1
12a	S	1.5	Sa-Rk	15.0	28.0	07, 09/76	2
12b	ST	15	Sa-Rk	—	—	07/76	1

recorded for most sampling sites (Table 1). Bottom temperature and salinity data inside and outside Passamaquoddy Bay came from routine monthly sampling by the Department of Fisheries and Oceans at a site opposite the Biological Station (near Station A) and at "Prince 5" 3.2 km south of Bliss Islands in the Bay of Fundy (near station B). Temperatures at deep stations were taken with a reversing thermometer attached to a Nansen bottle and at shallow stations with a hand thermometer. Salinities were determined with a laboratory salinometer from samples collected in the field. Substrate samples at deep stations were obtained with a PONAR grab. At shallow stations, substrate type was assessed visually.

Fishes were identified using Leim and Scott (1966) with the exception of red and white hake and redfish, which were determined by using Musick (1973) and Ni (1982), respectively. Because we were unaware of the problem of distinguishing between young *Raja ocellata* and *R. erinacea* (McEachran and Musick 1973), these determinations may be incorrect.

Coefficients of community were calculated using the formula:

$$\frac{C}{A + B - C} \times 100$$

where C = number of common species, A = number in assemblage 1, and B = number in assemblage 2 (Jaccard 1932; Kontkanen 1957). An index that compared presence and absence of species at each station (binary data) was used because species abundances among stations were not comparable due to different gear used.

RESULTS AND DISCUSSION

Station Environmental Characteristics

Temperature and salinity at stations A and B (Fig. 2) followed the typical, yearly cycle of a cold temperate sea (Fig. 3). Annual temperature range in the Bay of Fundy was less than in Passamaquoddy Bay. Summer temperatures at inshore sites were simlar to offshore sites with the exception of higher temperatures at some estuary stations (i.e., 1 and 2) (Table 1). Two notable variations occurred: The early months of 1977 and August 1978 were abnormally warm, particularly at station A (J. Hull[5]); and throughout the study period there was a generalized cooling trend.

Salinities were highest in late summer through the fall and lowest in spring at both sites. At all times of year, salinities were higher in Bay of Fundy (station B) than at station A (Fig. 2). Inshore sites had salinities of 1-2 ppt less than station B, and salinities at estuarine sites were as low as 21.0 ppt during summer (Table 1).

Substrates of most sites were composed of sand and/or mud (Table 1). Station A had the steepest slope, about 2:100 m. Slopes at stations B and C were 0.4:100 and 0.6:100 m, respectively. Slopes at coastal intertidal sites were gradual, about 1:100 m. Estuarine stations (1, 2, and 10) had extremely soft mud bottoms and station 2 had extensive eel grass beds.

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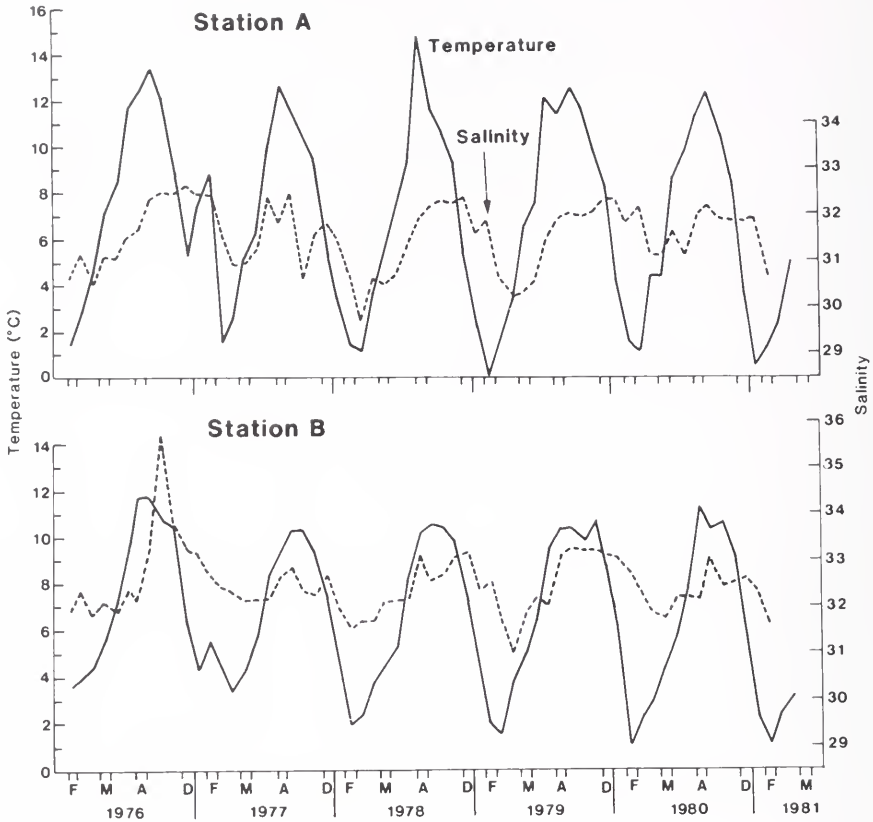

FIGURE 2.—Bottom temperature and salinities at station A in Passamaquoddy Bay and station B in the Bay of Fundy during 1976-81.

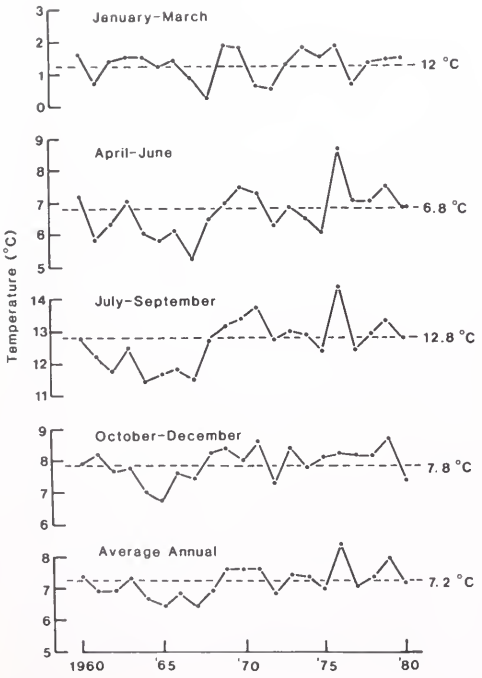

FIGURE 3.—Mean surface sea temperatures at station B by season during 1960-80 as compared with the 50-yr mean at this site.

Fishes and Seasonal Occurrence

Sixty-two species of fish were captured during the study period (Tables 2, 3). For those stations sampled regularly and intensively, residency period and abundance are indicated. Fish occurrence is expressed as part of the summer component (June-October), the winter component (November-May), the regular component (caught year round), or the occasional component. Fishes classified as occasional components show no seasonal abundance pattern and were collected <70 times (specimens captured $\times$ sampling trips) over 5 yr at stations A, B, and C, or <15 times at stations 1-12. We realize that some fish at all stations may have been missed entirely or are listed as rare simply because they were unavailable to the sampling gear used or could avoid capture (e.g., mackerel). Abundance of fishes in the catch was categorized as rare (1-10 specimens), com-

TABLE 2.—Residency and abundance of fishes occurring at deep sampling stations in the Bay of Fundy and Passamaquoddy Bay. Residency is R = regular; S = summer; W = winter; O = occasional; N = never encountered. Abundance is a = abundant; c = common; r = rare.

Species	Station			Species	Station		
	A	B	C		A	B	C
Mysine glutinosa	Oc	N	N	*Lumpenus lumpretaeformis*	Or	Or	N
Squalus acanthias	Oc	Sa	Oc	*Lumpenus maculatus*	Or	N	N
Raja radiata	Sc	Rc	Or	*Macrozoarces americanus*	Ra	Sc	Sc
Raja senta	Or	Rc	Or	*Nezumia bairdi*	N	Or	N
Raja erinacea	Ra	Wc	Oc	*Cyclopterus lumpus*	Or	Or	N
Raja ocellata	Rc	Or	Or	*Liparis coheni*	Wc	Or	N
Raja laevis	N	Or	N	*Liparis inquilinus*	Wr	N	N
Acipenser oxyrhynchus	N	Wr	N	*Sebastes fasciatus*	Wc	N	N
Alosa Aestivalis	N	N	Or	*Myoxocephalus octodecemspinosus*	Ra	Wc	Oc
Alosa pseudoharengus	Or	Or	Sc	*Myoxocephalus aeneus*	Wc	Or	N
Alosa sapidissima	Or	Sc	N	*Myoxocephalus scorpius*	Wc	Or	N
Clupea harengus	Wa	Wa	Wa	*Hemitripterus americanus*	Rc	Rc	Or
Osmerus mordax	Rc	Or	Sa	*Triglops murrayi*	Oc	Or	N
Mallotus villosus	N	N	Or	*Artediellus uncinatus*	Wc	N	N
Enchelyopus cimbrius	Sr	Rc	Or	*Aspidophoroides monopterygius*	Rc	N	N
Gadus morhua (adult)	Sc	Wc	Oc	*Poronotus triacanthus*	Oc	Or	Oc
G. morhua (juvenile)	Wa	Wc	Oc	*Pseudopleuronectes americanus*	Sa	Wa	Sa
Microgadus tomcod	Or	Or	Oc	*P. americanus (juvenile)*	Wa	Wr	Sa
Pollachius virens (juvenile)	Wa	Or	N	*Glyptocephalus cynoglossus* (adult)	Or	Sc	N
Melanogrammus aeglefinus (adult)	Sc	Oc	N	*G. cynoglossus* (juvenile)	Or	Wc	N
M. aeglefinus (juvenile)	Wc	N	N	*Hippoglossoides platessoides*	Rr	Ra	Sa
Merluccius bilinearis	Sa	Sa	Sc	*Limanda ferruginea*	Sr	Or	Or
Urophycis tenuis	Sc	Rc	Oc	*Liopsetta putnami*	N	N	Wc
Urophycis chuss	Sc	Sr	Or	*Hippoglossus hippoglossus* (juvenile)	Wr	N	N
Anarhichas lupus	Sr	N	N	*Paralichthys oblongus*	Or	N	N
Ulvaria subbifurcata	Wr	N	N	*Scopthalmus aquosus*	Or	Or	Rc
Cryptacanthodes maculatus	Or	Or	N	*Lophius americanus*	Sr	Or	N

TABLE 3.—Residency and abundance of fishes occurring at estuarine, intertidal, and shallow marine sites in Passamaquoddy Bay. Residency is R = regular; S = summer; W = winter; O = occasional; N = never encountered (station 3 only). Abundance is a = abundant; c = common; r = rare.

Species	Station											
	1	2	3	4	5	6	7	8	9	10	11	12
Squalus acanthias	—	—	N	—	Sc	—	Sc	—	—	—	—	—
Raja radiata (juvenile)	—	—	Sr	—	Oc	—	O	—	—	—	—	—
Raja erinacea	—	—	Sc	—	O	—	—	—	—	—	—	—
Raja ocellata	—	—	N	—	O	—	O	—	—	—	—	—
Alosa aestivalus	—	—	N	—	—	—	—	Sa	—	Sa	—	—
Alosa pseudoharengus	—	—	Sr	—	—	O	—	Sa	—	Sa	—	—
Clupea harengus	Sc	O	O	O	—	O	O	Sa	—	Sa	O	O
Salmo salar	—	—	S	—	—	—	—	—	—	O	O	—
Osmerus mordax	Rc	Rc	Wa	—	—	—	O	Sa	—	Wa	—	—
Mallotus villosus	—	—	N	—	—	—	—	—	—	—	Oc	Oc
Fundulus heteroclitus	Sa	Sc	Wc	—	—	—	—	Or	—	Sc	—	—
Gasterosteus aculeatus	Sc	Sa	Oc	O	O	O	—	Sc	—	Sc	O	O
Gasterosteus wheatlandi	Oc	Sa	Sr	—	—	—	—	Sr	—	Sr	—	—
Apeltes quadracus	—	Sc	N	—	—	—	—	—	—	—	—	—
Pungitius pungitius	—	Sa	N	—	—	—	—	—	—	—	—	—
Anguilla rostrata	Or	Sc	N	—	—	—	—	—	—	Sr	—	—
Enchelyopus cimbrius (larvae)	—	—	Sc	—	—	—	—	—	—	—	—	—
Gadus morhua (adult)	—	—	N	—	O	—	O	Sr	—	—	—	—
G. morhua (juvenile)	—	—	Sr	—	Sc	—	Sc	Sr	—	—	—	—
Microgadus tomcod	Wc	Wc	Wc	O	O	—	—	Sc	O	Wc	O	—
Pollachius virens (juvenile)	O	O	Sa	O	O	O	—	Sa	O	—	—	O
Urophycis tenuis (juvenile)	—	—	Sc	—	—	—	—	Sc	—	—	—	—
Ammodytes americanus	—	—	N	—	—	—	—	—	—	—	O	—
Scomber scombrus	—	—	Sr	—	Sc	—	Sc	—	—	—	—	O
Pholis gunnellus	O	—	Rc	O	—	—	—	S	—	—	—	O
Ulvaria subbifurcata	—	—	N	—	—	—	—	—	O	—	—	—
Cyclopterus lumpus (juvenile)	—	—	Sc	—	—	—	—	O	O	—	—	—
Macrozoarces americanus	—	—	N	—	—	—	—	O	O	—	—	O
Myoxocephalus octodecemspinosus	—	—	Sr	—	—	O	O	S	—	O	O	O
Myoxocephalus aeneus	—	—	Sc	—	—	—	—	Sc	O	—	—	—
Myoxocephalus scorpius	O	—	O	—	—	—	—	Sc	—	—	—	O
Hemitripterus americanus	Oc	—	Sc	O	—	—	O	O	—	—	—	—
Menidia menidia	Sa	Sa	Wc	—	—	—	—	O	—	—	—	—
Pseudopleuronectes americanus (adult)	Sr	—	Sr	O	Sa	—	Sa	O	O	—	—	—
P. americanus (juvenile)	O	—	Sa	O	Sa	—	Sa	Sa	O	—	—	—
Liopsetta putnami	Sc	O	Sr	—	—	—	—	—	—	Sc	—	—
Syngnathus fuscus	O	Sc	N	—	—	—	—	—	—	—	—	—

mon (11-100), and abundant (+100). Because of gear differences further quantification of catches was unjustified.

Eight species of flatfishes were captured during the study period (Table 2). The winter flounder, *Pseudopleuronectes americanus*, was the numerically dominant species (Figs. 4, 5). Juveniles (<22 cm, 2+ age group; Fig. 6) were abundant in shallow water during summer (Fig. 5) and at deep station over hard bottom in Passamaquoddy Bay during winter (Fig. 4). Adult winter flounder were abundant during summer in Passamaquoddy Bay, both inshore and offshore, but rare at the Bay of Fundy site (Fig. 4). During winter they were rare or absent inside Passamaquoddy Bay but common to abundant at the Bay of Fundy station. This pattern reflects the winter movement of this species into offshore water in the northern part of its range (Saila 1961; McCracken 1963; Van Guelpen and Davis 1979), which is probably triggered by temperature. Adults were seldom present in Passamaquoddy Bay when temperatures were below 6°C. McCracken (1963) found a similar relationship between minimum flounder catch-per-effort and minimum temperature. Surges of adult flounder abundance at offshore sites, which coincided with rapid temperature change in spring and fall, were evident in most years (Fig. 4; Tyler 1971) and may have been related to rapid onshore or

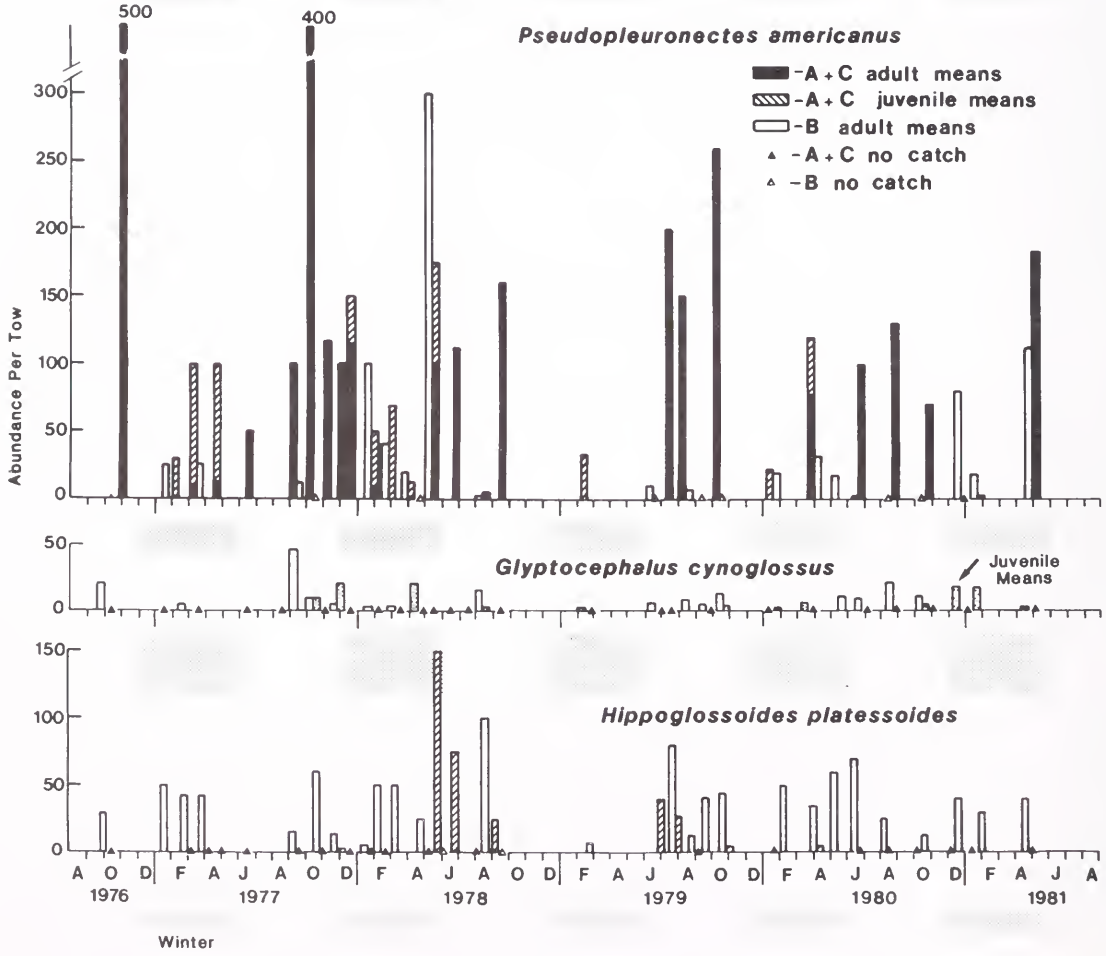

FIGURE 4.—Seasonal occurrence and abundance of juvenile and adult flatfishes (*Pseudopleuronectes americanus*, *Glyptocephalus cynoglossus*, and *Hippoglossoides platessoides*) at offshore station in the Bay of Fundy and Passamaquoddy Bay. For witch flounder (middle) dark bars are adults and lined bars are juveniles at site B. For American plaice (bottom) open bars are site B and lined bars are site C (all juveniles).

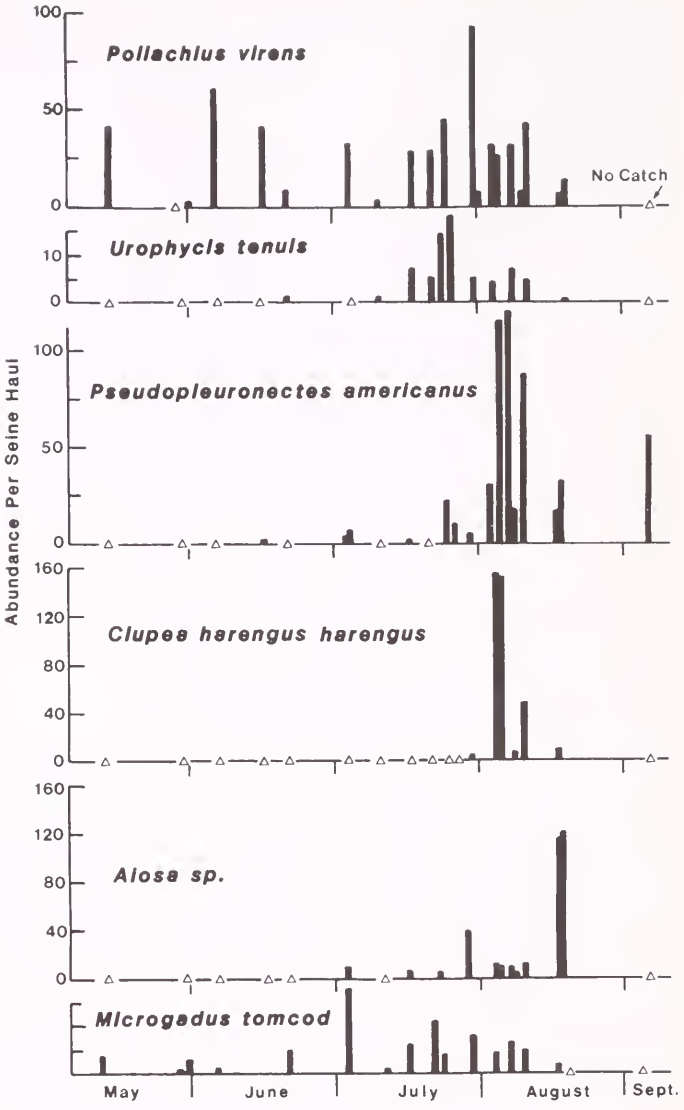

FIGURE 5.—Seasonal occurrence and abundance of fishes captured by seine at beach station 8 from May to September 1981.

offshore movement of the population.

The witch flounder, *Glyptocephalus cynoglossus*, was absent or rare at all times inside Passamaquoddy Bay, but was a regular component at the soft-bottom Bay of Fundy station (Fig. 4). Catches from June to October consisted of large adult witch flounder (30-60 cm, >6+ age group), but catches from November to May were 6-25 cm juveniles (0-6 yr) (Figs. 6, 7). Adult witch flounder on the Scotian Shelf also move from intermediate depths (100 m) in summer to deeper water in winter (Powles and Kohler 1970). Both Powles and Kohler (1970) and Markle (1975) reported juvenile witch flounder from deep water (150-1,000 m) over hard bottom, quite unlike the situation we encountered except for similar temperature regimes. Also, replacement of adults by juveniles during winter seems peculiar to our study, but may have been observed because of year-round sampling.

Juvenile American plaice, *Hippoglossoides platessoides*, were a major summer component of station C and a regular component of the Bay of Fundy station (Fig. 4), both soft-bottom habitats, but was only occasional at the hard-bottom station (A). Age-2 plaice (6-14 cm; Fig. 6) were first captured with our shrimp net in April. By the following year, recruitment to the gear appears complete at an average size for the age-class of 17 cm (Fig. 7). Juvenile plaice are

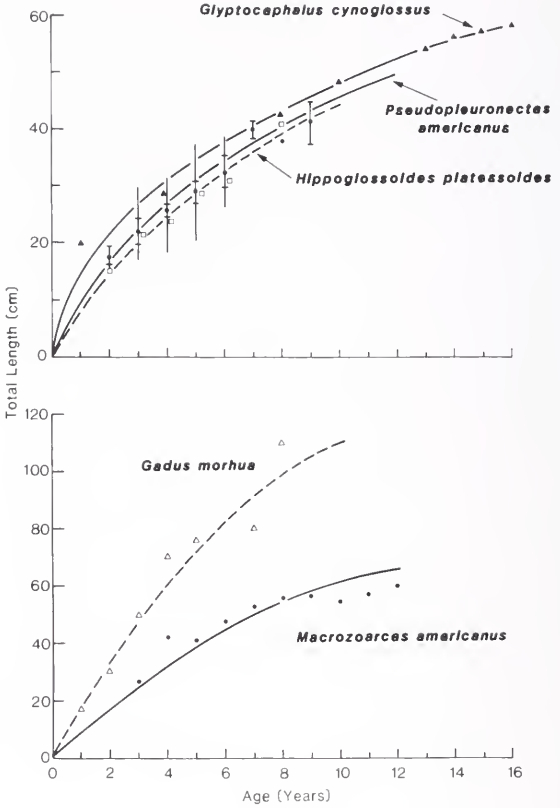

FIGURE 6.—Fish length versus age for five fish species caught at stations A and B; December 1980-June 1981. Lines are fitted by eye.

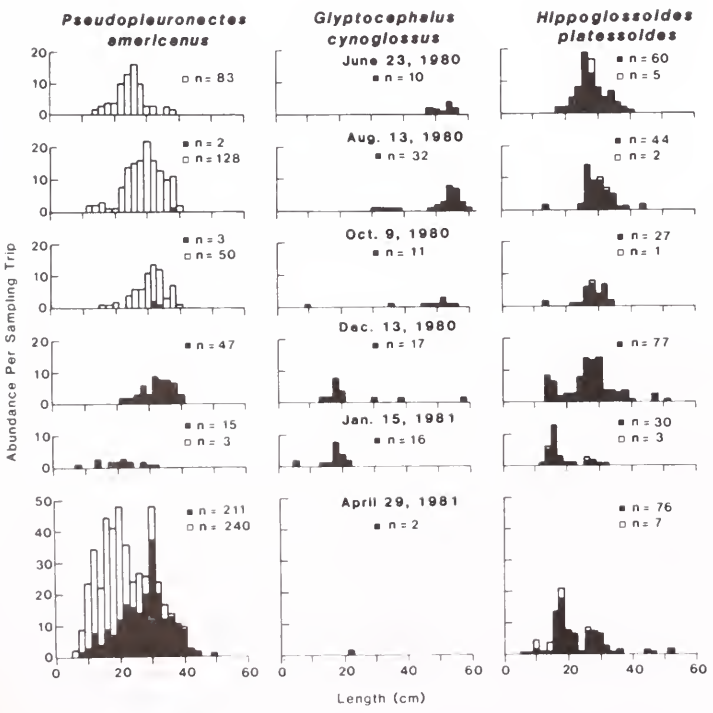

FIGURE 7.—Seasonal size distributions of flatfishes (*Pseudopleuronectes americanus*, *Glyptocephalus cynoglossus*, and *Hippoglossoides platessoides*) from offshore stations in the Bay of Fundy and Passamaquoddy Bay, 1980 and 1981. Shaded area is captures at station B; unshaded, station A inside Passamaquoddy Bay.

sedentary, soft-bottom dwellers, that exhibit little seasonal movement, and migration from nursery ground to adult stock is diffusive (Bigelow and Schroeder 1953; Leim and Scott 1966). However, some seasonal movement does occur when plaice leave soft-bottom, middepth habitat (30 m) for winter and return in summer (present study). Plaice were a regular, low-abundance component at station A in 1965 (Tyler 1971), but we found they were virtually absent between 1976 and 1981. The difference may be attributable to the general decline of groundfish abundance in the Bay of Fundy after 1970 (Hare 1977).

Among other flatfishes, windowpane, *Scophthalmus aquosus*, was a regular component at station C and the smooth flounder, *Liopsetta putnami*, was common among the inshore-estuarine communities during summer (Tables 2, 3). Yellowtail flounder, *Limanda ferruginea*, was a rare member (4-5/tow) of the summer assemblage at station A and occasional at the other two deep stations. Juvenile Atlantic halibut, *Hippoglossus hippoglossus*, was a low-abundance member (2-3/tow) of the winter assemblage at station A. The fourspot flounder, *Paralichthys oblongus*, was captured once at station A during the abnormally warm fall of 1978.

Eight species of gadoid fishes were captured during the study (Tables 2, 3). Adult Atlantic cod, *Gadus morhua*, was an abundant member of the summer component at offshore sites in Passamaquoddy Bay, particularly station A, but was absent from there in winter. It was a common member of the early winter assemblage in the Bay of Fundy but rare thereafter (Figs. 8, 9). During summer, juvenile Atlantic cod (10-20 cm) were captured occasionally while seining beach sites, but were more common in gill net catches at intermediate depth (30 m) inshore (stations 5 and 7; Table 3). The shallow water abundance maxima of

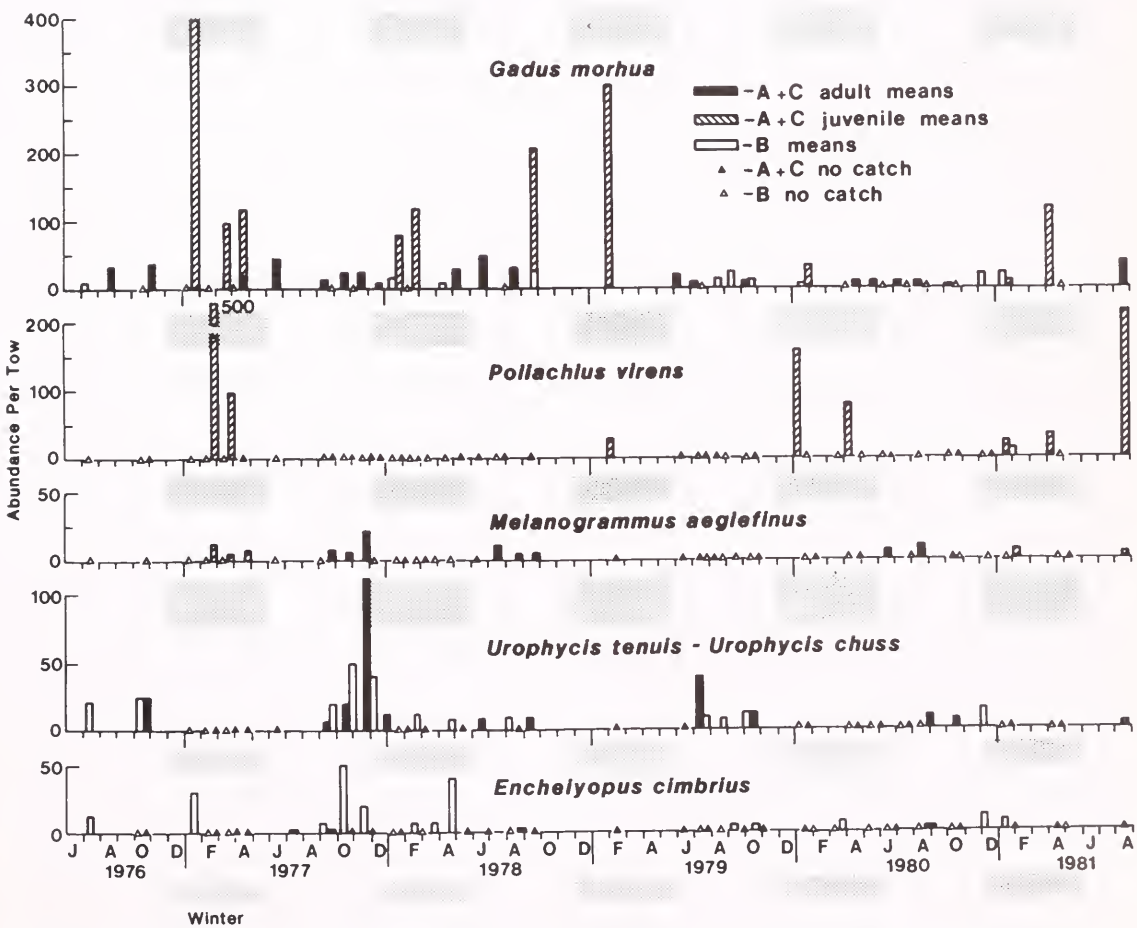

FIGURE 8.—Seasonal occurrence and abundance of gadoids at offshore stations in the Bay of Fundy and Passamaquoddy Bay, 1976-81.

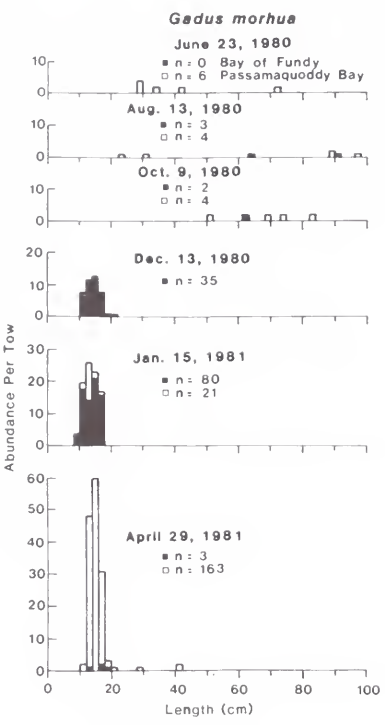

FIGURE 9.—Seasonal size distributions of *Gadus morhua* at station B in the Bay of Fundy and station A in Passamaquoddy Bay, 1980 and 1981.

young cod (0+, 1+, <17 cm) has been previously reported in the western North Atlantic (Schroeder 1930) but is not well documented. On the other hand, this occurrence of young cod in the North Sea is well known (Daan 1978). During winter, juvenile cod were abundant at station A or in colder winters at station B (Fig. 8, 1980 and 1981). Both juvenile and adult cod were more abundant at station A during our study than during 1965 (20-70/tow, Tyler (1971); 1976-81, 50-400/tow).

Haddock, *Melanogrammus aeglefinus*, were never abundant during our study. Adults were captured only at the hard-bottom station A during summer (Fig. 8) and juvenile haddock (1+) were occasionally captured at the same site in winter. Catches of haddock declined from a maximum of 25/tow to <5/tow during the study period (Fig. 8). However, up to 260 haddock/tow were caught at station A during 1965 (Tyler 1971). Decline in abundance after 1965 might be the cause for the collapse of the Gulf of Maine haddock stock in 1970 (Hare 1977; Clark et al. 1982).

Only juvenile pollock, *Pollachius virens*, were captured during the study. Pollock of the annual year class (0+) were either rare or extremely abundant at beach sites (100+/seine haul) in a given year, depending perhaps, on the size of the annual year class. Pollock dominated beach catches during early summer but disappeared from this region by September (Fig. 5). In years when 0+ pollock were abundant along the beach in summer, members of the same year class were also abundant the following winter at station A (1976-77, 1981) and, in summers of low abundance on the beach, they were correspondingly rare offshore in winter (1977-78; Fig. 8). Large numbers of pollock larvae were present in the plankton during March 1979 (Scott 1980), and we again encountered large number of 0+ juveniles at station A in the winter of 1979-80. Present findings suggest there may have been three large year classes produced during our study period, 1976, 1979, and 1981.

Adult white, *Urophycis tenuis*, and red, *U. chuss*, hakes were common summer components at offshore stations A and B (Markle et al. 1982). Juvenile white hake (<15 cm) were a summer component at beach stations (Fig. 5), but were rarely captured thereafter and only then at offshore sites in winter. Also in 1965 few small hake were captured after December (Tyler 1971). Apparently hake leave Passamaquoddy Bay in winter (Markle et al. 1982). In the present study, the one time hake were observed during winter was at station B in the Bay of Fundy (Fig. 8).

The fourbeard rockling, *Enchelyopus cimbrius*, was a regular component at station B in the Bay of Fundy and occasional in summer at station A (Fig. 8). The mesh size of our gear was just small enough to capture large individuals of this species, and it was probably more abundant than indicated. Larval rockling were a rare summer component of inshore sites (Table 4). Battle (1930) and Tyler (1971) both considered rockling a summer occasional in Passamaquoddy Bay, occurring there during spawning migration. Tyler's catch rate at station A (2-3/tow) was similar to ours at that site. Larger catch rates at station B (10-50/tow) may be due to rocklings preference for soft-bottom habitat (Bigelow and Schroeder 1939).

Silver hake, *Merluccius bilinearis*, was often the most abundant gadoid found at offshore stations during summer, and juveniles were a regular component at station B year round (Fig. 10). Large numbers of adult silver hake were present during fall (Fig. 10) in company with other migratory summer occasionals, including American shad, *Alosa sapidissima*; spiny dogfish, *Squalus acanthias*; and butterfish, *Poronotus triacanthus*. All these fishes may carry out counterclockwise spring to fall migrations around the Bay of Fundy similar to the shad (Dadswell et al. 1983).

The Atlantic tomcod, *Microgadus tomcod*, was a regular component of the inshore assemblage and was particularly abundant at beach sites during early summer (Fig. 5) and in estuaries in early winter (Table 3).

Clupeids and osmerids made up a major portion of

TABLE 4.—Catch of fishes at intertidal seining station 3 (Brandy Cove) during period May 1976-November 1977. Fish captured during three 5-min seine hauls (100 × 15 m) ([j] = juvenile; [l] = larvae).

Species	1976							1977								
	15/05	14/06	13/07	18/08	15/09	10/10	08/12	15/02	20/03	10/04	30/05	29/06	15/07	18/09	10/10	17/11
Raja radiata [j]	—	—	—	—	—	1	—	—	—	—	—	1	—	1	2	—
R. ernacea [j]	—	4	—	—	—	—	—	—	—	—	—	1	—	—	—	—
Alosa pseudoharengus	—	—	—	—	25	2	—	—	—	—	—	—	—	4	—	—
Clupea harengus	—	—	2	2	—	—	—	—	—	—	2	—	15	10	—	—
Salmo salar [j]	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
Osmerus mordax	3	—	—	11	—	5	1	—	—	4	—	—	3	—	6	4
Fundulus heteroclitus	—	—	—	—	—	—	5	3	1	—	—	—	—	—	—	1
Gasterosteus aculeatus	—	5	51	5	2	4	—	—	—	5	26	32	5	27	3	—
G. wheatlandi	—	—	1	—	—	—	—	—	—	—	—	3	1	—	—	—
Enchelyopus cimbrius [l]	—	—	—	2	1	—	—	—	—	—	—	—	—	3	—	—
Gadus morhua [j]	—	—	—	1	—	—	—	—	—	—	—	—	2	—	—	—
Microgadus tomcod	1	2	3	—	—	—	—	—	4	8	—	3	—	2	—	—
Pollachius virens [j]	115	132	15	12	2	—	—	—	—	2	—	—	—	—	—	—
Urophycis tenuis [j]	—	1	2	—	—	—	—	—	—	—	3	6	11	—	—	—
Scomber scombrus	- - -observed never captured - - -															
Pholis gunnellus	—	1	2	—	—	3	1	1	—	4	—	2	3	1	2	—
Cyclopterus lumpus	—	1	—	—	—	2	—	—	—	—	—	1	2	—	—	—
Myoxocephalus aeneus	1	—	—	—	—	1	—	—	—	—	1	1	—	3	—	1
M. scorpius [j]	—	—	—	—	—	—	1	—	—	—	2	—	—	—	—	—
M. octodecemspinosus [j]	—	3	—	—	—	2	—	—	1	—	—	—	—	3	1	1
Hemitripterus americanus	—	1	—	1	—	1	—	—	—	—	1	—	—	—	—	—
Pseudopleuronectes americanus	—	10	9	—	4	—	3	—	—	—	12	22	8	2	—	2
Liopsetta putnami	—	—	1	—	—	—	—	—	—	—	—	2	—	—	—	—
Menidia menidia	1	—	—	3	—	—	15	4	1	—	—	—	—	—	2	4

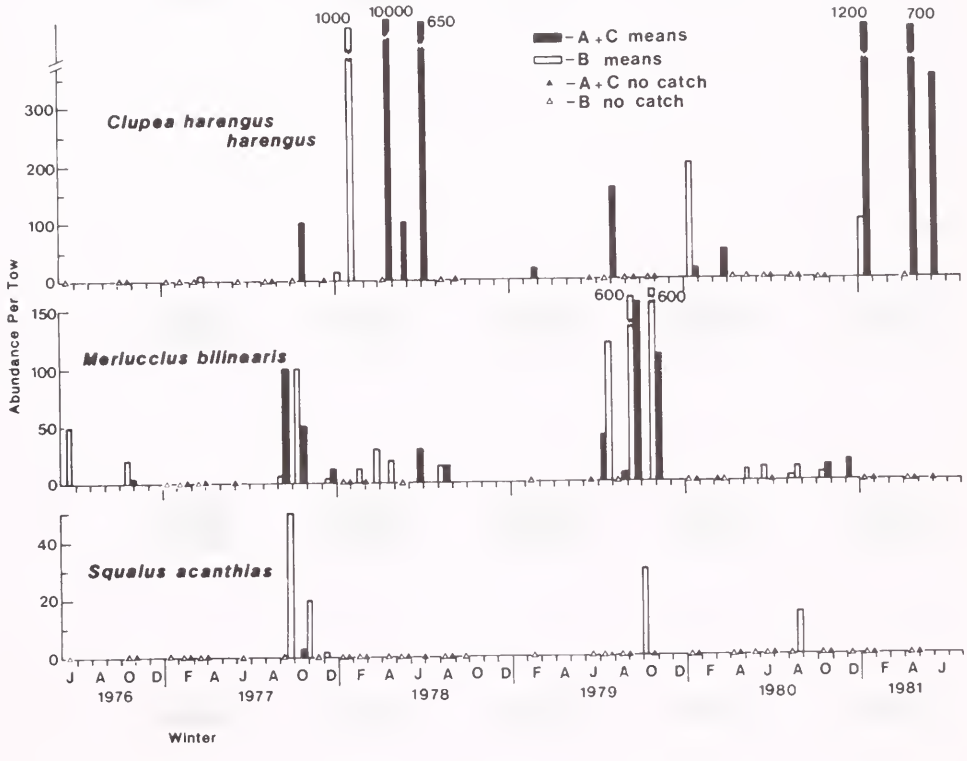

FIGURE 10.—Seasonal occurrence and abundance of pelagic fishes and dogfish at offshore stations in the Bay of Fundy and Passamaquoddy Bay, 1976-81.

the fishes caught at inshore sites (Table 2). At beach station 8, alewives, *Alosa pseudoharengus*; Atlantic herring, *Clupea harengus harengus*; and American smelt, *Osmerus mordax*; appeared in mid-July and increased in abundance during August (Fig. 5). Herring were abundant in estuaries during summer and were replaced there by smelt in winter (Table 3). Large American smelt were present at offshore sites in Passamaquoddy Bay in mid-summer as observed by Tyler (1971). During most winters, juvenile Atlantic herring (10-20 cm) were abundant at offshore sites, particularly inside Passamaquoddy Bay at intermediate depths (station C; Fig. 10). Catches were variable, possibly because of schooling behavior (Brawn 1960). Tagging experiments indicate herring move from inshore during summer to deeper water in winter (McKenzie and Tibbo 1961).

Six species of sculpin (Table 2) were commonly encountered at offshore station of which two—longhorn sculpin, *Myoxocephalus octodecemspinosus*, and sea raven, *Hemitripterus americanus*—were abundant, regular components (Fig. 11). Juveniles of most species were common at beach sites in summer (Table 4) and at station A in winter (Table 2). Increases in abundance of longhorn sculpins at station B during winter were observed (Fig. 11) and may be the result of migration out of Passamaquoddy Bay. Two small species, Arctic hookear sculpin, *Artediellus uncinatus*, and mailed sculpin, *Triglops murrayi*, were winter occasionals at station A. They were perhaps more abundant than catch rates indicated (2-5/tow) because their maximum size range was at the lower limit of catchability for our trawl.

The blennioid-like fishes were represented by seven species (Tables 2, 3) of which ocean pout, *Macrozoarces americanus*, was regular at offshore stations in Passamaquoddy Bay (Fig. 11), and rock gunnel, *Pholis gunnellus*, was a regular component at beach sites (Table 4). Ocean pout abundance in Passamaquoddy Bay was generally highest in early summer and declined thereafter (Tyler 1971; Fig. 11). Abundance of ocean pout usually increased at station B in late summer and fall, suggesting movement from Passamaquoddy Bay to the Bay of Fundy.

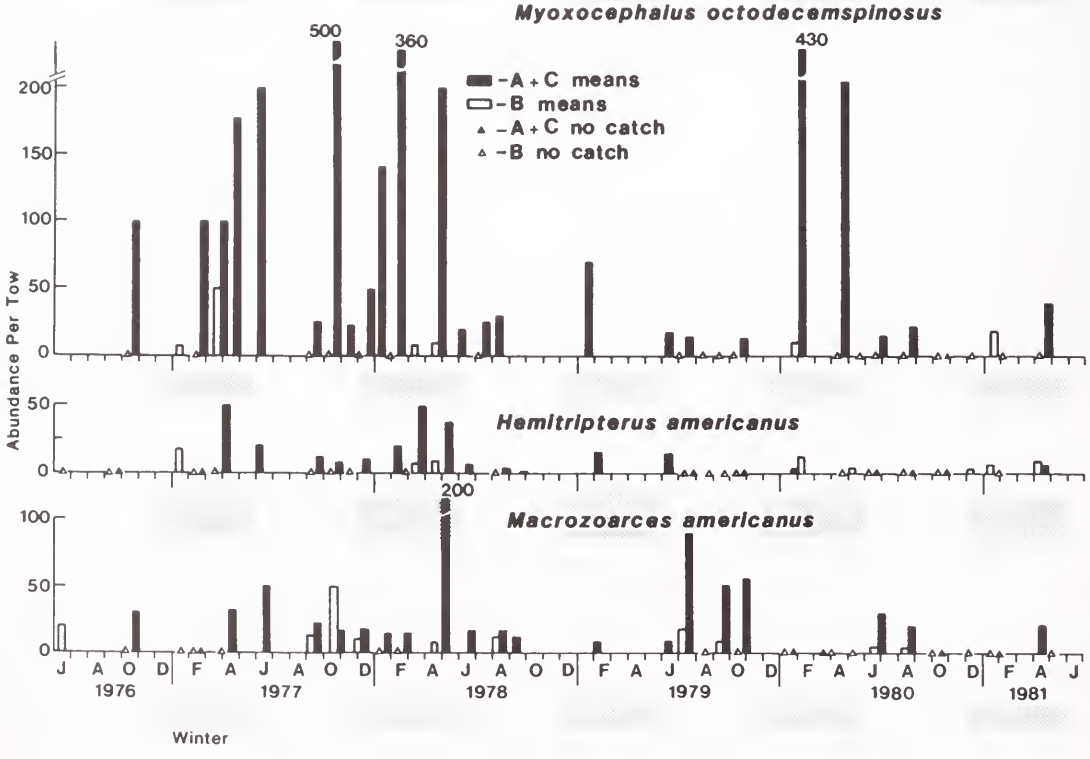

FIGURE 11.—Seasonal occurrence and abundance of sculpins and ocean pout at offshore stations in the Bay of Fundy and Passamaquoddy Bay, 1976-81.

It may be a response to avoid warm temperatures (Olsen and Merriman 1946). Movement of ocean pout is generally thought to cover only short distances (Orach-Maza 1975; Sheehy et al. 1977).

Other blennioids occurred infrequently at station A (Table 2). Selectivity of our shrimp trawl may have been a factor in these low catches. One species, radiated shanny, *Ulvaria subbifurcata*, which was thought to be rare in Passamaquoddy Bay (Leim and Scott 1966), was often captured (5/tow) at station A during winter. Scuba searches during summer revealed radiated shanny were abundant inshore, under rocks in 6-9 m of water (Dadswell and Melvin, pers. obs.).

Five species of skate were captured during the study (Table 2): Two species, thorny skate, *Raja radiata*, and smooth skate, *R. senta*, were common, regular components of the offshore site in the Bay of Fundy; two little skate, *R. erinacea*, and winter skate, *R. ocellata*, were regular components of station A in Passamaquoddy Bay; and one species, the barndoor skate, *R. laevis*, was encountered occasionally at station B. The species cooccurrences of skates and their habitat selection are as described by McEachran and Musick (1975). Some seasonal movement into Passamaquoddy Bay was exhibited. Abundance of smooth and thorny skates at station A increased during summer and declined after late fall. Juveniles of thorny, little, and winter skates were often captured at beach sites during summer (Table 3).

Several smaller fishes were captured at inshore sites only, but again this may be an artifact of sampling gear. Threespine stickleback, *Gasterosteus aculeatus*, was a regular component at most beach sites (Table 4). Other sticklebacks were more or less confined to estuarine areas (Table 3). Mummichog, *Fundulus heteroclitus*, and Atlantic silversides, *Menidia menidia*, occurred mainly in estuaries during summer but were part of the winter community at beach sites (Table 4).

Assemblages and Diversity

Species assemblages in the study area varied according to site and season. If juveniles and adults of some dominant species are considered as separate taxonomic units (Table 2), calculated coefficients of community show similarity between similar habitat types (e.g., soft bottom) at a given season, and between the summer assemblage of one habitat and the winter assemblage of the next seaward habitat (Table 5). In general, movement of assemblages was from inshore in summer to offshore in winter with some return movement in spring (Fig. 12). Some species, however, exhibited a partial reverse of this pattern (Atlantic tomcod, ocean pout).

Specific groupings of fish were segregated among the available habitats according to season. The "estuarine" assemblage was dominated by warmwater, euryhaline species, including sticklebacks, Atlantic silversides, mummichogs, and juvenile clupeids. Most of this group moved to adjacent, inshroe marine habitat in winter (Tables 3, 4), but Atlantic tomcod and American smelt moved in the reverse direction to form a winter estuarine group (Table 3).

The summer "beach" assemblage consisted of regulars such as threespine stickleback and rock gunnel and a summer component including juvenile gadids, juvenile sculpins, flounders, and juvenile alosids. Juvenile gadids (pollock, white hake, and Atlantic tomcod) were most abundant in early summer but were replaced by steadily increasing numbers of clupeids in late summer (Fig. 5). Numerous other postlarval and juvenile fishes, including fourbeard rockling and lumpfish, *Cyclopterus lumpus*, appeared in the beach zone during the summer (Table 3). In late fall, most of this assemblage left the beaches and occupied offshore sites in Passamaquoddy Bay. Atlantic herring concentrated at the soft-bottom station C and the gadids, sculpins, and winter flounder (juveniles) at the hard-bottom station A. Threespine stickleback and rock gunnel

TABLE 5.—Coefficients of community among seasonal fish assemblages in the lower Bay of Fundy.

					Seaward					
	Estuarine winter	Estuarine summer	Beach winter	Beach summer	C winter	C summer	A winter	A summer	B winter	B summer
Estuarine winter	—	10.0	20.0	7.0	0.0	12.5	0.0	2.0	0.0	0.0
Estuarine summer	—	—	50.0	12.5	20.0	0.0	0.0	0.0	0.0	0.0
Beach winter	—	—	—	6.6	14.3	3 8	4 2	0.0	0.0	0.0
Beach summer	—	—	—	—	6.6	33.3	36.1	17.3	21.2	0.0
C winter	—	—	—	—	—	12.5	4 2	5.7	6.6	0.0
C summer	—	—	—	—	—	—	4 8	40.0	40.0	47.0
A winter	—	—	—	—	—	—	—	20.9	43.0	26.3
A summer	—	—	—	—	—	—	—	—	36.4	42.8
B winter	—	—	—	—	—	—	—	—	—	25 8

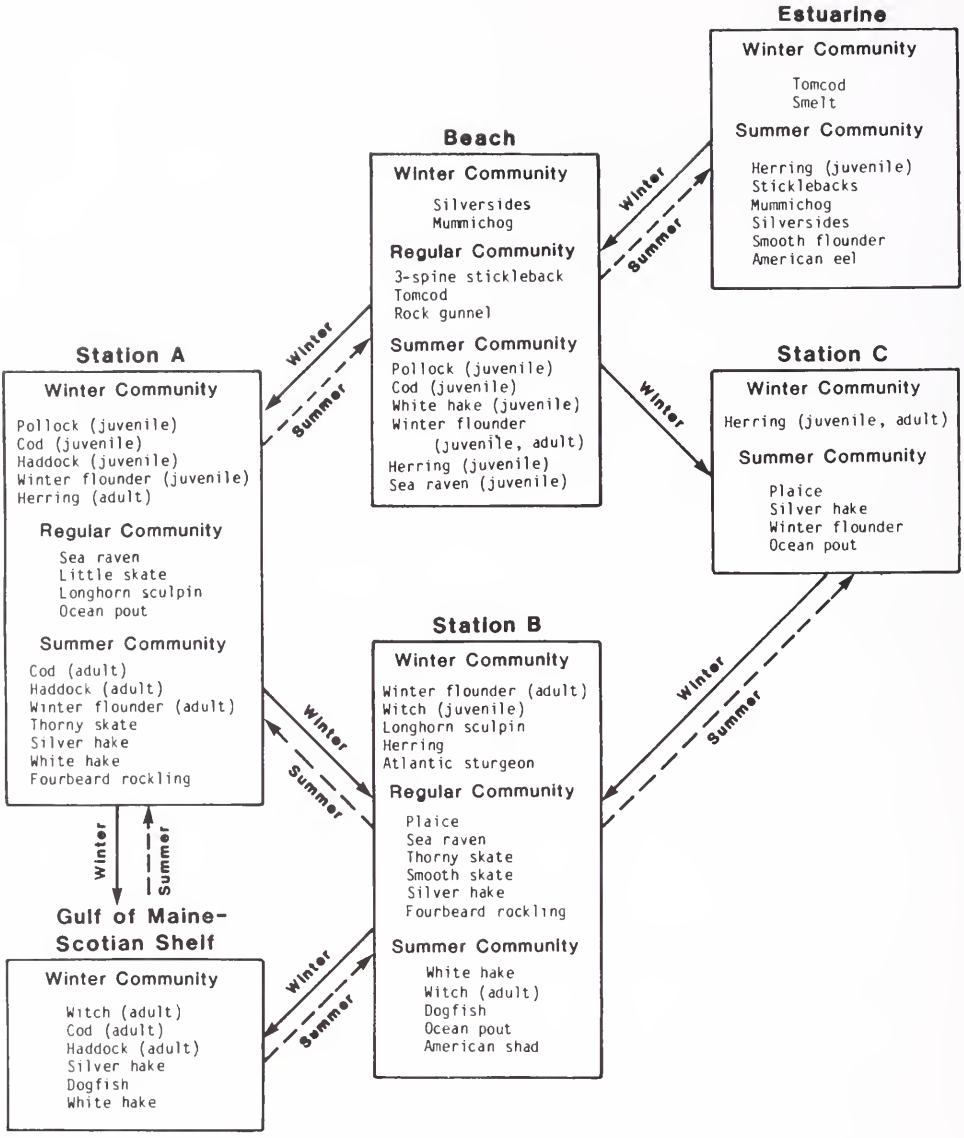

FIGURE 12.—Communities of fishes occurring at each site divided into summer component (SC), winter component (WC), and regular component (RC). Arrows indicate direction of seasonal movement.

remained at beach sites over winter and were joined by Atlantic silversides and mummichog to form a winter assemblage (Table 4).

During summer an "offshore, hard-bottom" assemblage consisting of adult gadids (Atlantic cod, haddock, white and red hake), adult flounders (winter yellowtail), ocean pout, adult sculpins, and skates assembled inside Passamaquoddy Bay. Sea raven, longhorn sculpin, ocean pout, and little skate remained at this site over winter and were joined by juvenile fishes from the beach zone. The other species apparently move to offshore sites in the Bay of Fundy and/or to the Scotian Shelf (McCracken 1959; Wise 1962; Edwards 1965; Kulka and Stobo 1981).

The "offshore, soft-bottom" assemblage consisted of American plaice, witch flounder, white hake, fourbeard rockling, and skates as described by Bigelow and Schroeder (1939). This group at station B was the most stable assemblage studied and had the largest regular component. Conversely, similar assemblages which occurred at the shallower, soft-

bottom station C were the most seasonally dynamic (Fig. 12). Adult witch flounder and most hakes left station B in winter for grounds further offshore in the Gulf of Maine (Powles and Kohler 1970; Kulka and Stobo 1981), and this site was occupied by adult winter flounder and longhorn sculpin, perhaps from inside Passamaquoddy Bay or other adjacent inshore sites (McCracken 1963).

Superimposed on the two offshore, essentially benthic fish assemblages was a seasonal semipelagic component. In summer, silver hake was the numerically dominant species. During fall, diversity increased with the arrival of spiny dogfish, butterfish, and American shad. In winter, Atlantic herring numerically dominated the pelagic component at all offshore sites (Fig. 12).

Diversity, expressed simply as number of species captured, varied appreciably at beach sites during the year. Diversity was 2-5 species in winter-spring, 9-13 species in summer, and 4-6 species in fall-winter (Fig. 13). Total number of species captured at inshore sites was 35, compared with 51 species captured at offshore sites.

Diveristy of assemblages at deep offshore sites (80+ m) was more stable on an annual basis because of the seasonal influx and departure of species from and to adjacent habitats (Fig. 14). Species number varied between 7 and 17 fishes at station B and 7 and 20 fishes at station A, fluctuating about a mean of 12/sampling trip. During 1965, Tyler (1971) observed a higher mean diversity of 17 species/trip at station A with a maximum occurrence of 24. The difference between his observations and ours may be accounted for partially by the decline in haddock abundance

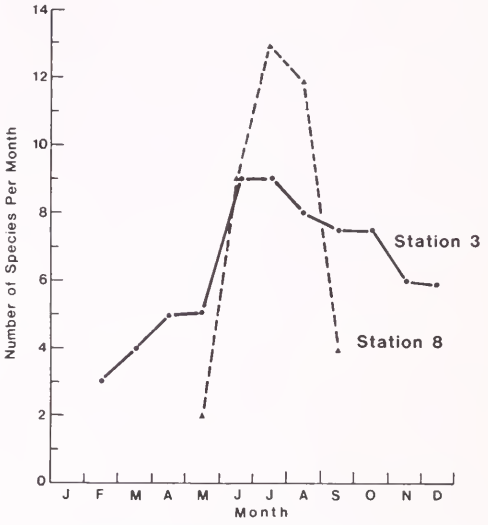

FIGURE 13.—Monthly diversity of fishes at intertidal stations 3 and 8 in Passamaquoddy Bay. Species/month for station 3 is mean of 1976 and 1977 samples.

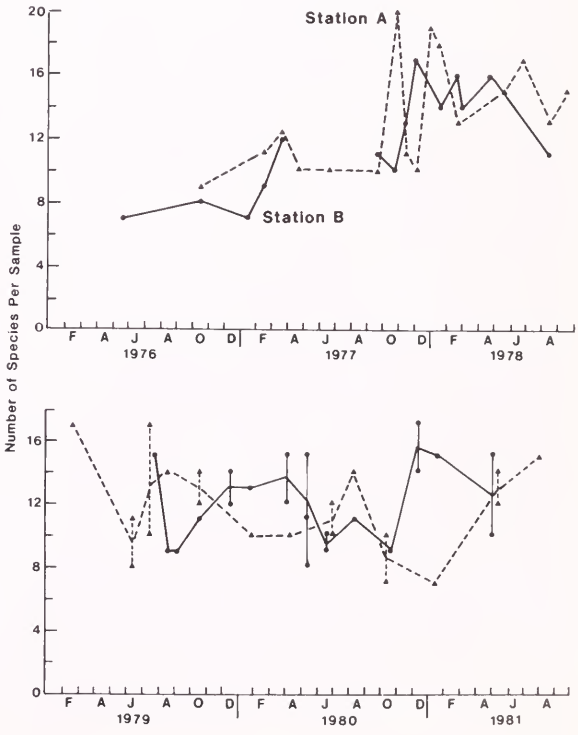

FIGURE 14.—Seasonal diversity of fishes at station A (Passamaquoddy Bay) and station B (Bay of Fundy). Vertical bars represent the range among replicated collections.

since 1965 and the recent absence of American plaice from this site, and partially by his use of a 0.6 cm cod end liner, which would have retained small, occasional species more often than our 2.5 cm cod end.

Highest diversities occurred during winter at station B and during summer at station A (Fig. 14) as a result of seasonal exchange between these sites and the arrival of periodics. The highest diversities recorded during the study period occurred at station A during the fall, coinciding with maximum annual temperatures (Fig. 2). Diversity at station C, the mid-depth site, decreased from 13 species in May 1978 to 4 species in May 1980, perhaps in response to a general decline in lower Bay of Fundy temperatures during the study period (Fig. 3).

GENERAL DISCUSSION

Most authors have related the occurrence and distribution of adult benthic fishes in the North Atlantic to substrate type and temperature (Edwards 1965; Colton 1972; McEachran and Musick 1975; Scott 1976) and have shown that there is a marked seasonal variation (Lux and Nichy 1971; Jeffries and Johnson 1974). Our findings agree and suggest yearly differences at the same site for a given time may be influenced mainly by annual ocean climate pertubation. Species occurrence and abundance appeared to change in response to seemingly small changes in temperature. Jeffries and Johnson (1974) reported a similar observation concerning winter flounder abundance over a 7-yr period in Narragansett Bay. Pelagic and semipelagic species (Atlantic herring, silver hake) demonstrated little or no substrate preference. Occurrence was apparently related to annual migratory behavior.

Seasonal movements of the various species was largely from an inshore, shallow-water locality in summer to an offshore, deepwater locality in winter with a reverse movement occurring in spring. Cause of this movement may have a large physiological component related to temperature effects on the osmoregulation of marine fishes (Potts and Parry 1964). In the southern part of their range, fish such as winter flounder migrate onshore in winter (Bigelow and Schroeder 1953) in response to availability of preferred temperature but never encounter the low temperatures found at northern latitudes. Atlantic tomcod, a species known to produce an antifreeze in its blood (Fletcher et al. 1982), was one of the few fishes exhibiting onshore migration to lower salinities during winter in this area. For many species (pollock, Atlantic herring, white hake), migration from inshore habitat to offshore is unidirectional for the individual, since each year the beach community consists of the new 0+ year class. For other species (winter flounder, juvenile sculpins, radiated shanny), the return inshore is an annual occurrence, triggered perhaps as much by resource availability and predator avoidance as by physiology.

Tyler (1971) concluded that in Passamaquoddy Bay movements of large fish independent of the small individuals of a species were not evident for fishes other than hake, but we found obvious differences in size-class distributions and abundance between summer and winter populations of winter flounder, witch flounder, Atlantic cod, and pollock at offshore sites and a complete lack of most fish inshore. This suggests marked segregation between juveniles (at least 0+ age group) and adults for these species. The use of shallow water habitat as nursery area by fishes of commercial important in the Canadian North Atlantic has received little attention. In Europe, this fact has been amply demonstrated for many fish species, including Atlantic cod and pollock (Zijlstra 1972; Daan 1978; Burd 1978; Rauck and Zijlstra 1978). The use of beach habitat as nursery by these fishes makes them susceptible to coastal pollution impacts and puts their adult fisheries at risk to coastal degradation and development.

Decline in haddock abundance in Passamaquoddy Bay since 1965 coincides with increased numbers of Atlantic cod. However, previous studies indicate little interaction between these two species (Tyler 1972; Jones 1978). Catches in 1965 (Tyler 1971) coincided with the largest haddock abundance on record (Clark et al. 1981). Fishermen in Passamaquoddy Bay may only catch haddock consistently during years preceded by large recruitment on Georges Bank, the Scotian Shelf, and the Gulf of Maine.

In the Bay of Fundy region, fish assemblages are segregated according to habitat and, although fish movement is influenced by seasonal climatic regime, assemblages appear cohesive through time. In summer, fishes assembled and exploited the available resources as members of 1) estuarine, 2) beach, 3) offshore, hard-bottom, 4) offshore, soft-bottom, and 5) migratory-pelagic assemblages. With winter, movement of species and/or age groups resulted in different seasonal assemblages in each habitat, but major groupings remained essentially intact and replaced each other seaward. The reverse movement occurred in spring. A large portion of benthic and pelagic components occurring at the offshore, hard-bottom habitat were migratory. In contrast, the offshore, soft-bottom assemblage was more sendentary. Smaller seasonal variation in the water tem-

perature at the Bay of Fundy, soft-bottom site, and the greater seasonal stability of invertebrate food resource production in this type of habitat (Wildish and Dadswell in press) may also be important. The dynamic nature of the hard-bottom community, particularly among commercially valuable species, emphasizes the need for well-designed, seasonal sampling programs in order to properly assess the occurrence of species and abundance of fish stocks in a local area. Long-term changes are apparent from annual assessment data (Brown et al. 1973), but higher resolution surveys at "type" localities are needed to properly determine causative factors, whether physical or biological.

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THE DETECTION AND DISTRIBUTION OF LARVAL ARCTO-NORWEGIAN COD, *GADUS MORHUA*, FOOD ORGANISMS BY AN IN SITU PARTICLE COUNTER

S. TILSETH AND B. ELLERTSEN[1]

ABSTRACT

An in situ particle counter system was developed to count measure food particles in numbers per liter within the size range 150-600 μm, the sizes of copepod nauplii captured by first feeding cod larvae. Patches of particles/nauplii of 50-100 per liter were found in the spawning and larval first feeding area. Different sizes of copepod nauplii showed diel vertical migration, and this influenced the formation of patches. Mixing of the water column by wind forces created a homogeneous vertical distribution of particles. Gut content analysis of cod larvae during these hydrographical conditions indicated reduced accessibility of food organisms to larvae.

During the last few years fisheries scientists have done a great deal of laboratory work on the behavior of fish larvae and their energy requirements for growth and survival (Hunter 1972; Laurence 1974; Lasker and Zweifel 1978; Houde 1978; Werner and Blaxter 1980). A review of these data (Hunter 1981) shows that differences exist between the required density of prey particles for first feeding larvae to survive and the densities found in the sea. Since pelagic fish larvae are successful in their environment, it is recognized that there must be patches of suitable concentrations of food organisms for first feeding larvae (Lasker and Zweifel 1978). This has been demonstrated for the northern anchovy, *Engraulis mordax*, in laboratory experiments by Hunter and Thomas (1974) and in a series of field investigations by Lasker (1978). Houde and Schekter (1978) have shown increased survival of larval bay anchovy, *Anchoa mitchilli*, and sea bream, *Archosargus rhomboidalis*, when exposed to simulated food patches in a laboratory experiment.

This work has been stimulated by Hjort's (1914) hypothesis which simply stated that larval mortality rates may be due to variable feeding conditions at a critical stage, which in turn causes variations in year-class strength. It has been difficult to test this simple hypothesis in field surveys because of the inadequacy of the sampling gear used (May 1974). To obtain a better understanding of the relationship between estimates of food densities required by fish larvae in the laboratory and densities found in the open sea, samples should be taken which are relevant to larval searching behavior. This would require an enormous number of plankton samples. It would be time-consuming to obtain these samples with conventional plankton gear. Furthermore, water movement and dispersion would make it difficult to obtain time and space relationships for studying the formation and dynamics of plankton patches (Steele 1978). One way of studying these relationships is by using in situ instruments (Boyd 1973; Pugh 1978; Tungate and Reynolds 1980).

In this study an instrument designed to count and measure particles in situ in the size range of food organisms most frequently captured by cod larvae was used. Investigations were made on the spawning and first feeding grounds of the Arcto-Norwegian cod, *Gadus morhua* Linnaeus, during two successive years (1980-81). During the first survey, investigations were made in a sheltered fjord where cod larvae are known to appear in high numbers (Ellertsen et al. 1977) and where the current system has been described (Furnes and Sundby 1981). The objective was to find and study the formation of microzooplankton patches and to study larval cod feeding under different environmental conditions with regard to food density, water turbulence, etc. In the following year, the main first feeding area, an open ocean bay, was surveyed in order to find and study the vertical and horizontal distribution of microzooplankton patches in this exposed area.

The present study is part of a project, started in 1975, dealing with growth, mortality, and drift of cod larvae in the Lofoten area (Ellertsen et al. 1976).

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MATERIALS AND METHODS

The Particle Counter

The in situ particle counter system was built and described by Mohus (1981), Eriksen (1981), and Eriksen and Mohus (1981). It is presented schematically in Figure 1. The system is based on a Hiac PC-320 Particle Counter[2] which works on the principle of light blockage. The sensor (E-2500, dynamic range 80-2500 μm) is installed in a pressure-proof box together with a depth detector. A pump is connected to the sensor, and the sensor and pump are mounted to a rig which is lowered into the sea by winch. Seawater is pumped through a 60 cm long by 2.5 cm diameter hose through the sensor orifice (3 mm), at a flow rate of 6.15 l/min. Particles are counted by the Hiac PC-320 Particle Counter and depth is monitored by the depth detector unit. The "Micro-count" datalogger unit contains an input-output interface to accomodate incoming data, a large internal data storage area, operator communication via a small CRT display, a keyboard, and a microprocessor with program to control the system. The microcomputer samples data from the Hiac PC-320 Particle Counter and the data sample time can be selected from 1 to 99 s. Finally, a Silent 733 terminal is connected to the microcomputer. This terminal contains a full text keyboard and a page printer used for initial operator communication and printout of data tables. Two cassette tape stations are included in the terminal.

The system operates from the surface to 50 m depth, and the registration of particles is presented on the TV monitor as the sensors are lowered into the sea. The vertical distribution of particles can be presented on the monitor at 1, 2 , or 5 m depth, depending on the selected depth intervals. Data are, however, printed out in 1 m depth intervals from the surface to 50 m depth as concentration of particles per liter in six different size groups (150-600 μm) on the Silent 733 terminal immediately after the samples have been made. An in situ particle profile is

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

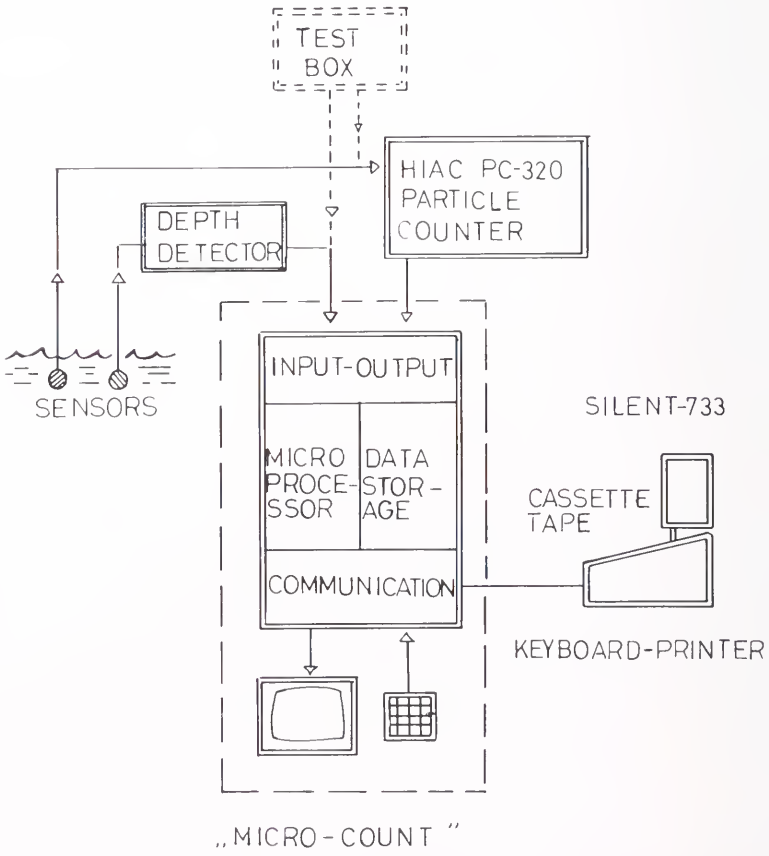

FIGURE 1.—The particle counter system.

defined in the present paper as the concentration of particles within the size range of 150-600 μm from the surface to 50 m depth in 1 m depth intervals.

An object found in the Hiac sensor was measured so that the largest projected area was converted to a circle of the same area. By calibration, the object was given a length similar to the diameter of this circle.

The contours of *Artemia* nauplii were drawn by using a microscope drawing tube. Their areas were estimated by planimeter and converted to areas of circles and their diameters calculated. Their size distribution was then divided into four 50 μm length groups of 200 to 400 μm. Four of the Hiac Particle Counter channels were set according to the sensor calibration diagram to the corresponding size groups.

The instrument system was tested and calibrated in the laboratory by comparing microscope and Hiac measurements of the size-frequency distribution of a sample of laboratory hatched *Artemia* nauplii. Tests were also made at sea when the research vessel was anchored. The in situ instrument data were compared with plankton pump samples taken simultaneously. These samples were taken by a submersible electric pump (Flygt 2051, 250 l/min) which pumped samples on deck through a 50 m long by 5 cm diameter hose. Samples were taken at 0, 2.5, 5, 7.5, 10, 12.5, 15, 20, 25, 30, and 40 m depths. This is defined as a zooplankton pump profile. Seawater was collected in calibrated tanks (23.7 l), and zooplankton were filtered through 90 μm mesh plankton nets. Zooplankton were identified and counted by microscope, the whole sample (23.7 l) was counted. Results of the samples from these 11 depths were statistically compared with the in situ counts from corresponding depths by paired *t*-tests.

Field Investigations

The main objectives of field investigations were to use the in situ instrument system to find particle patches and to identify larval cod food organisms and study their vertical distribution. Observations were made in the Lofoten area (Fig. 2). The effect of wind driven turbulence on the distribution of particles and the consequences on larval cod feeding incidence were studied in the Austnesfjord (Fig. 3), which is in the main spawning area of the Arcto-Norwegian cod. Stations and sections in the Austnesfjord are shown in Figure 3. A section is a transect with a series of stations. Austnesfjord was chosen because cod larvae are known to appear in high numbers (Ellertsen et al. 1977), and the dynamics of the current system are known (Furnes and Sundby 1981). During the 1980 cruise, a Wolfe wind recorder was placed on land in the fjord to continuously measure wind velocity and direction.

In 1981, observations were also made in the main first feeding area, an open ocean bay (Fig. 2), for cod larvae. The objectives were to find these food particle patches for cod larvae and to investigate the extent and densities of these patches in this exposed area.

Distribution of cod larvae in the first feeding areas was studied from the Juday net (80 cm, 375 μm mesh) samples taken in vertical hauls from 30 to 0 m. In the Austnesfjord, three stations were taken on eight sections (Fig. 3). The vertical distribution of cod larvae in the Austnesfjord was investigated only when the ship was anchored. A total of 42 samples were taken by a submersible electric pump (Flygt B2125, 3.4 m^3/min) at 5, 10, 15, 20, 25, 30, and 35 m depths every 3 h from 1600 h 13 May to 1000 h 14 May 1980. Fifteen cubic meters of seawater was sampled at each depth. Seawater was pumped through a 40 m long by 15 cm diameter hose and filtered through a Juday net (40 cm, 180 μm mesh) into a large tank on deck. Cod larvae were preserved in 4% Formalin in 10‰ seawater solution. Gut contents of

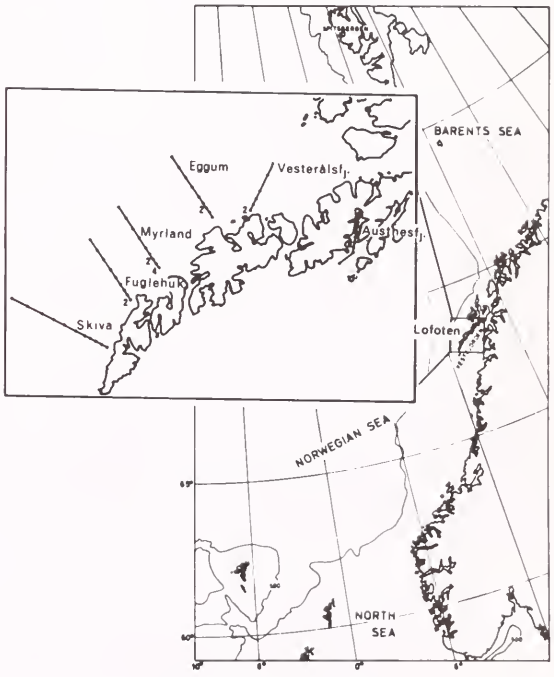

FIGURE 2.—Map of the Lofoten area with stations and sections 21 April-8 May 1981. The figures on the stations refer to number of cod larvae/m^2 surface.

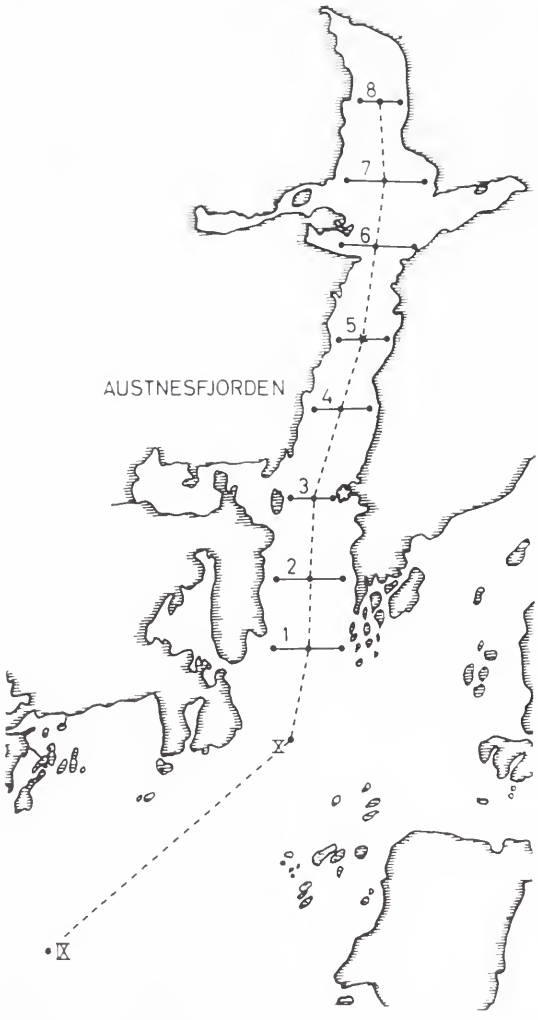

FIGURE 3.—Map of the Austnesfjord with stations. ● Juday net and particle/zooplankton stations, position of the 24 h station ★, and the Wolfe wind recorder ☆.

about 20 larvae from each depth were examined by dissecting the larval gut under the microscope.

During 24-h stations in situ particle profiles, CTD profiles, and zooplankton pump profiles were made simultaneously every 2 h. On sections, zooplankton pump profiles were made on every second station.

RESULTS

In Situ Instrument Tests

Results of the comparison between microscope and particle counter measurements is presented in Table 1. A chi-square test for independence in the 4×2 table (3 df) showed no significant difference ($P < 0.05$) between the two methods of measuring *Artemia* nauplii.

TABLE 1.—Size frequency distribution of *Artemia* nauplii measured by the Hiac Particle Counter ($n = 1542$) and by microscope ($n = 45$).

Size (μm)	No. of *Artemia* nauplii counted by	
	Particle counter	Microscope
200-249	101	5
250-299	416	14
300-349	848	23
350-399	177	3

Paired tests between microscope and in situ particle counts were done on data from two different 24-h stations in the Austnesfjord (Figs. 4, 5). Plankton pump samples were taken from 11 different depths on each profile, and the mean counts from these depths were tested against the mean in situ counts from the same depths. A comparison was also made between the mean of all plankton pump counts from each profile, and the mean of all in situ counts from the corresponding profile.

During the first 24-h station, 19 vertical profiles were made. No significant differences ($P < 0.05$) was found when the mean counts ($n = 19$) from each of 11 different depths were compared, nor when the mean counts from the different profiles were compared. The same statistical test was made on data from 14 vertical profiles on the second 24-h station. There had been an increase in the variability of microzooplankton both horizontally and vertically during this 24-h station (Fig. 5A, B). No significant differences ($P < 0.05$) was found between the mean in situ counts and the mean plankton pump counts when the different profiles were tested. We found, however, a significant difference ($P < 0.05$) when the mean counts from corresponding depths were tested. This difference was found between in situ and plankton pump counts both from 30 and 40 m depths. No significant difference ($P < 0.05$) was found between counts from 0, 0.5, 7.5, 10, 12.5, 15, 20, and 25 m depths. This difference may have resulted from samples having been taken at different depths. The in situ instrument was equipped with a depth detector, but the depth of the submersible pump was controlled only by the meter wheel on the winch.

Distribution of Particle/Nauplii in the Fjord

The vertical distribution of particles/nauplii for a 24-h station made during 22-24 April 1981 in the

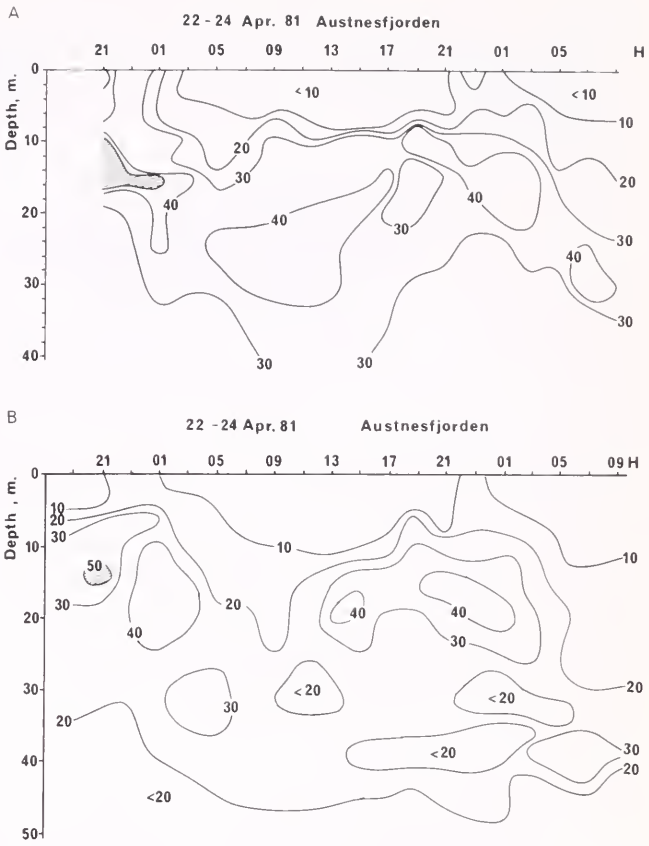

FIGURE 4.—Isopleth diagrams of the particle concentrations (per liter) (A), and nauplii (per liter) (B), center station, section 5 in Austnesfjord, 22-24 April 1981.

Austnesfjord is presented in Figure 4A and B. The maximum observed particle concentration was a small patch of 50 particles/l at about 15 m (Fig. 4A). A patch of 40 nauplii/l at the same depth was identified from pump samples (Fig. 4B). The particle/nauplii isolines in the upper 20 m show a tendency of ascending towards the surface at midnight, indicating their diel vertical migration. This observation was repeated on another 24-h station made 6 d later at the same position (Fig. 5A, B). Particle concentration had increased markedly during this period; more than 50 particles/l were found at 25-35 m depth on every profile. A very dense surface patch was found at midnight with more than 500 particles/l. Figure 5B shows a similar distribution of nauplii during the same 24-h station. Since there was no wind in the fjord and consequently little or no vertical turbulence, the hydrographic conditions during this 24-h station were perfect for this type of observation. This is shown in Figure 6 where the hydrographic conditions is presented by the temperature distribution in the upper 60 m.

Figure 7A and B presents the particle (150-600 μm) distribution from 0 to 40 m depth through a section of the Austnesfjord made at night on 27-28 April 1981 from 2130 to 0420 h. There was little or no wind in the fjord when the section was made. Patches of more than 100 particles/l were found in the surface water of the outer parts of the fjord. A particle minimum layer (<10/l) was observed at 10 m in the middle of the fjord. In the bottom of the fjord three patches of more than 50 particles/l were found at different depths. Figure 7B shows the naupliar distribution on the same section. Highest concentrations (>100/l) were observed in the bottom of the fjord, at intermediate depths and in the surface water of the outer parts of the fjord.

The same section made through the fjord the next day from 0950 to 1610 h (Fig. 8A, B) showed that the particle/nauplii distribution in the fjord had changed completely. A particle/nauplii minimum layer (<10/l) was found from the surface down to about 20 m through most of the fjord length. The surface patches in the outer parts of the fjord had disappeared. Only

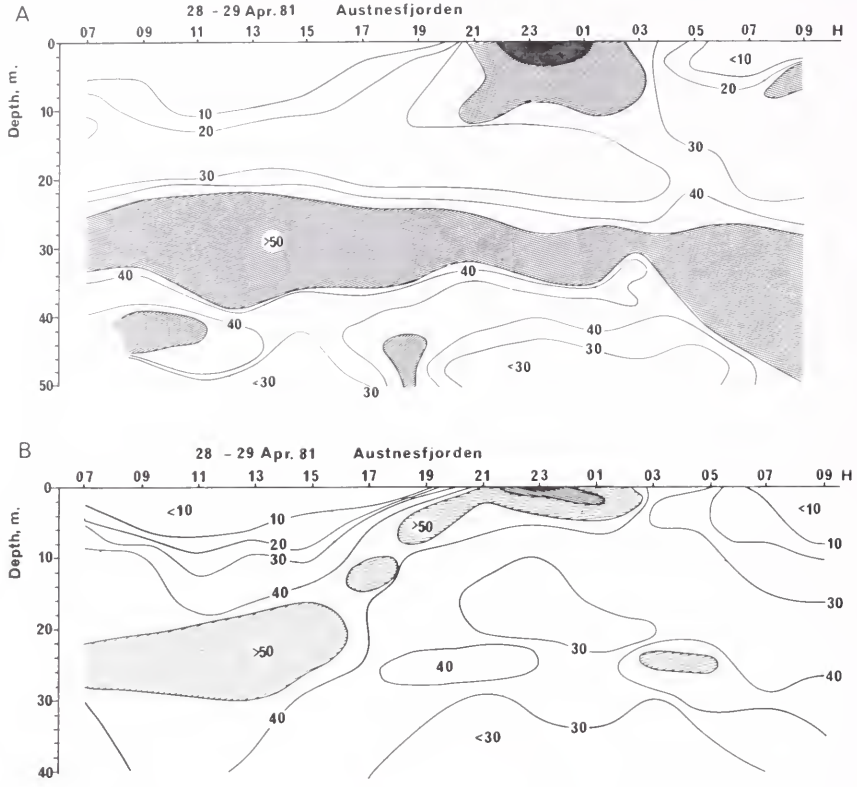

FIGURE 5.—Isopleth diagrams of the particle concentrations (per liter) (A), and nauplii (per liter) (B), center station, section 5 in Austnesfjord, 28-29 April 1981.

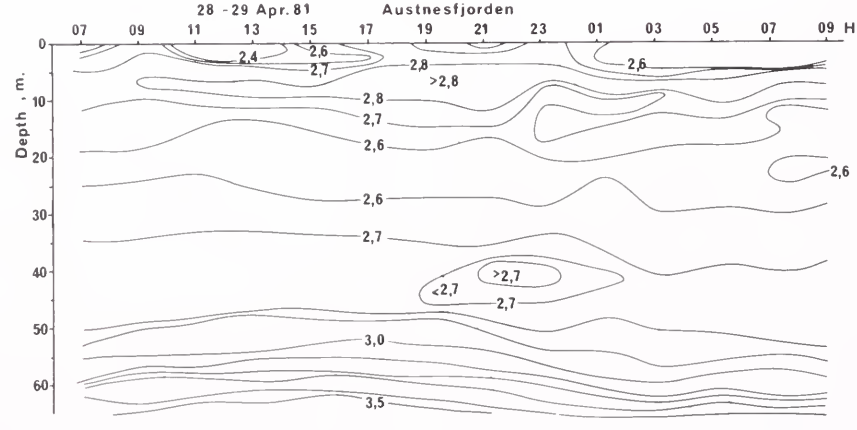

FIGURE 6.—Isopleth diagram of the temperature distribution, middle station, section 5 in Austnesfjord, 28-29 April 1981.

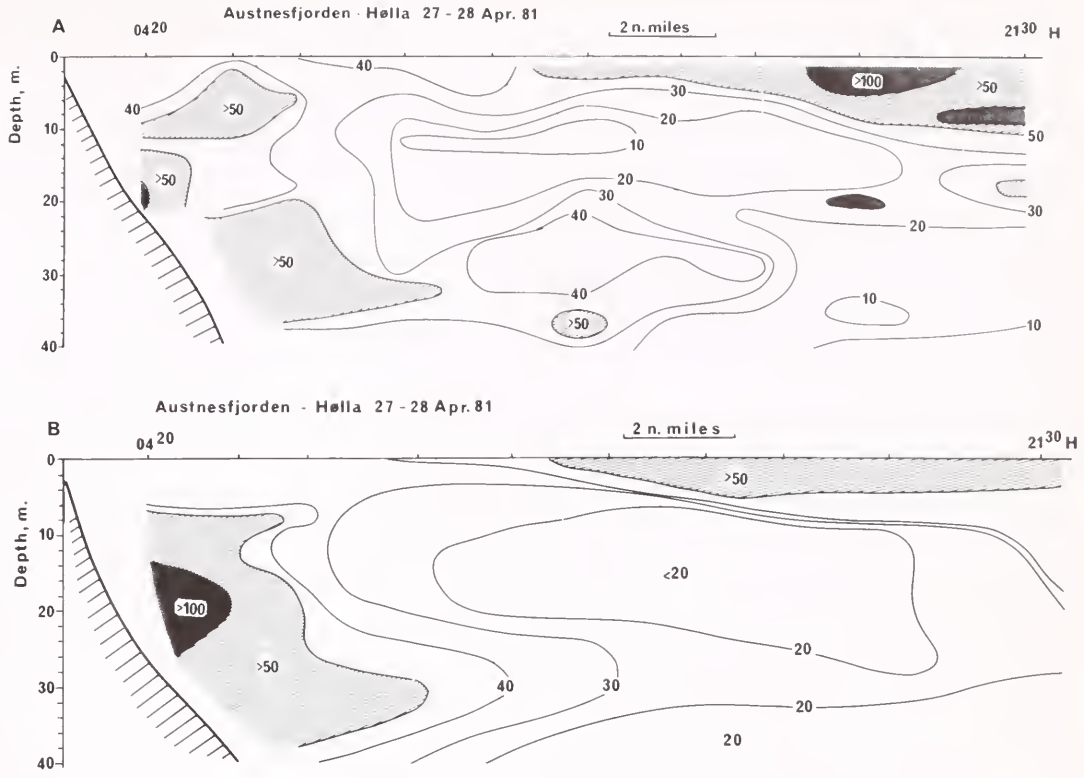

FIGURE 7.—Particle (A) and nauplii (B) distributions (per liter) in the upper 40 m of Austnesfjord, 27-28 April 1981, at 2130 to 0420 h. (Particle size range 150-600 μm, nauplii all sizes.)

one patch with >50 particles/nauplii per l was observed between 20 and 40 m at the bottom of the fjord.

Effect of wind driven turbulence on vertically migrating particles is presented in Figure 9A, B, and C. The figure presents data collected continuously from 9 to 15 May 1980, on wind velocity and direction, temperature, and particle distribution in the water column. Due to technical problems, only particles within the size range 300-500 μm were measured by the particle counter in 1980. From 9 to 12 May the wind was blowing downfjord with varying velocity. On 12 May the wind changed direction 180° and blew upfjord with a velocity of 5-10 m/s (Fig. 9A). Unfortunately, observations of temperature and particle distribution were not made from 10 to 11 May. However, one 24-h station was made on 9 May during the period when the wind was blowing downfjord. At this time, the upper 10 m of the water column showed tendencies of mixing, and colder intermediate water masses were observed from 15 to 55 m above the transition layer. Within the cold intermediate water masses a particle maximum layer was found (Fig. 9C). It is believed that the wind was blowing the surface water downfjord and this was compensated for by intermediate water masses moving in the opposite direction. On 9 May we observed a patch of particle-rich intermediate water moving in from the outer part of the fjord. The particle isolines in the upper 10 m followed the isotherms (Fig. 9B, C). When the wind direction reversed and increased in velocity on 12 May (Fig. 9A), the fjord became more exposed to the wind force and the wave action from the open ocean outside the fjord. Under this condition the current system will reverse (Furnes and Sundby 1981). The surface water became completely mixed within about 24 h (Fig 9B), and no particle diel vertical migration was observed during this condition (Fig. 9C). The particle concentration decreased and became almost homogeneous from the surface to 40 m.

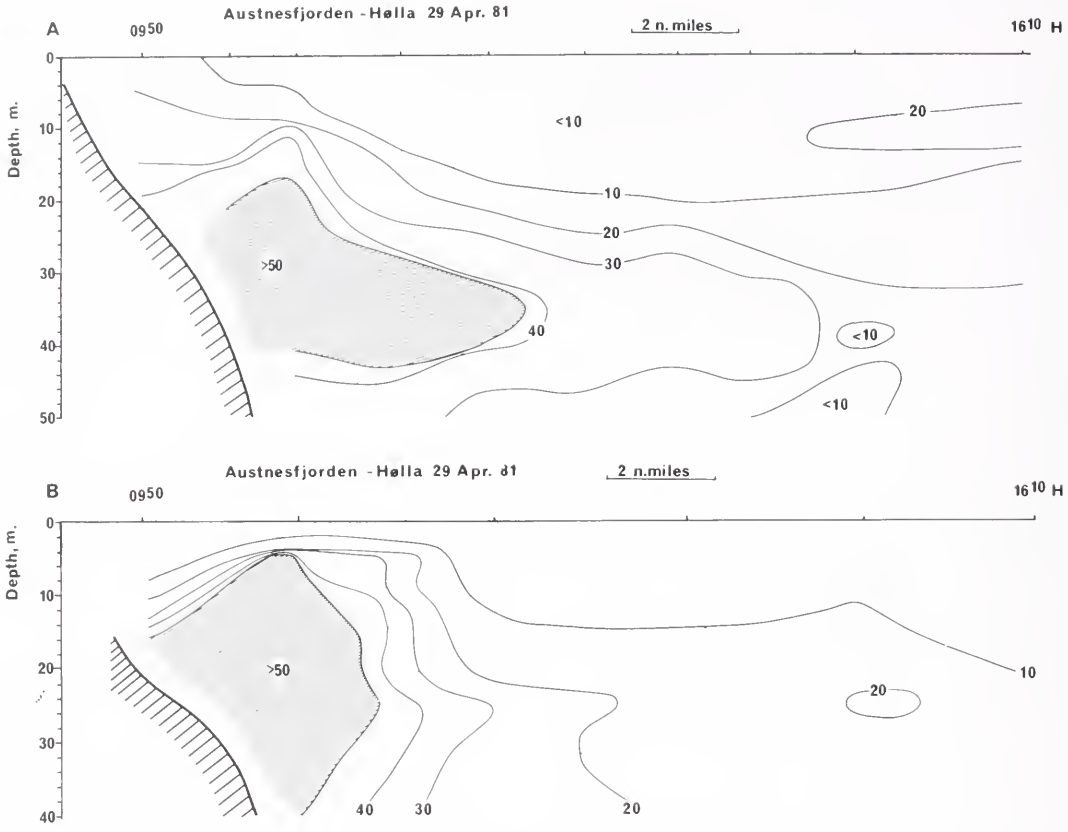

FIGURE 8.—Particle (A) and nauplii (B) distributions (per liter) in the upper 40 m of Austnesfjord, 29 April 1981, at 0950 to 1610 h.

Distribution of Cod Larvae

The highest concentration of cod larvae (140-290 larvae/m²) was observed in the middle of May at the bottom of the Austnesfjord both in 1980 and 1981 (Fig. 10). This has also been observed on previous cruises (Ellertsen et al. 1977). The research vessel was therefore anchored at the middle station on section 5, where 24-h stations were made.

In 1981, the study of the distribution of cod larvae in the exposed open ocean bay of Vesterålsfjorden showed that larvae were only found on the innermost stations with a maximum of 4 larvae/m² (Fig. 2), e.g., only two cod larvae in vertical Juday net hauls from 30 m depth.

Gut contents of 738 cod larvae were examined from 39 pump samples. Fewer than 10 larvae were found in pump samples from 30 and 35 m depths from the 01-02 h pump profile and from 35 m depth from the 04-05 h pump profile. These larvae have not been included in the analysis (Fig. 11B). A total of 1,204 prey organisms were found, out of which 96.5% were identified as copepod nauplii. Only 1.7% of the prey organisms could not be identified. About 0.5% of the larval cod gut content was bivalve veliger larvae, copepod eggs, and phytoplankton (*Peridinium* sp.), and 1.3% was identified as copepod fecal pellets. The size distribution of the main prey organisms (e.g., copepod nauplii) ranged from 140 to 520 μm with a mean size of 224 μm (all measurements as carapace length).

Gut content analysis of cod larvae is presented in Figure 11B as feeding incidence (percent larvae with gut content) and larval feeding ratio (number of prey organisms per larval gut). The feeding incidence varied between 73 and 100% in samples from the three pump profiles taken before midnight. In 61% of these samples the feeding incidence was as high as

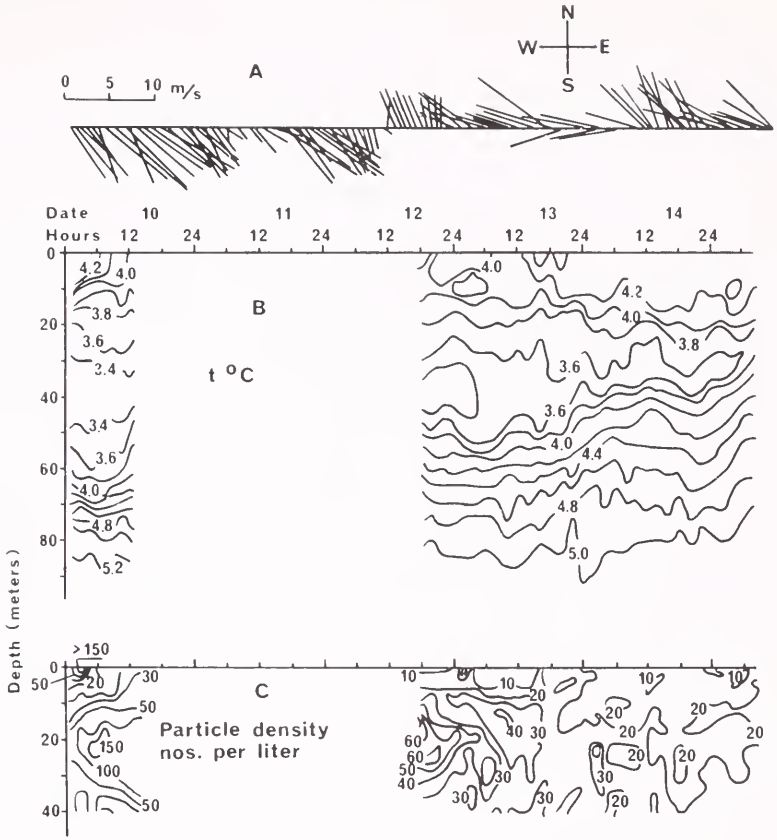

FIGURE 9.—Wind velocity (length of vector, see m/s scale) and direction from the abcissa (A), isopleth diagrams of temperature (B), and particle concentration (300-500 μm) distribution (C), at the middle station on section 5 in Austnesfjord, 9-15 May 1980.

90-100%. The larval feeding ratio was ≥1 prey/larval gut in all samples taken before midnight. In 71% of these samples the feeding ratio was ≥2 prey/larval gut and in 14% of the samples ≥3 prey/larval gut. In samples taken after midnight, however, the feeding incidence varied between 4 and 92%. The lowest level was found in pump samples from 25 m depth from the 01-02 h profile. In 38% of the samples taken after midnight the feeding incidence was <50%. Only in the last pump profile made at 09-10 h the larval feeding incidence was more than 50% in all samples. The feeding ratio was <1 prey/larval gut in all samples from 01-02 h profile, and ≤1 prey/larval gut in 61% of all samples taken after midnight. A feeding ratio level <1 prey/larval gut was not observed in samples taken before midnight. The highest feeding ratio observed in samples taken after midnight was 1.65 prey/larval gut from the 25 m depth samples taken from the 09-10 h pump profile.

Distribution of Particles/Nauplii in Open Ocean Waters

The main first feeding area of the Arcto-Norwegian cod is thought to be the waters outside the Lofoten islands and in the open ocean bay of the Vesterålsfjord (unpubl. data). Figure 12A and B shows the particle and nauplii distributions in the northeast section in the Vesterålsfjord. Plankton pump samples were only taken at every second station on the section. The figure shows a similar distribution pattern. However, due to the more frequent samples taken by the particle counter, a more accurate distribution picture of the particles on the section was achieved.

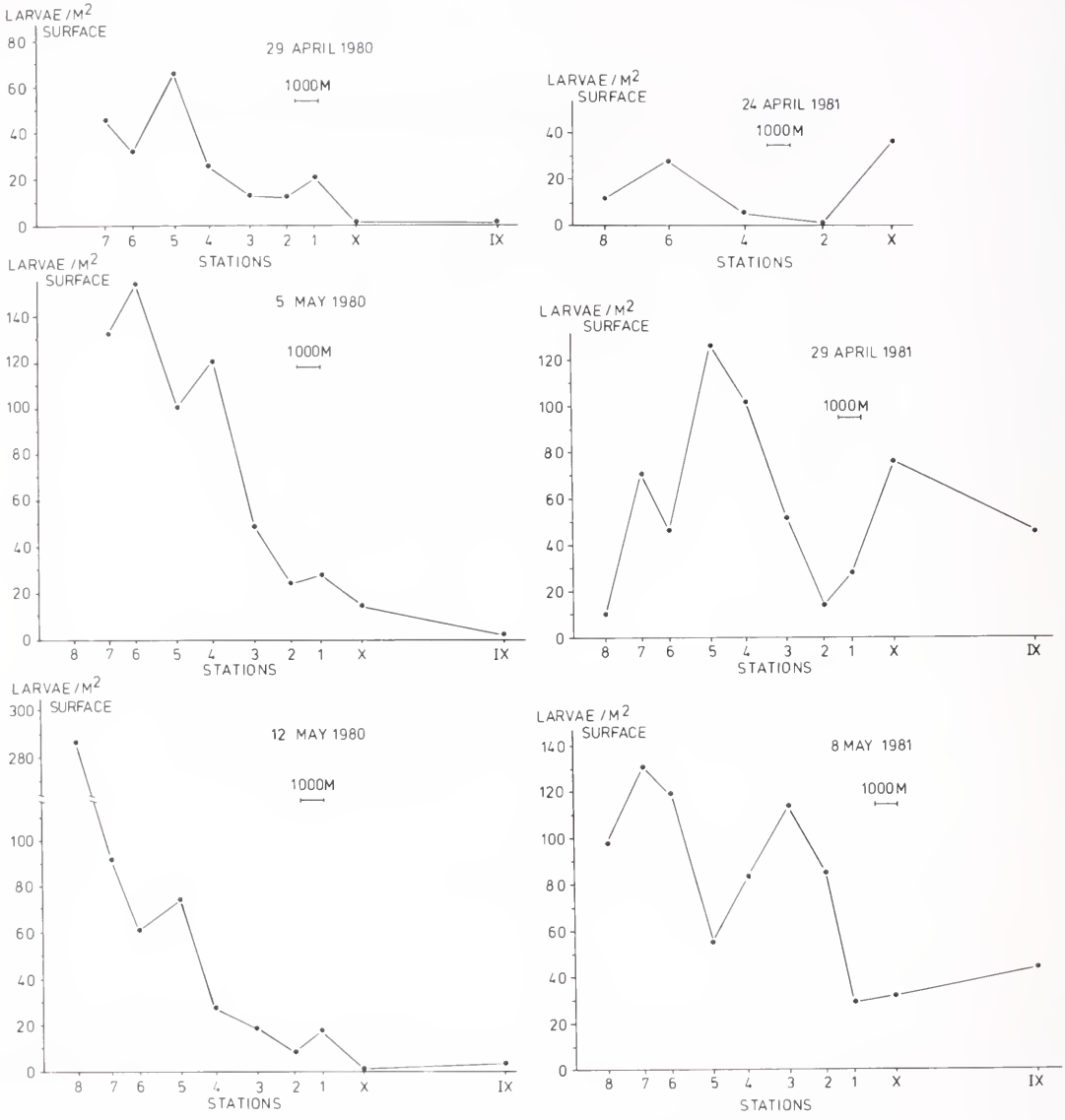

FIGURE 10.—The average number of cod larvae/m² surface on sections 1-8 and stations X and IX in the Austnesfjord, April-May 1980 and 1981.

Sections were also made at four locations in the open water off the Lofoten islands. On three of these sections (Eggum, Myrland, and Fuglehuk), patches with high particle concentrations (≥50/l) were observed about 11 km (8 n mi) off shore. All sections had low particle concentrations (10-30/l) in the surrounding water masses (Figs. 13-15). The similarity of the positions of these three patches suggests that they are components of the same water mass with higher particle concentrations than the surrounding water masses. On the Skiva section (Fig. 16A-D) the particle distribution patterns were more complicated. The section was surveyed during daytime and two patches were observed, one at about 5-10 m (>100 particles/l) and another 20-25 m (>50 particles/l). Particle concentration decreased further offshore. The same section was surveyed at night (Fig. 16C), and two surface patches were found.

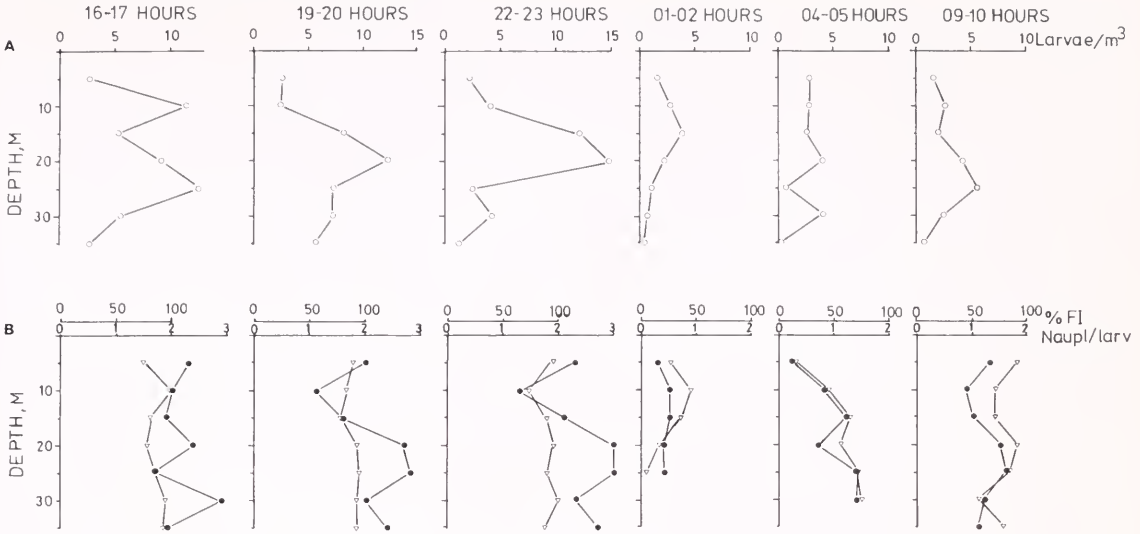

FIGURE 11.—Distribution of first feeding cod larvae (per m³) (A), and the larval feeding incidence (% larvae with gut content) ▽ and larval feeding ratio (nauplii/larval gut) ○ (B), during the 24 h sampling station, 13-14 May 1980, at middle station, section 5 in Austnesfjord.

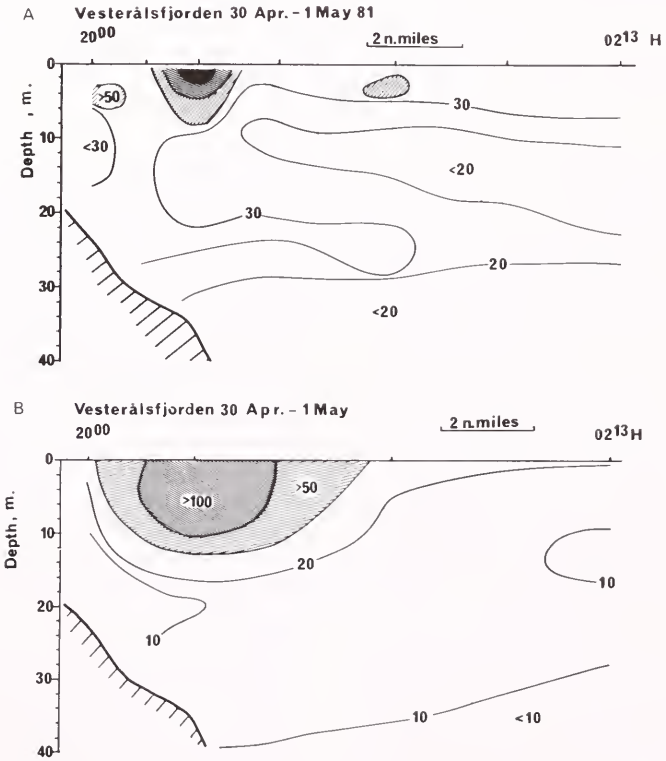

FIGURE 12. – Particle (A) and nauplii (B) distributions (per liter) in the upper 4 m on the section in Vesterålsfjord, 30 April-1 May 1981.

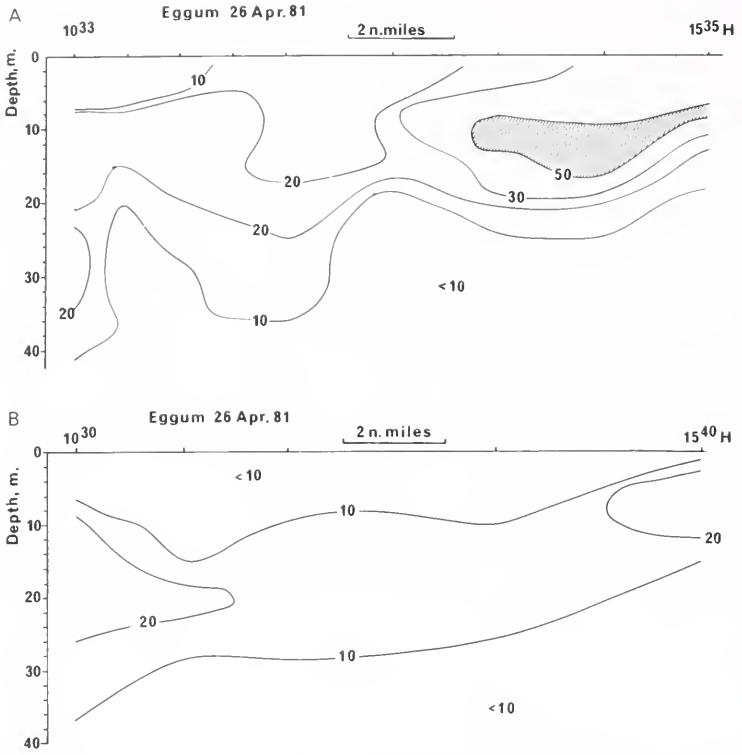

FIGURE 13.—Particle (A) and nauplii (B) distributions (per liter) in the upper 40 m on the Eggum section, 26 April 1981.

DISCUSSION

Food particles found in the alimentary tract of larval cod consist, with few exceptions, of copepod nauplii in the size range of 140-520 μm. This observation did not differ significantly from that of Ellertsen et al. (1977), who found the size variation to be within 140-600 μm. The in situ instrument was set to detect particles in this size range. Investigations have shown that in May copepod nauplii outnumber all other particles in this size range in the Lofoten area (Ellertsen et al. 1977; Wiborg 1948a, b). The main objective when designing this instrument was to obtain a quick, reliable impression of naupliar distributions without laborious, time-consuming countings by microscope. The tests performed to compare the in situ instrument system and the plankton pump samples showed good agreement between the two methods. The critical food concentrations for first feeding cod larvae are not precisely known. They are thought to be on the order of 40-200 nauplii/l based on studies of swimming activity, larval search volume, and oxygen requirements of first feeding cod larvae (Solberg and Tilseth 1984). Patches of particles/nauplii with the required densities for first feeding cod larvae to survive were found in the spawning and first feeding area by these methods.

The results presented in this paper show some of the dynamics in the formation and distribution in time and space of microzooplankton patches. The vertical distribution and density of nauplii changes due to the diel vertical migration of these organisms (Figs. 5, 6).

The concentration of particles/nauplii in a patch was dependent on the hydrographic situation and on the distribution and concentration of microzooplankton in the water column (Figs. 5, 6). Consequently the vertical distribution of particles and nauplii will be dependent on factors such as hydrographic conditions and time of day when the observations are made.

Increased wind force caused mixing of the surface layers and led to a homogeneous vertical particle distribution. No surface patch was observed at night during windy conditions, and the mean particle concentration in the water column dropped steadily dur-

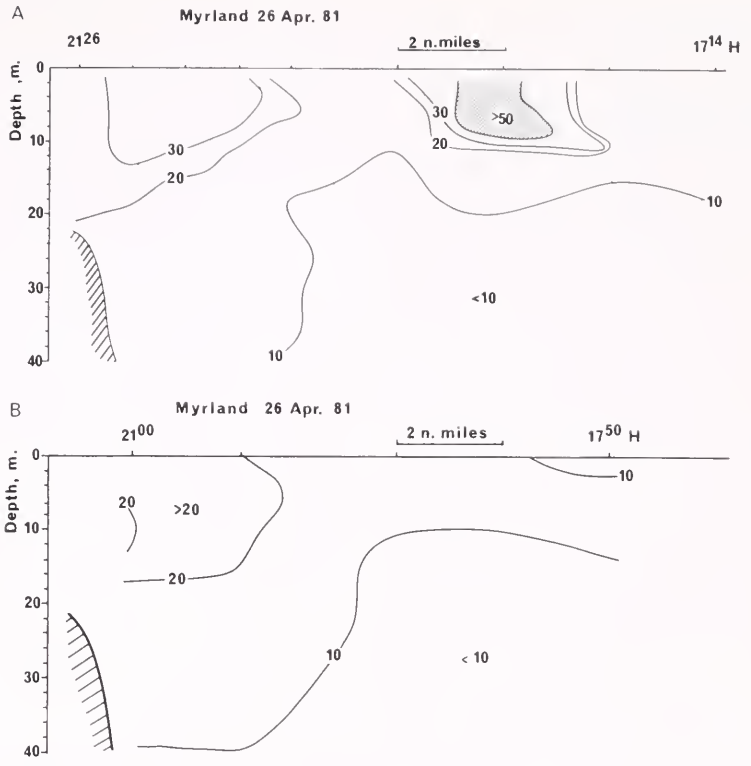

FIGURE 14.—Particle (A) and nauplii (B) distributions (per liter) in the upper 40 m on the Myrland section, 25 April 1981.

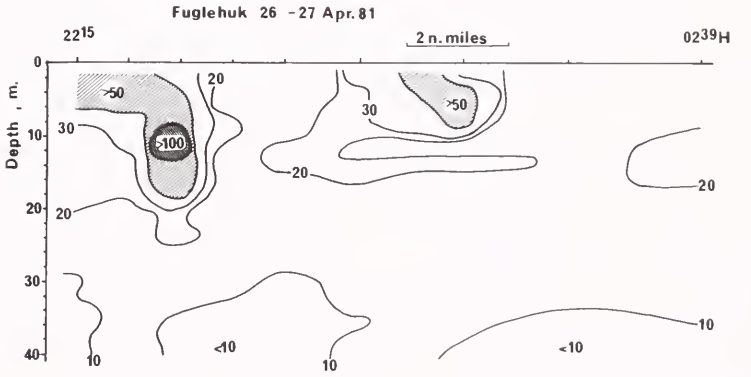

FIGURE 15.—The particle distribution (per liter) in the upper 40 m on the Fuglehuk section 26-27 April 1981.

ing the observation period (Fig. 10). This indicates that wind forces have caused increased water turbulence, and that these forces have exceeded the naupliar swimming rate. Mixing of surface layers and reduction in particle concentration occurred a few hours before midnight 13-14 May, and the water column became completely mixed down to a depth of 16 m (see Figure 10). Cod larvae were sampled both before and after this condition occurred (see Figure 11). Larval gut content analysis from these samples showed a reduction both in feeding incidence and feeding ratio in samples taken the first few hours

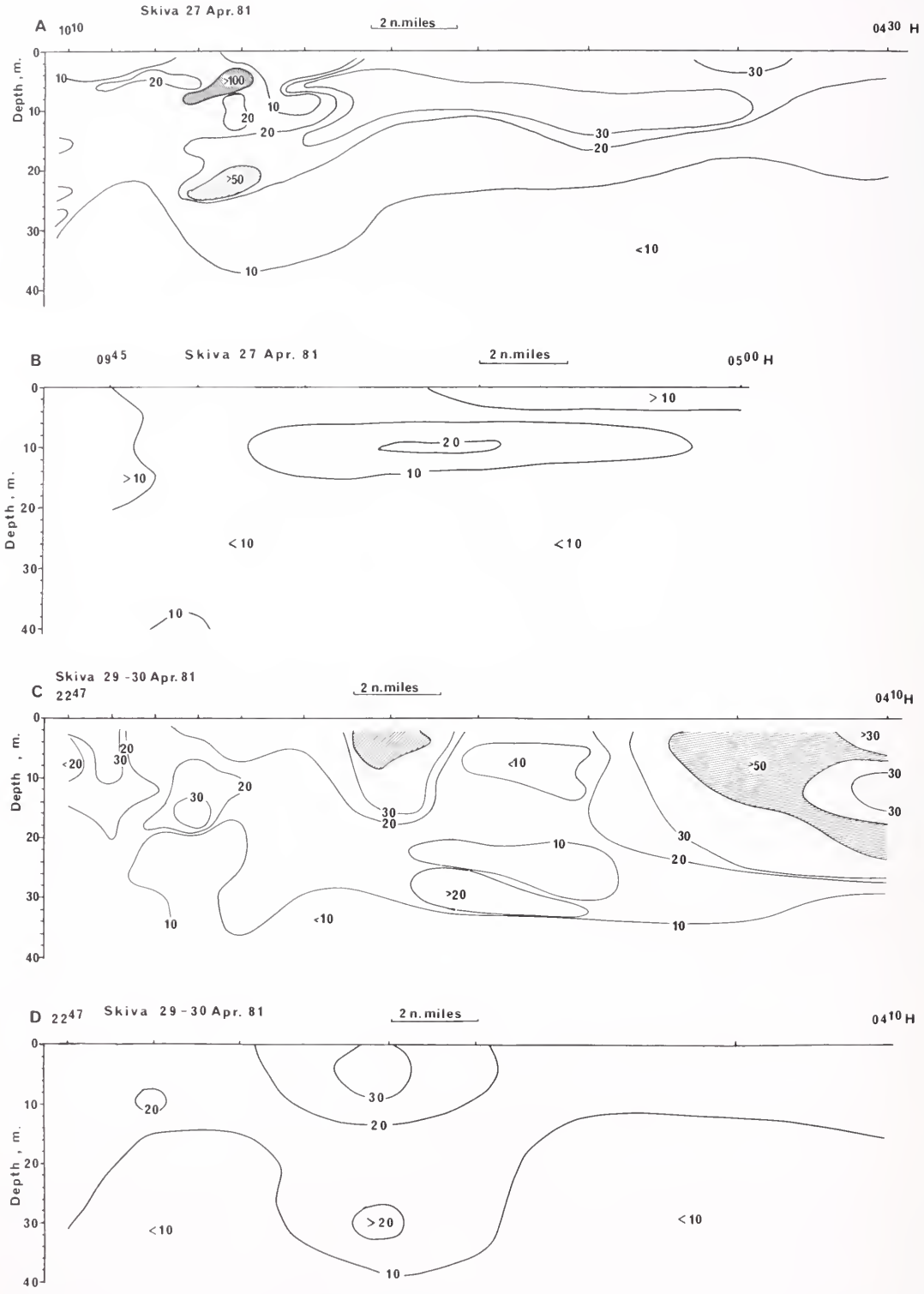

FIGURE 16.—The particle and nauplii distribution (per liter) in the upper 40 m on the Skiva section 27 April 1981 (A, B) and the particle and nauplii distribution 29-30 April 1981 (C, D).

after this hydrographic condition had occurred. During the following hours the larval feeding incidence increased again, most rapidly in larvae sampled at 15-30 m, indicating that food particle concentration did not become critical. (Note that the particle concentration in Figure 10C only represents particles within 300-500 μm size range.) However, the feeding ratio did not increase significantly, indicating a more difficult accessibility of food particles to the larvae. Similar observations were made by Lasker (1975, 1978), where stability of the water column in the upper 30 m was necessary for food organisms to aggregate in concentrations high enough to exceed the threshold for feeding stimulus of first feeding northern anchovy larvae. This observed reduced feeding in cod larvae cannot be explained by a diel feeding rhythm. Cod larvae are visual feeders; the light intensity threshold for feeding is 0.1 lx (Ellertsen et al. 1980). The light intensity in the upper 40 m does not drop below this level in Lofoten in May, and cod larvae are found with newly captured nauplii in the gut at all hours (Gjøsaeter and Tilseth 1981).

The number of cod larvae found in the main first feeding area was too small to do a comparison on larval feeding conditions. However, patches with particle/nauplii concentrations of more than 50/l were observed on every section made in this area. Sizes of these patches were, on the other hand, small compared with the volume of water surveyed. The life span of these patches is probably very short because of the influence of biological and physical factors, especially when the upper 50 m of the water column is unstable. This is the normal situation in the Lofoten area in May (Furnes and Sundby 1981). Therefore, prey organism patches with concentrations above the critical level for first feeding cod larvae would probably be broken down, due to increased water turbulence when the wind forces increase. A series of storms during the larval cod first feeding period could thereby have serious effects on larval feeding conditions and consequently on survival and recruitment.

ACKNOWLEDGMENTS

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EFFECTS OF SIZE AND TIME OF RELEASE ON SEAWARD MIGRATION OF SPRING CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*

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ABSTRACT

Juvenile spring chinook salmon, *Oncorhynchus tshawytscha*, from Round Butte Hatchery on the Deschutes River, Oregon, were released monthly into a 3.7 km fish ladder. Fish released into the ladder from February to May migrated through the ladder in mid-May in both 1977 and 1978. Fish released after mid-May migrated through the ladder within 2 weeks after release. The extent of migration decreased progressively in fish released after 15 June. The migration was presumably photoperiod dependent, although temperature may have acted both as a releasing factor for migration and as a stimulus for growth. In the fish ladder, size of the fish remained constant over a 3-week migration period, suggesting that larger fish migrated before smaller fish. After a migration of 213 km, fish captured at the Dalles Dam had very large apparent growth rates, suggesting that larger fish were faster migrants.

Maximum survival of juvenile salmonids after release from hatcheries is dependent upon their rapid migration to the sea (Raymond 1979). Delays in this seaward migration may subject the juveniles to starvation and stress which rapidly deplete their numbers (Miller 1952, 1958). Residual hatchery juveniles in a river often have an impact on wild stocks of fish through piscivory (Sholes and Hallock 1979) and competition for food (Chapman 1966). Rapid migration of hatchery juveniles ensures maximum survival to adulthood with minimal interaction with wild stocks.

Timing and duration of the physiological conditions which result in migratory behavior are still relatively unknown. Timing of seaward migration in juvenile salmonids depends upon a number of environmental factors, including photoperiod (Wagner 1974), temperature (Solomon 1978), water flow (Mains and Smith 1964), and fish size (Wagner 1974). The interrelationships between these are not well understood, but the available data suggest that these relationships may be complex. Hoar (1958) and Baggerman (1960) have postulated that these environmental factors act as "releasers" which, in conjunction with a physiological readiness to migrate, trigger overt migrational behavior.

In most river systems, the relative influence of such factors is estimated by extensive sampling programs which use multivariate analysis of the data. Control of environmental variables in such a system is not possible. Furthermore, the size of many river systems prevents an unbiased sampling of juveniles during migration. It is difficult, therefore, to obtain reliable estimates of the size of fish at migration, the timing of migration, and the influence of the environment on that timing.

In the present study, an unused fish ladder provided a relatively constant environment for migration of juvenile spring chinook salmon, *Oncorhynchus tshawytscha*, over a 3.7 km distance. Serial releases of hatchery-reared juveniles into this system permitted an investigation of the timing of seaward migration, the duration of the migration tendency of the juveniles, and the relationship of several environmental variables to seaward migration.

METHODS

Study Area

The study area included the lower 175 km of the Deschutes River, Oreg., and the lower Columbia River from its confluence with the Deschutes River to the Dalles Dam (Fig. 1).

Rearing Conditions

Progeny from spring chinook salmon spawned at

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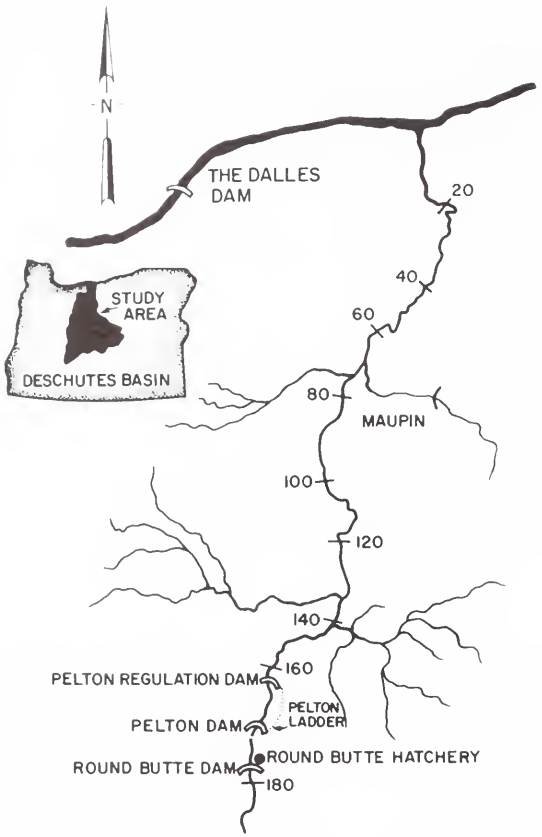

FIGURE 1.—Map of the lower 175 km of the Deschutes River and its confluence with the Columbia River. Numbers refer to kilometers from the mouth of the Deschutes River.

Round Butte Hatchery (river km 175 from the Columbia River) in 1976 and 1977 were used for experiments in 1977 and 1978, respectively. Eggs from 1976 brood fish were incubated in Heath[4] incubators in 10°C spring water, and the resulting fry were reared in raceways using the same water source. Eggs from 1977 brood fish were divided into two groups. One group was reared under conditions as described above and referred to as "fast-reared". The second group of eggs was incubated in Heath incubators in spring water chilled to 5°-6°C. The resulting fry were transferred to raceways and reared in 7°-8°C tail-race water from Round Butte Dam. After 2 mo, the group was transferred to 10°C spring water and reared there until release. This group was referred to as "slow-reared" and was released in March 1979 as yearlings.

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

In May and June, production lots of fast-reared spring chinook juveniles were released into the Deschutes River below Pelton Regulation Dam. At this time, experimental groups were transferred to oval fiber glass ponds supplied with 10°C spring water at 9.5 l/s. In May 1977, 5,600 fast-reared spring chinook juveniles (average fork length 10.0 cm) were transferred to a fiber glass pond and reared there through June 1978. In late March 1978, 2,500 fast-reared fish (average fork length 8.5 cm) were transferred to a fiber glass pond and reared there through August.

All fish were reared under a natural photoperiod and fed to repletion daily with Oregon Moist Pellet.

Seaward Migration

Migratory behavior of the spring chinook salmon was assessed by the release and recapture of hatchery-reared juveniles from two groups. Migration tendency of the experimental groups was assessed by monthly release of about 200 fish into the upper end of Pelton ladder during 1977 and 1978 (Fig. 1). The ladder is 3.7 km long and is constructed with concrete walls and bottom except for a 1.1 km central section which is a natural stream channel. It is supplied with water from Lake Simtustus (directly above Pelton Dam) at a constant flow rate of 1,130 l/s. Maximum depth of the ladder is 2.1 m. The ladder is closed by revolving screens at both the upper and lower ends. A trap located at the lower end of the ladder was used to capture migrants. Temperature of the water at the lower end of the ladder was measured by a thermograph placed near the trap.

Fish from the various experimental groups were identified upon recapture in the trap at the lower end of the ladder by unique combinations of polystyrene dye (Phinney et al. 1967) and fin clips. The trap was checked 5 d a week during May and June and 2 d a week during the remainder of the year. Fish captured in the trap were considered migrants while those remaining in the ladder following the date of peak recapture were assumed to be residuals. Fork lengths and marks of each migrant were recorded upon capture. In January 1978, the ladder was drained and all residual fish from the 1977 studies were removed before the 1978 releases.

The second group of hatchery-reared fish used for assessment of migration were production lots of fast-reared juvenile chinook released into the Deschutes River immediately below Pelton Regulation Dam (river km 161). These fish were marked with coded wire tags (Jefferts et al. 1963). In 1977, 62,000 fast-reared fish were released on 2 May and 73,000 fast-

reared fish were released on 3 June. These fish averaged 9.7 cm and 11.2 cm FL, respectively. On 31 May 1978, 121,000 fast-reared fish, which had been graded according to fork length, were released in two groups of 95,000 and 26,000 fish to test the effects of size on migration and survival to adulthood. These fish averaged 10.9 and 11.8 cm FL, respectively. Downstream movement in both years was monitored in the Columbia River at the Dalles Dam (52 km downstream from the mouth of the Deschutes River) by gatewell sampling conducted by the National Marine Fisheries Service and the Oregon Department of Fish and Wildlife. Sampling was conducted 5 d a week throughout May and June. Juveniles originating at Round Butte Hatchery were identified by analysis of coded wire tags.

Apparent Growth Rates

Apparent growth rates in Pelton ladder and in the Deschutes River were calculated from the size of the juveniles released into the ladder or the river and the size and time at which they were recaptured. Actual growth rates could not be measured, because selective mortality of small fish or migration of larger ones could not be estimated. Differences in fork lengths were tested for significance at the 95% confidence level using Student's t test.

RESULTS

Timing of Migration

Maximum migration of chinook salmon juveniles released in February and March into Pelton ladder occurred between mid-May and the first of June in both 1977 and 1978. There was little migration in these groups before or after this 4-wk period (Tables 1, 2). Fish released in April showed two peaks in migration. A large percentage of the fish moved through the ladder within 2 wk after release, while a second peak of migration occurred during the last 2 wk of May. Fish released in early May also had a large percent migration within 2 wk after release, but the greatest percent migration occurred during the first 2 wk in June. When chinook salmon juveniles were released from June to November, most of the fish moved through the ladder within 7 d after release. The maximum percent migration within 7 d after release occurred in fish released in early June 1977 (Fig. 2) and in mid-June 1978 (Fig. 3). Fish released in August and at later times had reduced migration and had a higher tendency to become residual (Tables 1, 2). Migration of slow-reared fish released into Pelton ladder from May to August 1978 was less than half that of fast-reared fish released at the same time (Fig. 3B).

Daily migrations of two groups released in February and March 1978 were compared with those from 8 May to 8 June. Movement of both groups was coincidental throughout this period (Fig. 4), suggesting that environmental factors such as temperature influenced migration tendency. Temperatures in the ladder varied seasonally due to solar warming (Fig. 5). Maximum temperatures of 17°C were attained in August 1977 and in July and August 1978. Temperatures in both years exceeded 13°C by June, suggesting a possible temperature threshold for migration. While the relationship between migration and temperature was very poor (correlation coefficient, $R^2 = 0.074$), there may have been a tendency for peaks in seaward migration to occur 1-2 d after transient increases in temperature (Fig. 4).

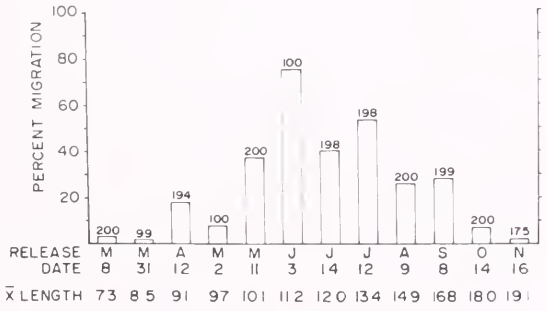

FIGURE 2.—Percentage seaward migration within 7 d following release for each group of fast-reared spring chinook salmon released into Pelton ladder in 1977. Above each bar is the number of fish released. Lengths are means of samples of 30 fish taken from the population at the time of release.

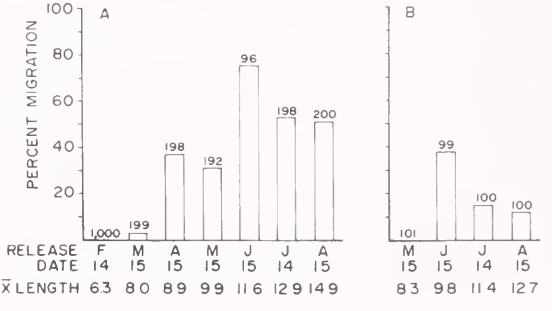

FIGURE 3.—Percentage seaward migration within 7 d following release for each group of spring chinook salmon released into Pelton ladder in 1978. A) Fast-reared chinook salmon. B) Slow-reared chinook salmon. Above each bar is the number of fish released. Lengths are means of samples of 30 fish taken from the population at the time of release.

TABLE 1.—Percentage downstream migration for fast-reared spring chinook salmon released into the Pelton ladder in 1977.

Capture dates	Release date: $\bar{X}$ length (cm): n:	8 Mar. 7.2 200	31 Mar 8.5 99	12 Apr. 9.1 194	2 May 9.7 100	11 May 10.2 200	3 June 11.2 100	14 June 12.0 198	12 July 13.4 198	9 Aug 14.9 200	9 Sept. 16.8 199	15 Oct. 18.0 200	16 Nov. 19.1 175
3/1-3/15		3.5											
3/16-3/31		1.0											
4/1-4/15		1.0	1.0	17.5									
4/16-4/30		0.0	0.0	0.5									
5/1-5/15		1.5	1.0	3.0	9.0	37.0							
5/16-5/31		34.5	42.0	27.0	19.0	5.5							
6/1-6/15		8.0	16.0	18.0	37.0	35.5	78.0	7.0					
6/16-6/30		0.0	1.0	0.5	6.0	3.0	4.0	35.0					
7/1-7/15		0.5	0.0	0.0	0.0	0.5	1.0	2.0	40.0				
7/16-7/31		0.5	0.0	0.0	1.0	0.0	0.0	0.5	18.5				
8/1-8/15		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	26.0			
8/16-8/31		0.0	0.0	0.5	0.0	0.0	1.0	1.0	0.5	7.5			
9/1-9/15		0.0	0.0	0.0	1.0	0.0	1.0	3.5	0.5	2.0	29.0		
9/16-9/30		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	3.0		
10/1-10/15		0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0		
10/16-10/31		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.5	
11/1-11/15		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
11/16-11/30		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.5	2.5	5.0
12/1-12.15		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	1.5	0.5
12/16-12/31		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1/1-1/15		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	1.5	1.0
Total percentage migration		50.5	61.0	62.0	73.0	81.5	85.0	49.0	60.0	37.0	36.0	13.0	6.5
Percent residuals		0.0	0.0	0.0	2.0	0.0	0.0	0.0	2.0	14.5	31.5	43.5	55.0
Total percentage recovered		50.5	61.0	62.0	75.0	81.5	85.0	49.0	62.0	51.5	67.5	56.5	61.5

TABLE 2.—Percentage downstream migration over semimonthly intervals for fast-reared spring chinook salmon released into the Pelton ladder in 1978.

Capture dates	Release date: $\bar{X}$ length (cm): n:	14 Feb. 6.3 1,000	15 Mar. 8.0 199	15 Apr 8.9 198	15 May 9.9 192	15 June 11.6 96	14 July 12.9 192	15 Aug 14.9 200
2/15-2/28		0.1						
3/1-3/15		0.0						
3/16-3/31		0.0	3.0					
4/1-4/15		0.0	0.0					
4/16-4/30		0.1	1.0	37.0				
5/1-5/15		17.3	8.0	2.5				
5/16-5/31		64.8	62.8	32.8	41.7			
6/1-6/15		3.8	8.5	12.0	33.8			
6/16-6/30		1.7	0.0	1.0	3.1	77.0		
7/1-7/15		0.5	0.0	0.0	0.0	0.0		
7/16-7/31		1.3	1.0	0.0	0.0	2.0	55.0	
8/1-8/15		0.0	0.0	0.0	0.0	0.0	0.5	
8/16-8/31		0.7	0.0	0.0	0.5	1.0	0.5	54.5
9/1-9/15		2.2	0.5	0.0	2.5	1.0	2.5	5.0
Total percent migration		92.5	84.8	85.3	81.6	81.0	58.5	59.5

Recovery of Released Fish

In 1978, the greatest recovery of fish liberated into Pelton ladder (92.5%) was from the large group of 1,000 fish released on 14 February (Table 2). From 81.0 to 85.3% of the fish released from 15 March through 15 June were recovered. Only 58.5 and 59.5% of the fish released on 14 July and 15 August, respectively, were recovered in the trap as migrants. Presumably the remainder were residuals in the ladder.

In 1977, recovery of both migrants and nonmigrants from all groups was lower than in 1978 (Table 1), although the extent of migration of fish released near the time of maximum migration tendency on 11 May and 3 June was 81.5 and 85%, respectively, similar to that observed for most release groups in 1978. Few residual chinook salmon from releases before August 1977 were found when the ladder was drained in January 1978. Nonmigrant fish were recaptured in increasing numbers from releases from 12 July on.

Size and Growth Relationships

Growth rates of juvenile chinook salmon reared at Round Butte Hatchery were 0.046 and 0.058 cm/d

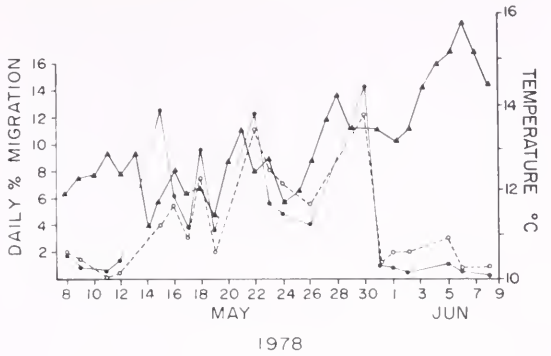

FIGURE 4.—Daily percent seaward migration from 8 May to 8 June for groups released 14 February (solid circles) and 15 March (open circles). Temperature (triangles) is the average daily temperature.

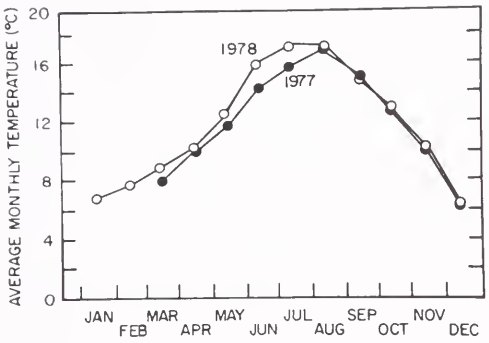

FIGURE 5.—Average monthly temperature in Pelton ladder in 1977 (solid circles) and 1978 (open circles).

TABLE 3.—Apparent growth rates of juvenile chinook salmon released into Pelton ladder, 1977 and 1978.

	Release date	Average recapture date	Apparent growth rate (cm/d)
1977	3/8	5/24	0.078
	4/12	6/1	0.081
	5/2	5/28	0.124
	5/11	6/4	0.120
Hatchery	—	—	0.048
1978	2/14	5/27	0.034
	3/15	5/20	0.071
	4/15	5/26	0.097
	5/15	6/7	0 097
Hatchery	—	—	0 046

TABLE 4.—Fork lengths of juvenile chinook salmon at time of release into Pelton ladder and at time of recapture, 1977 and 1978. Values are means ± standard errors. Number of samples is given in parentheses.

Date of release	Mean fork length at release (cm)	Date of recapture	Mean fork length at recapture (cm)
1978:			
2/14	6.5±0.1 (60)	5/15-6/9	13 4±0.1 (245)
3/15	8 2±0.1 (30)	5/16-5/24	13.0±0.1 (81)
4/15	9.0±0.1 (100)	5/22-5/31	13.0±0.2 (42)
5/15	10.1±0.1 (29)	6/5-6/9	12.3±0.1 (54)
6/15	11.3±0.1 (30)	6/16	11.9±0 1 (30)
7/14	13.7±0.1 (30)	7/17	13.2±0.2 (30)
8/15	15 1±0.3 (30)	8/16	15.5±0.4 (9)
9/15	17.1±0 3 (28)	9/18	17 2±0 2 (30)
1977			
3/8	7.5±0.1 (30)	5/24	13.5±0.1 (25)
3/31	8 5±0.1 (30)	5/24-5/28	13 5±0.1 (26)
4/12	9 4±0 1 (30)	6/1	13 4±0 1 (26)
5/2	9.7±0.1 (30)	5/28	12.9±0 1 (7)
5/11	9.9±0.1 (29)	5/12-6/4	11.7±0.1 (61)
6/3	11.2±0.1 (30)	6/3	11.4±0 1 (25)
6/14	12.0±0.1 (30)	6/17	12 3±0 1 (30)
7/12	13.5±0.1 (60)	7/15	13 9±0.1 (28)
8/9	15.1±0.2 (88)	8/15	16 1±0 2 (20)
9/9	16.7±0 2 (88)	9/9-9/13	16.8±0 2 (42)
10/15	17.5±0 5 (30)	10/17	18 4±0.4 (15)

for fast-reared fish in 1977 and 1978, respectively. Slow-reared fish in 1978 grew at 0.043 cm/d. Apparent growth rates of fish placed in Pelton ladder varied from 0.034 to 0.124 cm/d (Table 3). These apparent growth rates increased in later introductions, reflecting the increasing water temperature of the ladder (Fig. 5).

There was no evidence for differences in migration timing by fish of different sizes. Fork lengths of fish recaptured in the trap within a few days of release were usually not significantly different ($P > 0.05$) from those of fish at release (Table 4). However, fish recaptured from the large group of juveniles released on 14 February 1978 were similar over a 3-wk period (Table 5), suggesting that faster growing fish were migrating more rapidly that slower growing fish.

Apparent growth rates of marked spring chinook juveniles released below Pelton Regulation Dam in 1977 were calculated from fork lengths of recaptured fish at the Dalles Dam, after a migration distance of 213 km (Table 6). This apparent growth rate is nearly twice that of fish reared at Round Butte Hatchery.

TABLE 5.—Mean fork lengths of juvenile spring chinook salmon recovered in 1978 after release into Pelton ladder on 14 February 1978. Values are means ± standard errors. Number of samples is given in parentheses.

Date of recovery	Fork length (cm)
2/17	6.7±0 1 (30)
5/15	12.8±0.1 (30)
5/16	13.2±0.1 (30)
5/18	13 1±0.1 (30)
5/22	13.4±0.1 (30)
5/24	13.2±0.1 (30)
5/30	13.9±0.1 (30)
6/1	13.5±0.2 (19)
6/5	13.6±0.1 (21)
6/9	11.2±0.1 (25)

TABLE 6.—Fork lengths and apparent growth rates of juvenile spring chinook salmon recaptured at the Dalles Dam after release into the Deschutes River, 1977. Fork lengths are means ± standard errors for the number of samples shown in parentheses.

Recapture date	Fork length (cm)	Apparent growth rate (cm/d)
2 May release (9 7±0.1 cm fork length)		
5/27	11 6±0.2 (12)	0.075
6/3	12.2±0.1 (19)	0 078
6/7	12 2±0.1 (22)	0 077
6/8	12 2±0.1 (21)	0 076
3 June release (11 2±0 1 cm fork length)		
6/7	11.9±0.1 (23)	0 168
6/8	11.8±0.1 (30)	0.120

DISCUSSION

Determination of the migratory characteristics of juvenile chinook salmon during smolting has been complicated by the variety of migratory behaviors displayed by the juveniles. Some fry migrate from tributaries shortly after emergence from the gravel (Reimers 1973; Ewing et al. 1980), but there is little evidence that the fry move into the estuary at that time (Schluchter and Lichatowich 1977). In some stocks, a general movement of fish through the river occurs during the fall of the first year (Reimers 1973) with a majority of the fish entering the ocean during the fall of the first year (Reimers 1973; Schluchter and Lichatowich 1977; Buckman and Ewing 1982). In other stocks, seaward movement occurs primarily in the following spring when the fish are more than 1 yr old (Mains and Smith 1964; Diamond and Pribble 1978; Raymond 1979). Krema and Raleigh (1970) reported migration of juvenile chinook salmon into Brownlee Reservoir (Snake River, Idaho) in fall and spring for 2 consecutive years. The migration pattern seems to depend upon stock, size, and rearing conditions and may be highly variable. It is therefore important in the culture of various stocks of juvenile chinook salmon to determine the timing of maximum migration tendency.

In the present study, the major migration of fish released early into Pelton ladder occurred in mid-May. Fish from the same brood released into the Deschutes River at about this time were found to migrate 213 km to the Dalles Dam within 7 d, suggesting that the migrational behavior was seaward directed (Hart et al. 1981). It is difficult to confirm in the Deschutes River that the release of fish into Pelton ladder 1 mo before the time of maximal migration tends to increase the time during which the fish will migrate. Release of the fish 1 mo later than the time of maximal migration tends to decrease the time for migration. It is important to note that it is not necessary to release the fish early to insure that all migrate to sea. Releases late in the migration period were recovered to the same extent as those released earlier. Migration tendency seems to be retained for some time, even though the fish are not permitted to begin migration. These results suggest that late releases hasten the seaward migration, thus removing the populations of hatchery fish quickly from the river system and affording maximum protection to the wild stocks.

Those groups released later than July were recaptured in the trap in decreasing numbers (Tables 1, 2). In 1977, nonmigrant fish were recaptured in increasing numbers from releases after 12 July (Table 1). This result indicates that the decrease in numbers of fish recaptured at the trap was due to decreased migration tendency and not due to increased mortalities at the higher water temperatures.

A major advantage of utilizing a closed system such as the Pelton ladder for studies of migration was that fish populations and flows could be effectively controlled. Variables which remained uncontrolled included photoperiod, lunar periodicity, temperature, and food supply. Of these, photoperiod seems the most important in stimulating seaward migration. Previous studies utilizing a closed system for studying seaward migration of steelhead trout, *Salmo gairdneri*, (Zaugg and Wagner 1973; Wagner 1974) and coho salmon, *Oncorhynchus kisutch*, (Lorz and McPherson 1976) also concluded that photoperiod was an important factor affecting the timing of seaward migration.

Lunar phase has been suggested to affect the onset of migration, based on the correlation between peaks in plasma thyroxine levels and lunar phase (Grau et al. 1981). Assuming maximal migration occurred on 22 May in both 1977 and 1978, this date corresponded to the time of a new moon in 1977 and that of a full moon in 1978. These brief data do not support the hypothesis that the migration is influenced by the lunar phase.

Temperature may have had a dual influence on migration. Temperature has been suggested as a releasing factor for salmon migration (Hoar 1958; Baggerman 1960), but we were unable to show a statistical relationship between daily migration and average daily temperature (Fig. 4).

Temperature also serves to increase growth rates in salmonids in the presence of abundant food supplies. Wagner (1974) suggested that a critical size was required in steelhead if migration were to take place. The importance of size on migration of spring chinook salmon can be seen by comparing the extent of migration of the slow- and fast-reared fish in 1978 (Fig 3). The slow-reared fish may have failed to mi-

grate because they did not reach a critical size and/or growth rate by the appropriate photoperiod. Migration from Pelton ladder seemed to occur as fish reached a particular size, since during a 3-wk period of migration, there was no difference in average fork length of the fish recaptured (Table 5). From estimated growth rates (Table 3), fish at the end of the migration period might be expected to be nearly 2 cm larger than those at the beginning. This influence of size on migration could be best demonstrated in fish recaptured at the Dalles Dam after a migration distance of 213 km. Apparent growth rates were much higher than that of fish reared at Round Butte Hatchery, suggesting that a selection for larger fish occurs during the long migration distance.

A major concern in utilizing a closed system for studying seaward migration is the importance of aggressive behavior by resident fish toward newly introduced fish. Chapman (1962) found that aggressive behavior of resident fish may be partly responsible for emigration of fish introduced into the system. Aggressive behavior may have caused the rapid movement immediately following release for the March and April release groups in both 1977 and 1978. Further movement of these fish was not observed until May. Alternatively, migration in these fish immediately after release may have been due to disorientation of the fish upon release and a passive drifting downstream with the current. Fish released earliest into Pelton ladder migrated first in both 1977 and 1978.

The importance of determining appropriate times for hatchery releases of spring chinook salmon in order to obtain maximum seaward migration is demonstrated by the short time during which maximum migration occurred (Tables 1, 2). In both 1977 and 1978 peak migration occurred within a period of a few weeks. Releases made on either side of this time period exhibited decreased migratory activity. The use of model systems, such as the Pelton ladder, to determine when peak migration occurs can benefit hatchery programs by suggesting sizes and times for release of salmonids which maximize seaward migration.

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INTERACTIVE EFFECTS OF AGE AND ENVIRONMENTAL MODIFIERS ON THE PRODUCTION OF DAILY GROWTH INCREMENTS IN OTOLITHS OF PLAINFIN MIDSHIPMAN, *PORICHTHYS NOTATUS*

STEVEN E. CAMPANA[1]

ABSTRACT

Plainfin midshipman, *Porichthys notatus*, were reared in the laboratory under three environmental regimes to determine the influence of certain variables upon otolith growth increment formation. Both larval and juvenile midshipman were used to test diel cycles and constant conditions of light and temperature. Daily growth increments were formed upon hatch unless a diel photoperiod was absent. However, under constant light, an endogenous circadian rhythm became evident after a 2-3 week acclimation period, resulting in daily increment production. With increasing age, the influence of light as a zeitgeber decreased, while daily increments became more prominent in all environments. Temperature fluctuation affected increment appearance, but did not entrain increment deposition.

Daily growth increments in the otoliths of fishes have been observed in a large number of species (Pannella 1971; Brothers et al. 1976; Taubert and Coble 1977; Wilson and Larkin 1980). These concentrically formed increments may be counted or measured to provide a chronological record of past fish growth. Information on hatching date/age (Ralston 1976; Struhsaker and Uchiyama 1976), daily growth rates (Methot 1981), and timing of life history transitions (Pannella 1980; Brothers and McFarland 1981) has been derived from the examination of otolith microstructure. Such data are difficult to obtain from larval and juvenile fishes by other means.

Daily increments are produced through a diel periodicity in the deposition of calcium carbonate on the otolith (Mugiya et al. 1981). However, there is some controversy as to the zeitgeber behind the daily cycle of deposition, if indeed one exists. In a series of experiments upon larval *Lepomis*, Taubert and Coble (1977) determined that a 24-h light-dark cycle was necessary to entrain an endogenous rhythm of increment production. Reversal of the light-dark cycle reversed the daily sequence of increment formation in larval *Tilapia* (Tanaka et al. 1981). However, 36-h "days" and constant light conditions had no effect on daily increment production in juvenile starry flounders, *Platichthys stellatus* (Campana and Neilson 1982). Similarly, constant light or dark conditions did not inhibit the formation of daily increments in young chinook salmon, *Oncorhynchus tshawytscha* (Neilson and Geen 1982). The contradictory results of the above studies suggest that photoperiod effects on increment production may vary with age or species of fish.

Other environmental variables may influence the daily rhythm of otolith deposition. Diel temperature fluctuation has been implicated as a factor in daily increment production of temperate stream fishes (Brothers 1981), although this suggestion has not been supported by other studies (Campana and Neilson 1982; Neilson and Geen 1982). Feeding frequency may also influence otolith increment production; fish given multiple daily feedings have been reported to produce nondaily increments (Pannella 1980; Neilson and Geen 1982), although recent studies suggest that feeding effects are limited (Tanaka et al. 1981; Marshall and Parker 1982; Campana 1983).

Confidence in the reliability of otolith microstructure examination requires knowledge of those factors that may influence otolith increment production. Conflicting results in the literature suggest that age influences the response of daily increment production to environmental variables such as photoperiod and temperature. This study was undertaken to test that hypothesis. Plainfin midshipman, *Porichthys notatus*, were reared from the egg stage under various light and temperature regimes; constant conditions and diel cycles of each variable were tested. The effect of the regimes on otolith microstructure was noted for both newly hatched and juvenile fish.

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Juveniles were then subdivided and transferred to different regimes, allowing an examination of the interactive influence of greater age and novel environment on increment production.

MATERIALS AND METHODS

Fertilized *Porichthys* eggs were collected intertidally from White Rock, British Columbia, on 9 and 22 June 1982. Yolk-sac larvae remain attached to the rock upon which the eggs were originally deposited (Arora 1948), necessitating the collection of both rocks and egg masses. Upon return to the laboratory, eight separate egg masses (50-250 ova each) were isolated in individual saltwater aquaria and maintained under a diel photoperiod and a temperature of 13°C. Small amounts of methylene blue, streptomycin sulphate, and penicillin G were used to control bacterial and fungal infection. Embryo development varied both among and within egg masses, but the difference appeared to be <2-3 d.

On 1 July, egg masses were exposed to an experimental environment. Environmental regimes were selected to provide a diel periodicity of either photoperiod or temperature. A third regime maintained constant conditions of both variables. In this manner, the influence of both factors on increment formation could be determined for newly hatched larvae. Daily increment production in the constant environment would suggest the presence of an endogenous circadian rhythm. Regimes were as follows:

14L:10D at a constant temperature of 19°C (14L:10D/CT)
24L with 14 h at 21°C and 10 h at 19°C (24L/$14T_1$:$10T_2$)
24L at a constant temperature of 19°C (24L/CT)

Duplicate aquaria, each containing an egg mass (or 2 small masses, if at similar developmental stages), were kept in light-proof, temperature-controlled cubicles under each of the above environments. All lighting was fluorescent (30 μEs/m^2/s). Temperature fluctuations were timer-controlled and conducted parallel to the light cycle. New temperatures were reached 1½ h after initiation. Mean temperatures approximated those of the egg collection site; diel temperature fluctuations were present at the site, but were not recorded. Aquarium water was changed at 7-10 d intervals. Hatching date varied among and within egg masses, beginning between 7 and 11 July. Release from the rock (before completion of yolk-sac resorption) was more variable, and occurred between 23 July and 9 August. Live adult *Artemia* were first provided as food on 30 July and were consumed by both released and attached larvae. Thereafter, *Artemia* were maintained in all aquaria at all times, with the exception of two 3-d periods when food was not available. Food abundance did not differ among the aquaria. Observations of feeding fish indicated that the accessibility of *Artemia* did not limit growth.

By 10 August, all fish were about 32-d old (posthatch) and had become juveniles (i.e., had assumed the appearance of an adult). To test the effect of an altered photoperiod or temperature cycle on juveniles, one tank from each of the environmental regimes was subdivided (Fig. 1). About 25 fish were transferred from one aquarium ("cohort") to each of the remaining environments, while leaving 25 fish in the original environment as a control. Sagittae were removed from up to 25 of the excess fish to determine the effect of the original environment on newly hatched larvae. In order to remove any intercohort variability of hatching dates, only one of the two available cohorts from each environment was subdivided and sampled. However, low numbers of 14L:10D/CT fish necessitated the transfer of an entire cohort.

For processing, the sagittae were brushed free of tissue and glued sulcus-side up with instant glue on a standard microscope slide. Sagittae were ground and polished with metallurgical lapping film (grit size 30

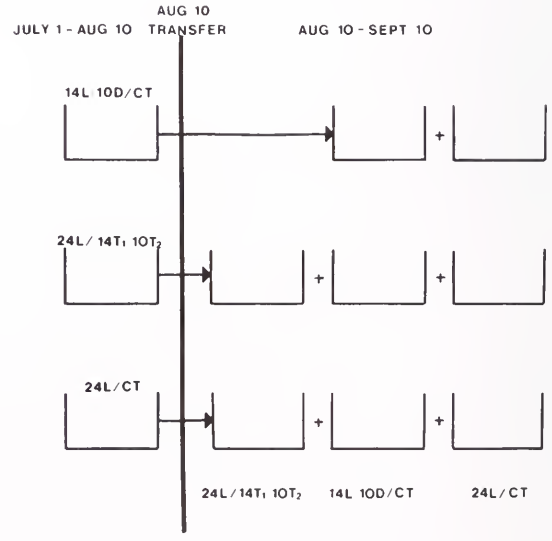


FIGURE 1.—Summary of experimental environmental regimes of plainfin midshipman through time. Fish transferred to new environments on 10 August came from the same egg mass as that sampled on 10 August.

μm to 0.3 μm) until the growth increments in the region of maximal growth were most visible. I defined a growth increment as a bipartite structure, consisting of a narrow opaque band and an adjacent broad translucent region. Growth increments between the otolith periphery and the hatch check were counted at least twice through a compound microscope at a magnification of 400×. Duplicate counts of an otolith never differed by more than 10%. The use of a hand counter eliminated the possibility of a count converging on an expected value. There was little doubt concerning the nature of the hatch check; its radius matched that of radii of otoliths removed at hatch. Growth increments in 14L:10D/CT fish sampled 10 September were counted as above. However, a second series of counts was made from the hatch check to the prominent 10 August check; the second data set served as a substitute for the actual sampling of 14L:10D/CT fish on 10 August.

Increment counts were made from both the left- and right-hand side sagittae. Since the two sides did not differ systematically under any of the environments (paired t-test, $P > 0.05$), the means were used in all data analyses.

Increment widths were measured from photographs with a micrometer. Expected increment widths were calculated from radial measurements (central nucleus to rostral tip) of otoliths from all environments and a variety of sampling dates ($N = 10$ per date). Values for mean increase in radial otolith growth per day were then compared to observed values.

Since individual otoliths often displayed erratic but discernable width trends through time, a measure of the similarity of the widths of two adjacent daily increments was calculated:

$$IR_i = \frac{W_i - W_{i-1}}{(W_i + W_{i-1})/2}$$

where IR_i is the index of increment width regularity for day i, and W_i is the increment width for day i. Such an index gives low values when adjacent increments are similar in width, despite any trends in the data. Index values were calculated for a range of ages in otoliths from a given environment.

RESULTS

Porichthys larvae and juveniles survived and grew under all laboratory environments. Survival exceeded 95% after hatch. Fish sampled about 1 mo after hatch (10 August) did not differ significantly in standard length (ANOVA, $P > 0.05$). By the end of the study, only those fish maintained in the 24L/$14T_1$:$10T_2$ environment were significantly smaller in length (Scheffe's test $P < 0.01$); the difference was apparently due to unintentional overcrowding from the date of transfer.

Hatching was initiated simultaneously in two of the three initial environments, but started 4 d later in the 24L/CT aquaria. The delay did not appear to be due to the artificial environment, since embryo development among the 24L/CT egg masses lagged behind that of the others at the time of collection. In the aquarium, about 95% of the viable ova hatched within 4 d of hatch initiation. Intratank hatch-date variance would be expected to affect the variance of increment counts. However, the 17-d range of larval release dates (from the rock) was not reflected in the otolith microstructure.

Unground sagittae derived from both pre- and posthatch fish were extremely lobulated in structure. The origin of the numerous lobes was 5-10 "peripheral" nuclei, from which the majority of the growth increments emanated. A central nucleus also had growth increments associated with it, although these were incorporated into the peripheral increments within 10-20 d/increments. A prominent hatch check occurred within 5-10 major increments of the central nucleus. The most prominent check of the older otoliths was that associated with the subdivision/transfer date of 10 August.

Many growth increments were visible in the polished otoliths sampled after hatch. When plotted as a function of time, total increment counts were significantly greater than those expected of daily production ($P < 0.05$) (Fig. 2). Diel light and temperature cycles both produced an increment: age slope of about 3.0, suggesting that numerous subdaily increments were being counted with any daily increments present. Increment clarity, prominence, and width varied substantially within an otolith. However, most increments could be assigned to one of two "levels"—visually prominent/relatively wide and visually faint/relatively narrow. To determine if the first level consisted primarily of daily increments, the expected width of a daily increment was calculated.

	23 July	30 July	9 Aug.	10 Sept.
Mean otolith radius (μm):	270	430	620	875

Daily increments on the order of 12-23 and 5-8 μm wide would be expected in the first and second month posthatch, respectively. These expected increment widths were similar to those observed in the first "level" of growth increments.

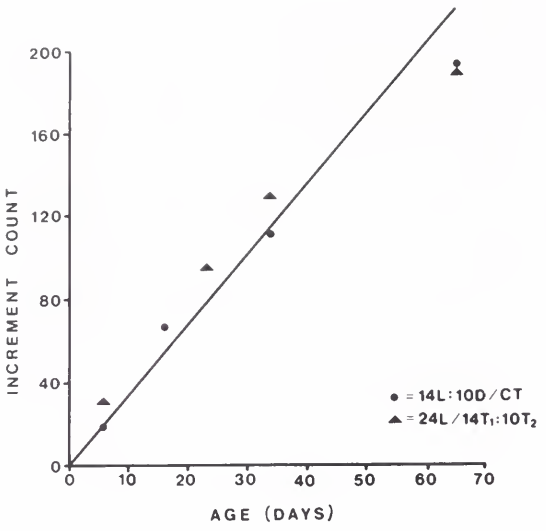


FIGURE 2.—Total otolith increment count as a function of age for plainfin midshipman from two cyclic experimental environments. A straight line has been fitted to the data, although the relationship is probably curvilinear. $N = 5$ for each data point.

Criteria for distinguishing daily from subdaily increments have been reported previously (Taubert and Coble 1977; Campana and Neilson 1982; Marshall and Parker 1982). Nevertheless, no objective criteria have yet been defined which can be applied to all otoliths. In this study, I have used visual prominence and increment width as guides for differentiating daily and subdaily increments. Increments assigned as daily were 1) of similar visual prominence (contrast) to adjacent daily increments (±30%), 2) of similar increment width to adjacent daily increments (±50%), 3) not merged with adjacent daily increments in the nearest radial groove of the sagitta. Some increments met only some of the criteria and were subjectively assigned as daily or subdaily. The observed widths of daily increments, as classified above, were similar to those expected on the basis of otolith growth calculations (see previous paragraph).

Diel Light Cycle

Otoliths of fish reared under a diel photoperiod and constant temperature (14L:10D/CT) produced clear daily growth increments from the time of hatch. Regression of major increment number against elapsed time produced a slope not significantly different from 1.0 ($P > 0.05$); a slope of 1.0 would indicate that one increment was formed every day.

Increment width varied with location on the otolith and fish age (Fig. 3). Subdaily increments were common at all ages, numbering up to 5 between adjacent daily increments. They were most abundant in the first month after hatch. The distinction between daily and subdaily increments was generally clear; however, increments produced 5-20 d after hatch were the most irregular on the otolith, and were sometimes difficult to interpret. Subdaily increments tended to be prominent in this region, so that distinction was a matter of degree (Fig. 4A).

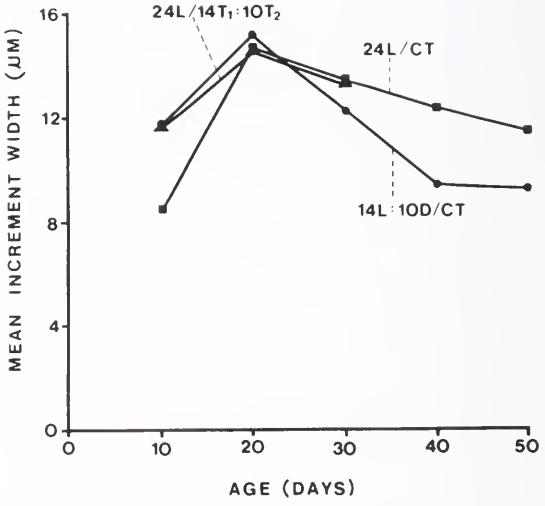


FIGURE 3.—Daily increment width as a function of age for otolith samples of plainfin midshipman from each of the three experimental environments. At a given age, mean widths do not differ significantly among environments, with the exception of values at age 40 d ($P < 0.05$).

Fish transferred to a constant environment (24L/CT) as juveniles produced posttransfer increments that were very different from those produced prior to transfer. Posttransfer increments were visually faint and, in some cases, virtually invisible (Fig. 5A). Subdaily increments were also present. Transfer to a constant environment was not associated with a recognizable lag period during which increments gradually shifted their appearance. Increments produced within 1-2 d of transfer were virtually nonexistent. Nevertheless, posttransfer increments were daily in nature, as indicated by increment counts similar to those expected of daily increment production (Table 1). Daily increments gradually became more prominent after about 15 d posttransfer, their visual contrast improving until the end of the experiment.

TABLE 1.—Growth increment counts in otoliths of plainfin midshipman, *Porichthys notatus*, in relation to elapsed time for various experimental environments. Fish were transferred to new environments (or kept in the original environment as a control) on 10 August.

	10 Aug. samples				10 Sept. samples		
Environment 1	Days after hatch	No. major increments	SE	Environment 2	Days after hatch	No. major increments	SE
14L:10D/CT	34	[1]34.3	0.57	14L:10D/CT	65	66.7	0.80
14L:10D/CT	—	—	—	24L/CT	65	65.1	1.21
24L/$14T_1$:$10T_2$	34	41.1	1.29	24L/CT	65	71.2	0.70
24L/CT	30	49.1	1.33	24L/CT	61	76.9	1.04
24L/CT	—	—	—	14L:10D/CT	61	72.7	1.10
24L/CT	—	—	—	24L/$14T_1$ $10T_2$	61	69.3	0.92

[1]This value was derived from 14L: 10D/CT otoliths sampled 10 September; counts were made from the hatch check to the prominent subdivision/transfer check

Diel Temperature Cycle

Fish hatched under a 24L/$14T_1$:$10T_2$ regime deposited growth increments that differed in many respects from those produced under a cyclic photoperiod (14L:10D/CT). Increments produced up to 8 d medial and distal of the peripheral nuclei were characterized by a high incidence of prominent subdaily increments (Fig. 4B), more so than was the case under a cyclic photoperiod. Daily/subdaily similarities are reflected in the data of 10 August (Table 1), where the observed major increment count was significantly different from that expected of daily increments ($P < 0.05$). The high increment count indicates that some subdaily increments were prominent enough to be classified as daily.

Increments produced in the 15-20 d before transfer were generally distinct and regular in appearance. Increment width and the incidence of subdaily increments were similar to those observed in the corresponding region of the cyclic photoperiod otoliths (Fig. 3). However, the appearance of the major increments was unusual in that the opaque portion of each increment was relatively broad and sharply delineated (Fig. 6).

Fish maintained in the 24L/$14T_1$:$10T_2$ environment after 10 August were overcrowded and did not grow well. As a result, posttransfer otolith growth was limited, increments were very narrow, and reliable counts could not be made. However, increment counts of representative otoliths suggested that daily increments were deposited after the transfer date.

Juvenile fish transferred from the fluctuating temperature regime to a constant environment (24L/CT) produced posttransfer increments similar to those of fish transferred from 14L:10D/CT to 24L/CT (Fig. 5B). The difference between August and September increment counts corresponds to that expected of daily increment deposition ($P > 0.05$) (Table 1). The first five posttransfer increments were faint and virtually nonexistent; subsequent increments became more distinct and regular with time. Opaque regions within each increment never became as broad and discrete as was observed prior to transfer.

Constant Environment

Otoliths of fish hatched under constant conditions (24L/CT) initially resembled those of the other two environments (with respect to the first 5-8 increments). The subsequent region resembled that of 24L/$14T_1$: $10T_2$ fish in that subdaily increments were prominent (Fig. 4C). Although the difference was not significant (Scheffe's test, $P = 0.07$), increment widths tended to be more irregular than those of 14L:10D/CT fish of similar age (Fig. 7). The confusion of daily and subdaily increments in the early larval region resulted in a high variance and a mean increment count that was significantly higher than would be expected of daily increments ($P < 0.05$) (Table 1). After age 10-25 d, daily increments decreased in width (Fig. 3) and became more regular in width (Fig. 7) and appearance, although subdaily increments were still present. Increments with broad, discrete opaque portions were not observed in the 24L/CT fish, as they were in the fluctuating temperature regime. For an unknown reason, otolith growth (but not fish growth) under a 24L/CT regime significantly exceeded that observed under 14L:10D/CT ($P < 0.05$).

Fish remaining in a constant environment after the 10 August transfer date continued to produce distinct increments, although daily and subdaily increments were occasionally difficult to differentiate. Increment width was significantly more irregular than in the posttransfer region of 14L:10D/CT fish (t-test, $P < 0.05$) (Fig. 7). Major increments in the posttransfer region were daily; the regression of increment number against elapsed time resulted in a slope not significantly different from unity ($P > 0.05$).

Posttransfer increments of fish hatched and reared under constant conditions were prominent, although

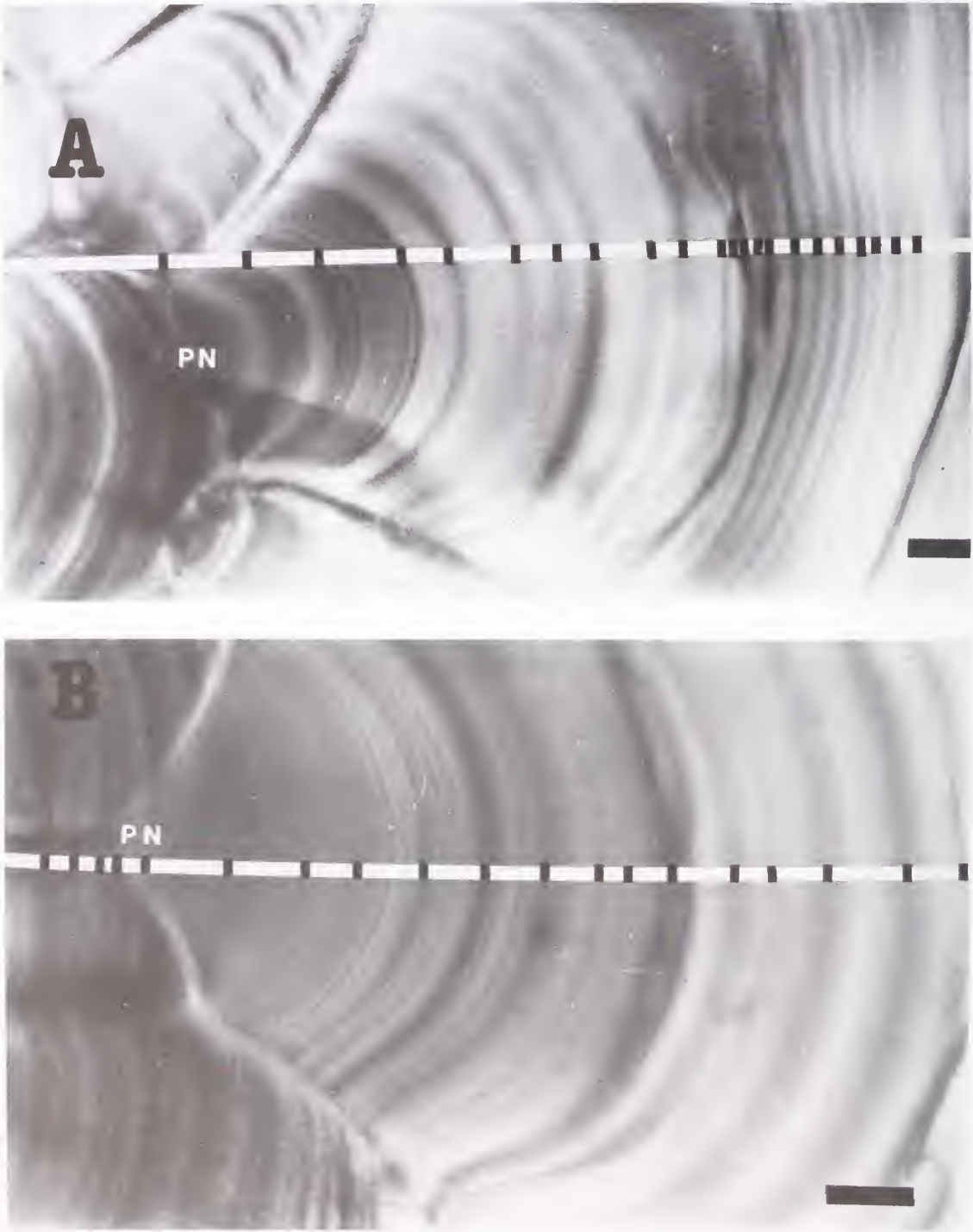
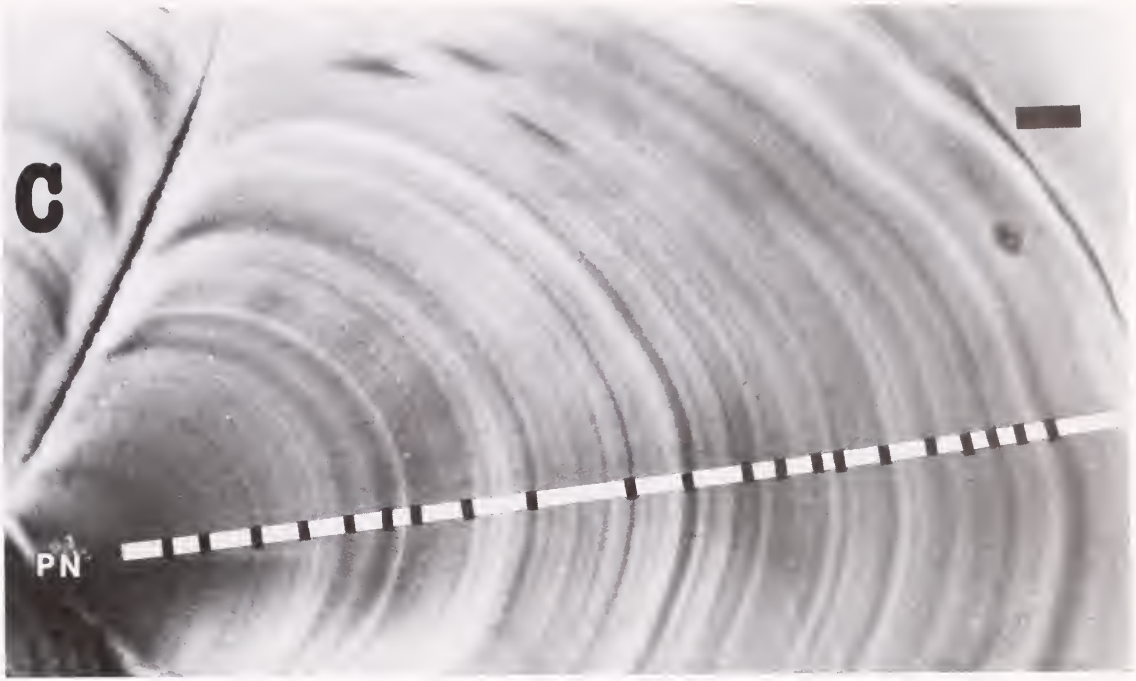


FIGURE 4.—Growth increments on the polished sagittae of larval plainfin midshipman. Subdaily increments are visible between some of the indicated daily increments. Daily increments became more clear with age, but were most prominent/consistent in width in (A). Bar = 30 μm.



PN = peripheral nucleus. (A) Hatched under a diel light cycle; (B) hatched under a diel temperature cycle; (C) hatched under a constant environment.

irregular in width (Fig. 5C). In contrast, increments of fish transferred to the constant environment as juveniles were visually faint, becoming more prominent after 2-3 wk. Juveniles transferred from a constant environment to a cyclic regime deposited similar-appearing increments before and after transfer. However, posttransfer increments tended to be more regular in width than in constant environment fish; the change generally became apparent 2-4 d after transfer. Visual contrast of daily increments may have increased in the fluctuating temperature regime, but the change was not consistent among all otoliths. No such change was evident among the posttransfer increments of fish shifted from 24L/CT to 14L:10D/CT, although the incidence of subdaily increments appeared to decrease. Fish transferred from the constant environment to either of the cyclic regimes produced daily increments after transfer; high increment counts (Table 1) were derived from the irregular, pretransfer region of the otolith.

DISCUSSION

Daily growth increments were deposited on the otoliths of plainfin midshipman under a variety of environmental conditions. My results indicated that light, temperature, age, and an endogenous circadian rhythm may all influence the production and/or appearance of daily and subdaily increments. However, some of the variables tested interacted to a large degree, and their influence on increment production was subject to alteration through time.

A cyclic light regime influenced increment production in larval fish more than any other variable tested. Under a natural photoperiod, daily increments were produced from the time of hatch. In contrast, constant light conditions disrupted the production of posthatch increments, resulting in a high incidence of prominent nondaily increments (>1 increment/24 h) and irregular increment widths. My observations are consistent with those of Taubert and Coble (1977), who observed numerous, nondaily increments in larval *Tilapia* hatched under constant light conditions. Those authors concluded that light acted as a zeitgeber for an endogenous rhythm and that without a cyclic photoperiod, daily increment production was not possible. My results only partially support their conclusion. Photoperiod entrained daily increment production in newly hatched midshipman. However, in the absence of cyclic light or temperature stimuli, an endogenous circadian rhythm of increment deposition became apparent after an acclimation

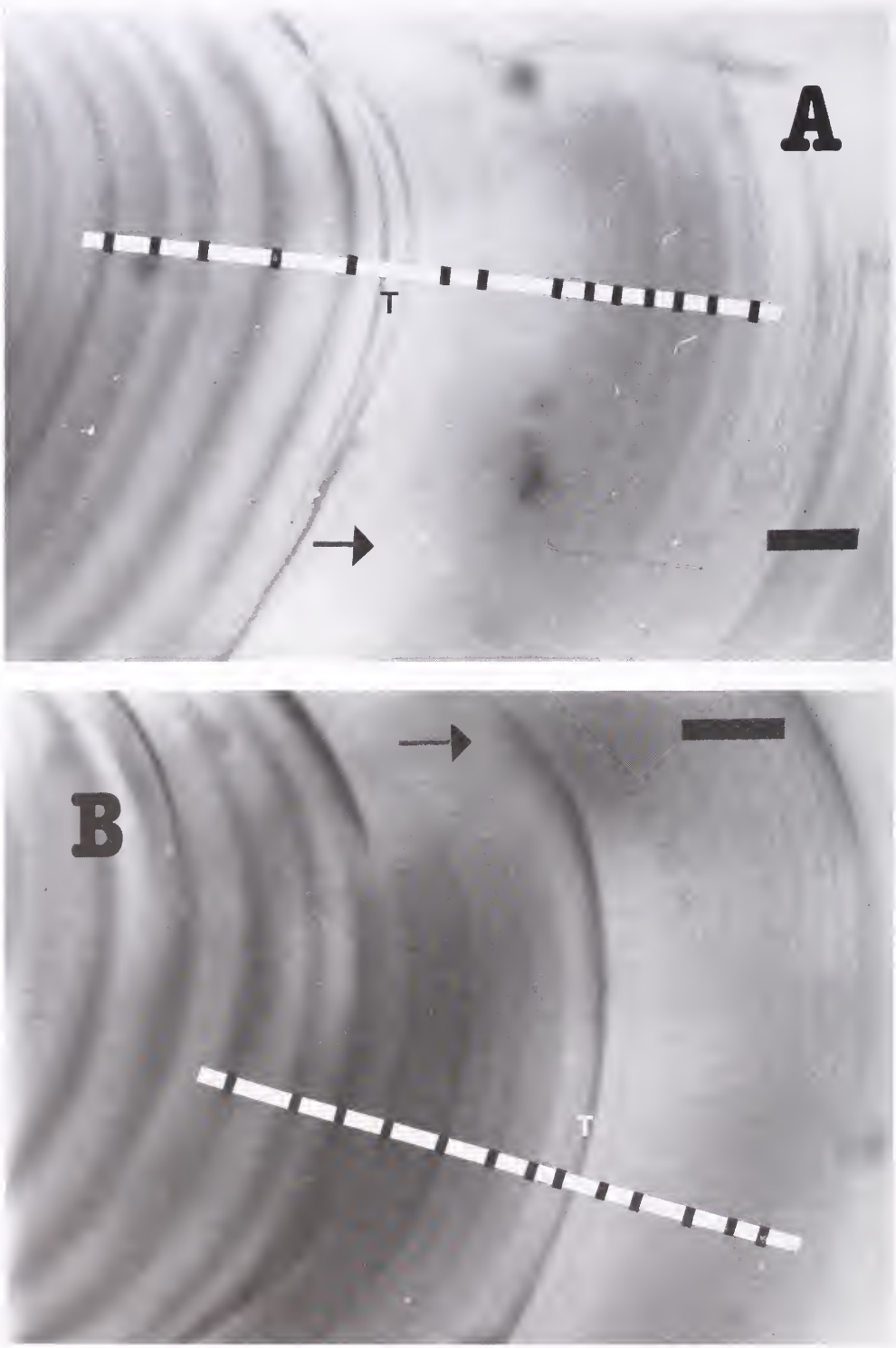
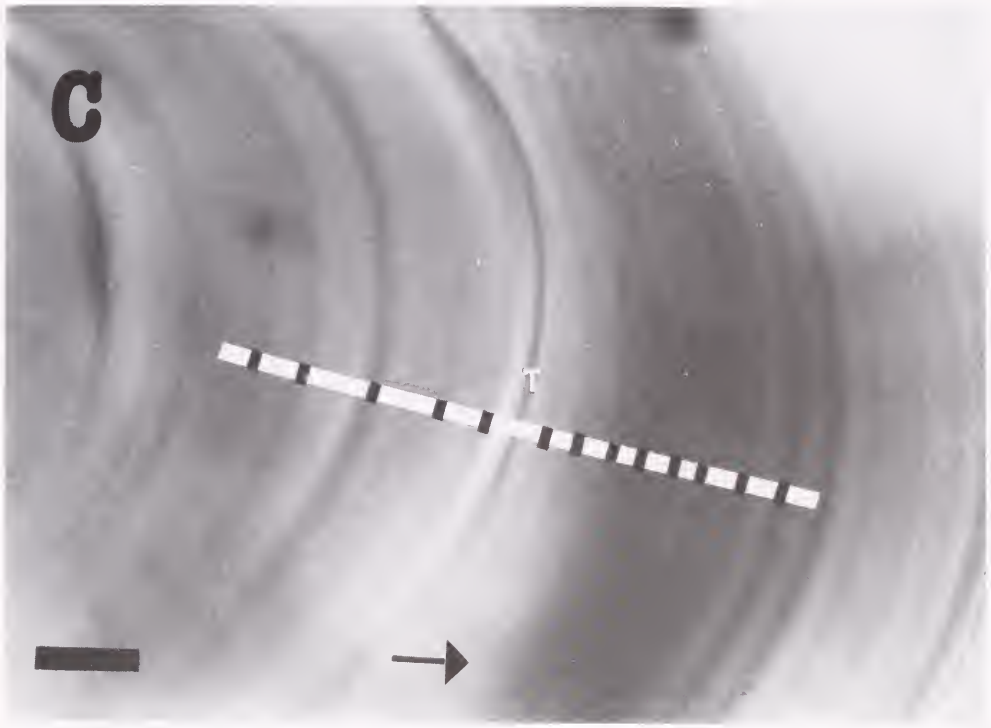


FIGURE 5.— Growth increments in sagittae of plainfin midshipman produced before and after transfer to a constant environment. Fish hatched under 24L/CT produced clearer daily increments than those transferred from a different



environment. Daily increments are indicated, as is direction of sagittal growth (arrow). T = transfer check. Bar = 30 μm. (A) 14L:10D/CT to 24L/CT; (B) 24L/14T_1:10T_2 to 24L/CT; (C) 24L/CT to 24L/CT.

period of 2-4 wk. Therefore, photoperiod acted as a zeitgeber for an endogenous rhythm during the early larval stages, but became unnecessary with increasing age. The nondaily increments produced after hatch in this study (and that of Taubert and Coble 1977), probably comprised both daily and subdaily increments. The combination resulted in the deposition of more than 1 increment/24 h.

If a constant photoperiod was present at hatch, an endogenous rhythm of increment deposition became apparent after an acclimation period. Acclimation also occurred when older fish were transferred from a natural light cycle to constant light conditions. However, the pattern of increment production during acclimation differed at the two ages (Table 2). The larval fish acclimation period may be analogous to that of newborn rats transferred from a diel photoperiod to constant conditions. An arhythmic activity pattern continues for almost 2 wk in rats before an endogenous circadian rhythm becomes apparent (Davis 1981).

The length of the acclimation period could not be determined with accuracy. A shift in increment appearance after transfer from a constant to a cyclic environment generally occurred in 2-5 d. The reverse transfer resulted in almost nonexistent increments for a period of 5 d, but the visual contrast of the growth patterns improved over the subsequent 10-15 d. Therefore, the critical stage of the adaptation process appears to have been completed in 2-5 d. This result is consistent with that of Tanaka et al. (1981), who observed a 6-d transitory period of increment formation when a 24-h light-dark cycle was suddenly reversed.

TABLE 2.—Age effects on growth increment production in otoliths of plainfin midshipman, *Porichthys notatus*, reared under three artificial environments.

Larvae	Juveniles
Light important as zeitgeber	Light not important as zeitgeber
Daily & subdaily increments similar during acclimation to 24L	Faint daily increments, but subdaily increments dissimilar during acclimation to 24L
Long acclimation to 24L	Short acclimation to 24L
Immature circadian rhythm	Mature circadian rhythm

Age-related changes in endogenous circadian rhythms have not been examined in fishes. Mammalian studies indicate that endogenous rhythms often appear after birth; once present, cycle amplitude tends to increase with time until the rhythm is "mature" (Davis 1981). *Porichthys* larvae hatched under constant light appear to fit this pattern. Daily and subdaily increments were not easily

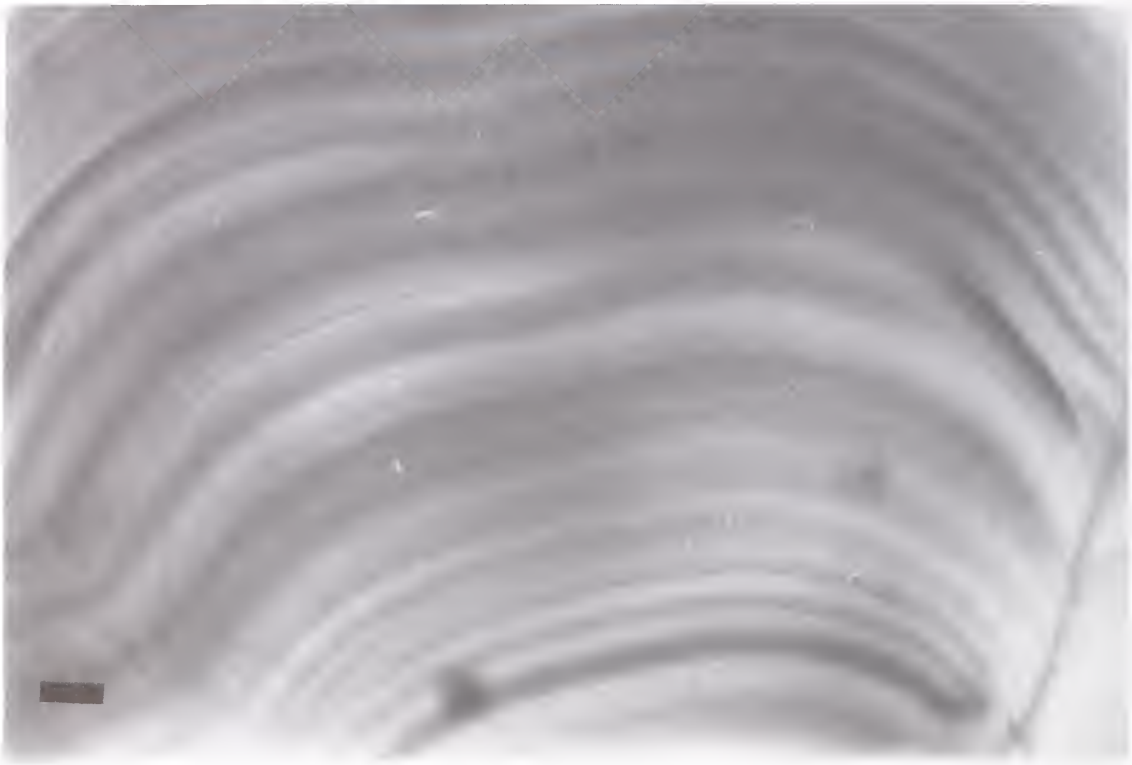


FIGURE 6.—Daily growth increments produced on the sagittae of plainfin midshipman after 15-25 d of rearing under a diel temperature cycle. The increments were visually prominent and sharply delineated relative to those produced under other environmental regimes. Bar = 20 μm.

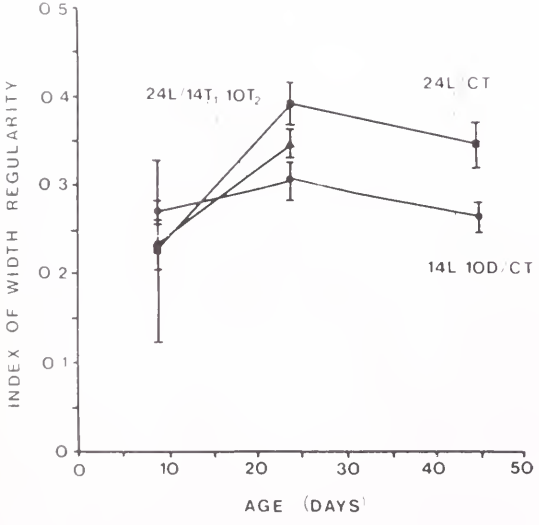


FIGURE 7.—Index of daily increment width regularity as a function of age for otolith samples of plainfin midshipman from each of the three experimental environments. Bars represent ±1 SE.

differentiated at first, suggesting that the circadian deposition rhythm was not yet mature. Maturation apparently occurred by days 10-20. Early larval increments were only indistinct temporarily in the 14L:10D/CT fish, suggesting that the cyclic photoperiod entrained the maturing rhythm fairly quickly. In addition, very young animals may be more responsive to a diel light cycle, due to age-related characters of the rhythm cycle (Sacher and Duffy 1978). For instance, the metabolic rate of newly hatched rats is very sensitive to changes in light level, while older rats are less affected. In this study, larval fish exposed to a constant environment took longer to produce daily increments than did juvenile fish, suggesting an analogy with the rat study. Similar age-related results were reported by Gibson et al. (1978) in an ontogenetic study of flatfish activity cycles. A constant photoperiod eliminated a diel activity cycle in larval plaice (*Pleuronectes platessa*), but had no such effect on juveniles of the same species.

Increasing age of midshipman was correlated with decreasing increment width and fewer subdaily

increments in all environments. However, foremost among the age-associated effects (Table 2) was the prominence of daily increments in juveniles relative to larvae. Distinction between daily and subdaily increments was seldom difficult in juveniles (outside of the acclimation period) unlike the situation in larval otoliths. If this age-related difference in daily increment formation is universal, daily increment counts in larvae may be unreliable relative to slightly older fish. This suggestion has serious implications for the application of growth increments in aging larval fish. Similarly, the absence of definitive criteria for differentiating daily and subdaily increments could cause problems in aging field-collected fish. Subdaily increments can be numerous and confusing in some species (Campana, unpubl. data).

The demonstration of and age-related rhythm and the existence of an acclimation period may have resolved some of the conflicting results in the literature concerning the zeitgeber effect of light. In a previous study, a constant light regime did not influence the production of daily increments in juvenile starry flounders (Campana and Neilson 1982). The flounders were about 8 mo-old, suggesting that the necessary acclimation period would be short. In addition, the fish were exposed to the experimental environment for 2 wk prior to tetracycline injection (marking the start of the experiment); it is probable that acclimation occurred during this period, resulting in clear daily increment production by the time the experiment began. An analogous explanation may explain the results of another study, where chinook salmon eggs, reared in darkness, produced daily increments after hatch (Neilson and Geen 1982). The embryos were held in total darkness for 50 d before hatch, suggesting that their endogenous circadian rhythm had time to acclimate before hatch.

A fluctuating temperature regime did not entrain increment production under constant light conditions. Fish reared in this environment produced more increments than would be expected of daily production, similar to those of 24L/CT fish. The variance of larval increment counts was similar to that produced under a constant environment, both of which were significantly larger than the 14L:10D/CT variance (Bartlett's test, $P < 0.01$). Once acclimation occurred, daily increments were produced through an apparently endogenous periodicity, and not through temperature entrainment of an internal clock. However, the formation of a broad, optically dense, sharply delineated opaque zone in postacclimation daily increments indicates that temperature fluctuation did affect increment production. The opaque portion of a daily increment consists of calcium carbonate and a proteinaceous matrix, with the latter component predominating (Brothers 1981; Mugiya et al. 1981). Falling temperatures, such as would occur at night, may have increased the proportion of protein deposited in the opaque region, resulting in an increment that had increased visual contrast. Accentuation of contrast renders increments visually prominent, and could easily be interpreted as an entraining mechanism. Diel temperature fluctuations noticeably accentuated increment contrast in young chinook salmon otoliths (J. D. Neilson[2]). A correlation of increasing protein deposition with decreasing temperature suggests that the broad opaque zone formed during the low temperature, 10-h, experimental "night", overlaid the opaque zone formed under circadian control through a 3-h period (Mugiya et al. 1981). If temperature does exert a "masking" effect (Enright 1981), a low temperature-induced opaque zone would appear independently of any endogenous circadian rhythm of deposition. Therefore, multiple daily oscillations in temperature could conceivably produce a distinct increment after each cycle, in addition to the daily increment formed under endogenous control. In some situations, the masking effect of temperature fluctuations may be substantial, obscuring most of the increments formed through the action of an endogenous rhythm of deposition (E. B. Brothers[3]). This hypothesis is consistent with studies that demonstrated that temperature cycles do not entrain daily increment production (Campana and Neilson 1982; Neilson and Geen 1982), but can influence increment formation (Brothers 1981).

My results suggest that a diel light cycle entrains an endogenous circadian rhythm of increment deposition. Increasing age mitigated the zeitgeber effect of photoperiod, while temperature fluctuation influenced increment appearance, rather than periodicity. In other studies, the incidence of subdaily increments was correlated with feeding periodicity (Neilson and Geen 1982; Campana 1983). The fact that so many variables may affect increment deposition suggests that the environment does not influence the rhythm of otolith deposition directly, but acts through some penultimate process. Metabolic rate is susceptible to environmental influence, as well as being subject to an endogenous circadian rhythm (Matty 1978) that changes with age (Davis 1981). However, metabolic rate is in turn

[2]J. D. Neilson, Marine Fish Division, Biological Station, St. Andrews, New Brunswick, Canada E0G 2X0, pers. commun. January 1983.

[3]E. B. Brothers, Division of Biological Sciences, Cornell University, Ithaca, NY 14850, pers. commun. May 1983.

regulated by endocrine levels, and it may be the environmental modulation of endocrine rhythms that ultimately controls increment periodicity on the otolith (Menaker and Binkley 1981). Endocrine secretion often follows a circadian pattern (Simpson 1978) and, in mammals at least, is closely linked to the circadian pacemaker itself (Menaker and Binkley 1981). Hormones regulate many aspects of metabolism and growth, including skeletal calcification (Simpson 1978). Therefore, it seems reasonable to postulate that those factors that entrain and/or moderate the circadian rhythm of endocrine secretion will have a subsequent effect on increment deposition in the otolith.

ACKNOWLEDGMENTS

Jim McNutt of Ayerst Laboratories kindly donated the antibiotics used in this study. I appreciate the assistance and technical innovation of Doug Begle in the field and laboratory. John D. Neilson and Norman J. Wilimovsky provided many helpful comments on an earlier draft of the manuscript. This study was supported by a grant from the Natural Sciences and Engineering Research Council of Canada to Norman J. Wilimovsky.

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ASPECTS OF THE LIFE HISTORY AND FISHERY OF THE WHITE CROAKER, *GENYONEMUS LINEATUS* (SCIAENIDAE), OFF CALIFORNIA

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ROBERT J. LAVENBERG,[2] AND LINDA MARTIN[3]

ABSTRACT

White croaker, *Genyonemus lineatus* (Ayres), was a dominant species off southern California in nearshore, sandy substratum waters, and comprised 29.7% of all fish taxa taken in otter trawl hauls. Juveniles occurred in waters <27 m and the mean length of all individuals increased with depth. The maximum depth of capture was 183 m.

White croaker live to 12 years, exhibiting rapid growth which is essentially constant throughout the species' life. Females grew at a slightly faster rate than males. Von Bertalanffy age-length parameters for females were $L_\infty = 60.7, k = 0.04, t_0 = -7.6$, and for males $L_\infty = 59.2, k = 0.03, t_0 = -8.7$. After 1 year, more than 50% of the individuals are mature, but others delay maturity for 4 years. Larger females had longer spawning seasons than did smaller individuals. Although spawning occurred throughout the year, principal spawning occurred between November and April, with a February-March peak. White croaker are batch spawners; females spawned 18-24 times a season. Batch fecundities ranged from 800 to 37,200 eggs. White croaker reproduction off Monterey differed significantly from that off southern California. Large-scale spawning occurred from at least July through February, and continued throughout the year. Colder water off Monterey may have allowed for extended spawning activity.

White croaker larvae were a significant constituent of the southern California ichthyoplankton fauna, second in abundance to northern anchovy, *Engraulis mordax*, in waters <36 m deep. Data from ichthyoplankton surveys indicated two spawning centers, one located from Redondo Beach to Laguna Beach and a smaller one centered about Ventura. Highest larval densities were found near the substratum in 15-22 m of water. White croaker is an important part of the skiff sportfishery and the basis of a growing commercial gill net fishery. Size frequencies of white croaker taken in both fisheries indicated that few juveniles were captured.

Fishes of the family Sciaenidae (drums) are a major constituent of the fauna of the eastern temperate Pacific coast off California (Skogsberg 1939; Frey 1971). Eight species have been recorded off California, primarily in inshore waters. With the exception of the shortfin corvina, *Cynoscion parvipinnis*, and black croaker, *Cheilotrema saturnum*, all six of the other species known from off California (white seabass, *Atractoscion nobilis*; white croaker, *Genyonemus lineatus*; California corbina, *Menticirrhus undulatus*; spotfin croaker, *Roncador stearnsii*; queenfish, *Seriphus politus*; yellowfin croaker, *Umbrina roncador*) are of sport or commercial importance.

The white croaker is an abundant species that associates with soft (primarily sand) substrata in the coastal zone. White croaker are small (reaching lengths of 41.4 cm total length, Miller and Lea 1972) and active fishes that range from the surf zone to depths of 183 m between Vancouver Island, British Columbia, Canada, south to Magdalena Bay, Baja California, Mexico. Within this geographic range, they are most abundant between San Francisco Bay and northern Baja California. White croaker are omnivores, feeding on a variety of benthic and epibenthic forms (crustaceans, clams, polychaetes, and small fishes, particularly the northern anchovy, *Engraulis mordax* (Phillips et al. 1972; Morejohn et al. 1978; Ware 1979)).

White croaker are the mainstay of pier and small boat sportfish catches in both southern (Pinkas et al. 1968; Wine and Hoban 1976) and central California (Miller and Gotshall 1965). In addition, commercial catches have increased in recent years to 200,000 kg/yr.[4] Despite this, *G. lineatus* is a much maligned species, as it is small and adept at bait-stealing. More-

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over, there is a firmly held belief that white croaker are unusually wormy. In fact, the frequency of occurrence of nematodes (larval *Anisakis* and *Phocanema*) in white croaker muscle is lower than that for at least some other important sport and commercial species such as California halibut, *Paralichthys californicus*, and chilipepper rockfish, *Sebastes goodei* (Dailey et al. 1981).

Because white croaker are abundant around sewage outfalls and tolerant of degraded environments, much of the recent research on this species has been pollution-centered. Several published works deal with pesticide levels (Castle and Woods 1972; MacGregor 1972; Stout and Beezhold 1981) and pollution-implicated diseases and abnormalities (Russell and Kotin 1957; Mearns 1974, 1979; Mearns and Sherwood 1977; Sherwood 1978). Five small-scale studies have been conducted on its life history (Issacson 1964, 1967; Goldberg 1976; Morejohn et al. 1978; Ware 1979)

This contribution represents a summation of unpublished white croaker data obtained from three sources: a life history and fishery study by Love, ichthyoplankton work by McGowen and Lavenberg, and a trawling survey by Westphal.

METHODS

Collection of Juveniles and Adults

Samples were collected monthly (3-6 per month) from October 1978 to February 1981 with a 7.6 m or 4.9 m headrope otter trawl in 15-65 m of water between Palos Verdes and Huntington Beach, Calif. Reduced numbers of white croaker also were collected monthly from April 1979 to September 1981 in Monterey Bay with a 4.9 m otter trawl in 10-60 m of water or were purchased from local fishermen. All of these specimens were frozen for later dissection. After thawing, all fish were measured (total length, fork length, standard length), weighed, sexed, and the gonads were weighed.

Collection of Depth Preference Data for Adults and Juveniles

Information on white croaker depth preference was based on data from a trawling program aboard the RV *Vantuna*. Trawling was conducted at a speed of 2-3 kn for 20 min with a 7.6 m (occasionally 4.9 m) otter trawl having a net of 0.6 cm stretch mesh. From September 1972 through December 1980, 18 stations (Fig. 1) were sporadically sampled at 10 depths, although most of the trawling effort was performed at depths between 59 and 91 m. After shipboard sorting, fishes were measured (board standard length) and discarded. All lengths were converted to total length (TL) using conversion factors based on measurements of 100 white croaker (Table 1).

TABLE 1.—Conversion factors between standard (SL), fork (FL), and total (TL) lengths (cm), based on measurements of 100 white croaker from southern California.

SL = 0.442 + 0.79 TL	FL = 0.088 + 0.96 TL	TL = 0.892 + 1.19 SL
= 0.379 + 0.82 FL	= 0.849 + 1.14 SL	= 0.023 + 1.04 FL

Techniques for Aging Juveniles and Adults

Sagitta were removed from each side of the head, and the otoliths were cleaned, air dried, and stored in vials. Because whole croaker otoliths are difficult to age, they were sectioned on a Buehler Isomet[5] low speed saw, Otoliths were placed on wood blocks and completely embedded in clear epoxy (Ciba 825 hardener and Ciba 6010 resin). Each block with its otolith was emplaced on the saw and a dorsal-ventral 0.05 cm wafer was cut through the otolith, using two diamond-edge blades separated by a stainless steel shim. Wafers were stored in water for a few days to soften the epoxy (which was removed), then the wafers were placed in a black-bottomed water glass filled with water and read under a dissecting microscope at a magnification of 10×. All otoliths were read twice, about 4 mo apart, by Love. When readings did not agree, the otoliths were read again. The value of two coincident readings was accepted as the best estimate of age. Fifteen percent of all otoliths were unreadable due to a lack of recognizable annuli.

Procedures for Determining the Timing of Maturation and Reproduction

We estimated length at first maturity by classifying gonads as immature or mature based on the techniques of Bagenal and Braum (1971). Smaller mature fish and fish just entering their first mature season become reproductive later in the spawning season. Hence we estimated length at first maturity during the peak spawning period of January, February, and March. To ascertain spawning season duration and its relation to body size, we sampled at least 150 females/mo in 1 cm size intervals throughout the

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

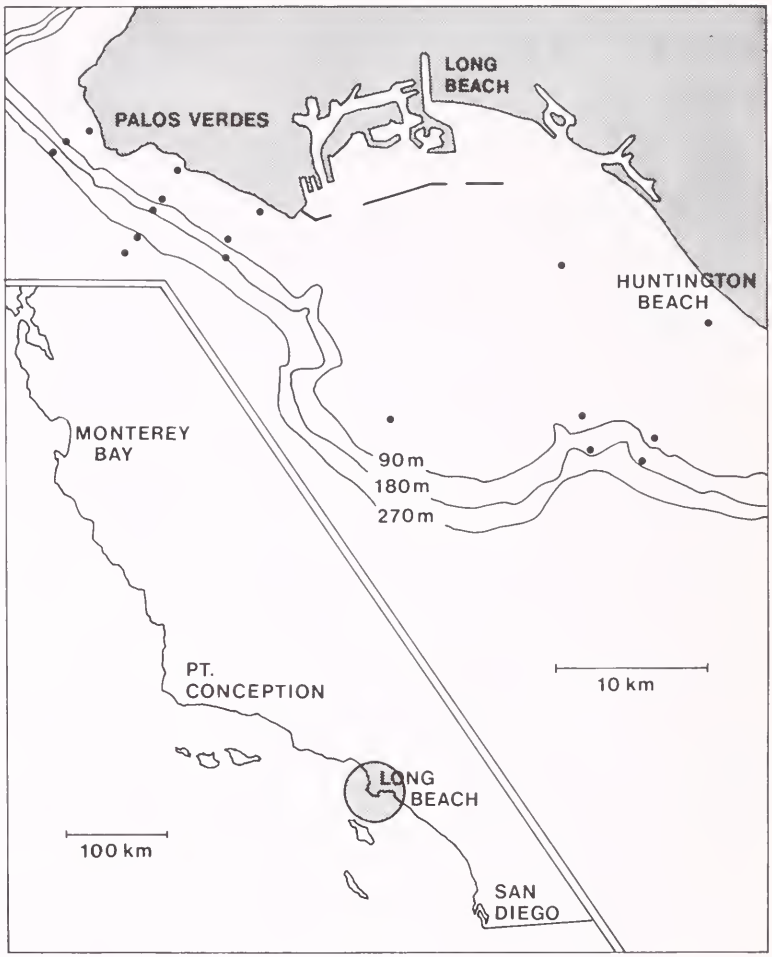

FIGURE 1.—Location of white croaker sampling sites.

year. A gonadosomatic index (gonad weight)/(total body weight) × 100 was computed from frozen specimens to quantify changes in gonad size with season. Ovaries for use in fecundity studies were fixed in modified Gilson's fluid (Bagenal and Braum 1971) for 4-8 mo. We measured fixed egg diameters from 11 individuals, all of which contained some hydrated eggs. Batch fecundity was estimated by the gravimetric method of Bagenal and Braum (1971). The time between spawning events per female was computed by estimating the percent of females with hydrated eggs on any given night during the spawning season.

We computed condition factor $\frac{100\,(W-GW)}{L^3}$, where W = body weight in grams, GW = gonad weight in grams, and L = total length in centimeters—of mature southern California and Monterey croaker. Condition factor was computed using body weight with gonad weight subtracted to minimize the effects of seasonal changes in gonad size.

Larval Sampling

Ichthyoplankton data presented here were collected monthly between August 1979 and July 1980 along 20 sites within the Southern California Bight aboard the RV *Seawatch* (Table 2). Stations were established at 8 and 22 m along each transect (with exception of Palos Verdes and Laguna Beach where 15 m was substituted for 8 m). Additional stations at 15 and 36 m depths were maintained at three sites (Ormond Beach, Redondo Beach, San Onofre). Oblique bongo tows from the bottom to the surface were made at all stations. A 70 cm diameter bongo net sampler (McGowan and Brown 1966), equipped with wheels to prevent damage when the sampler encountered the bottom, was lowered to the bottom with canvas

TABLE 2.—Southern California ichthyoplankton collection sites, August 1979-July 1980. Location abbreviations used in Figures 13-15 are in parentheses.

Collection sites	Lat. N	Long. W
Coho Bay (80)	34°26′	120°26′
Refugio to El Capitan, 8 m (DR)	34°27′	120°02′-120°05′
North of Refugio, 22 m	34°27′	120°06′
Santa Barbara to Goleta Pt. (8.15)	34°25′	119°44′-119°51′
Pt. Gorda to Rincon Pt. (RN)	34°22′-34°23′	119°28′
Ventura (83)	34°16′	119°17′
Ormond Beach (OB)	34°07′	119°10′
Arroyo Sequit (85)	34°03′	118°57′
Malibu Beach (MU)	34°02′	118°41′
Playa del Rey (87)	33°57′	118°27′
Redondo Beach (RB)		
Redondo Breakwater, 8, 15, and 22 m	33°51′	118°24′
Hermosa Pier, 36 m	33°52′	118°25′
Palos Verdes (PV)	33°43′	118°25′
Huntington Harbor (88)	33°41′	118°04′
Balboa (BA)	33°36′	117°54′
Aliso Creek (Laguna Beach) (90)	33°31′	117°46′
San Onofre (SO)	33°21′	117°33′
Santa Margarita River (91)	33°15′	117°28′
Agua Hedionda (Carlsbad) (CD)	33°08′	117°23′
San Dieguito River (Del Mar) (93)	32°58′	117°16′
Mission Beach (MB)	32°48′	117°16′
San Diego (95)	32°38′	117°09′

doors over the mouth openings. The canvas doors were removed by a cable messenger, allowing the nets to fish. Immediately thereafter the sampler was retrieved at a constant rate of about 10 m/min (0.17 m/s); a wire angle of 51 ± 5° was maintained. The ship's speed (0.95 ± 0.03 m/s) plus the retrieval rate brought the net speed to about 1.12 m/s.

In addition, stratified (surface, midwater, bottom) tows were made at each of the four stations on transects at Ormond Beach, Redondo Beach, and San Onofre. Horizontal midwater tows were made with the previously described bongo sampler towed at a rate of 1.06 ± 0.06 m/s. For these tows the sampler was lowered to a depth about half-way between the surface and the bottom, opened via cable messenger, fished, closed via cable messenger, and retrieved. Surface samples were taken with a manta sampler (Brown 1979) towed at a rate of 1.07 ± 0.06 m/s. This net had a rectangular opening (88 × 16 cm). Bottom collections were taken using an auriga net[6] with a 200 × 50 cm mouth. The auriga net fished a zone 2 m wide by 0.5 m deep, about 0.25 m above the substratum, and was fished at a rate of 1.07 ± 0.46 m/s. All nets were equipped with 335 μ mesh. A General Oceanics flowmeter was mounted in the mouth of each net. The field program is described in greater detail by Lavenberg and McGowen.[7]

Additional data from a 4-yr study off Redondo Beach were derived from monthly surface tows made from January 1974 to February 1977, using meter nets with 335 μ mesh. A TSK flowmeter was mounted in the mouth of each net. This field program is described in greater detail by McGowen.[8]

Fishery

Although white croaker are usually the most important species in the private vessel sportfishery, no size-frequency data were available. For this reason, 4,941 croaker taken by anglers aboard skiffs and other small private vessels were measured during the period June 1980 to July 1981, between Oxnard and Dana Point. From September 1980 through August 1981, 1,748 white croaker were taken off southern California by commercial gill net vessels and were measured.

RESULTS

Depth Preference

Our trawling study indicated that white croaker preferred nearshore habitats and their abundance declined in deeper waters. Ranking first of all species taken, white croaker was the dominant species at the shallowest (18-27 m) stations (Table 3), and composed 29.7% by number of the total catch and appeared in 68% of the trawls. At the 59-73 m stations, white croaker catches had declined to 3.3% of total catch, frequency of occurrence 20.7%, and at the 91-109 m station, the species made up 1.2% of total catch, frequency of occurrence 14.0%. At stations between 165 and 183 m, white croaker comprised 0.6% of the total catch, with a frequency of occurrence of 1.7%. On the basis that no individuals were captured at greater depths, we accept 183 m as their maximum depth.

Though white croaker was supplanted as the dominant species at deeper stations, it remained an important community component to depths of 109 m. Two other species, the California tonguefish, *Symphurus atricauda*, and the Pacific sanddab, *Citharichthys sordidus*, were among the 10 most abundant species throughout these depths. Pacific

[6]Mitchell, C. T. Auriga: A wheeled epibenthic plankton sampler for rocky bottoms. Unpubl. rep., 12 p. Marine Biological Consultants Inc., 947 Newhall Street, Costa Mesa, CA 92627.

[7]Lavenberg, R. J., and G. E. McGowen. Coastal ichthyoplankton of the Southern California Bight: temporal and spatial distribution (August 1979-July 1980). Manuscr. in prep. Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, CA 90007.

[8]McGowen, G. E. 1978. Effects of thermal effluent from Southern California Edison's Redondo Beach steam generating plant on the warm temperate fish fauna of King Harbor Marina. SCE Research and Development Series: 78-RD-47, 65 p.

TABLE 3.—The 10 most abundant fish species taken by otter trawls in three depth intervals off Southern California, 1972-80.

	Total no. taken	% total no.	% frequency occurence
Depth interval, 18-27 m Number of collections, 109 Total no. of fish, 14,313 Total Species, 80			
Genyonemus lineatus	4,252	29.7	67.9
Citharichthys stigmaeus	2,221	15.5	63.3
Symphurus atricauda	2,031	14.2	60.6
Seriphus politus	1,341	9.4	44.0
Phanerodon furcatus	595	4.2	59.6
Engraulis mordax	591	4.1	22.0
Pleuronichthys verticalis	476	3.3	62.4
Hyperprosopon argenteum	395	2.8	33.0
Citharichthys sordidus	301	2.1	12.8
Synodus lucioceps	206	1.4	38.5
Depth interval, 59-73 m Number of collections, 82 Total no. of fish, 13,337 Total species, 62			
Citharichthys sordidus	3,196	24.0	72.0
Microstomus pacificus	2,769	20.8	65.9
Sebastes dalli	1,565	11.3	65.9
Sebastes saxicola	867	6.5	29.3
Porichthys notatus	786	5.9	59.8
Sebastes jordani	694	5.2	17.1
Symphurus atricauda	512	3.8	51.2
Scorpaena guttata	506	3.8	63.4
Genyonemus lineatus	436	3.3	20.7
Icelinus quadriseriatus	297	2.2	25.6
Depth interval, 81-109 m Number of collections, 172 Total no. of fish, 35,488 Total species, 77			
Microstomus pacificus	12,386	34.9	76.2
Citharichthys sordidus	9,655	27.2	73.8
Sebastes saxicola	4,262	12.0	65.1
Porichthys notatus	1,688	4.8	63.4
Glyptocephalus zachirus	1,249	3.5	30.2
Scorpaena guttata	875	2.5	44.2
Sebastes jordani	802	2.3	21.5
Genyonemus lineatus	441	1.2	14.0
Symphurus atricauda	377	1.1	24.4
Zaniolepis frenata	299	0.8	25.0

sanddab dominated in waters between 59 and 109 m, declining in numbers both inshore and offshore. California tonguefish exhibited an abundance pattern like white croaker, with numbers peaking in inshore waters and declining with greater depth.

Most juvenile white croaker (50% mature by 15 cm) were limited to the inshore (18-27 m) stations (Fig. 2). Larger individuals inhabited greater depths. In fact, the mean size of white croaker was successively larger as depth increased (ANOVA, $F = 284.2, P < 0.001$).

Age and Growth

Lengths at ages were estimated by direct observation of otolith annuli and through the von Bertalanffy growth curve model

$$L_t = L_\infty [1 - \exp - k (t - t_0)]$$

where L_t = length at time t
L_∞ = theoretical maximum length
k = constant expressing the rate of approach to L_∞
t_0 = theoretical age at which $L_t = 0$

was fitted to the direct observation age-length data.

We transformed male and female growth equations to linear form (Allen 1976) and compared these by analysis of variance. Females were found to grow significantly faster than males ($F = 16.8, P < 0.05$), hence we separated growth data by sex (Table 4).

TABLE 4.—Parameters of the von Bertalanffy equation for white croaker off southern California.

Sex	L_∞	SE	k	SE	t_0	SE
Female	60.72	0.23	0.037	0.02	−7.54	1.1
Male	59.17	0.29	0.033	0.03	−8.66	1.3

The oldest male and female white croaker we examined were 12 yr old (Fig. 3). Females grew slightly faster than males and reached a greater size. Females from age 1 (at which over 50% of the fish were mature) outgrew males.

White croaker grew at a fairly constant rate throughout their lives, exemplified in their very low k values. No asymptote was reached within the observed 12-yr life span. Thus, the maximum predicted lengths were longer than both published (41.4 cm TL, Miller and Lea 1972) and unpublished (44.2 cm[9]) records, although the r values for the von Bertalanffy equations were high (0.84 for both sexes).

Length - Weight Relationships

A total of 581 males and 665 females from southern California and a total of 94 males and 161 females from Monterey Bay were weighed and measured. The relationships between total length and weight fit the relationship $W = aL^b$, where W = weight in grams, L = total length in centimeters, and a and b are constants, with values determined using $\log_{10}$ transformation and fitting the values to a straight line by least squares (Figs. 4, 5). In southern California, males tended to be heavier at a given length than females (analysis of variance, $F = 10.18, P < 0.01$), whereas off Monterey no significant difference was found (analysis of variance, $F = 0.67, P > 0.4$). To test whether this difference was an artifact caused by seasonal and gender-related factors, we subtracted

[9]R. N. Lea, California Department of Fish and Game, 2201 Garden Road, Monterey, CA 93940, pers. commun. May 1982.

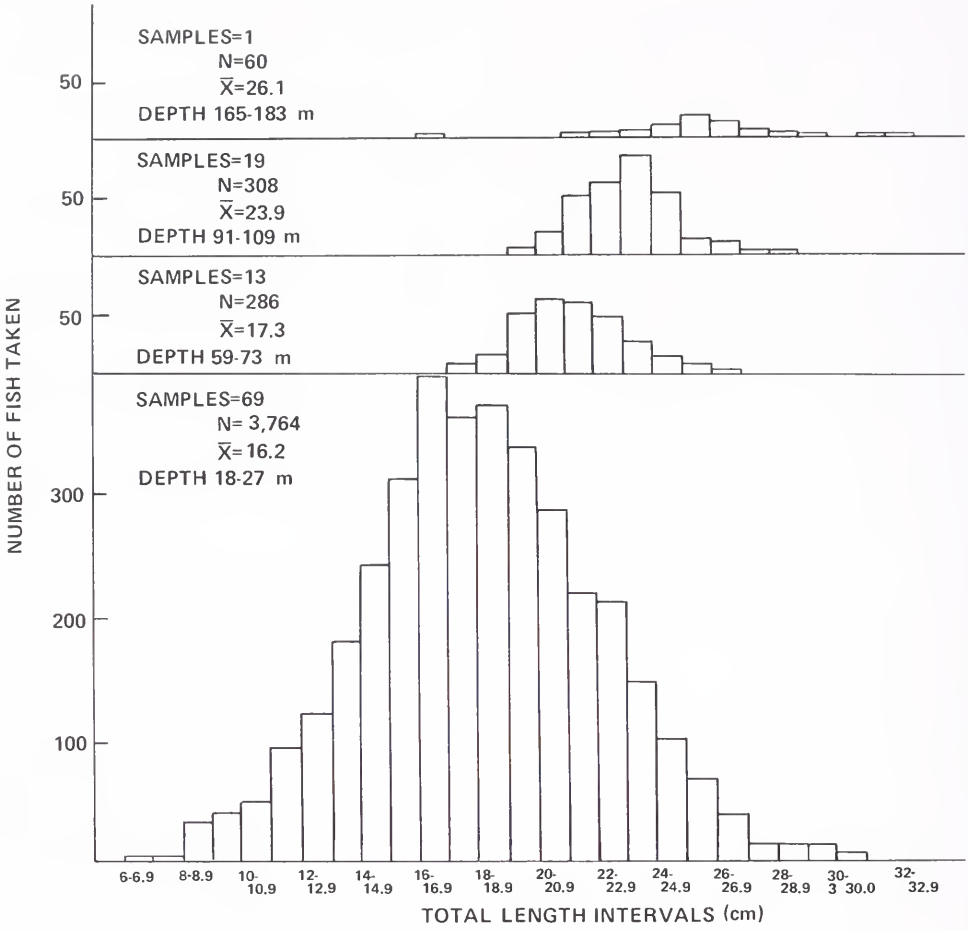

FIGURE 2.—Length intervals of white croaker taken by otter trawl off southern California.

gonad weight from body weight, generated the length-weight relationships for each sex and tested these between sexes. Again, differences between sexes existed in southern California (ANOVA, $F = 11.13, P < 0.01$), but not in Monterey Bay (ANOVA, $F = 1.33, P > 0.05$).

Condition Factor

Both male and female southern California white croaker displayed differences in condition between peak spawning and resting seasons (Table 5). In both sexes, fish were more robust during the resting season, perhaps because energy normally utilized for somatic maintenance and growth was shifted to egg and sperm production and spawning behavior. Over all seasons, whereas southern California females were more robust than males (Table 5), no such sex-

TABLE 5.—Condition factor (K) of white croaker from southern California 1978-81 and Monterey Bay, Calif., 1979-81.

	N	K	SD	F	P
Southern California					
Males					
Jan.-Mar.	264	0.34	0.53	117.4	<0.001
May-Aug.	91	0.98	0.32		
Females					
Jan.-Mar.	280	0.46	0.56	24.4	<0.001
May-Aug.	76	0.80	0.49		
Sexes Combined					
Jan.-Mar.	544	0.40	0.55	118.3	<0.001
May-Aug.	167	0.90	0.41		
All Seasons					
Males	535	0.71	0.56	4.5	<0.05
Females	617	0.78	0.54		
Monterey—All seasons					
Males	80	1.03	0.09	1.29	>0.2
Females	142	1.02	0.10		
Southern California and Monterey					
Males					
Monterey	80	1.03	0.09	26.54	<0.001
S. Calif.	535	0.71	0.56		
Females					
Monterey	142	1.02	0.10	27.83	<0.001
S. Calif.	617	0.78	0.54		

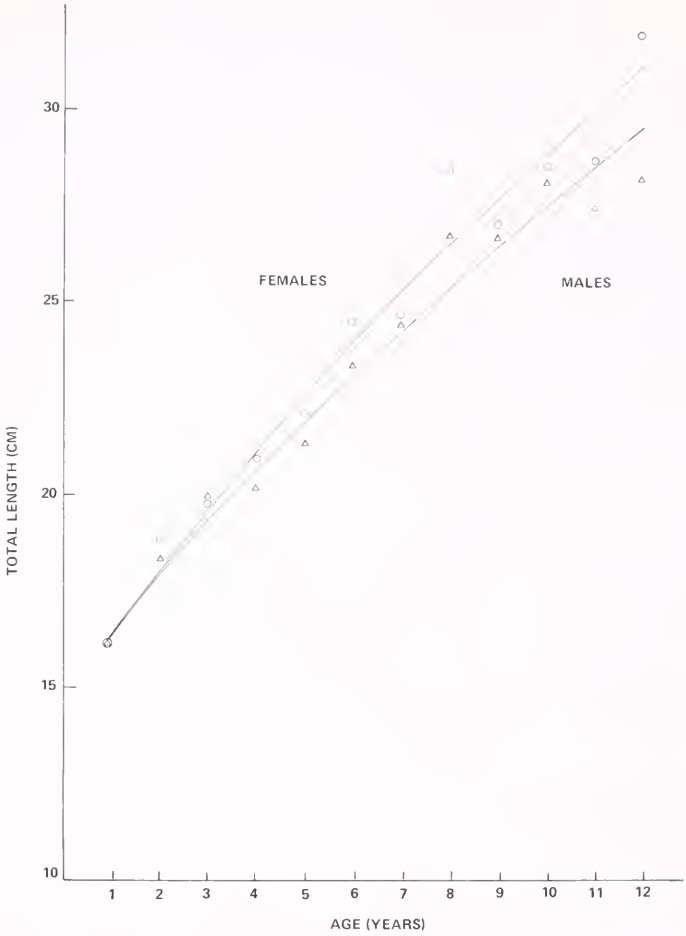

FIGURE 3.—Von Bertalanffy growth curves of female and male white croaker. Also included are mean lengths at ages (females-circles, males-triangles) computed from direct observation of otolith annuli. Based on 332 females and 250 males taken off southern California, 1977-81.

ual dimorphism was observed off Monterey. Both males and females off Monterey were more robust than their southern California counterparts (Table 5).

Maturation and Reproduction

Although a few white croaker matured before 1 yr (12.9-13.4 cm TL), over 50% of the males were mature by 14 cm TL and over 50% of the females by about 15 cm TL, which equals an age of 1 yr (Fig. 6). All fish were mature by 19 cm TL (3-4 yr).

Larger females (greater than about 17 cm TL and 1-2+ yr) spawned earlier in the year and continued to spawn later than smaller and younger individuals (Table 6). The smallest spawning females may spawn for 3-4 mo whereas larger individuals may spawn for as long as 7 mo.

Off Long Beach, white croaker spawned primarily from November through April, with January through March the peak months, based on the occurrence of hydrated eggs within ovaries. A few individuals (>18 cm TL) spawned from May through October. Ovaries increased in size in the fall and peaked in January, when they averaged 4.6% of body weight (maximum 11.8%, minimum 0.8%). Thereafter, ovarian size declined in summer to a minimum of about 1.0% of body weight (maximum 1.3%, minimum 0.07%) and remained constant through August (Fig. 7).

Similarly, testes were small during summer months

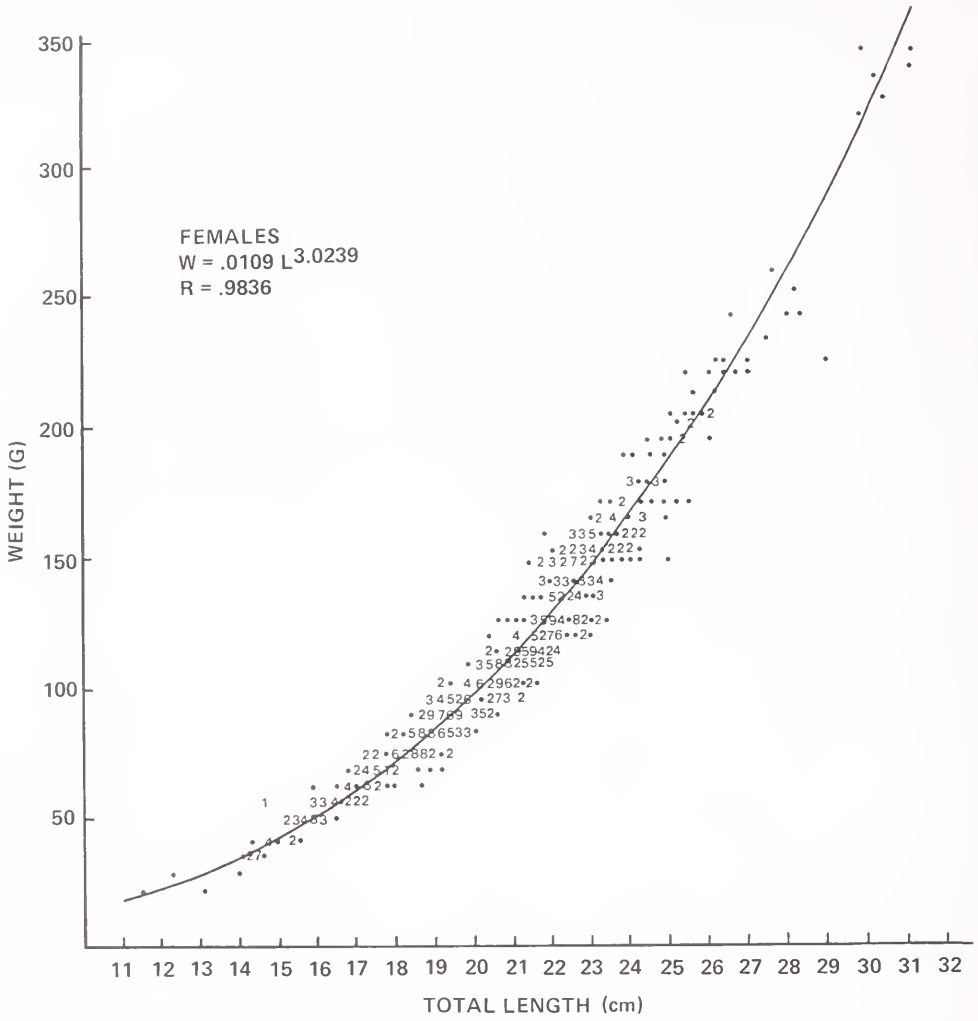

FIGURE 4.—Length-weight relationship based on 665 female white croaker sampled off southern California, 1978-81.

TABLE 6.—The percent per month of female white croaker from southern California (1978-81) that were sexually mature.

Mean total length (cm)	Percent sexually mature											
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug
13.0	0	0	0	2	16	15	6	0	0	0	0	0
14.0	0	0	0	11	26	26	8	0	0	0	0	0
15.0	0	0	0	21	73	72	15	0	0	0	0	0
16.0	0	0	0	18	88	88	27	0	0	0	0	0
17.0	0	0	2	20	91	90	35	tr[1]	1	0	0	0
18.0	0	0	6	21	96	94	61	tr	tr	0	0	0
19.0	0	0	7	21	100	100	83	48	tr	0	0	0
20.0	0	tr	7	23	100	100	82	52	tr	0	tr	tr
21.0	0	0	5	31	100	100	94	51	2	tr	0	0
22.0	tr	0	6	32	99	99	93	58	1	0	0	0
23.0	0	0	7	48	100	100	95	60	tr	0	0	tr
24.0	tr	0	6	47	100	100	93	58	2	0	0	0
25.0	0	0	6	47	100	100	99	57	2	0	0	0
26.0	0	tr	6	46	100	100	98	59	1	0	tr	0

[1]Trace <1%.

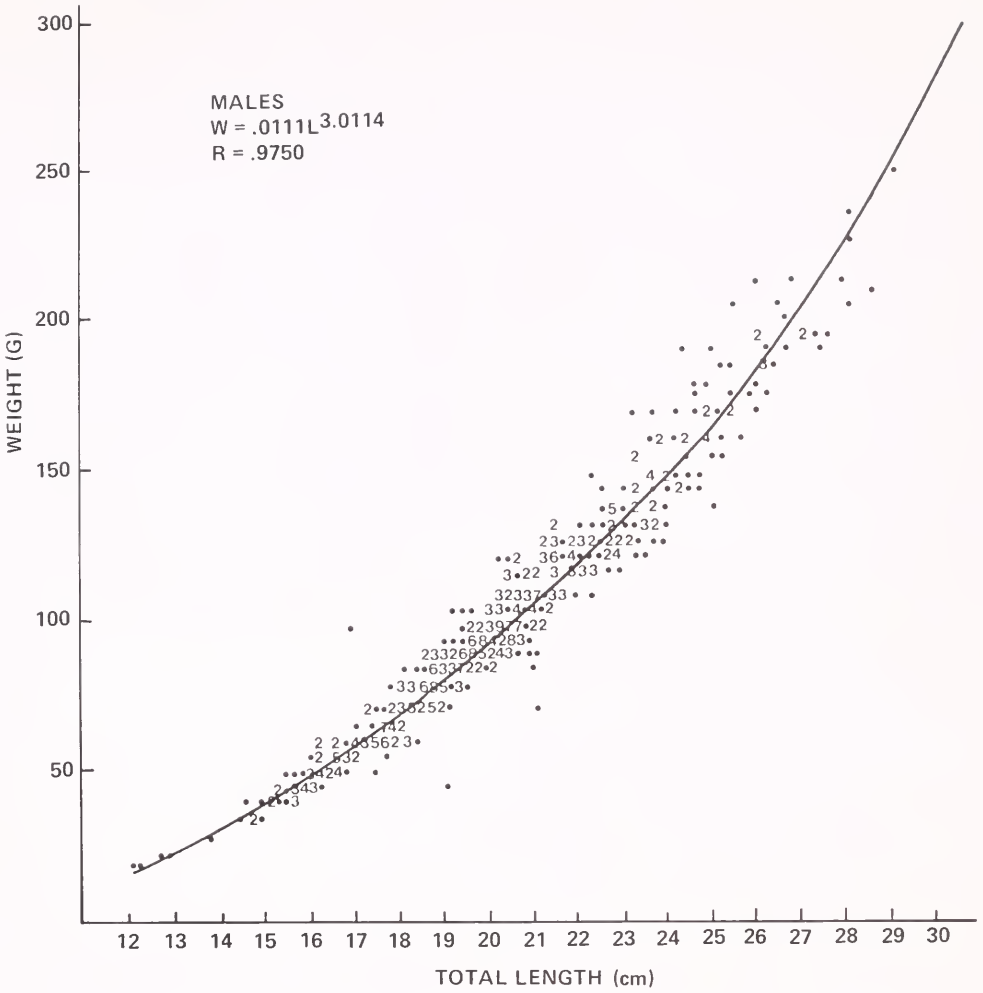

FIGURE 5.—Length-weight relationship based on 581 male white croaker sampled off southern California, 1978-81.

(Fig. 8), averaging 0.3% of body weight (maximum 0.9%, minimum 0.05%), and increased in the fall to a January peak averaging 2.6% of body weight (maximum 7.7%, minimum 0.4%).

In contrast, white croaker off Monterey Bay spawned over a longer period and may have winter and summer spawning peaks. Ovarian weights were highest in January and September (averaging about 6.5 and 7.0% of body weight, respectively) and lowest in May (1.3% of body weight). Ovaries never shrank to the minimum sizes typical of individuals in the southern California population during summer months. Testes grew to a much larger maximum size (4.6% vs. 2.6%) off Monterey. Northern white croaker spawned nearly every month, though spring spawning might have been limited. In limited sampling during the following year,[10] the second (January) peak was not evident, and thus may not be an annual event.

Batch fecundities ranged from an estimated 800 eggs in a 15.5 cm female to about 37,200 in a 26 cm female (Fig. 9). During the spawning period about 19% of all mature female white croaker sampled contained hydrated eggs, implying that a female spawned about once every 5 d. Females of ages 1 and 2 (13-18 cm) have a spawning season of 3 mo (Table 6) and spawn about 18 times per season, whereas older fish (19 cm and larger) spawn over a period of 4 mo, about 24 times/season.

[10]T. Keating, Moss Landing Marine Laboratory, P.O. Box 223, Moss Landing, CA 95039, pers. commun. January 1982.

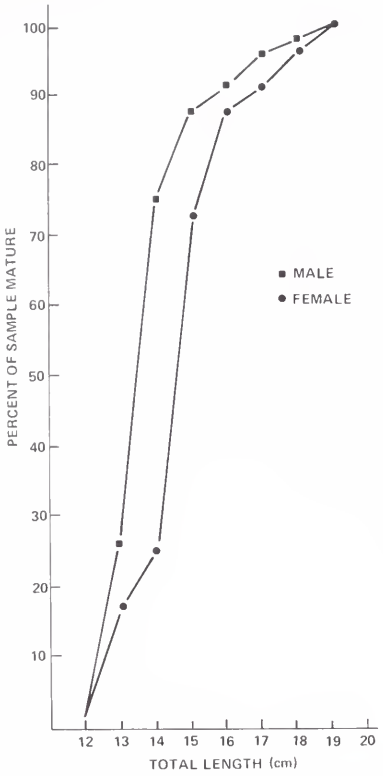

FIGURE 6.—Length-maturity relationship in 995 female and 941 male white croaker collected off southern California, 1978-81.

Larvae

Data from our ichthyoplankton surveys showed that white croaker spawning occurs every month of the year (Fig. 10). However, a distinct seasonal spawning period can be deduced from findings that few larvae were collected from June through November, whereas high densities were encountered from January through April with a strong peak in March. Results of our study in King Harbor, Redondo Beach (Fig. 11), confirm the peak densities of white croaker larvae in January, February, and March.

White croaker larvae constitute an important component of the neritic ichthyoplankton fauna of the Southern California Bight, ranking second in overall abundance behind the northern anchovy, *Engraulis mordax*. On a per transect basis (Fig. 12), white croaker larvae ranked first in abundance at all transects between Palos Verdes[11] and Laguna Beach and

[11] *Genyonemus* and *Engraulis* were virtually tied for first place at Redondo Beach with 40.1% and 40.3%, respectively.

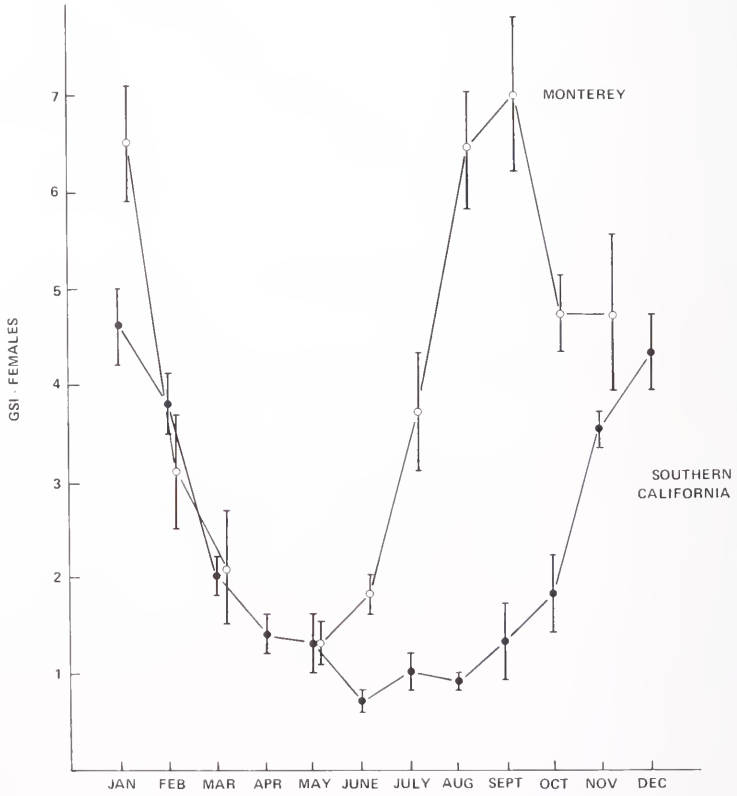

FIGURE 7.—Seasonal changes in the gonosomatic index (GSI-gonad weight as a percentage of total body weight) of female white croaker (based on 720 southern California and 223 Monterey individuals). Vertical lines indicate 95% confidence intervals of the mean.

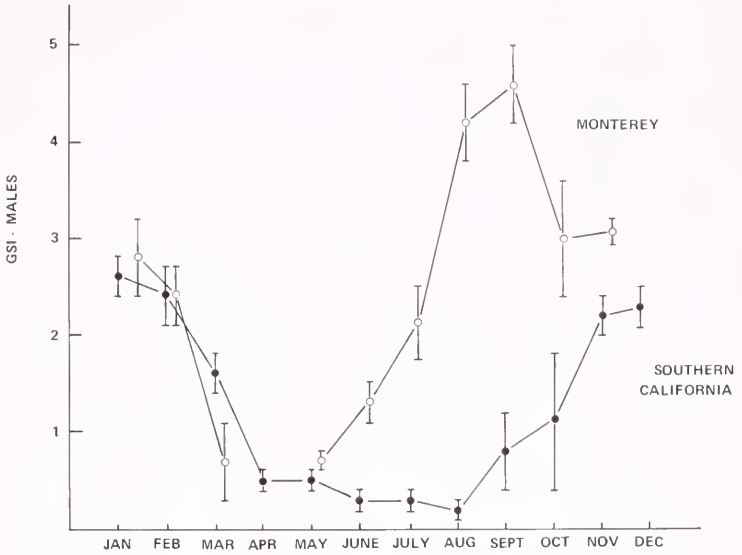

FIGURE 8.—Seasonal changes in the gonosomatic index of male white croaker (based on 631 southern California and 114 Monterey individuals). Vertical lines indicate 95% confidence intervals of the mean.

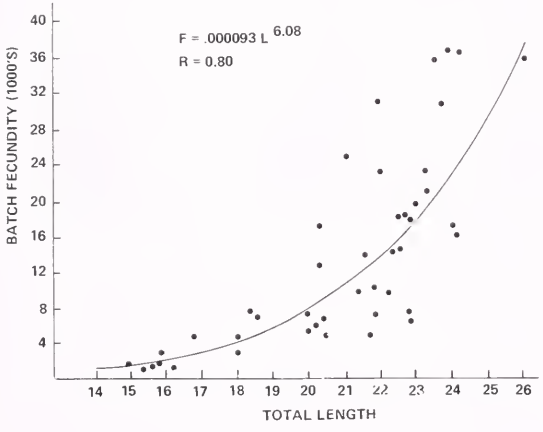

FIGURE 9.—Batch fecundity—total length relationship for 44 white croaker collected off southern California during February and March 1979-81.

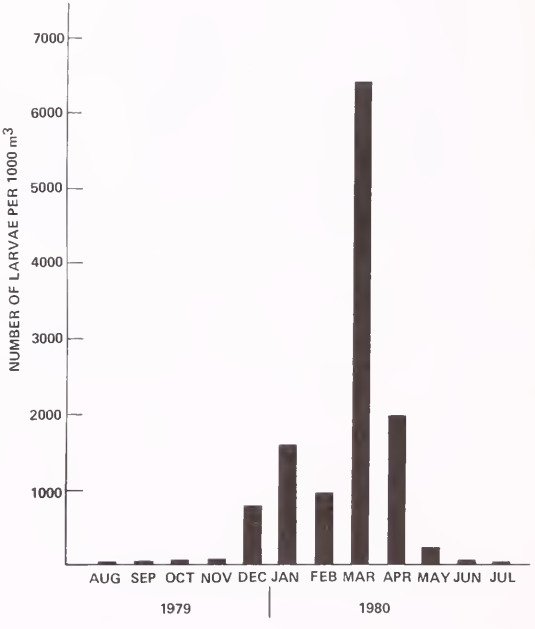

FIGURE 10.—Mean density of white croaker larvae collected in the oblique bongo tows per month between August 1979 and July 1980.

second at the remaining transects, except Mission Beach where it ranked third behind *Engraulis* and an unidentified goby. In the King Harbor study, white croaker larvae ranked either fourth or fifth depending on the year and the stations sampled.

Larval density data (number of individuals per unit volume of water) indicate two spawning centers between Point Conception and the U.S.-Mexican border (Fig. 13): The larger one extends north and south of the Palos Verdes Peninsula, from Redondo Beach to Laguna Beach, whereas the smaller one is further north around Ventura. That area from San Onofre south to the international border was striking for its low densities of white croaker larvae. Along this sec-

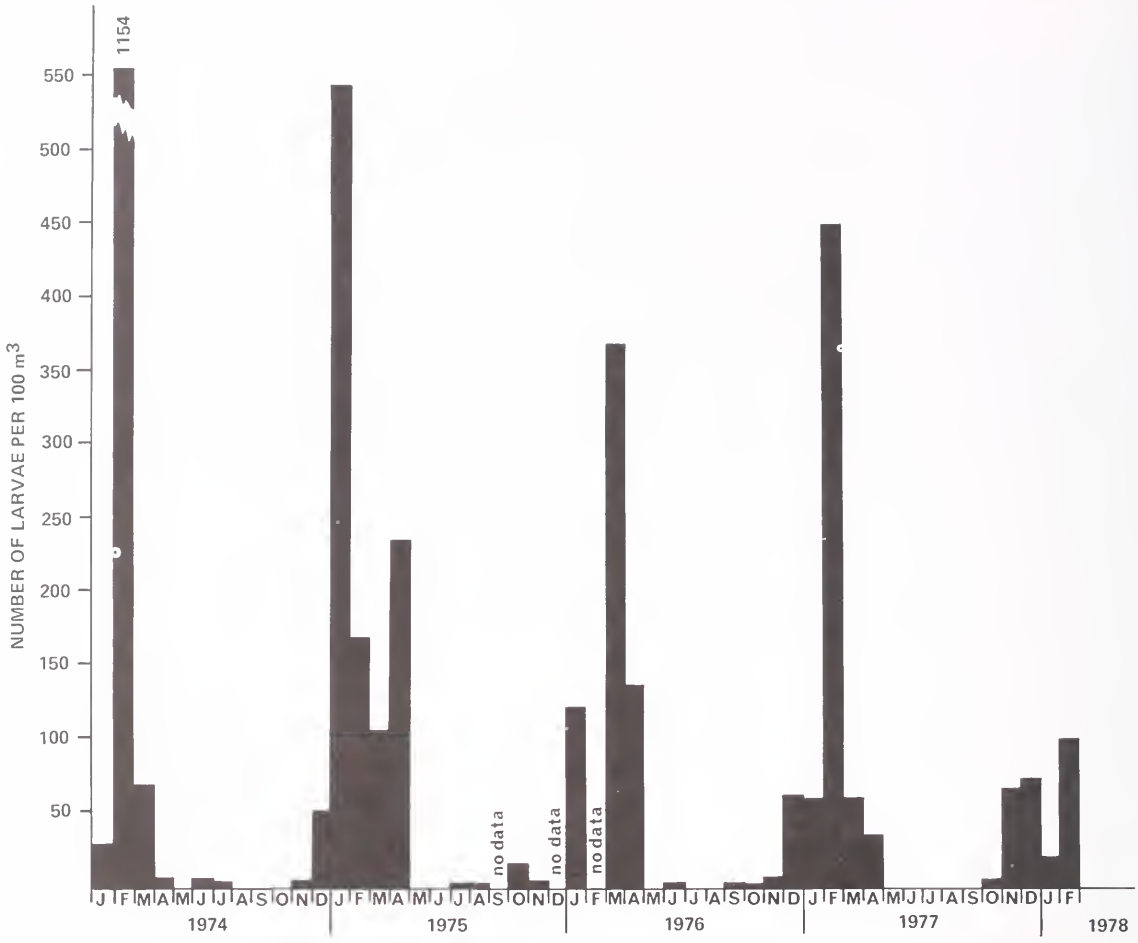

FIGURE 11.—Mean densities of white croaker larvae in the vicinity of King Harbor, Redondo Beach, Calif., between January 1974 and February 1978.

tion of the coast, white croaker larvae accounted for 11.7% of the larval fishes collected in oblique tows versus 43.6% from Laguna Beach to Redondo Beach and 17.9% from Playa del Rey to Point Conception (Fig. 14).

Our data indicate that highest densities of white croaker larvae occur near the bottom (Fig. 15). In the coastal zone, between the 15 and 36 m isobaths, relative densities indicate little variation through the water column, being 1.5-3.5% with surface waters, 55.0-58.0% in the bottom waters, and 40.0-42.5% in middepth waters (Fig. 16). Relative densities in the surface waters at the shallow 8 m stations dramatically increased to 17.5% with a corresponding decrease in both bottom and middepth waters.

White croaker larval densities peaked at stations located at 15 and 22 m depths (Fig. 15). The densities declined sharply at the deeper (36 m) and shallower stations (8 m). The only exception to this trend was in surface water where densities steadily decreased in an offshore direction.

Only 15 of our 20 transects had stations at 8 and 22 m isobaths. Data in Figure 15 suggest that an abundance estimate based on the 8 and 22 m stations may approximate one based on the 15 and 36 m stations. If so, an estimate based on either of those station pairs should approximate one based on all four. We examined this at the three transects (OB, RB, SO), where data for all four stations were available. We tested the data from each transect for each of the 12 mo of the sampling program using the sign test (Dixon and Massey 1957). The estimated number of white croaker larvae per 1,000 m^3 based on the 8 and 22 m stations was compared with the estimate based

on the 8, 15, 22, and 36 m stations; no statistically significant difference was found ($N = 26$; $P > 0.05$). The similarities of the overall estimates based on these two station groupings are shown in Figure 13.

On the basis of our 8 and 22 m stations we have extrapolated density estimates to 36 m. Estimates were made for the truncated Palos Verdes and Laguna Beach transects as well, which are likely to be upwardly biased as they are based on two high density stations (15 and 22 m). Data in Figure 13 show that these two transects are not high density ones; in fact, Palos Verdes is low for that section of the coast. The Laguna Beach transect is lower than the next two transects to the north. We included the Laguna Beach transect in the portion of the Southern California Bight where white croaker larvae are in high abundance, on the basis that the density would still be higher than the portion of the coast from San Onofre to San Diego, based on just the 8 and 22 m stations, even if the 8 m station contributed no larvae.

We estimated, from oblique bongo tows taken at the 8 and 22 m stations (15 and 22 m stations at Palos Verdes and Laguna Beach), the average density of white croaker larvae between August 1979 and July 1980 to have been 740/1,000 m^3, 2,203/1,000 m^3, and 411/1,000 m^3 for the regions between Point Conception and Playa del Rey, Redondo Beach and Laguna Beach, and San Onofre and the international border, respectively. On the basis that there is no significant difference between estimates based on the 8 and 22 m stations and one based on the 8, 15, 22, and 36 m stations, we use the 8 and 22 m density estimates to project the average number of white croaker larvae to the 36 m isobath.

It has been estimated (Lavenberg and McGowen footnote 7) that about 31 km^3 of water are located in a band along the coast between Point Conception and the U.S.-Mexican international border and extending seaward to the 36 m isobath. Of this, 15.6 km^3 (50.6%) is located in the region between Point Conception and Playa del Rey, 7.9 km^3 (25.9%) between Redondo Beach and Laguna Beach, and 7.2 km^3

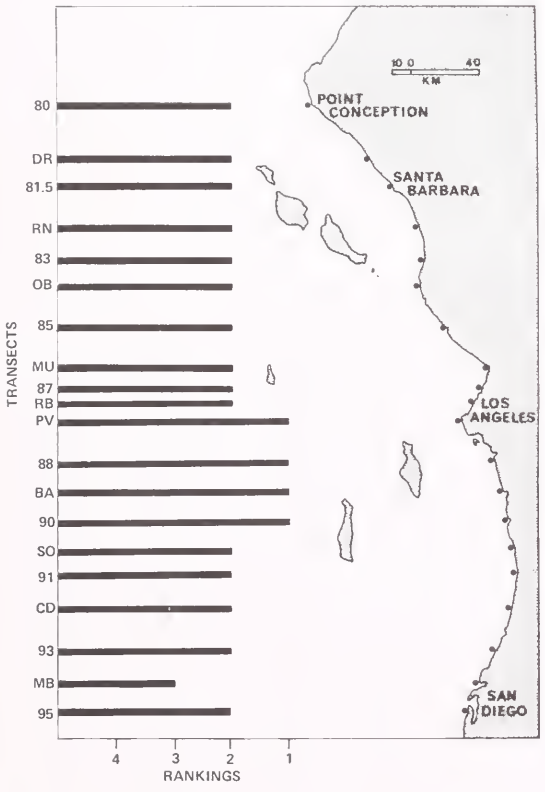

FIGURE 12.—Rank abundance of white croaker larvae collected in oblique bongo tows taken along 20 transects in the Southern California Bight between August 1979 and July 1980. See Table 2 for station abbreviation definitions.

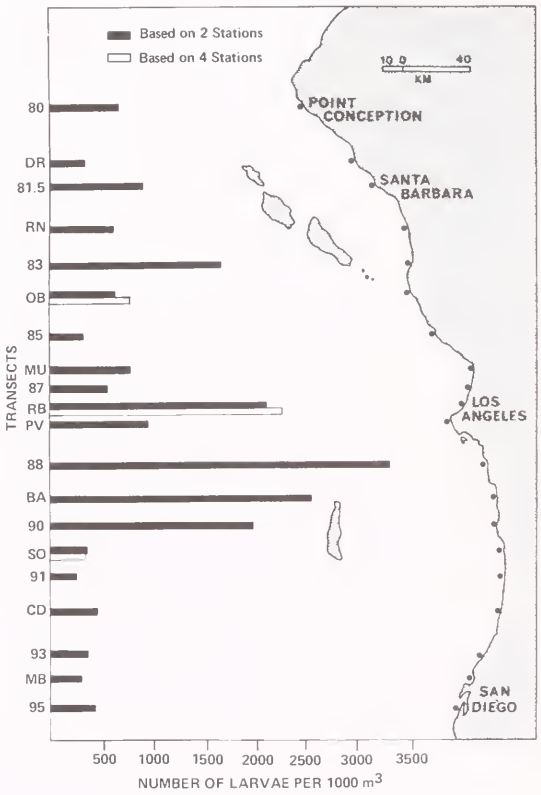

FIGURE 13.—Mean densities of white croaker larvae along 20 transects in the Southern California Bight between August 1979 and July 1980. See Table 2 for station abbreviation definitions.

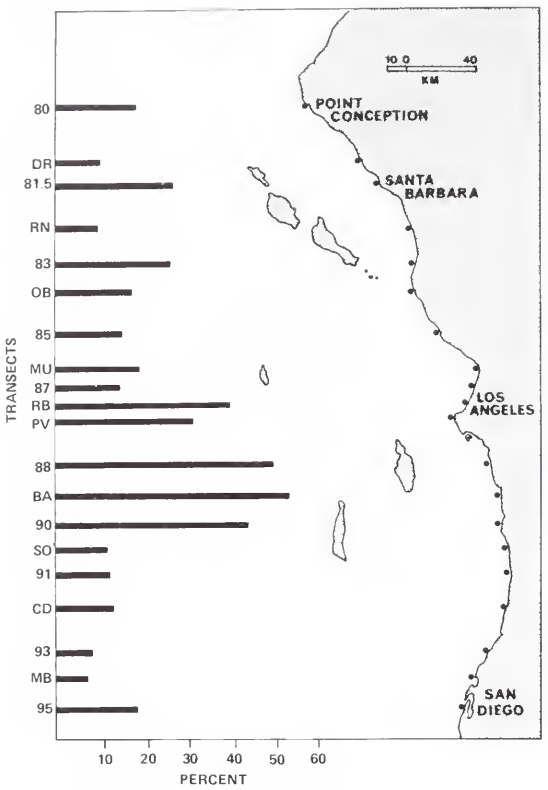

FIGURE 14.—The percentage contributed by white croaker to the total number of larvae collected along each of 20 transects in the Southern California Bight between August 1979 and July 1980. See Table 2 for station abbreviation definitions.

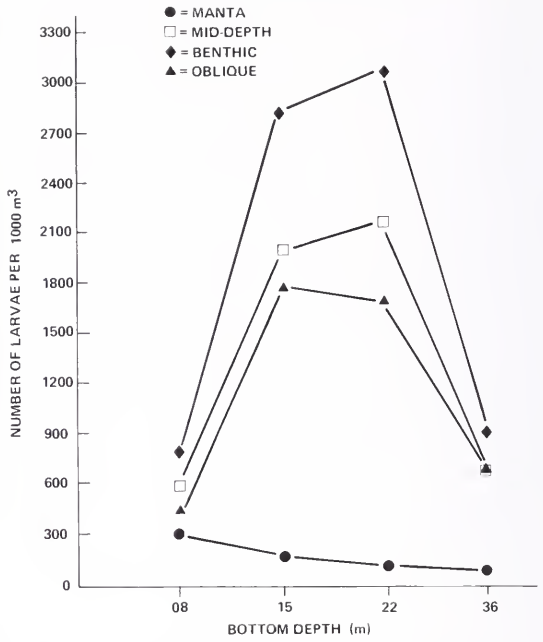

FIGURE 15.—Mean density of white croaker larvae collected with each of four different tow types along four isobaths—8, 15, 22, and 36 m—in the Southern California Bight between August 1979 and July 1980.

(23.5%) between San Onofre and the international border. Based on these values plus the density estimates, we project the average number of white croaker larvae in each of the three areas during this period to have been 1.15×10^{10}, 1.75×10^{10}, and 2.97×10^{9}, respectively. Thus, about 55% of the white croaker spawned in the area between Redondo Beach and Laguna Beach, 36% between Playa del Rey and Point Conception, and about 9% between San Onofre and the border.

Fishery

Most of the white croaker retained by sportfishermen were adults (Fig. 17), being 21-25 cm and 5-7 yr

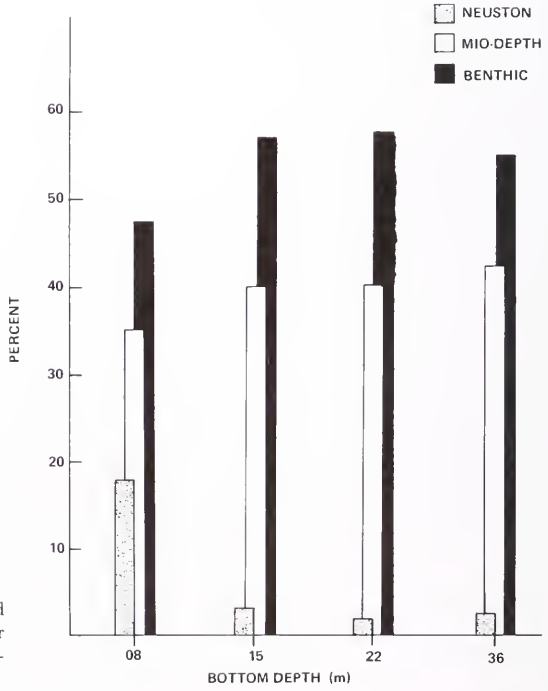

FIGURE 16.—Mean percentage of white croaker larvae collected near the surface, near the bottom and in between along each of four isobaths—8, 15, 22, and 36 m—in the Southern California Bight between August 1979 and July 1980.

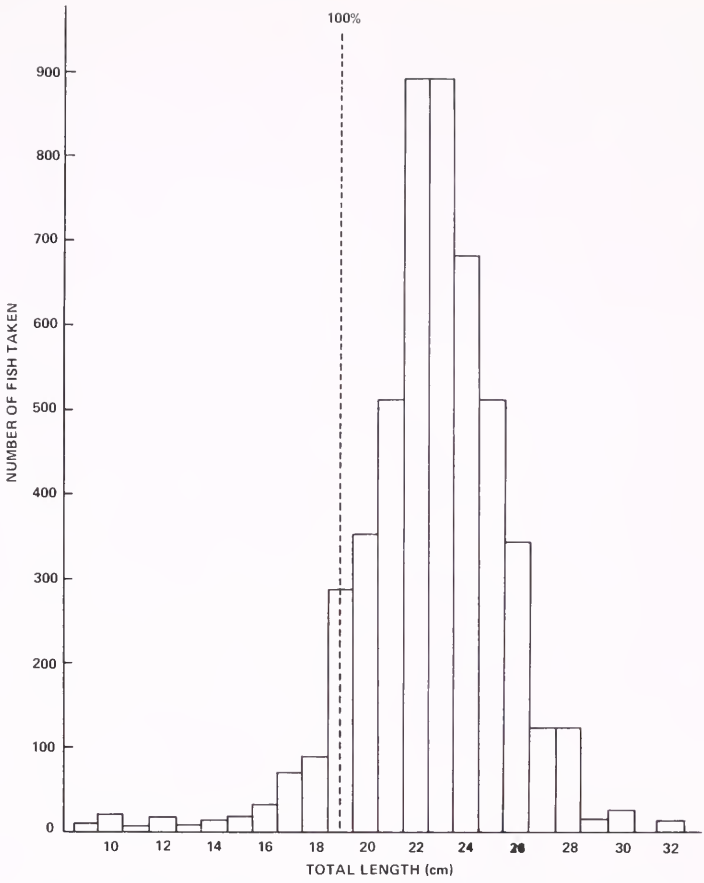

FIGURE 17.—Lengths of white croaker retained by skiff sportfishermen off southern California, 1980-81, with length at 100% maturity noted.

old. Small fish were only occasionally hooked, and rarely retained.

Within the Southern California Bight, about 10 vessels fished white croaker full time. Two areas, Long Beach south to Dana Point and Oxnard to Santa Barbara, were fished most heavily, which corresponded to the sites of peak white croaker larvae concentrations reported here.

This is a gill net fishery, and an informal agreement among fishermen sets the net mesh at 7.0 cm (2.75 in) stretch. Nets are 1.3 km (0.8 mi) long and are set on the bottom in depths of 5.5-37 m (3-20 fathoms). Mean catches of white croaker are 270-400 kg (600-900 lb) per set with maximum catches of 680-770 kg (1,500-1,700 lb). Largest catches occurred in January and February, during spawning season, when white croaker aggregated in large numbers. The prices for 1982 to fishermen were 13-18¢/kg (30-40¢/lb). Most fish taken during our study were 26-29 cm long (Fig. 18) and 8-10 yr old. We found no immature fish.

DISCUSSION

Depth Preference

Though most species of Sciaenidae prefer inshore waters, white croaker are distributed over a wider depth range than other northeastern Pacific species. Queenfish was the fourth most abundant species taken in our survey at the shallowest station (Table 3); its abundance declined rapidly with depth. Though it was present in deeper water, it contributed <0.1% of the fishes taken at 59-73 m. The white seabass is common within the 30 m contour (though they are taken as deep as 90 m during winter months). *Umbrina roncador*, *Roncador stearnsi*, and *Menticirrhus undulatus* prefer sandy beaches and bays to

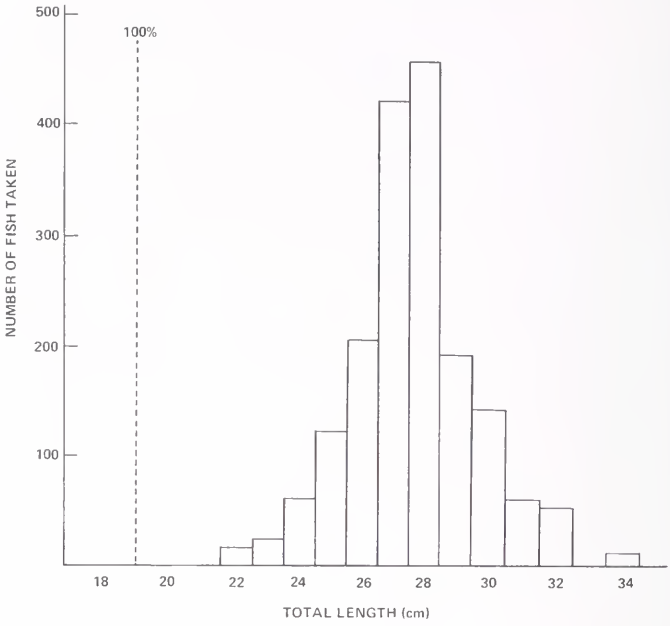

FIGURE 18.—Lengths of white croaker retained by commercial gill net fishermen off southern California, 1980-81.

depths of perhaps 9 m (Skogsberg 1939), whereas *Cheilotrema saturnum* are common over reefs to perhaps 15 m (occasionally to 45 m) (Limbaugh 1961).

Most eastern Pacific drums are limited to the warmer waters south of Point Conception (Miller and Lea 1972) or, like the queenfish and white seabass, are rare north of the Point. Conversely, white croaker are abundant north to San Francisco. Temperature preference experiments[12] indicate that juvenile white croaker have wide metabolic thermal optima (11°-17°C, based on routine oxygen consumption rates) that may account for their wide depth and latitudinal ranges.

Though white croaker are most abundant over sandy, featureless substrata, they are occasionally found in large numbers in kelp beds. This is particularly the case in beds anchored on sand, such as those off San Onofre and Santa Barbara. Similarly, though they spend most of their time near the bottom, we have noted schools in midwater, 20-40 m or more above the substrata. We have also seen white croaker at the surface, chasing anchovy schools.

Maturation and Reproduction

We computed the length-maturity relationship using standard length to compare our results with those of Issacson (1967). We found 50% of the males mature by 12.0 cm SL and 50% of females by 13.0 cm SL, both at 1 yr. This was in sharp contrast to Issacson's statement that "The white croaker matures between 147 and 164 mm standard length at an age of 3 to 4 years." Why such a disparity should exist is unclear.

White croaker is the only southern California drum that spawns in the winter. Winter spawning is unusual even among tropically derived temperate species off California. All species in the families Blenniidae, Carangidae, Labridae, Pomacentridae, Scombridae, and Sphyraenidae are either summer spawners or spring and summer spawners with a summer spawning peak. An exception are the rockfishes (Scorpaenidae), the vast majority of which spawn in winter and/or spring.

The more or less continuous (or perhaps dual-peaked) spawning season seen in white croaker in Monterey Bay is an interesting phenomenon. Most California marine fishes have restricted spawning seasons. If spawning does continue for extended periods (as in the bocaccio, *Sebastes paucispinis*), there is usually only one peak spawning period. An exception is the northern anchovy, *Engraulis mordax*, that may spawn year-round and which exhibits a major peak in late winter-early spring and a minor one in early fall.

Fishes of the northeastern Pacific tend to have a longer spawning season in the southern part of their range, as favorable conditions are usually more re-

[12]Hose, J. E., and W. H. Hunt. 1981. Physiological responses of juvenile marine fish to temperature. Occidental College Annual Report submitted to Southern California Edison, 17 p.

stricted in northern waters (Westrheim 1975). However, on examination, the water temperatures in Monterey Bay more closely approximate optimal white croaker spawning conditions than those off southern California. The peak spawning periods, based on gonosomatic indices and ichthyoplankton surveys, in southern California occur between January and March, when mean surface temperatures decrease to 13°-14°C (U.S. Department of Commerce 1956). Off Monterey, the mean temperatures of the warmest months are 13°-14°C (June-October), whereas the other months are 1°-3°C cooler. Thus white croaker encounter temperatures conducive to spawning for more months off Monterey than off southern California.

White croaker reproductive behavior is in some respects the opposite of the cooccuring queenfish. White croaker spawn almost entirely during late winter and early spring (peak February-March), but our ichthyoplankton survey gives a March-April peak, whereas queenfish are spring and summer spawners (peak April-May, DeMartini and Fountain 1981). Most egg hydration in white croaker takes place during the night, with spawning occurring from just before dawn to midmorning. Queenfish spawn between late afternoon and evening. We have not ascertained the extent that habitat partitioning has played in this separation. Off Monterey, where queenfish are rare, white croaker spawn virtually year round. As discussed before, this is perhaps a reflection of a more favorable temperature regime. It would be instructive to know if in the absence of queenfish, egg hydration and spawning time are simlar to those off southern California.

Larvae

Data from both gonosomatic indices and ichthyoplankton surveys show white croaker spawn year-round in southern California waters. However, peak spawning clearly is in the winter and spring. Our data, combined with Watson's (1982), indicate that peak densities of white croaker larvae were in either January, February, or March from 1974 through 1980. This is out of phase with other southern California sciaenids, all of which spawn primarily in the spring and summer (Lavenberg and McGowen footnote 7).

White croaker larvae are an important component of the southern California neritic ichthyoplankton fauna. Along the three sections of the Southern California Bight, defined and studied during this investigation, white croaker larvae contributed 11.7, 43.6, and 17.9% of the total larvae from south to north. Highest densities were found at stations located in 15-22 m depths (Fig. 15). The decreasing densities, as one moves shoreward of the 15 m isobath, apparently continues into the enclosed bays and estuaries of southern California. McGowen (1981) did not collect any white croaker larvae in south San Diego Bay during a 13-mo study. Larval white croaker ranked sixth, contributing 0.6% of the larvae collected in Newport Bay during an 18-mo study by White (1977). The percentage reported by White may have a bias toward lower values because the period of peak spawning was sampled only once during the 18 mo. However, even a doubling of White's percentages does not make white croaker larvae dominant members of the Newport Bay ichthyoplankton assemblage. Leithiser (1981) reported white croaker to contribute 1.9% of the total catch of larval fishes in Anaheim Bay during a 12-mo study.

King Harbor is typical of the estuarine-enclosed bay habitat rather than that of the open coast and is dominated by blennies, clinids, gobies, and engraulids (McGowen footnote 8). White croaker larvae ranked either fourth or fifth in the King Harbor study, depending on the year and the stations sampled.

Densities of white croaker larvae also decreased between the 22 and 36 m isobaths (Fig. 15). This indication that white croaker larvae are not common in offshore waters is supported by CalCOFI data. The highest any sciaenid ranked in these collections between 1955 and 1958 was 18th, contributing 0.30% of the total larval catch (Ahlstrom 1965).

This pattern of white croaker larvae being distributed in a narrow band along the coast, between the 15 and 22 m isobaths, is similar to the pattern reported by Watson (1982) and Barnett et al.[13] off San Onofre. They designated white croaker larvae as having an inner nearshore epibenthic pattern. Barnett et al. (footnote 13) indicated highest densities on the bottom, shoreward of the 22 m isobath, and the second highest densities in the water column between the 12 and 22 m isobaths and on the bottom between the 22 and 45 m isobaths. The major discrepancy between their data and ours is the higher epibenthic densities that they report shoreward of the 12 m isobath and seaward of the 22 m isobath. This discrepancy may be partially explained by dif-

[13]Barnett, A. M., A. E. Jahn, P. E. Sertic, and W. Watson. 1980. Long term spatial patterns of ichthyoplankton off San Onofre and their relationship to the position of the SONGS cooling system. A study submitted to the Marine Review Committee of the California Coastal Commission, July 22, 1980, Unpubl. rep., 32 p. Marine Ecological Consultants of Southern California, 533 Stevens Ave., Suite D-57, Solana Beach, CA 92075.

ferences in sampling strategy. They sampled within blocks defined by depth contours whereas we sampled at specific isobaths. Thus, part of their block D (between the 22 and 45 m isobaths) is located at a depth where we found high densities (22 m) and part of it where we found low densities (36 m). All of their block B (between 9 and 12 m) is located at depths where we did not sample. Their block A (between 6 and 9 m) is located in a zone where our data suggest lower densities.

Our trawling data also support this narrow band as important for the young stages of white croaker. Almost all of the juvenile white croaker taken during our study were collected at stations located between the 18 and 27 m isobaths (Fig. 2).

In summary, these data suggest that adult white croaker migrate shoreward (larger adults were taken at deeper depths; Fig. 2) and spawn in a narrow band along the coast. This band has its shoreward boundary located between the 8 and 12 m isobaths, and its seaward boundary located between the 22 and 36 m isobaths. Furthermore, the pelagic stages remain primarily within this band. At the end of the pelagic phase young white croaker move into 3-6 m and take up residence near the bottom. As these juvenile fish mature, they migrate to deeper waters (Fig. 2).

Based on this hypothesis, we believe that a realistic evaluation of the spawning activities of the white croaker can be based on data collected from the shore to the 36 m isobath. We have done this and found that about 9% of the spawning by white croaker occurred along the coast from San Onofre to the international border, about 55% from Laguna Beach to Redondo Beach, and around 36% from Playa del Rey to Point Conception. If this represents the typical annual pattern, the portion of the Southern California Bight from Laguna Beach to at least Point Conception is important for white croaker, especially the region around the Palos Verdes Peninsula from Redondo Beach to Laguna Beach. However, that portion of the bight from San Onofre to the border is relatively insignificant. The only remaining coastal zone in the U.S. portion of the Southern California Bight is around the Channel Islands. We have not investigated the coastal zones of these islands and cannot appraise their significance to the spawning activities of white croaker in the Southern California Bight.

Fishery

Historically, the commercial white croaker fishery has been minor, rarely exceeding 1 million lb/yr (Frey 1971). Most fish were caught and landed in the Long Beach-San Pedro region and Monterey Bay. Southern California accounted for about two-thirds of the catch and Monterey one-third, although during World War II, Monterey produced over one-half the total catch. Until recently, white croaker were taken commercially by otter trawl, round haul net, multifilament gill net, and hook and line. However, in the past few years, significant changes have occurred in the fishery. Gill nets, particularly monofilament nets, have almost entirely supplanted other methods.

The ubiquity of white croaker along the southern California mainland makes this species accessible to small boat sportfishermen. The ease with which it may be taken, using minimum skill or equipment, ensures that this species will be caught in considerable numbers. We commonly found two fishermen with at least 50 or more white croaker after a half day's effort. Though traditionally scorned by many, we found that the species is popular with a number of ethnic groups.

The Monterey fishery has been revived in the past 2-3 yr by newly arrived Vietnamese fishermen.[14] White croaker are fished throughout Monterey Bay, over the entire year, in 12-24 m (40-80 ft), occasionally to 37 m (120 ft) with 1.6-2.4 km (1-1.5 mi) long monofilament gill nets [6.3 cm (2.5 in) stretch mesh]. Nets are tended daily, and 450-900 kg (1,000-2,000 lb) catches are common with maximum catches to 1,800 kg (4,000 lb). Depending on catch size and fish condition, payment to fishermen ranges from 6 to 22¢/kg (15 to 50¢/lb). These white croaker are sold principally within central California (particularly the San Francisco area), although a small amount is shipped to southern California. Demand is increasing, particularly among various Asian communities.[15]

SUMMARY

In this study, white croaker was the most abundant species in nearshore (18-27 m) otter trawl collections in southern California. This species dwelled principally in shallow water and juveniles were restricted to the shallower (<27 m) parts of the species depth range. Living to 12 yr, white croaker grew at a nearly

[14]D.J. Miller, California Department of Fish and Game, 2201 Garden Road, Monterey, CA 93940, and T. Keating, Moss Landing Marine Laboratory, P.O. Box 233, Moss Landing, CA 95039, pers. commun. August 1981.

[15]Though most white croaker are retailed fresh, there is reason to believe that a potential market exists for them as surimi (fish cakes). A fish cake plant existed in Ventura during 1979, processing 3,000-4,000 lb (1,360-1,800 kg) of white croaker per day. All cakes were sold to the Asian community in Los Angeles. Demand for the product was very strong and the plant closed for reasons unrelated to profitability.

constant rate throughout the species' life. A majority of both males and females matured at about 1 yr and all were mature by 4 yr. We noted a difference in spawning season between southern and central California. Off southern California, significant spawning occurred between November and April, while central California individuals spawned all year, with large-scale activity occurring from July through February. Our ichthyoplankton survey indicated that two spawning centers occurred off southern California—one located from Redondo Beach to Long Beach and the other centered about Ventura. White croaker larvae, which were second in abundance to northern anchovy in nearshore waters, were found in greatest abundance near the substratum in 15-22 m of water. The abundance of white croaker and its ease of capture make it a major sportfish in the skiff fishery and a growing component of the commercial gill net fishery. Our study indicates that the vast majority of fishes taken in both fisheries were adults.

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L. McCluskey helped estimate batch fecundities, and L. Natanson and E. Taylor conducted the small vessel creel census. T. Keating supplied numerous Monterey specimens, and J. Balesteri supplied data on the southern California commercial operation.

Majority of the larval identifications were made by D. Carlson, D. Chandler, D. Eto, R. Feeney, S. Goodman, N. Singleton, D. Winkler, and R. Woodsum of the University of Southern California and the Natural History Museum of Los Angeles County. E. Gray and L. Games of the Southern California Edison Company and the Natural History Museum of Los Angeles County, respectively, assisted with data reduction and computer programming. We also thank M. Butler (illustrations) and R. Meier (photography) of the Los Angeles County Natural History Museum. Lastly, we thank the many people who assisted in the sorting and collecting of samples, especially the crews of RV *Vantuna* and RV *Seawatch*.

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FEEDING HABITS OF BLACKSMITH, *CHROMIS PUNCTIPINNIS*, ASSOCIATED WITH A THERMAL OUTFALL

PAMELA A. MORRIS[1]

ABSTRACT

The availability and use of food by blacksmith, *Chromis punctipinnis*, were examined at a thermal outfall and a control site in King Harbor, California. Stomach analysis showed that blacksmith from the outfall area consumed a significantly greater amount of food, consisting of larger prey items, than control fish. Movements of water created by the outflow may provide dietary benefits by reducing zooplankton predator avoidance and by entraining and entrapping organisms not normally planktonic. This dietary enrichment may result in attraction of blacksmith to the King Harbor outfall.

An increased demand for energy resulting in growth of coastal power plant activity has created concern for the effects of heated effluents upon the fish community (Miller 1977; Stephens 1978,[2] 1980[3]; Stephens and Palmer 1979[4]). Few studies have examined the factors attracting fish to outfall areas. White et al. (1977) found less diversity and lower abundance of fish at an outfall station, while Kelso (1976) and Minns et al. (1978) reported a clustering of fish in the vicinity of thermal outfalls. Underwater observations suggest that fish are attracted to thermal outfalls to feed. Kelso (1976) found that fish in proximity to a thermal discharge exhibited a complex swimming behavior that could represent feeding activity. Moreover, this behavior continued when unheated effluent was discharged.

The blacksmith, *Chromis punctipinnis* (family Pomacentridae), an abundant planktivorous temperate reef inhabitant, has been regularly observed feeding at the thermal outfall of a steam electrical generating station in King Harbor, Redondo Beach, Calif. Recent studies on the effects of thermal effluents upon blacksmith have concentrated on behavioral responses to intermittent chlorination (Hose and Stoffel 1980; Hose et al. in press). The objective of this study was to examine the feeding habits of blacksmith and determine whether the discharge was attracting them through dietary enrichment.

MATERIALS AND METHODS

This study was conducted at King Harbor, Redondo Beach, Calif., at the southern end of Santa Monica Bay, just north of the Palos Verdes Peninsula (Fig. 1, lat. 33°51'N, long. 188°24'W) (Terry and Stephens 1976; Stephens and Zerba 1981). Situated just offshore is the head of the Redondo Submarine Canyon, a source of cold upwelling water for the harbor. In contrast, thermal effluent from Units 7 and 8 of Southern California Edison's Redondo Beach steam electrical generating plant is discharged just inside the harbor mouth.

The thermal outfall study site consists of a vertical conduit, 4 m in diameter, out of which the effluent is pumped. The circular outlet is level with the substrate at a depth of 7 m. Effluent is discharged at a rate of 1.78×10^6 l/min during peak operation.

A control site was chosen about 500 m from the discharge. This area, referred to as the Point, is located at the tip of the breakwater that partially encloses the harbor. This site has been surveyed by Stephens and Zerba (1981) who note that blacksmith are an abundant resident species.

A form of presence/absence monitoring was used as an indicator of fish abundance at the discharge. Mean estimates (0-25, 26-50, 51-75, 76-100, or >100) were made by two scuba divers swimming a circular transect around the discharge. The position of fish was recorded: in the plume (the column of water directly over the discharge), in the outer plume (the area of

[1]VANTUNA Research Group, Department of Biology, Occidental College, Los Angeles, CA 90041.

[2]Stephens, J. S., Jr. 1978. Effects of thermal effluent from Southern California Edison's Redondo Beach steam generating plant on the warm temperate fish fauna of King Harbor Marina. Fish and laboratory study reports for Phase III. VANTUNA Research Group, Department of Biology, Occidental College, Los Angeles, CA 90041.

[3]Stephens, J. S., Jr. 1980. Effects of thermal effluent from Southern California Edison's Redondo Beach steam generating plant on the warm temperate fish fauna of King Harbor Marina. Fish and laboratory study reports for 1977-1978. VANTUNA Research Group, Department of Biology, Occidental College, Los Angeles, CA 90041.

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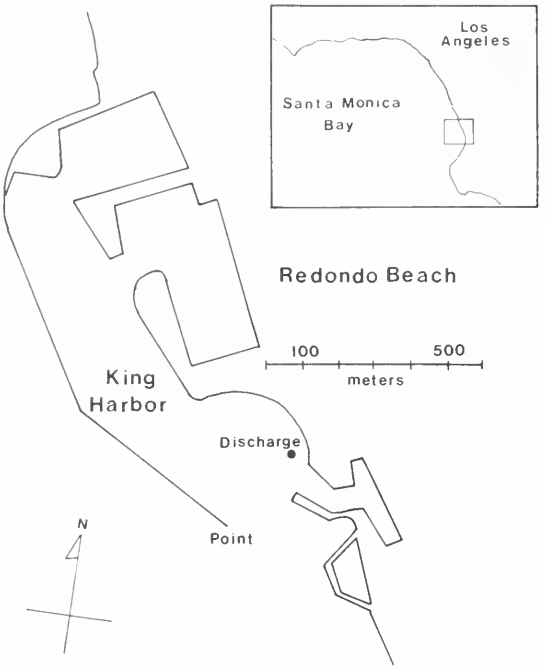

FIGURE 1.—Study area at King Harbor, Redondo Beach, Calif.

water immediately surrounding the plume), or at the base (the substrate surrounding the discharge).

The abundance of fishes at the Point has been documented since 1974 (Stephens and Zerba 1981), and work continued at this area during the same time period the discharge was examined. Two divers equipped with slates and depth gauges swam in one direction along the rock breakwater at a fixed depth for 5 min, counting all fish seen 1.5 m above and below them and within sight to either side. Transects were run at depths of 1.5, 4.5, 7.5, and 10.5 m, with replicates at each depth.

In order to determine the nature of the feeding habits of blacksmith at the discharge versus those feeding at the Point, utilization of food items based on stomach analysis was examined for each area. General availability of food was estimated by sampling plankton at both sites.

Stomach analysis closely followed methods employed by Ellison et al. (1979). Fish were collected from each study site by scuba divers using pole spears. During fish collection, a temperature profile was taken using a temperature probe coupled to a telethermometer (Yellow Springs Instruments Co., Model 431D[5]). After capture the fish were placed on ice. The body wall was cut open and the stomach injected with a 20% Formalin solution. The fish were then preserved in a 10% Formalin solution for at least 48 h, rinsed in running water for 2 h, and placed in 70% isopropyl alcohol.

Within 2 wk from date of capture, fish stomachs were removed and placed in vials of 70% isopropyl alcohol. At this time the standard length, wet weight, and sex of each fish were noted. Each stomach was then blotted dry (with special care taken to remove the internal fluid) and weighed, food items dissected out, and the empty stomach weighed again. Stomach fullness was estimated using a scale from 0 (empty) to 5 (full).

Individual prey items were separated into the lowest identifiable taxa and counted, and the percent of the total volume estimated. In most cases, only whole organisms or whole organism indicators were counted. In prey items which were not eaten whole (i.e., algae and ectoprocts), only the percent volume was estimated.

In 1979-80, 73 fish were collected at the discharge area from 13 sampling days during a 15-mo period. Four sampling days were in the afternoon (1430-1830 h) and 10 were in the morning (0830-1100 h). A total of 35 blacksmith were collected from the Point area before noon (1000-1130 h).

During the study period, 28 plankton samples from the discharge plume and 13 plankton samples from the Point were collected. The mean rank order abundance of prey items from each site was determined for comparison with blacksmith stomach contents.

Observations comparing different prey items from two locations were tested using contingency table analysis, the G-test (Crow 1982), and Kendall's coefficient of rank correlation. When only one variable (fish weight, stomach fullness etc.) was tested between two locations, a two-sample t-test was used, assuming separate variances. Values of the Index of Relative Importance (IRI) were calculated for consumed prey from the sum of the percent number and the percent volume, multiplied by the frequency of occurrence (Foc) (Pinkas et al. 1971).

Dietary overlap between blacksmth from the Point and discharge was examined using the formula of Schoener (1970):

$$a = 1-0.5\left(\sum_{i=1}^{n} |Px_i - Py_i|\right)$$

where n is the number of food categories, x_i is the average percentage of estimated volume that food category i contributed to species at location x, and y_i is the average percentage of estimated volume that food category i contributed to species at location y.

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

An estimate of mean prey size was obtained by dividing the total number of prey consumed into the stomach weight for each fish collected.

RESULTS

Thirty species of fish were identified from the area surrounding the discharge. Blacksmith were the most abundant and frequently occurring fish (mean estimate of abundance per transect >100 individuals, rank of the mean number per transect = 1, and frequency of occurrence per transect = 92.3). Large schools arrived in the morning and began feeding in the plume and outer plume. When feeding in the outer plume, blacksmith would orient themselves toward the plume, surrounding it, and feed on the organisms that settled out of the rising effluent. When in the plume, blacksmith were in constant motion, being tossed about by the irregular flow, but it was apparent from mouth action that these fish were also feeding on suspended food items.

The mean abundance per transect of blacksmith at the Point for the quarterly sampling days in 1979 and 1980 was 148.4. They ranked first in mean number per transect, with a mean frequency of occurrence of 86.2, and used the breakwater as their primary nocturnal sheltering site.

There were no significant differences in either fish length or fish weight, but there were significant differences in stomach weight and stomach fullness between the two collection sites (Table 1). Fish collected from the discharge had a greater amount of food in their stomachs (an increase of 138%).

Stomach fullness was not influenced by collection time. The stomach weight and stomach fullness were not significantly different between morning and afternoon collections (t-test: $t = 1.359, P = 0.181$ and $t = 1.471, P = 0.147$, respectively). Consequently, the data collected from the discharge samples were combined.

The mean prey abundance, percent number, percent volume, frequency of occurrence, and the calculated IRI value of the 30 most abundant prey items from each location are given in Table 2. A contingency table analysis of the mean abundance indicates that there was a significant difference in the stomach contents between the two locations ($G = 570.6$, $P < 0.001$, df = 17). The 10 most abundant prey from each site (eliminating the smaller values) are significantly different ($G = 561.1, P < 0.001$, df = 12). A comparison of the 10 highest IRI values from each site are not significantly correlated (Kendall's tau, $t = 0.1868, P = 0.324, n = 14$). A pictorial representation of the IRI values is given in Figures 2 and 3.

A comparison of the mean prey weight from each sampling site revealed that blacksmith from the discharge ate larger prey than blacksmith from the Point (discharge mean prey weight = 3.22 mg, SD = 4.01, Point = 0.82 mg, SD = 0.81, $t = 4.439, P < 0.001$).

Temperatures from the discharge plume and base were compared with surface and bottom temperatures at the Point. The mean plume temperature (26.3°C, SD = 3.3, $n = 15$) was significantly greater (t-test: $t = 5.69$, $P < 0.001$) than the mean surface temperature from the Point (20.8°C, SD = 2.5, $n = 30$). Similarly, the mean base temperature (18.2°C, SD = 2.4, $n = 17$) was significantly greater ($t = 4.12$, $P < 0.001$) than the mean bottom temperature from the Point (15.2° C, SD = 2.4, $n = 30$).

The rank of the 10 most abundantly consumed prey items was compared with the rank of the 10 most abundant plankton items for both the discharge and Point. There was no significant correlation for either study site (discharge $t = 0.0110, P = 0.956, n = 14$; Point $t = 0.2051, P = 0.329, n = 13$).

Between-site comparisons of the mean abundance of six abundantly consumed prey items from both stomach contents and plankton samples (Table 3) show that two prey items, gammarids and *Polyophthalmus pictus*, had a significantly higher usage and availability at the discharge than the Point, and that *Calanus* sp. and mysids had a higher usage at the discharge but were not significantly more available. There was no significant difference in the usage or availability of *Oikopleura* sp. between the Point and discharge (although blacksmith from the Point tended to eat a greater amount).

The diets of blacksmith at the discharge and Point

TABLE 1.—Comparison of blacksmith, *Chromis punctipinnis*, collected from the discharge (thermal outfall) and the Point (Control Site), King Harbor, Calif.

	Discharge $n = 73$	Point $n = 35$
Fish weight (g)	Mean = 175.6 g SD = 38.4 $t = 0.819$ $P = 0.416$	Mean = 168.3 g SD = 44.7
Fish length (SL mm)	Mean = 172.8 mm SD = 12.9 $t = 0.569$ $P = 0.571$	Mean = 172.2 mm SD = 14.3
Stomach weight (g)	Mean = 1.10 g SD = 0.53 $t = 9.726$ [1]$P < 0.001$	Mean = 0.30 g SD = 0.25
Stomach fullness (0-5)	Mean = 3.89 SD = 1.06 $t = 10.175$ $P < 0.001$	Mean = 1.63 SD = 1.09

[1]Note: The statistical package (SPSS) used was unable to compute P values lower than 0.001. Values below this number are represented as $P < 0.001$.

TABLE 2.—The 30 most abundant food items consumed by blacksmith, *Chromis punctipinnis*, at the discharge (thermal outfall) and the Point (control site), King Harbor, Calif. Foc = frequency of occurrence; IRI = index of relative importance.

	Point					Discharge				
	$\bar{x}$ no.	% no.	% vol.	Foc.	IRI	$\bar{x}$ no.	% no.	% vol.	Foc.	IRI
Oikopleura	430.49	77 5	41.3	77.1	9,159 5	290.63	33.7	10.8	87.7	3,902.7
Acartia	59.03	10.6	3 2	71.4	985.3	46.38	5.4	2 1	67.1	503.3
Calanoids, misc.	26.11	4.7	3.2	71.4	564 1	14 86	1 7	1 4	75.3	233.4
Polychaeta, misc.	8.03	1.4	1.6	57.1	171 2	2.53	0.3	1.2	50.7	76.1
Corycaeus	6.51	1.2	1 4	45.7	118.8	3 68	0.4	0.5	42.5	38.3
Calanus	5.29	0.9	5.7	62.9	415.1	298.36	34 6	11.0	76.7	3,497.5
Chaetognath	4 51	0.8	3.4	57.1	239.8	4 14	0.5	0.5	34.2	27.4
Labidocera	2 60	0.5	2.2	48.6	131 2	2.12	0.2	0.6	52.1	41.7
Brachyuran zoea	1 89	0.3	0.9	22.9	27.5	8.14	0.9	1.2	46.6	97.9
Gammaridae	1 83	0.3	1.1	42.9	60.1	111.33	12.9	25.3	91.8	3,506.8
Pagurid zoea	1 63	0.3	0.6	25.7	23.1	3.27	0.4	0.5	43.8	39.4
Cladocera	1.60	0.3	0.4	28.6	20.0	0.49	0.1	0.1	20.5	5.7
Rhincalanus	1.17	0.2	0.6	34.3	27.4	2 27	0.3	0.6	41.1	30.9
Euphausids	0.97	0.2	0.4	25.7	15.4	0.82	0.1	0.1	26.0	5.2
Tortanus	0.77	0.1	1 2	28.6	37.2	1.52	0.2	0.4	32.9	17.2
Cypris larvae	0.54	0.1	0.2	22.9	6.9	1.10	0.1	0.2	37.0	11.1
Fish eggs	0.49	0.1	0.2	28.6	8.6	0.53	0.1	0.1	24 7	4.9
Cirripide exoskel.	0.46	0.1	0.1	14.3	2 9	0.42	0.1	0.6	27.4	10.0
Polyophthalmus pictus	0.34	0.1	0.1	2.9	0.3	25.70	3.0	6.8	28.8	282.2
Gastropoda	0.34	0.1	0.2	22.9	6.9	0.37	0.1	0.1	20.5	4 1
Fish larvae	0.31	0.1	0.3	17.1	6.8	3 29	0.4	1.4	35.6	64.1
Mysids	0.31	0.1	0.2	20.0	6.0	36.01	4 2	7.7	80.8	961.5
Opheliidae	0.14	0.1	0.1	8 6	1.7	0.90	0.1	0.3	30.1	12.0
Decapoda, misc.	0.06	0.1	0.2	5.7	1 1	0.55	0.1	0.9	30.1	30.1
Caprellidae	0.03	0.1	0.1	2.9	0.3	1.90	0.2	1.0	46.6	55.9
Porcellanid zoea	0.03	0.1	0.1	2.9	0.3	0.89	0.1	0.2	32.9	9.9
Pelecypoda	0	0	0	0	0	0.60	0.1	0 4	24.7	12 4
Anemone	0	0	0	0	0	3.29	0.4	0.5	15.1	13.6
Ecto-Entoprocta	—	—	0.1	2.9	0.3	—	—	1 5	8.6	12.9
Unidentified, misc.	—	—	11.2	35.3	395.4	—	—	6.9	42.9	296.0

TABLE 3.—Usage and availability of selected prey items from the Point (control site) and discharge (thermal outfall), King Harbor, Calif.

	In stomachs[1]		In plankton[2]	
Prey items	Discharge	Point	Discharge	Point
Polyophthalmus pictus				
Mean	25.70	0.34	30.59	0
SD	67 49	2.03	86.52	0
	$t = 3.207$	$P = 0.002$	[3]$P < 0.001$	
Acartia				
Mean	46.38	59.03	181,987.13	167,487.59
SD	112.02	130.95	323,297.81	133,525.13
	$t = 0.492$	$P = 0.625$	$t = 0.031$	$P > 0.840$
Calanus				
Mean	299.36	5.29	364 41	721.00
SD	753.29	11.96	717.27	1,260.84
	$t = 3.323$	$P = 0.001$	$t = -0.959$	$P = 0.353$
Mysidacea				
Mean	36.01	0.31	943.28	306.38
SD	75.38	0.72	3,562.00	568.29
	$t = 4.046$	$P < 0.001$	$t = 0.981$	$P = 0.333$
Grammaridae				
Mean	111.33	1.83	6,291.81	472.92
SD	174.51	4.52	10,784.44	845.73
	$t = 5.357$	$P < 0.001$	$t = 3.029$	$P = 0.005$
Oikopleura				
Mean	290.63	430.49	6,829.81	4,582.08
SD	471.00	557.59	19,821.55	9,906.22
	$t = -1.281$	$P = 0.205$	$t = 0.505$	$P = 0.616$

[1]Mean number of prey consumed per fish.
[2]Mean number per 100 m^3 of water sampled.
[3]Note: The statistical package (SPSS) used was unable to compute P values lower than 0.001. Values below this number are represented as $P < 0.001$.

did not overlap ($a = 0.522$, with a value >0.60 considered significant, Zaret and Rand 1971).

DISCUSSION

Blacksmith were a numerically dominant species at both study sites. The daytime abundance of blacksmith was similar at the discharge and the Point. Blacksmith may travel to the discharge from the breakwater and other nearby jetties during the day, since they do not seek shelter around the discharge at night. Such diel migrations of blacksmith between the Units 7 and 8 intake of Southern California Edison's Redondo Beach Station and the nocturnal rocky shelters at the Point have been previously observed.[6]

The feeding habits of blacksmith were significantly different between the Point and discharge (Figures 2 and 3 best illustrate this difference). At the Point, *Oikopleura* and calanoid copepods (primarily *Acartia*) were the most heavily utilized organisms. At the discharge, blacksmith consumed larger organisms, gammarids, calanoid copepods of the genus *Calanus*,

[6]M. Helvey, VANTUNA Research Group, Occidental College, Los Angeles, CA 90041, pers. commun. 1980.

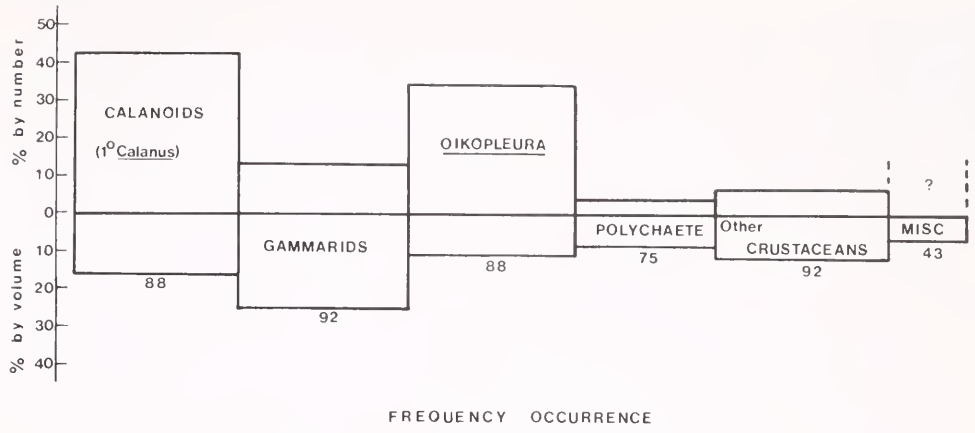

FIGURE 2.—Graphic representation of the Index of Relative Importance of prey items consumed by blacksmith, *Chromis punctipinnis*, at the discharge (thermal outfall) in King Harbor, Calif.

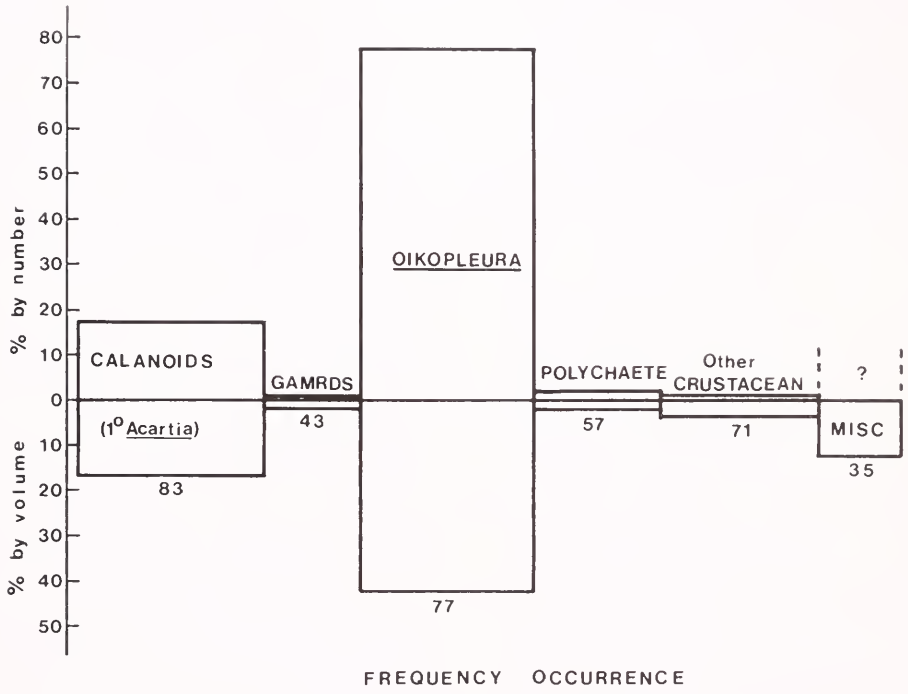

FIGURE 3.—Graphic representation of the Index of Relative Importance of prey items consumed by blacksmith, *Chromis punctipinnis*, at the Point (control site) in King Harbor, Calif.

large polychaetes, other crustaceans, as well as *Oikopleura*. At both sites blacksmith were selective in their planktonic feeding, consuming the largest prey items available. Brooks (1968) stated that there is selection for larger zooplankters, with smaller ones eaten as the larger ones become scarce. At the Point, *Oikopleura* was the largest prey item found in abundance, while at the discharge other larger food items

were common along with *Oikopleura* (gammarids, *Polyophthalmus pictus*, and mysids). The amount of dietary overlap between the two locations was not considered significant.

Although more abundant at the Point, a significantly greater amount of *Calanus* sp. was eaten by blacksmith at the discharge than at the Point. A possible explanation for the high usage of *Calanus* at the discharge could be the increased susceptibility of zooplankton to predation as a result of turbulent outflow. Entrained *Calanus* are more accessible to planktivorous fishes, since the mortality rate of copepods passing through a power plant may reach 70% (Carpenter et al. 1974). Dead or damaged copepods would appear as viable prey upon discharge from the plant and could be easily consumed. Increased mortality from turbulence has also been shown for other zooplankters (Gregg and Bergersen 1980).

There is evidence that alterations in plankton distributions at outfall areas are the result of upward vertical displacement of deep-water organisms. Evans (1981) noted that deeper living zooplankton are carried vertically upward to the turbulent waters over the discharge jets. Although analysis of plankton sampled did not prove the existence of such currents, in a previous study at King Harbor dye injections were carried to the plume from bottom water 20 m away from the discharge.[7]

Large gammarids, polychaetes, and juvenile anemones, all of which were common in stomachs of blacksmith from the discharge, are not normal constituents of King Harbor plankton. The force of the swirling effluent is strong enough to detach and entrap these organisms from their normal habitat inside and around the discharge pipe. Once entrapped in the plume, these large invertebrates are accessible to the planktivorous blacksmith.

Zooplankton avoid predation through escape movements upon detection of suction currents created by predatory fish (Dreener et al. 1978; Kettle and O'Brien 1978). Once entrained in the effluent plume, the ability of zooplankton to detect these currents becomes impaired (Evans 1981). As a result, fish frequenting the plume have the potential for feeding on a high concentration of zooplankton with limited predator avoidance. The greater stomach weight and stomach fullness of blacksmith feeding at the discharge support this theory.

Results from other studies examining the feeding habits of blacksmith appear to be similar to those found at the Point. The food items consumed by blacksmth at Santa Catalina Island are (listed in decreasing abundance) *Oikopleura*, calanoid and cyclopoid copepods, fish eggs, cladocerans, and other crustaceans (Hobson and Chess 1976). At Naples Reef, off Santa Barbara, Calif., Bray (1981) found the diet of blacksmith to consist of larvaceans (*Oikopleura*), copepods, cladocerans, chaetognaths, decapods, and polychaetes. In the two abovementioned studies and from the Point, blacksmith consumed at least twice as many *Oikopleura* as any of the other food items, while at the discharge, *Calanus* was the most abundantly consumed prey and gammarids comprised the greatest volume of prey eaten (Table 2). When *Calanus*, gammarids, mysids, and the polychaete *Polyophthalmus pictus* are removed from the analysis of the 10 most abundant prey consumed, no significant difference was observed between the two locations ($G = 9.4$, n.s. at $P = 0.05$, df = 7).

It has long been recognized that blacksmith forage on plankton in areas where currents are present (Limbaugh 1955, 1964; Feder et al. 1974; Ebeling and Bray 1976; Hobson and Chess 1976; Bray 1981). The tropical species of damselfish (family Pomacentridae) also prefer feeding in areas where currents are strong (Hobson and Chess 1978). Blacksmith have been shown to prefer incoming currents (Limbaugh 1955, 1964; Ebeling and Bray 1976; Bray 1981), and Limbaugh believed they materially affected the amount of plankton entering the kelp beds. In Bray's (1981) study, stomach fullness was greater in fish at the incurrent end of the reef than in fish at the excurrent end.

Areas of strong currents are rich in zooplankters (Hobson and Chess 1978) as is the discharge which receives both entrained and entrapped organisms. Although the discharge releases warm water, the current created by the outflow is the major attractant. Blacksmith, a species which prefers warm water (mean preferred temperature = 14°-15°C), are found in 26°-32°C discharge plume water, above their upper temperature avoidance limit of 23°-25°C (Shrode et al. 1982). In the presence of food, blacksmith will disregard their normal avoidance limits for chlorine, intermittently present in most power plant effluents (Hose and Stoffel 1980).

It can be concluded that the outflowing effluent and its related phenomena attract blacksmith to the discharge. This theory is further supported by documentation of similar attraction and rheotropic behavior by blacksmith at an offshore water intake structure (Helvey and Dorn 1981).

[7]Kinnetic Laboratories, Inc. 1981. Hydrodynamic characteristics of offshore intake structures. Field verification studies. Kinnetic Labs., Inc., P.O. Box 1040, 1 Potrero St., Santa Cruz, CA 95061.

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CALIBRATION OF DENTAL LAYERS IN SEVEN CAPTIVE HAWAIIAN SPINNER DOLPHINS, *STENELLA LONGIROSTRIS*, BASED ON TETRACYCLINE LABELING

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ABSTRACT

To calibrate dentinal and cemental growth layer groups (GLGs) with real time, a study was conducted on the teeth from seven captive Hawaiian spinner dolphins that had been treated clinically with tetracycline (TCL) at numerous times over multiple years at Sea Life Park, Hawaii. To monitor layer accumulation as it occurred for 1 year, we gave single injections to three animals every 3 months and pulled a tooth from each every 6 months. By comparing dental-layer patterns between TCL labels that had been introduced at 6-month and 1-year intervals, annual patterns were distinguished. In the dentine, a thin, light layer (the first being the neonatal line) was formed about every 6 months. Each annual GLG contained 13 lunar monthly layers (LMLs). Using LML or light-layer counts, age, month, and year of birth were estimated for each of the seven specimens. All seven deposited nearly the same dentinal GLG thickness in the same year of life. Estimates of birth months indicated that five of the animals were born in late summer or early autumn and two were born in spring. Comparisons of dentinal labels with clinical records for a captive-born animal showed that TCL given to its mother was imparted via milk to the nursing calf. Time calibration of cemental GLGs showed that usually one cemental GLG was deposited annually, but in some cases a GLG was formed every second year or twice a year.

The technique of "reading" layers or growth layer groups (GLGs, terminology of Perrin and Myrick 1980) in teeth, developed to determine ages for pinnipeds in the early 1950's by Scheffer (1950) and Laws (1952), is now used routinely in dolphin studies (see reviews by Klevezal' and Kleinenberg 1967; Jonsgård 1969; Scheffer and Myrick 1980). Early work on dolphins (e.g., Nishiwaki and Yagi 1953; Sergeant 1959), showing a correlation between apparent age and number of GLGs led to the working assumption that GLG-deposition cycles are constant, each GLG usually, but not always, interpreted as representing 1 yr. Critical analysis of this assumption has been impaired by a lack of suitable material.

Three approaches have been used in efforts to calibrate dental GLGs with time and to determine their deposition rate: 1) In vivo labeling of tooth layers, 2) multiple extractions of teeth over time, and 3) examination of teeth from animals of known age. Nishiwaki and Yagi (1953) labeled the layered dentine in four wild-caught striped dolphins, *Stenella coeruleoalba*, by intramuscular injection of lead acetate paste. None of the four survived long enough for the labels to provide useful data.

Nielsen (1972) treated a young wild-caught harbor porpoise, *Phocoena phocoena*, with tetracycline (TCL) three times over a 370-d period. Three fluorescent labels were found in thin sections of its teeth examined in ultraviolet (UV) light "... but the uniform [unlayered] dentine made it impossible to determine the number of growth-layers formed per year" (Nielsen 1972:72).

Best (1976) administered oral doses of TCL hydrochloride, "Mysteclin-V", on each day over an 8-d period to each of three wild-caught dusky dolphins, *Lagenorhynchus obscurus*. Labels were detected in teeth of two of the three specimens after their deaths. In one specimen, dentine accumulated for 703 d between treatment and death averaged 200 μm/yr and 0.56 μm/d. In the other (older) specimen, the average deposition rate in dentine between the treatment label and the pulp-cavity wall was 77 μm/yr and 0.21 μm/d. Best concluded that the thickness of GLGs decreases significantly with age in dusky dolphins.

Gurevich et al. (1980) successfully introduced a single TCL label into the teeth of three of four wild-caught adult common dolphins, *Delphinus delphis*. The three labeled animals died 328, 354, and 441 d, respectively, after the date of treatment. By estimating the dentinal pattern laid down in about 1 yr, the investigators characterized an annual GLG. They estimated the ages of the animals by assuming that the GLGs in the unlabeled regions of the teeth rep-

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resented the same amount of time as the single GLG interpreted from the labeled region of each tooth.

A study by Hui (1978) included two tooth extractions made 2.5 yr apart from a captive male bottlenose dolphin, *Tursiops truncatus* (No. 10, "Kona"). Comparisons of longitudinal thin sections of the two teeth led Hui to conclude that "... almost three dentin layers [GLGs] had been deposited during the intervening period..." (p. 11). Other than indicating GLG boundaries in figures of the two thin sections (his fig. 3), Hui did not describe the GLGs or their components.

Three published studies (Sergeant 1959; Sergeant et al. 1973; Hui 1978) have attempted to demonstrate time content in GLGs using teeth of known-age, i.e., captive-born dolphins. All three had access to only a small number of specimens, all of *Tursiops truncatus*. Apparently, the investigators knew the ages of the specimens before defining and counting dentinal GLGs in the teeth, and no assurance was provided that the GLGs counted corresponded to annual periods between birth and death. Hui's study demonstrated that GLGs may be defined in such a manner as to verify the age that is already known for a specimen (Myrick 1980a). The incorrect age data (3.3 yr) provided to Hui for one of two "known-age" specimens studied by him (Hui 1978) led to his subsequent division of its dentinal layering pattern into three GLGs and a small fraction (Hui[4]). The original clinical records for the specimen (Hui's No. 29, LACM 54698) show, however, that the dolphin was born on 28 August 1965 and died on 8 August 1969, at nearly 4 yr of age.

Used independently, teeth of known-age animals, single-labeled teeth, or teeth extracted on two dates do not provide reliable means by which to determine tissue accumulation rates fully or to define GLGs with precision. Each method yields only two dates bracketing a segment of layered tissue into which the known elapsed time is divided. Myrick (1980b) described approaches that combine the use of two or more labels and two or more tooth extractions over an extended period to monitor rates and calibrate GLGs. The present paper is an account of such a study which used TCL-labeled teeth from seven captive Hawaiian spinner dolphins, *Stenella longirostris*.

MATERIALS AND METHODS

The study consisted of two phases. The first was a retrospective examination of TCL labels in the dolphins' dental tissues produced incidentally by clinical treatments administered during their captivity at Sea Life Park, Hawaii. Teeth were used from four frozen carcasses (Nos. WFP 606, 669, 670, and 671[5]), including one specimen of known age, and three live animals (Nos. ACM 103, 104, and 106) from which teeth were extracted in early 1980.

The second phase was a 1-yr monitoring of tissue-accumulation rates in teeth of three live animals. Each animal was given intramuscular injections of TCL at about 3-mo intervals and underwent three tooth extractions during the monitored period.

To restrain the dolphins during injections and extractions, an elevated rigid litter was placed near the edge of the dolphin holding tank in which the water level had been lowered to a depth of 0.5 m. The sloped tank bottom inclined the litter at an angle of 20° relative to the water surface. Each dolphin in turn was guided on its belly onto the litter until the front half of its body was above the water surface. In this position the dolphin could be held firmly with little apparent discomfort to the animal.

The procedure used to extract teeth was adapted for the spinners from the method described by Ridgway et al. (1975) for bottlenose dolphins. The dolphin's mouth was held open by moistened rolled toweling placed around the upper and lower jaws. Carbocaine[6] (5-10 cc) was injected into the right or left interalveolar nerve immediately behind the anterior border of the mandibular foramen. After allowing about 10 min for the anesthetic to take effect, a tooth was removed from the middle of the corresponding mandibular tooth row using an elevator and an extractor. The vacated alveolus was packed with cotton soaked with a ferric solution to control bleeding and promote healing.

Liquamycin 100, a form of TCL, was injected into the dorsal musculature between the dorsal fin and the blow hole. To reduce the possibility of local inflammation of the tissue—a problem known to result from concentrations of TCL—each dose (25 mg/kg body weight) was distributed along the dorsum at three separate sites.

Untreated (cut or ground) thin sections and decalcified and haematoxylin-stained (D/S) thin sections are the two most widely used preparations for dolphin teeth in age determination studies (see Perrin and Myrick 1980: 21 ff.). D/S sections produce simpler, more uniform GLG patterns, but de-

[4]Clifford Hui, Naval Ocean Systems Center, San Diego, Calif., pers. commun. 1981.

[5]Skeletons are in the synoptic collection at Southwest Fisheries Center, NMFS, La Jolla, Calif.

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

calcification removes TCL labels (Nielsen 1972). We prepared the spinner teeth using both methods.

Untreated, mid-longitudinal thin sections, 100 μm thick, were prepared by hand grinding and polishing teeth using 240 and 600 grit Al_2O_3 on a glass plate. Other teeth were decalcified in RDO[7] for 6-8 h, rinsed, and cut with a microtome in longitudinal plane to produce 30 μm thick sections that were stained in Mayer's haematoxylin for 15-30 min. Untreated and D/S preparations were mounted on slides in Permount or glycerin gel and covered with coverslips.

To determine the pattern components of GLGs, the D/S and untreated thin sections were examined in plain transmitted light 39× and 150× with a Zeiss photomicroscope. TCL labels were viewed at the same magnifications with UV reflected light using a Zeiss fluorescent vertical illuminator with a filter-reflector No. 44-75-05 combination attached to the same instrument.

Retrospective Calibration of Dentinal GLGs

Dates and durations of treatment, date of birth (for one specimen) or capture, and dates of death (for four carcasses) were taken from clinical records maintained for each dolphin during its captive life at Sea Life Park (for summaries see Myrick et al. in press). Data for each specimen were transcribed onto a calibration chart as the chronological series of event blocks, the relative width of a given block corresponding to the length of a given period of treatment.

In each thin section showing distinct fluorescent labels under UV light, label thicknesses and interlabel distances were measured. Label-measurement data for each dolphin were entered on its chart as a series of blocks below the event blocks, with spacing and thickness scaled to the corresponding measurements. The treatment and label blocks were compared for spacing and thickness to identify the date each label was introduced. Connecting lines were drawn from the beginning and the end of each matched pair of blocks (Fig. 1C).

A UV photograph of each thin section was used to identify and letter key labels that enclosed 6- or 12-mo segments of dentine. Labels and structural landmarks in the UV photograph were traced with a china marker on an overlay of transparent plastic. Using the landmarks, the tracing was lined up on the corresponding plain-light photograph onto which the labels were reproduced to delineate layering patterns within the time segments. Each marked photograph was then inspected for repeating layer components to define GLGs and their subunits in the untreated thin section. GLGs defined in the labeled dentine of each thin section were used as a basis for identifying similar GLGs in the unlabeled regions of the dentine and permitted a complete series of GLG-thickness measurements and an estimate of dentinal age in years to be made for each animal.

Dentinal GLGs in dolphin teeth are most easily discerned in the region of the "shoulder", i.e., along a transect from near the base of the neonatal line (the first layer of the postnatal dentine), downward and inward at about a 30°-40° angle to the margin of the pulp cavity (for examples see Perrin and Myrick 1980: fig. 2; Hui 1978: figs. 1, 2, 3). For consistency, measurements of GLG and label thickness, taken perpendicular to the long axis of the teeth of the Hawaiian spinner dolphins, were made along transects at a similar position and angle (Figs. 1A, B). However, a GLG or label may vary in thickness in localized regions of the dentine and may not be the same on both sides of a tooth because of tooth asymmetry. For these reasons, measurements were made on the most symmetrical side of a tooth and in regions where GLGs and labels were clearest and least variable in thickness; departing slightly from a uniform angle of transect. GLGs in the dentine of the corresponding D/S thin sections were defined and counted with the aid of GLG-thickness measurements obtained from the untreated section.

Retrospective Calibration of Cemental GLGs

Because fewer labels were observed in the cementum than in the dentine of the same untreated thin section, it was assumed that those visible represented condensed forms of only the brightest, thickest, or closely spaced groups of dentinal labels. This has been verified in bottlenose dolphins (Myrick 1980b) and recently in the present sample of Hawaiian spinners by observations that bright dentinal labels at the tooth base are continuous with cemental labels. Hence, cemental labels were lettered to correspond to the brightest dentinal labels, and the cemental layers between labels were calibrated using the time segments represented between the dentinal labels.

The annual GLG pattern was defined as precisely as possible using the calibrated segments of the tissue, and the cemental GLG definition was tested by comparing the dentinal GLG count with the cemental GLG count in untreated thin sections. In D/S thin

[7] A commercial rapid decalcifying agent available through Dupage Kinetic Laboratories, Inc., Plainfield, Ill.

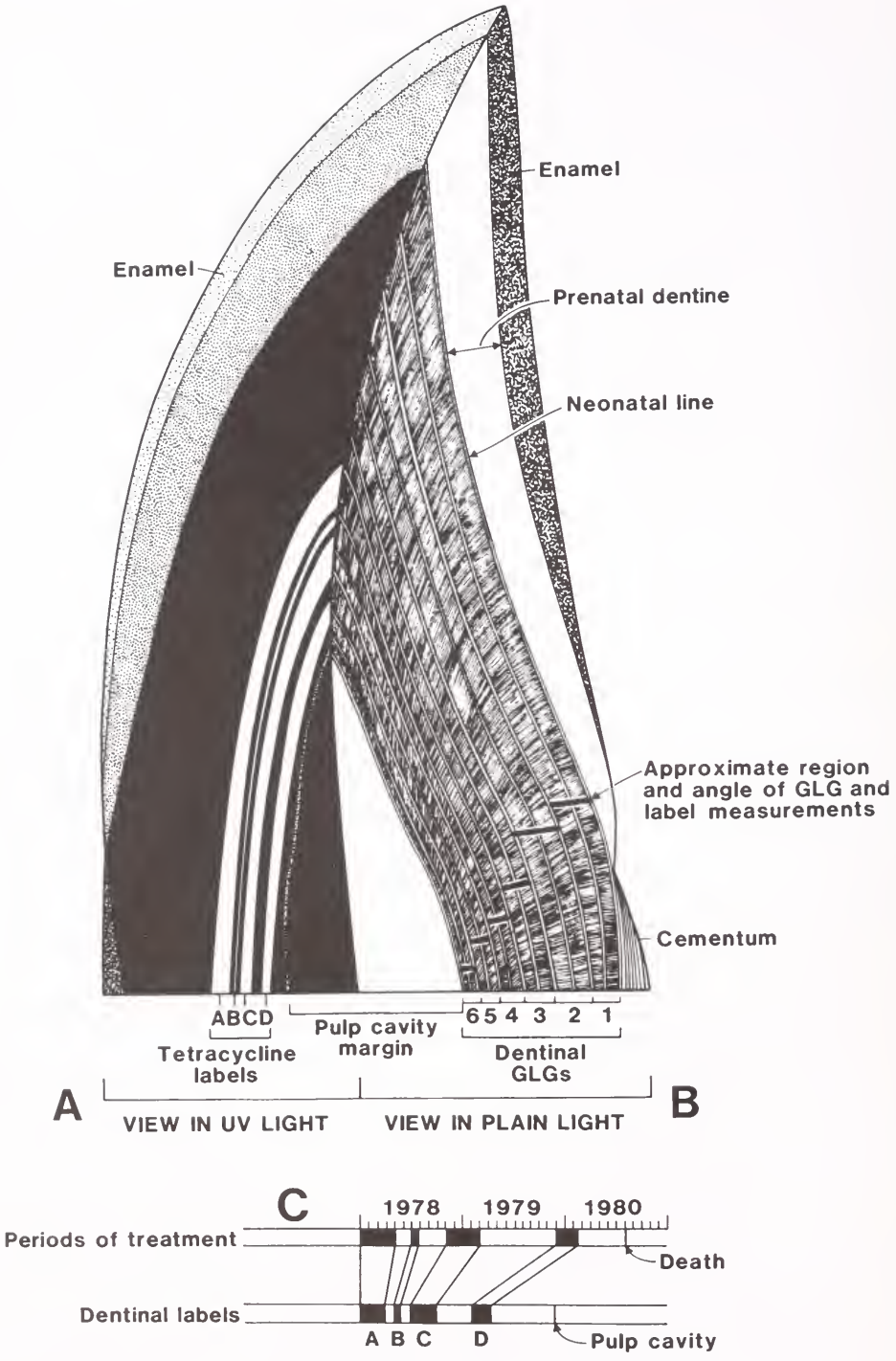

FIGURE 1.—Line drawing of hypothetical dolphin tooth in thin section showing appearance of TCL labels, A, B, C, D, under ultraviolet light (1A, left-hand side) and dentinal growth layer group (GLG) layering patterns under plain transmitted light (1B, right-hand side), and standard positions in tooth where label and GLG thickness are measured. 1C illustrates method of identifying labels in tooth section with TCL treatment dates by comparing relative thickness and spacing of labels with treatment periods.

sections, cemental GLGs were defined indirectly by comparing them with the pattern and number of cemental GLGs determined in untreated sections.

Direct Monitoring

Calculation of depositional rates and calibration and definition of GLGs in dentine and cementum were achieved by comparing tooth specimens containing successively introduced labels and/or additional tissue accumulated over the 1-yr period of monitoring. To make determinations, for cases in which labels were not distinct or not successfully produced, the additional tissue was measured from structural landmarks or labels in the extracted series of thin sections.

RESULTS

Dentinal labels.—The untreated thin sections for all seven specimens contained multiple labels. Most attempts to match labels with treatments were successful (Figs. 2-6). However, in four specimens more labels occurred than could be accounted for from clinical records. In the only captive-born specimen, WFP 670, numerous TCL labels were observed (Fig. 7A, B), but only three were found to have been caused by intentional therapeutic treatments (Fig. 7D, labels C, F, and G). Labels A and B apparently were a result of TCL impaired to the then-calf through the milk of its mother, who was treated with the drug for two periods while the calf nursed. The other labels appear to have resulted from frequent ingestion of stolen TCL-dosed smelt intended for other dolphins being treated at various times while sharing a common tank with this animal.

No treatment was recorded for label A found in the dentine of dolphin carcass WFP 669 (Fig. 4A, C) and live dolphin ACM 104 (Fig. 6A, C). Judging from the relative positions of the "A" labels to the other labels for which matches were found with recorded treatments, "A" labels were introduced into both specimens at or about their respective dates of capture. It is a fairly common practice in commercial aquaria to give medication (often tetracycline) to newly captured dolphins recovering from stress of capture and adjusting to the captive environment[8].

Labels B and G in the dentine of dolphin carcass WFP 671 could not be identified from clinical records (Fig. 5A, C), although the numerous other labels match well in relative thickness and spacing with the treatment dates for this specimen.

In teeth of live dolphin ACM 103 the labels were indistinct. The presence of TCL, introduced clinically during three periods of treatment over 2 yr and experimentally at 3-mo intervals in 1980, was indicated only by several areas of hazy fluorescence in the dentine near the pulp cavity.

Dentinal GLG pattern.—The use of plastic overlays of key labels enclosing 6-mo or 1-yr segments of dentine on plain-light photographs of the dentine for each specimen permitted repeated calibrations of the annual dentinal layering pattern for six of the seven specimens (the seventh specimen, ACM 103, had no discrete labels). In untreated thin sections, a dentinal GLG contained four major components deposited in the following sequence: 1) A thin, light (GLG-boundary) layer, 2) a thicker dark layer, 3) another thin, light (mid-GLG) layer, and 4) a second thick, dark layer (Figs. 3A, 4B, 5B, 6B).

In addition to the four components, many of the earliest deposited GLGs had an infrastructure composed of finer alternating dark and light layers. Counts made at 150× under low transmitted light showed that each of these annual GLGs contained 13 pairs of fine layers (Figs. 3A, 4B, 6D, 7C). Where layers were sufficiently distinct to be counted between labels (e.g., between label B and M, Fig. 4A, B), counts indicated that each pair ["LML," (lunar monthly layer) Myrick 1980b] represented about 1 lunar month. The full complement of LMLs was visible throughout the dentine in the captive-born specimen, WFP 670, i.e., 13 LMLs in each of the first three complete GLGs and 9 in the incomplete fourth GLG (Fig. 7C). In specimen ACM 103, 13 LMLs were observed in the first 12 of the 14.5 GLGs present (Fig. 8). But in other specimens, LMLs were clear enough to be counted only in the first five or six GLGs.

In D/S thin sections, the annual GLG pattern consisted of two lightly stained and two darkly stained layers. The thin, light, GLG-boundary layers and mid-GLG layers in untreated thin sections corresponded to the lightly stained layers in D/S thin-sections (Fig. 9A, B). LMLs were indistinct in almost all GLGs in D/S preparations.

Age-specific GLG thickness.—Table 1, showing dentinal GLG thickness measurements made from the most symmetrical side of the tooth of each of the seven dolphins, indicates that for each animal a GLG of a specific thickness was produced that appears to be related to the year of life in which the GLG was formed, i.e., an age-specific GLG thickness.

[8] William A. Walker, Los Angeles County Museum of Natural History, Los Angeles, Calif., pers. commun. 1982.

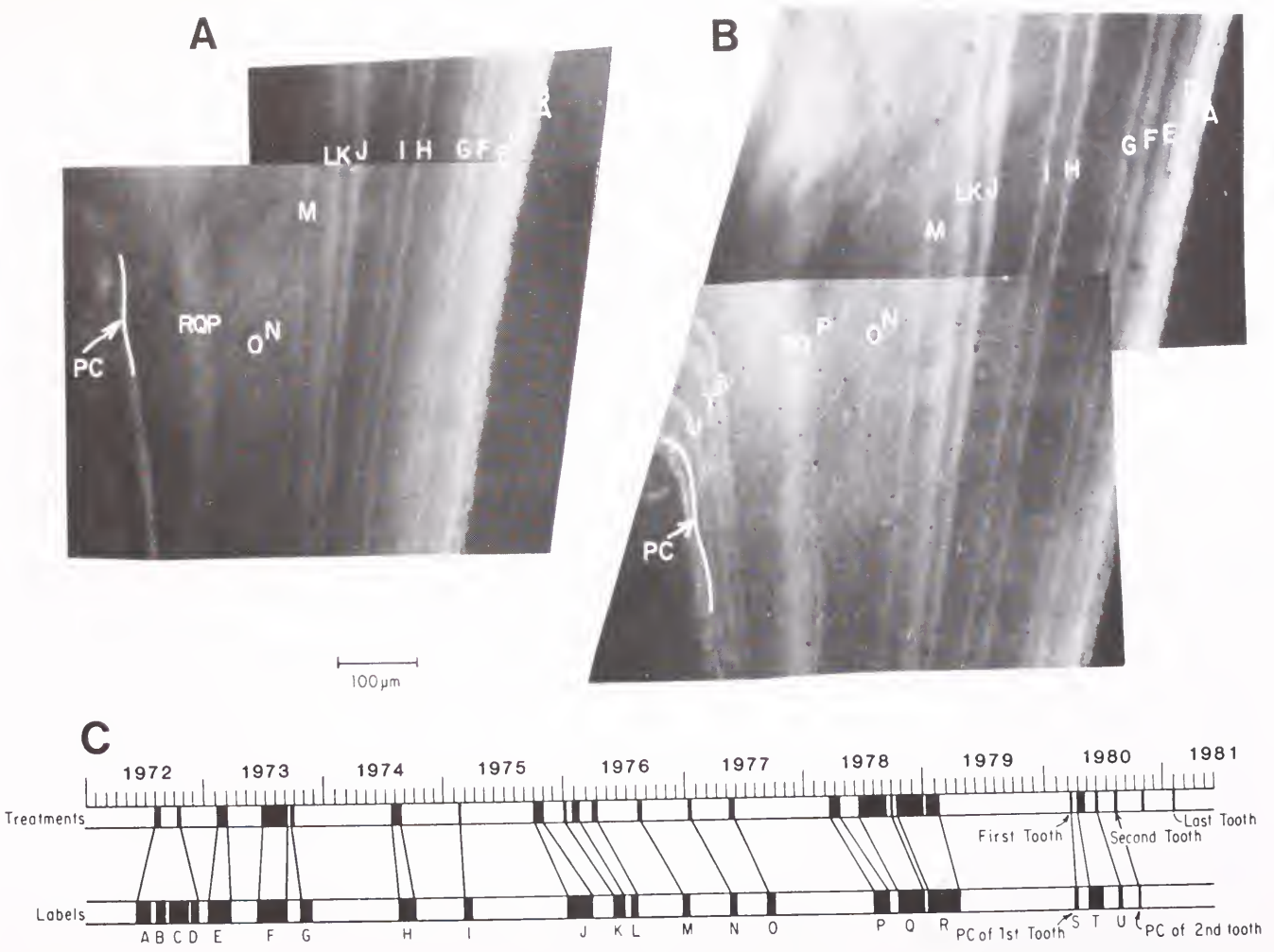

FIGURE 2.—Labeled teeth from live dolphin ACM 106. A. Untreated thin section of tooth extracted in March 1980, showing labels (lettered) introduced through TCL treatments from 1972 through 1979 (UV, 150×). B. Tooth extracted 4 mo after tooth in 2A showing three labels introduced during first part of the experimental labeling period. Label T was produced from a clinical treatment administered over 1-mo period (UV, 150×). C. Chart showing treatments and corresponding dentinal labels as interpreted from relative label positions and thicknesses.

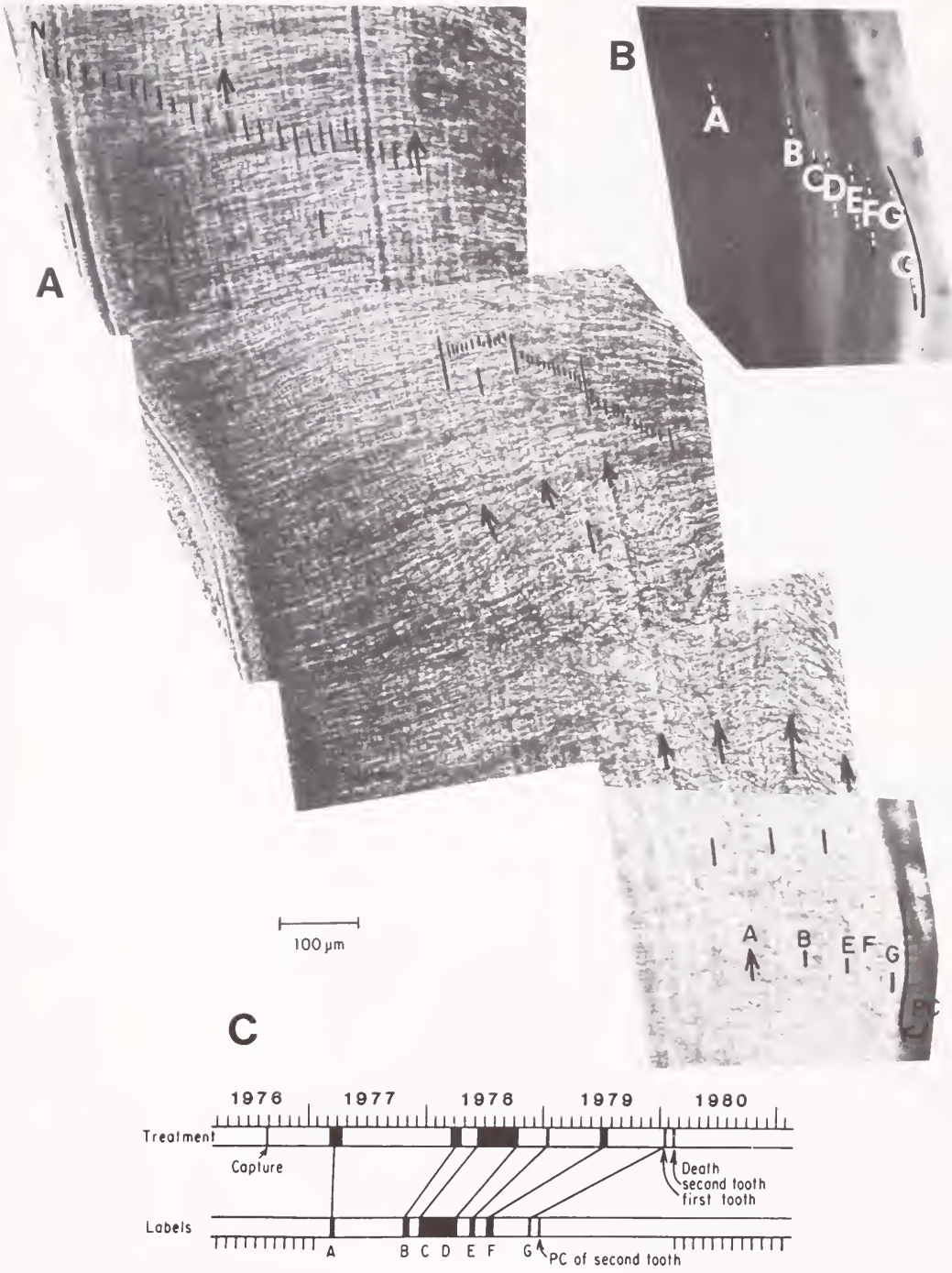

FIGURE 3.—Labeled tooth taken from dolphin carcass WFP 606. A. Untreated thin section in plain light showing about eight annual GLGs in dentine (separated by arrows). GLGs divided approximately in half by thin, light mid-GLG layers (heavy dark marks). GLGs 6, 7, and 8 were interpreted from positions of tetracycline labels (lettered). Finer dark layers represent lunar monthly layers (150×). B. Dentine labels in UV light (150×). C. Chart showing dates labels were introduced.

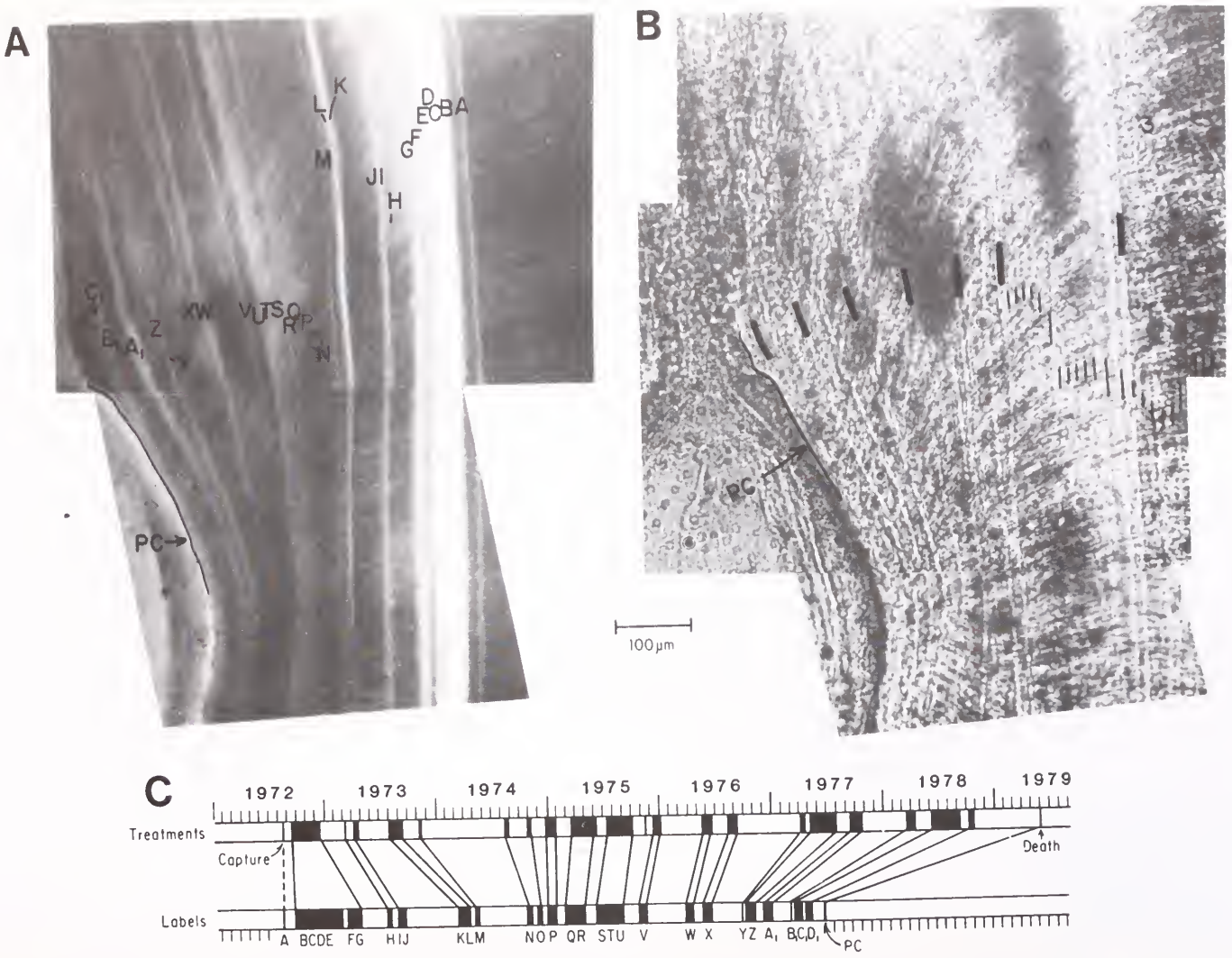

FIGURE 4.—Labeled tooth from dolphin carcass WFP 669. A. TCL labels (lettered) in region of dentine pulp cavity (PC) (UV, 150×). B. Plain-light view of dentine as in 3A showing annual GLGs bordered by light boundary layers (heavy dark marks) as interpreted from key TCL labels. Fine dark lines represent LMLs. (Heavy lines delineating GLGs are not placed at the standard positions used to measure GLG and label thickness.) C. Chart showing TCL treatments and corresponding dentinal labels identified by comparing relative positions and thicknesses of labels with spacing of treatment blocks.

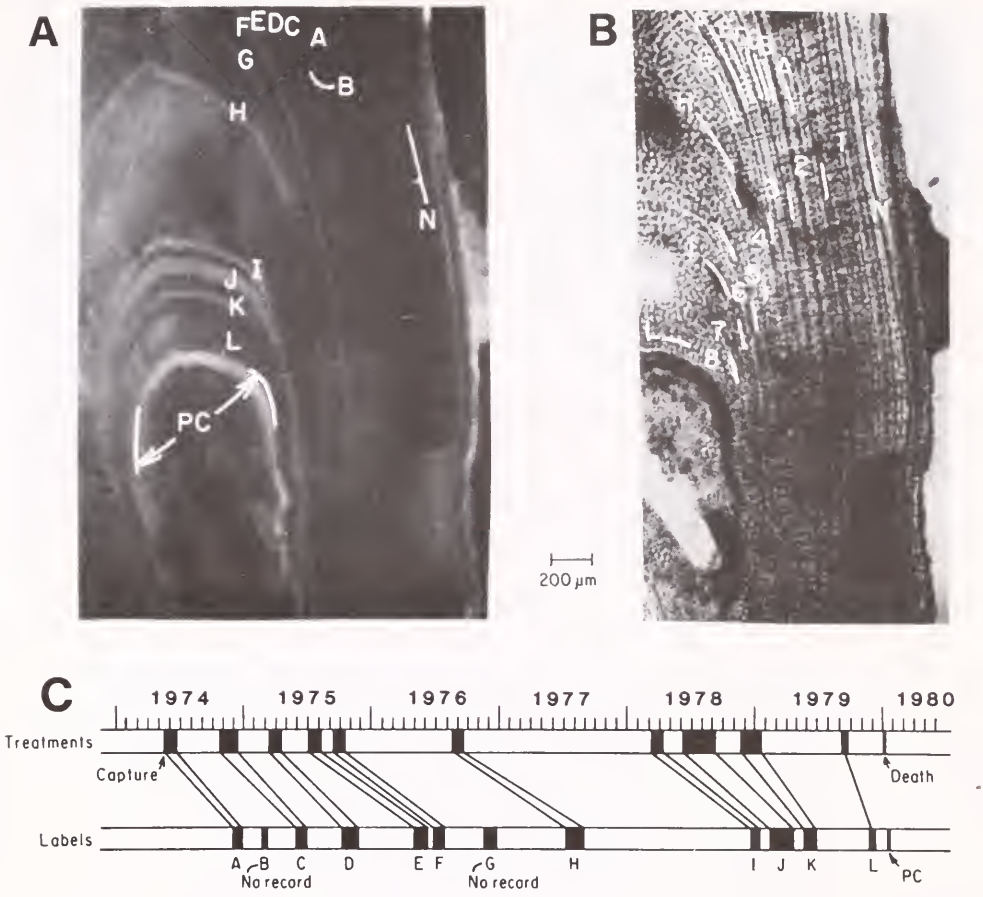

FIGURE 5.—Labeled tooth of dolphin carcass WFP 671. A. Untreated thin section in UV light showing TCL labels (39×). B. Thin section in plain light showing almost eight complete GLGs as interpreted from labels. Light GLG boundary layers appear to have been deposited in or about March (39×). C. Chart showing match between labels and treatments.

TABLE 1.—Mean age-specific thicknesses (µm) of completed dentinal growth layer groups (GLGs) in teeth of seven Hawaiian spinner dolphins, *Stenella longirostris*. Values are averages of at least three measurements per specimen, taken perpendicular to the long axis of the tooth in a stairstep fashion downward and inward from the base of the neonatal line to the pulp-cavity wall.

Specimen	GLG number														
no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
WFP 670	240	240	180	—	—	—	—	—	—	—	—	—	—	—	—
WFP 669[1]	240	240	172.5	150	127.5	127.5	92.5	85	65	57.5	—	—	—	—	—
WFP 671	240	240	165	140	120	95	80	—	—	—	—	—	—	—	—
ACM 104	240	230	170	140	130	90	90	70	70	60	55	—	—	—	—
ACM 103	240	240	180	160	110	80	80	70	60	60	60	65	55	40	40
ACM 106	240	240	150	130	110	90	90	60	60	60	55	—	—	—	—
WFP 606	240	240	180	150	120	90	90	—	—	—	—	—	—	—	—
N	7	7	7	6	6	6	6	4	4	4	3	1	1	1	1
$\bar{x}$	—	238.6	171.0	145.0	119.6	95.4	87.0	71.3	61.3	58.1	55.0	—	—	—	—
SD	—	3.8	11.0	10.5	8.4	16.5	5.6	10.3	2.5	2.4	5.0	—	—	—	—
SE	—	1.4	4.2	4.3	3.4	6.7	2.3	5.2	1.3	1.2	2.9	—	—	—	—

[1]Mean values of measurements in untreated and D/S (decalcified and haematoxylin-stained) sections

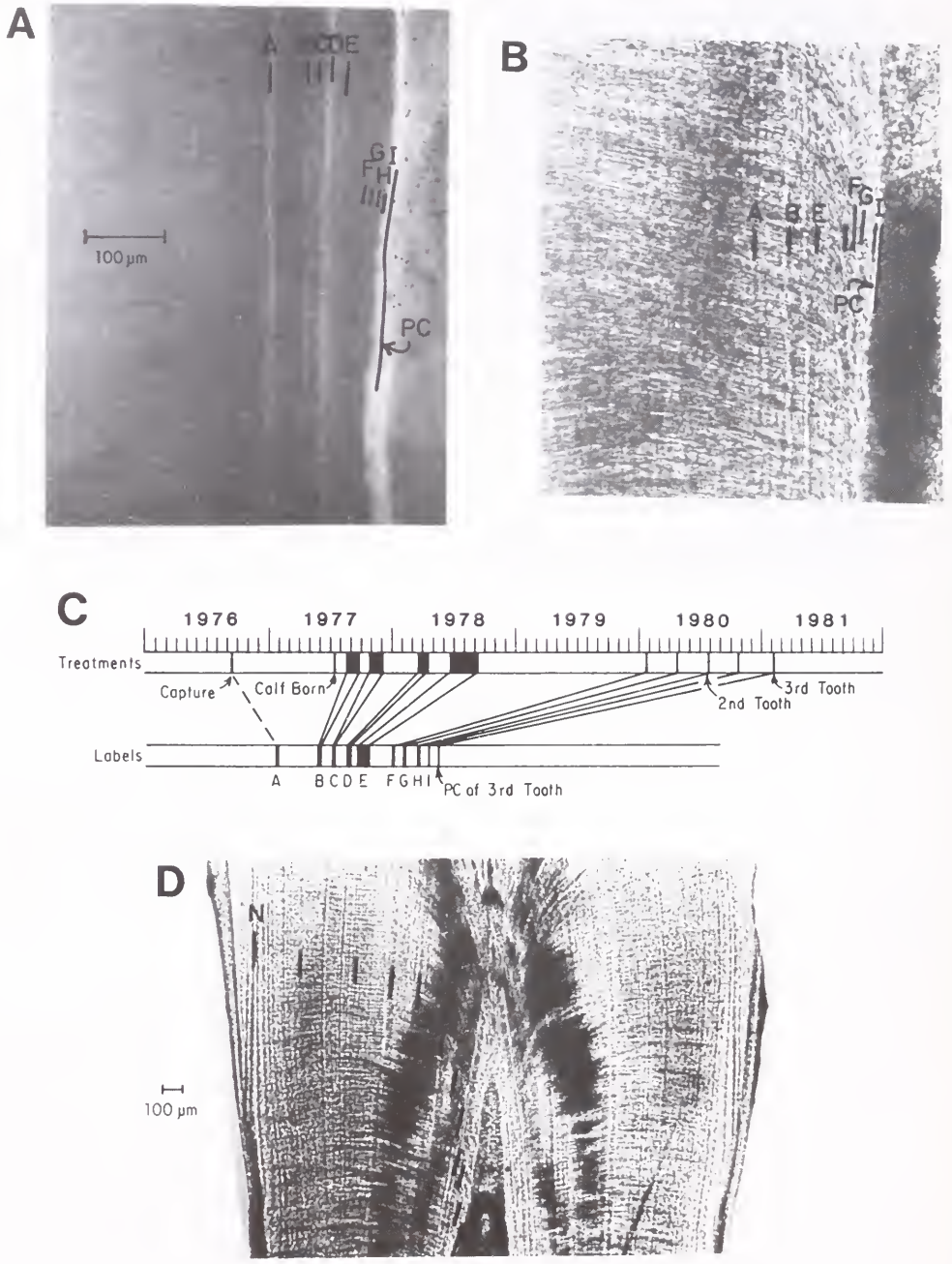

FIGURE 6.—Tooth of live dolphin ACM 104 extracted 2 February 1981. A. Untreated thin section in UV light showing location of TCL labels (150×). B. Same section as in 6A in plain light showing position of key labels bracketing last 4 yr of deposition. Light GLG boundary layers appear to have been deposited in or about August. C. Chart showing match of labels and treatments. D. Thin section showing 11 complete annual GLGs (separated by dark marks) as interpreted from labels (39×).

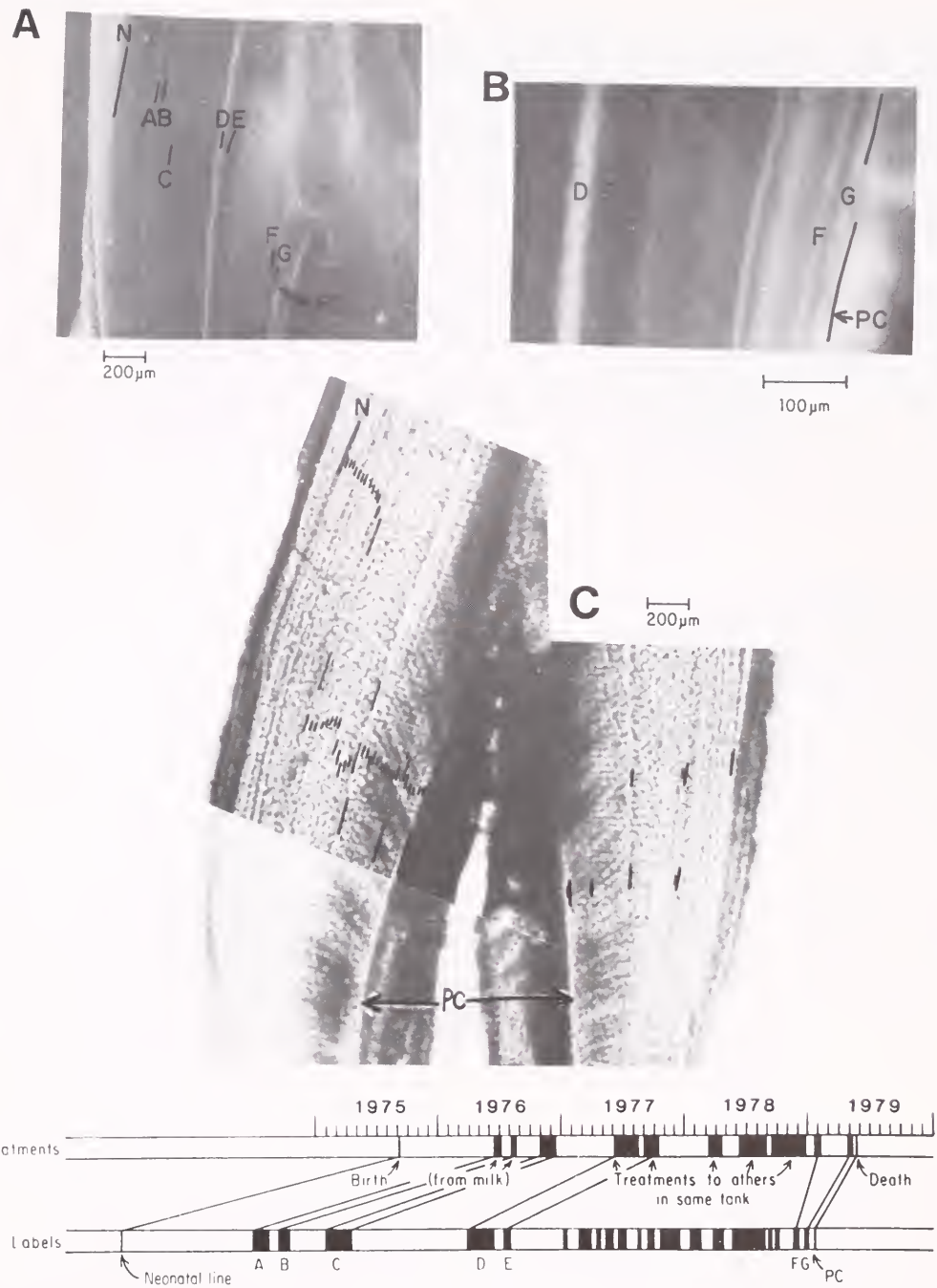

FIGURE 7.—Teeth from dolphin carcass WFP 670 (captive-born animal). A. Untreated thin section showing TCL labels in dentine. Labels A-B apparently represent TCL imparted to this animal through its mother's milk (UV, 39×). N = neonatal line; PC = pulp cavity margin. B. Portion as shown in 1A showing numerous labels from TCL-dosed smelt stolen from other dolphins occupying the same tank. Labels F and G represent direct treatments administered shortly before death (UV, 150×). C. Thin-sectioned tooth showing three entire and one partial GLGs (indicated by heavy dark marks) in the postnatal dentine as interpreted from TCL labels. LMLs are indicated by fine dark markers (plain transmitted light, 150×). D. Chart showing dates of direct and presumed incidental introduction of TCL and corresponding labels identified in the dentine by relative label position and thickness.

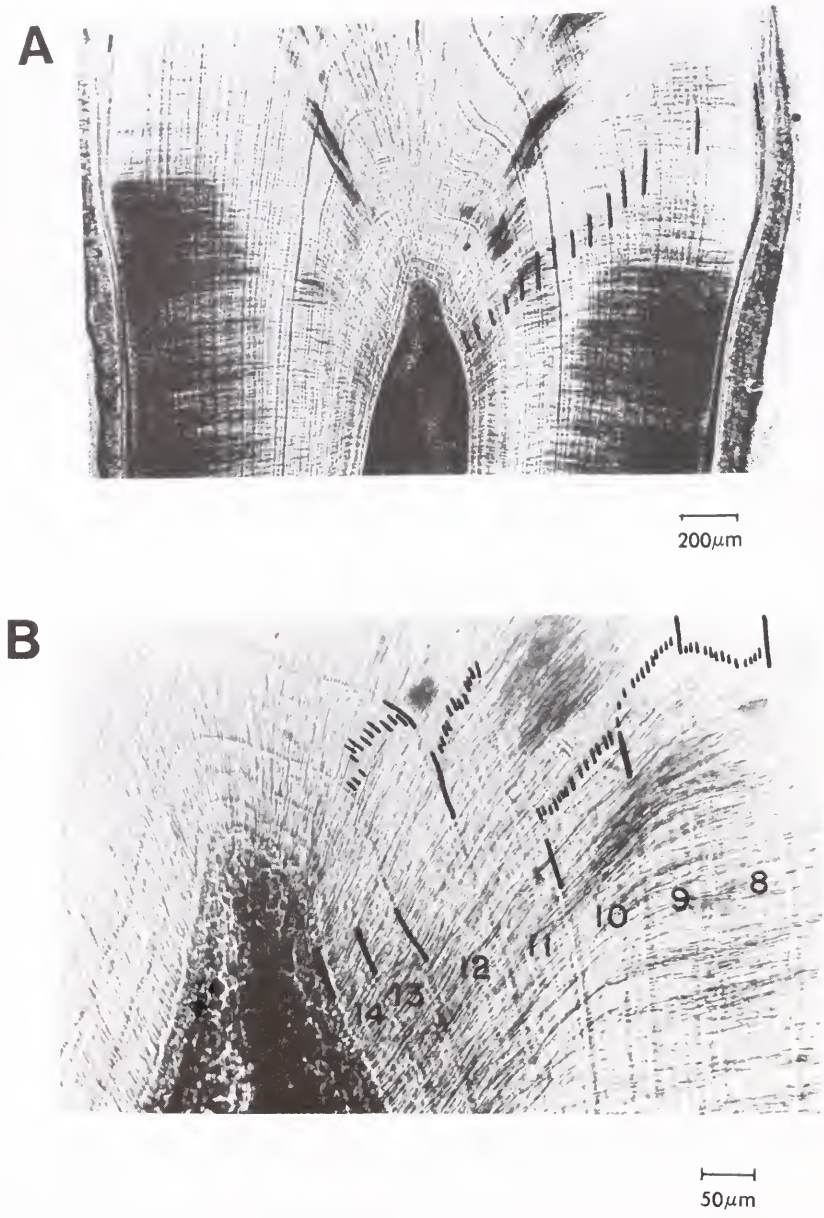

FIGURE 8.—Untreated tooth of live dolphin ACM 103 extracted 25 January 1980. A. About 14½GLGs indicated (heavy dark marks) (39×). B. GLGs 8-14½ showing thin, light boundary layers with dark margins. Thirteen LMLs indicated in each GLG 8-12 are particularly well developed (150×).

Comparisons of age-specific GLG thickness among the specimens suggest that the animals deposited a GLG of similar thickness in the same year of life. In the first and second year, 240 μm thick GLGs were deposited. In the third, fourth, fifth, sixth, and seventh years, thickness of GLGs averaged 171, 145, 119, 95, and 87 μm respectively. From the 8th to the 11th year, GLGs were between 71 and 55 μm thick. The data in Table 1 represent averages of at least three measurements per GLG per specimen.

Cemental labels.—Relatively few TCL labels were

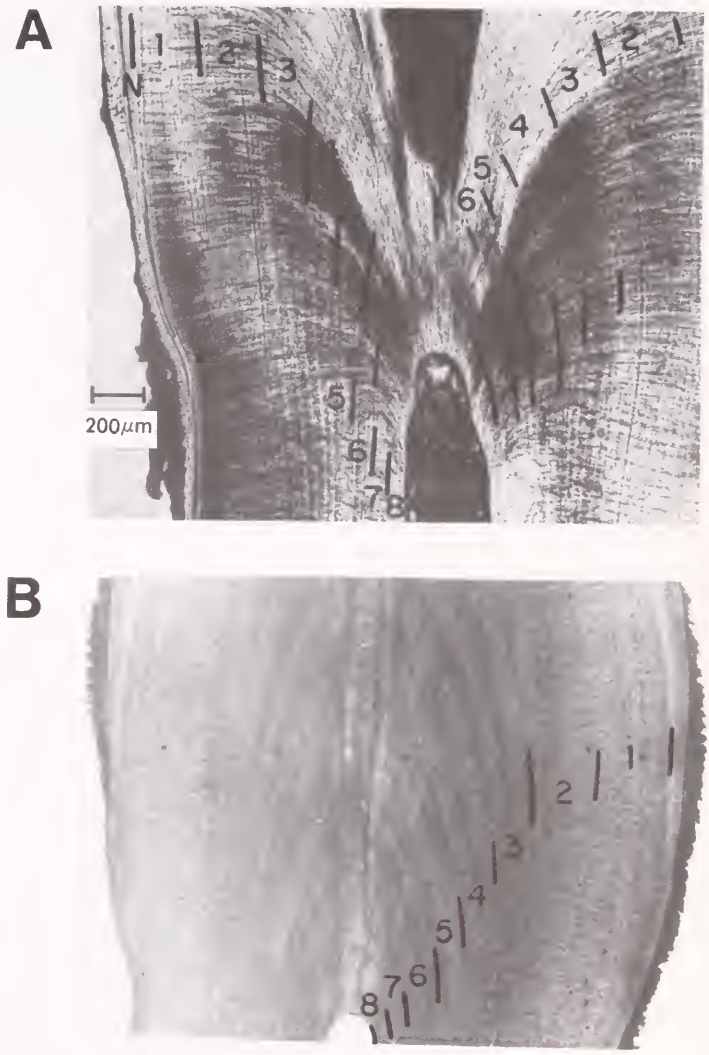

FIGURE 9.—Comparison of GLG patterns in teeth from dolphin carcass WFP 606 prepared by two methods: A. Untreated thin section (39×). B. Decalcified and stained thin section (39×).

found in the cementum compared with those in the dentine of the specimens. In the captive-born specimen, WFP 670, with about 25 dentinal labels, the cementum contained only three labels. In specimen WFP 669, only four cemental labels were observed (Fig. 10A) compared with 30 dentinal labels (Fig. 4A). The cementum in the other specimens had either zero or 1 label, despite the numerous dentinal labels observed for each.

Cemental GLG pattern.—In untreated thin sections, a cemental GLG consisted of a dark layer and a light layer (Fig. 10B). In D/S sections it was composed of a dark-stained layer, corresponding to the dark layer in untreated sections, and a lightly stained layer (Fig. 11). In both types of preparations, the dark layers contained larger concentrations of cementocytes than did the light layers.

Calibration of cemental GLGs.—Calibrations of cemental GLGs with those in the dentine were carried out using the assumption that cementum is a less sensitive recording structure than dentine (Klevezal' 1980) and that labels occurring in the cementum corresponded only to the brightest and thickest labels or label groups in the dentine. Thus, for example, the four labels detected in the cementum of specimen WFP 669 (Fig. 10A) were flagged with the same letters used to identify multiple label concentrations in the dentine (Fig. 4A).

In some cases, such as in WFP 669, plastic overlays were used to determine that a cemental GLG rep-

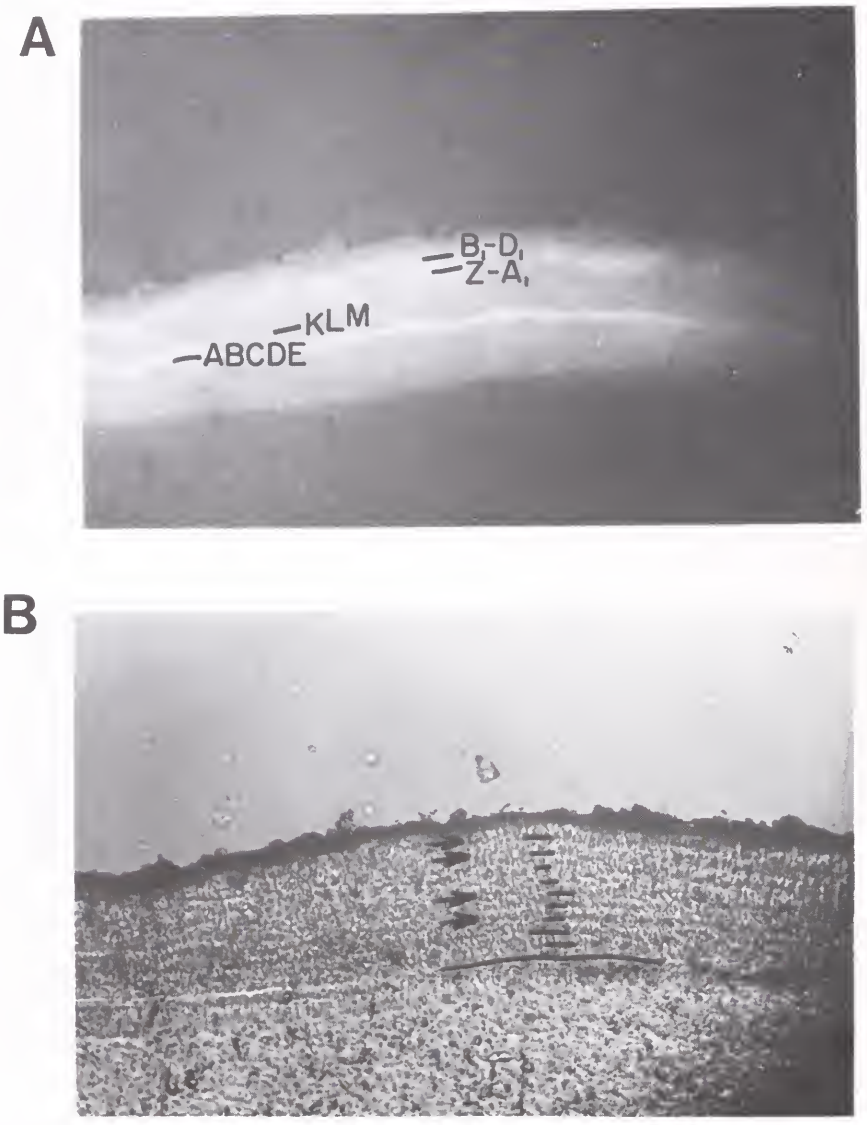

FIGURE 10.—Tooth cementum of dolphin carcass WFP 669. A. TCL labels interpreted as corresponding to lettered dentinal labels (150×). B. Positions of TCL labels (arrows) in layered cement. About 10 GLGs are indicated (150×).

resented the same amount of time as a dentinal GLG, i.e., 1 yr (e.g., Fig. 10B). In other cases, where labels were absent or where only one label occurred, calibration of cemental GLGs with dentinal GLGs was made indirectly by comparing GLG counts from both tissues. This method usually demonstrated a one-to-one relationship of GLGs in dentine and cementum, but in a few regions of the cementum of the captive-born specimen, WFP 670, there were twice as many GLGs as in the dentine (Fig. 11), indicating that a GLG may have been deposited twice a year in the cementum. In expanded regions of the cementum in another specimen (ACM 104; see Table 2), the cemental count was equal to the dentinal count; but in thinner regions the cemental count was only half that of the dentine, suggesting a cemental GLG being deposited every 2 yr in some cases.

Direct monitoring.—The results of examinations of thin sections of the series of three teeth from each of three live animals, taken at the beginning, at midpoint, and at the end of a 1-yr monitored period are

FIGURE 11.—Cementum of dolphin carcass WFP 670 tooth in decalcified and stained thin section. The number of dark layers is eight, about double the age in years of this captive-born specimen (150×, plain transmitted light).

presented in Table 2. Although distinct labels were not always successfully introduced, dentinal and cemental GLGs continued to be accumulated at a uniform rate of one per year. A comparison of accumulated dentine and labels in the first two extracted teeth of specimen ACM 106 (Fig. 12) showed two experimental treatments and one (unscheduled) clinical treatment accounted for in the second tooth (Fig. 2A-C). Specimen ACM 103, in which premonitor labels were indistinct, showed no experimental labels but clearly showed continued accumulation of dentine, the third extracted tooth having added about one GLG over the 1-yr period. No experimentally introduced labels were observed in the (less sensitive) cementum in any teeth of the three animals, but cemental deposition of about one complete GLG occurred in each animal for the period.

Seasons of birth.—By determining the dates of key dentinal labels introduced at or near the thin, light component layers of GLGs and by noting the approximate time of formulation of component layers in the teeth extracted during the monitor period, it was found that GLG-boundary and mid-GLG layers were formed at about 6 mo intervals. In five specimens, GLG-boundary layers were deposited in or about August and the mid-GLG layers were deposited in or about March. In the two other specimens the timing was reversed, i.e., GLG-boundary layers formed in March, mid-GLG layers in or near August. Proceeding on the assumption that the timing of layer formation (determined from the labeled or monitored

TABLE 2.—Results of examinations of teeth extracted from three live Hawaiian spinner dolphins, *Stenella longirostris*, over a 1-yr period monitoring accumulation of layers and labels. GLGs = growth layer groups.

Specimen no. and tooth	Date of tooth extraction	Date label introduced	Dentine		Cementum	
			Additional labels	No. GLGs	Additional labels	No. GLGs
ACM 103						
First	25 Jan. 1980	25 Jan. 1980 30 Apr. 1980	—	14 5	—	14.5
Second	30 July 1980	30 July 1980 30 Nov. 1980	indistinct	15.0	None	15.0
Third	2 Feb. 1981	—	indistinct	15.5	None	15.5
ACM 106						
First	19 Mar. 1980	19 Mar. 1980 11-28 Apr 1980[1] 5 June 1980	—	10.3	—	10
Second	30 July 1980	30 July 1980 30 Nov. 1980	3	10.7	None	10+
Third	2 Feb. 1981	—	indistinct	11 2	None	11
ACM 104						
First	25 Jan. 1980	25 Jan. 1980 30 Apr. 1980	—	([2])	—	([2])
Second	30 July 1980	30 July 1980 30 Nov. 1980	2	10.7	None	[3]5/10
Third	2 Feb. 1981	—	4	11.3	None	[3]6/11

[1]Unscheduled medical treatment 18 d in duration.
[2]Not examined because of poor preparation of section.
[3]Cementum showed a number of GLGs equal to that of the dentine as well as half that of the dentine.

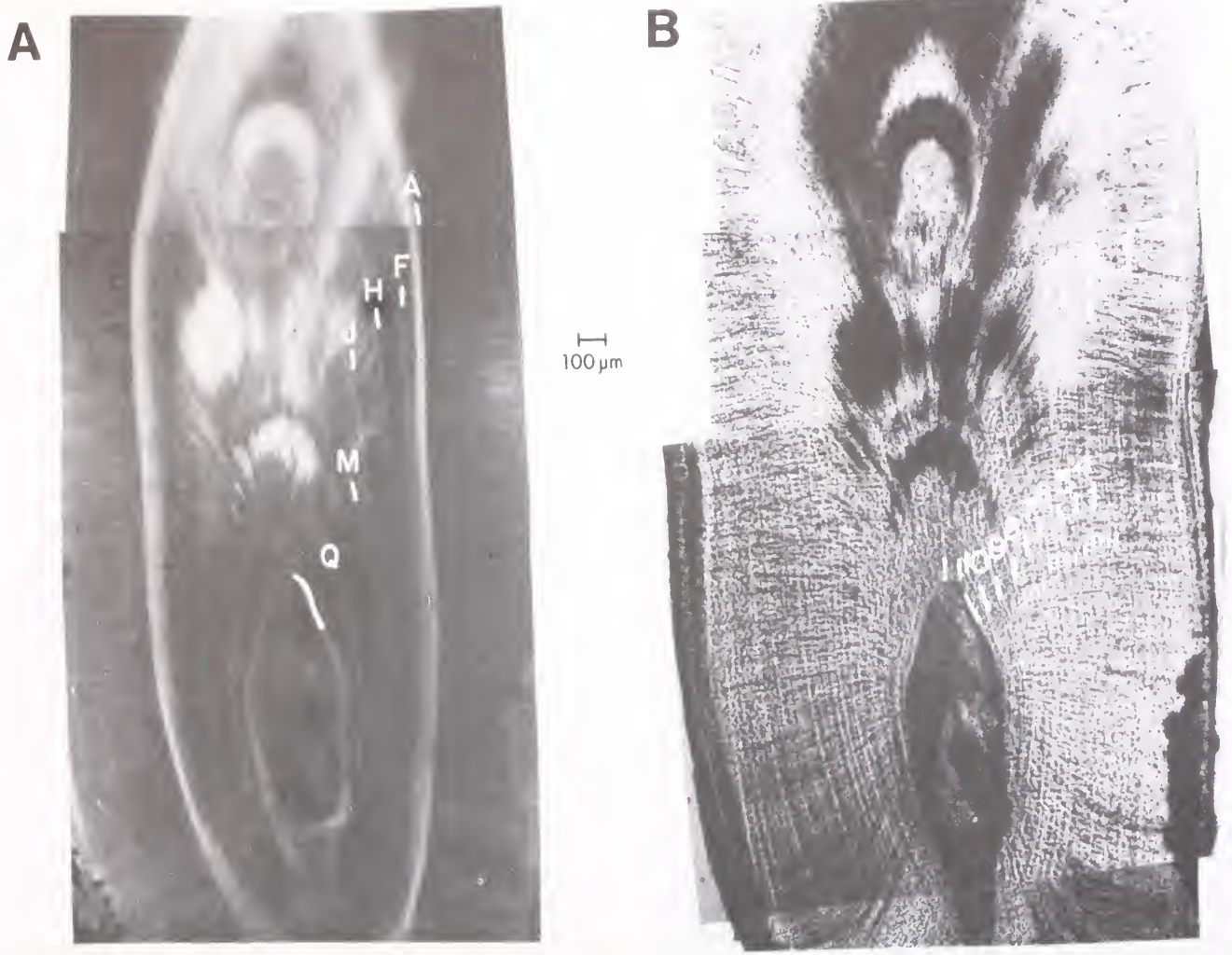

FIGURE 12.—Tooth of live dolphin ACM 106 extracted 30 July 1980. A. Untreated thin section in UV light showing key labels A-M each introduced 1 yr apart, M and Q 2 yr apart, and almost 1 yr of dentine accumulation represented between Q and the pulp-cavity margin (39×). B. Thin section as in 12A (plain light) showing GLGs as interpreted from labels. Positions of labels A and F are indicated. Horizontal white lines indicate positions and angle of transect. GLG thickness measurements were taken for GLGs 1-3.

regions of the dentine) was uniform throughout all of the dentine for a given specimen, GLG-boundary and mid-GLG layers were counted in reverse order of deposition up to the first boundary layer, the neonatal line, to estimate month and year of birth.

Table 3 summarizes the month- and year-of-birth estimates made from boundary-layer counts in six specimens and birth dates taken from park records of two captive-born specimens, WFP 670 and the calf of ACM 104. Six were born in late summer/early autumn and two in March.

TABLE 3.—Estimated birthdates of eight captive Hawaiian spinner dolphins, *Stenella longirostris*..

Specimen no.	Month and year of birth
ACM 103	August 1964
ACM 106	August 1969
WFP 669	August 1969
ACM 104	September 1969
WFP 606	March 1972
WFP 671	March 1973
WFP 670[1]	8 September 1975
Calf of ACM 104[2]	21 July 1977

[1]Born in captivity.
[2]Born in captivity, survived 3 d

DISCUSSION

Age-Specific GLG Thickness

Dentinal GLG thickness appears to be age-specific for the Hawaiian spinner dolphin teeth examined. There was little variability from tooth to tooth or from animal to animal in the sequence of GLG thickness through the 11th GLG, despite deposition of a specific GLG in some specimens while still in the wild and in other specimens during their captive lives. This suggests that, to some extent at least, the amount of dentine deposited by animals at a given age may be predetermined and that animals of a given stock, species, or higher common phylogenetic affinity may follow the same or similar pattern of age-specific GLG deposition unaffected by environment.

Used in conjunction with the GLG component-layer pattern, the regularity in thickness of age-specific GLGs may be useful as an aid in locating GLG boundaries and counting GLGs in teeth of wild Hawaiian spinner dolphins and dolphins of related species in which GLG thickness and component-layer patterns are found to be similar. When measurements are taken at standard positions in the teeth of such dolphins, one may make fairly rapid age estimates without having to examine each GLG in detail (see Myrick et al. 1983).

Lunar Monthly Layers (LMLs)

Laws (1962) was the first to suggest that the system of fine layers within dentinal GLGs of pinniped teeth corresponded to lunar monthly cycles. Putative LMLs have been reported in dentine of dugongs (Kasuya and Nishiwaki 1978; Marsh 1980), in dentine of beaked whales ("short cycles," Kasuya 1977; "accessory layers," Perrin and Myrick 1980:3, 5), in fossil dolphin teeth (Myrick 1979), and in the mandibular bone (Myrick 1980b) and dentine of modern dolphins (Myrick 1980b; Hohn 1980a, b). Hui (1978) reported finding no relationship between the fine layers that he counted in a tooth from a known-age bottlenose dolphin and its age in lunar months; but with no prior knowledge of its age, Myrick (1980b) made dentinal LML counts in the same specimen that closely agreed with its known age.

The present study has furnished verification that LMLs are deposited with lunar-monthly regularity in the animals studied. In the 3.7-yr-old captive-born spinner dolphin (WFP 670), 13 LMLs were counted in each of the three complete annual dentinal GLGs and 9 were counted in the partial fourth GLG. Where LMLs were visible between TCL labels in the dentine in this and other specimens, they were found to correspond consistently in number to the time in months represented between labeling dates.

Where LMLs could be seen clearly, no departure from the 13 LML/GLG pattern was detected in the teeth used in the present study. Variability has been reported in studies of other marine mammals. Marsh (1980:197) found only "about 12 [LMLs] per GLG" in the dentine of the deciduous incisor of a dugong. Ten to 15 LMLs/GLG were observed in dugong tusks by Kasuya and Nishiwaki (1978). Kasuya (1977) found between 11 and 13.4 LMLs ("short cycles")/GLG in teeth of Baird's beaked whales, *Berardius bairdii*. Hohn (1980b) counted 10-13 LMLs/dentinal GLG in Atlantic bottlenose dolphin teeth. Presumably, LML variability will be found to occur also in Hawaiian spinner dolphins when larger samples are examined.

Relationship of Cemental GLGs to Dentinal GLGs

None of the teeth of the studied specimens had reached the stage of pulp-cavity occlusion or dentinal irregularity that necessitated age estimation solely from cemental GLG counts (Kasuya 1976; Myrick et al. 1983). Although the pulp cavities were small in some specimens and some later-administered TCL

failed to produce distinct labels, none showed evidence of cessation of dentine deposition.

All cemental GLG counts corresponded in number to dentinal annual GLG counts except in the case of specimen WFP 670, where some regions of the cementum showed double the number, and in specimen ACM 104, where in some places the cemental count was half that of the dentine. The finding that in some cases cemental GLGs may form at half or twice the rate of dentinal GLG deposition points up the problem of using cemental GLGs to estimate ages without reference to the dentine (Myrick et al. 1983).

Evidence for an Internal Clock

In the dentine of the animals studied, a thin GLG boundary layer, beginning with the neonatal line, was formed in the month of birth and on anniversaries of the month of birth. Mid-GLG layers were formed about 6 mo after formation of boundary layers. Where LMLs could be calibrated, one was found to form about every (lunar) month with high uniformity in relative spacing. Such a cycle of deposition is indicative of an internal clock, or clocks. The pattern commences at birth and apparently is reset with solar and/or lunar regularity without perceptible alteration by fluctuation in the dolphins' natural or captive environment or in calendric season of birth. That it may not be a totally free-running system, i.e., not without external cues, is suggested by the precisely synchorized deposition of the fine and coarse patterns of the dentine repeated over many years.

Age at Sexual Maturity

Perrin et al. (1977) indicated that sexual maturity may be reached in females of *Stenella longirostris* at an average 5.5 yr (range of 5-9 yr) and the average period of gestation may be about 11 mo. From the study of dentinal GLGs and TCL labels of specimen ACM 104, it was possible to determine that this animal was about 8-yr-old when she gave birth to her calf. Assuming an 11-mo gestation, we estimate that she would have been 7-yr-old when she conceived. It is not known whether the pregnancy resulted from fertilization at her first or subsequent ovulations. ACM 104 remains alive. This precludes examination of her ovaries for ovulation scars.

Reproductive Seasonality

Based on the birth records of specimen WFP 670 and the calf of ACM 104 and the deductions made from dentinal layers, six animals were born in late summer/early fall, and two were born in March. Since all animals in the study represented the same population off Kona, Hawaii, the early-spring and early-fall birth patterns might indicate a corresponding two-cycle pattern of reproductive peaks for the wild population generally. Such a seasonal pattern has been suggested by Norris and Dohl (1980, fig. 16), but Wells (in press), who has studied the population in considerable detail, concluded that the breeding season occurs from spring to fall, with most births in the fall. Our sample was too small to verify Wells' findings.

Tetracycline Exposure to the Calf Through the Milk

The first two labels found in the dentine of specimen WFP 670, the captive-born animal, were interpreted as having been introduced through milk received by the calf while the mother was being treated with TCL. This recommends a possible practical application in indirectly treating newborns in ill health. Excessive handling of such animals frequently results in a worsening of their condition, making the treatment more dangerous than the malady. (Nursing calves not on solid food cannot be treated with TCL-dosed fish and must be force-fed or injected with drugs.) Separating the young calf from its mother may produce additional complications.[9] If treatments for the calf could be administered through the milk by treating the mother with TCL-dosed food, it seems likely that most of the problem could be minimized. The question invites further study.

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REPRODUCTION OF THE BANDED DRUM, *LARIMUS FASCIATUS*, IN NORTH CAROLINA[1]

STEVE W. ROSS[2]

ABSTRACT

The reproductive biology of *Larimus fasciatus* was examined in coastal North Carolina from September 1975 through September 1976. Spawning occurred in nearshore waters from April through September with a peak in August. Maturity in fameles was reached by the first year between 120 and 130 mm SL. Generally the larger, older fish matured earlier and also continued spawning later in the season than the younger ones.

Fecundity ranged from 12,750 to 320,819 ova with first spawners predicted to have between 31,088 and 65,038 eggs. Fecundity was best predicted by ovary weights during August. Sex ratios generally favored more females. As fish grew the sex ratio changed from predominately males to predominately females.

The banded drum, *Larimus fasciatus* Holbrook, occurs from Massachusetts to southeastern Florida and along the northern Gulf of Mexico from the Florida west coast to Mexico. Unlike other drums it appears to be largely restricted to nearshore coastal waters at all sizes and is rarely collected in estuaries or from the outer continental shelf (Gunter 1938; Dahlberg 1972; Chao 1978; Powles 1980). *Larimus fasciatus* is a small sciaenid reported by Holbrook (1860) to reach 305 mm TL (total length), but it seldom grows larger than 220 mm (Chao 1978). Its small size, low abundance, and lack of status as a food or game fish afford this species little commercial or recreational value, although it was reported as a component of the North Carolina (Wolff 1972) and Gulf of Mexico (Gutherz et al. 1975) industrial fisheries.

Published data on life history aspects of *L. fasciatus* are largely lacking. Hildebrand and Cable (1934) reported limited information on spawning, growth, and juvenile descriptions of North Carolina specimens, and Powles (1980) presented data on larval description, spawning seasons, and areas in the South Atlantic Bight. Feeding habits were briefly examined by Welsh and Breder (1923) and Chao and Musick (1977). Standard and Chittenden (in press) have studied banded drum life history off of Texas.

This study describes the following aspects of *L. fasciatus* life history in North Carolina: 1) spawning seasonality, 2) age and size at maturity, 3) fecundity, and 4) sex ratios.

METHODS

Most banded drum were collected in the ocean near the mouth of the Cape Fear River, N.C., about 4-6 km off Oak Island in depths of 4-14 m (Fig. 1). Bottom topography was uniform with sediments of fine sand and mud. Hydrographic conditions were heavily influenced by discharge from the Cape Fear River (Ross 1978).

This area was sampled weekly from September 1975 through September 1976, except only monthly samples were made during January, June, July, and August. Each sample consisted of repetitive (4-12) 30-min trawls with a 12.4 m semiballoon otter trawl of 3.85 cm stretched mesh during daylight hours.

Additional specimens were collected from September 1975 through September 1976 during twice monthly, daylight sampling between Beaufort Inlet and Cape Lookout, N.C. (Fig. 1), except that there was no sampling in December 1975 and only monthly sampling in January and February 1976. Repetitive trawls were made in this area in a depth range of 9-12 m over a flat, sand bottom using the aforementioned gear and tow times. Specimens were also collected near Cape Hatteras (9-17 m depth) in November and December 1975 and April 1976 by the North Carolina Division of Marine Fisheries (Fig. 1).

Larimus fasciatus were preserved in the field in 10% Formalin[3] and later stored in 40% isopropanol. Total length (TL) and standard length (SL) were measured to the nearest mm. Body weights (BW) were determined to the nearest 0.1 g, and gonads $\geq$0.01 g were

[1]Adapted from part of a thesis submitted to the Zoology Department, University of North Carolina, in partial fulfillment of the requirements for the MA degree.

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

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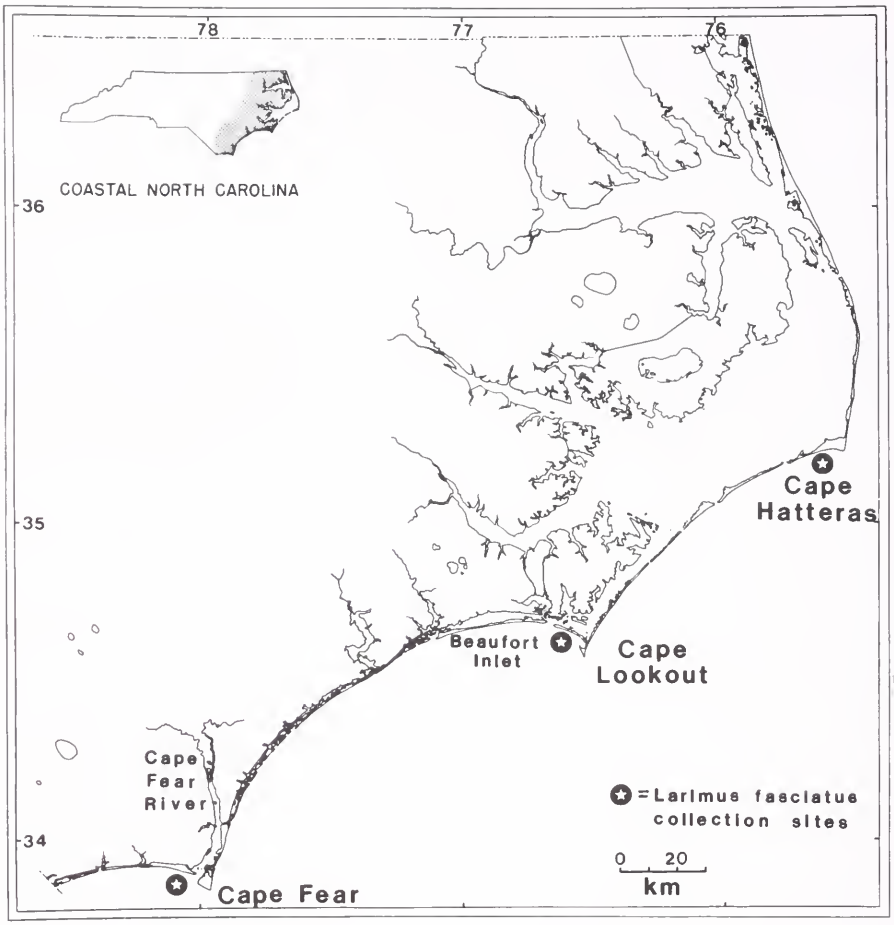

FIGURE 1.—Collection sites for *Larimus fasciatus* in North Carolina.

blotted dry and weighed (gonad weight (GW)) to the nearest 0.01 g. Gonad indices (GI) were calculated as follows:

$$GI = GW \text{ (both)} \times 100/(BW - GW)$$

and were used to determine spawning seasons and maturity.

Fecundity was determined for both maturing gonads by relating the number of eggs in a subsample to the whole gonad. Each subsample (weighed to the nearest 0.001 g), removed from the middle and both ends of each alcohol-preserved gonad, represented roughly 5% of the total gonad weight. All eggs (excluding those <0.01 mm in diameter and atretic eggs) in the subsample were counted, and the modal ovum diameter was measured to the nearest 0.05 mm. Total fecundity used in the analysis equaled the number of eggs in both gonads combined.

RESULTS

Spawning

Larimus fasciatus spawned from April through September with peak activity in August as indicated by female gonad indices ($n = 126$, Fig. 2). Male gonad indices ($n = 53$) somewhat mirrored the female pattern, but the spawning cycle was not clearly illustrated because the testes composed a small percentage of the body weight at any maturity stage in all months (Fig. 2). Some running ripe males were observed in the field from June through August. Since the mean gonad index was still high in September (Fig. 2), spawning may have continued after September, although I have no collections to substantiate this.

The large size range of juveniles and the collection of young-of-the-year ≤40 mm SL in all months ex-

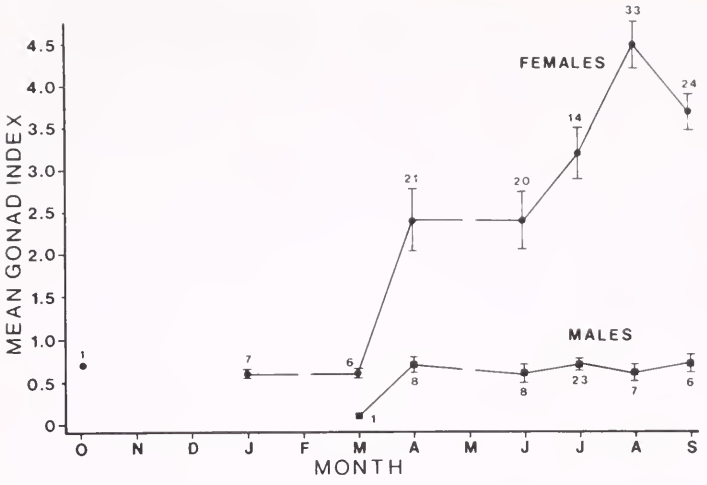

FIGURE 2.—Monthly mean gonad index of male and female banded drum from October 1975 to September 1976 in North Carolina, including sample size and ±1 standard error of the mean.

cept December 1975 and January, April, May, and June 1976 (Fig. 3) support an extended late spring through early fall spawning season. Major young-of-the-year (1976 year class) recruitment, evidently from Spring spawning, first appeared in July 1976 and continued through September 1976. Young-of-the-year from the 1975 year class were evident from September 1975 through November 1975 and appeared again in February 1976 (Fig. 3). This young-of-the-year recruitment over a long period with a lack of bimodal length frequencies indicated sustained spawning effort. Other collections in and near the lower Cape Fear River of *Larimus fasciatus* <40 mm SL in January, February, April, June, July, September, November, and December also indicated extended spawning (K. A. MacPherson[4]).

The majority of the reproductively active adults were collected near the Cape Lookout area (Fig. 1), especially during August and September where bottom water temperature averaged 27° (August) to 20°C (September). A high percentage (48.9-100%) of the total number of females collected in the Cape Lookout area exhibited maturing or ripe gonads while corresponding percentages from Cape Fear

[4]K. A. MacPherson, biologist, Carolina Power and Light Company, Brunswick Biological Laboratory, P.O. Box 10429, Southport, N.C. 28461, pers. commun. 1977.

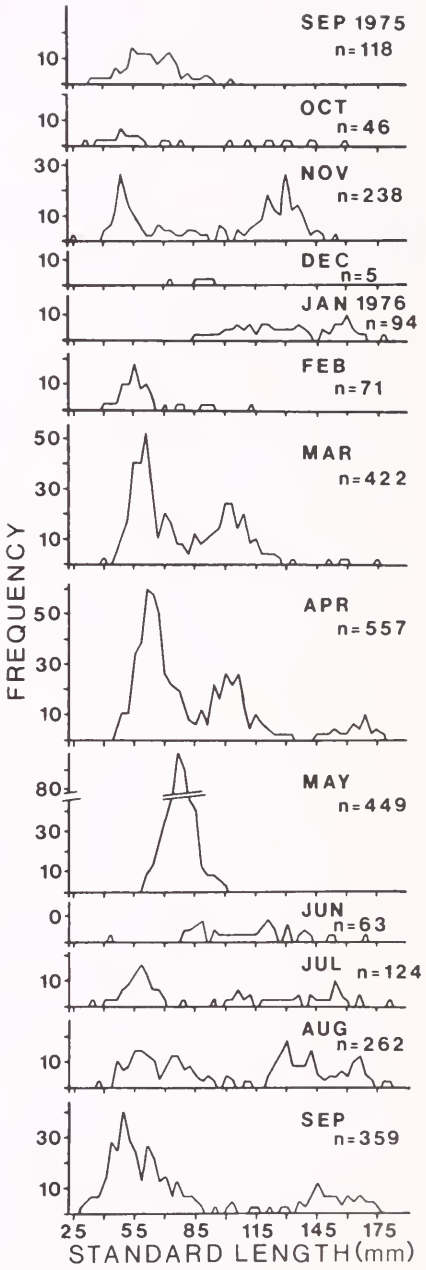

FIGURE 3.—Length frequencies of *Larimus fasciatus* collected in North Carolina from September 1975 through September 1976.

were low (0-8.1%) (Table 1). Although sampling effort in the Cape Fear area was half of that near Cape Lookout from June through August, more female banded drum were collected near Cape Fear; however, the percent of females with large gonads was much greater in the Cape Lookout area (Table 1). Cape Fear area sampling effort doubled over that near Cape Lookout in September and yielded many more female banded drum, but only 0.7% were reproductively active compared with 48.9% in the Cape Lookout area (Table 1). Irregular sampling from the Cape Hatteras area (Fig. 1) yielded maturing or ripe *L. fasciatus* only during April when 82.4% of the females collected had gonad indices between 1.7 and 6.1 (Table 1). Bottom water temperature in this area was 17°C.

Ovum diameter is often an indication of sexual maturity (Higham and Nicholson 1964), and the relationship between egg size (OD) and gonad index (GI) for banded drum ($n = 90$) was

$$OD = 0.34 + 0.11 \text{ (ln GI)}, r = 0.77$$

(Fig. 4). This relationship is an objective, quantitative way to determine degree of maturity (Yuen 1955; Schaefer and Orange 1956) and was used to differentiate maturing from immature female banded drum. The point on the graph (Fig. 4) where gonad index began to increase more rapidly than egg size was used as the boundary between immature and maturing gonads and occurred around a gonad index of 1.0 and an ovum diameter of 0.35 mm. Mean ova diameters peaked from July through September at 0.48 mm (Table 2), which also coincided with the highest gonad indices.

Maturity

Female banded drum reached sexual maturity between 120 and 130 mm SL ($n = 112$). All fish ≤120 mm SL were immature (GI ≤1.0) and 97% of those ≥130 mm were mature, with 60% between 120 and 130 mm reaching maturity (Table 3). During the spawning season, females between 120 and 130 mm indicated increased gonad activity. Females smaller than 120 mm displayed no seasonal gonad activity, while only three fish ≥130 mm were not maturing during the spawning season (Fig. 5). Only the larger adults ≥150 mm matured and spawned early (April), and generally a higher proportion of the older

TABLE 1.—Percent of female *Larimus fasciatus* with gonad indices ≥1.0 and sample size (*N*) from each collection area during the spawning months of 1976.

Area	April	May	June	July	Aug	Sept.	Total
Cape Fear	0 (274)	0 (219)	0 (9)	2.8 (36)	8.1 (111)	0.7 (153)	1.4 (802)
Cape Lookout	0 (1)	—	53.8 (26)	100 (12)	75.0 (28)	48.9 (45)	61.6 (112)
Cape Hatteras	82.4 (17)	—	—	—	—	—	82.4 (17)
Total	4 8 (292)	0 (219)	40.0 (35)	27.1 (48)	21.6 (139)	11 6 (198)	10.1 (931)

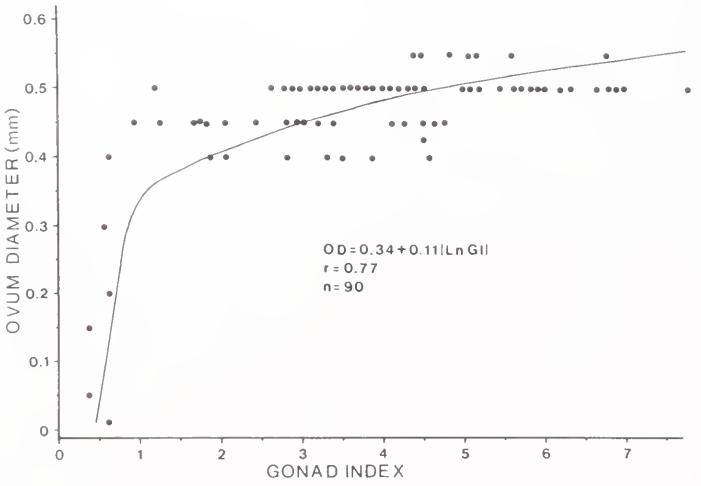

FIGURE 4.—Relationship between famale gonad index and ova diameters of North Carolina *Larimus fasciatus*.

TABLE 2.—Mean monthly ova diameters of *Larimus fasciatus* from March through September 1976.

Month	Mean ova diameter (mm)	Sample size
March	0.01	1
April	0.41	7
June	0.46	16
July	0.48	13
August	0.48	32
September	0.48	21

females continued spawning later (September) (Fig. 5). Most of the smallest reproductively active females (between 120 and 130 mm SL) matured from June to August (Fig. 5).

Using age-length relationships of Ross (1978), *Larimus fasciatus* reached maturity shortly after turning 1-yr-old. They continued spawning throughout life until age 3, which was the maximum age encountered.

Fecundity

Number of ova increased with increasing fish size, ranging from 12,750 ova in a 118 mm SL female to 320,819 in a 179 mm female. The relationship between fecundity (F) and SL for 86 females was linear and expressed by the equation:

$$F = -376{,}312 + 3{,}395\ (SL),\ r = 0.76$$

(Fig. 6). Length at first spawning is between 120 and 130 mm SL and predicted fecundity in this size range is 31,088-65,038 ova. Body weight (BW) minus the gonad weight (GW) was regressed onto fecundity yielding the equation:

$$F = -52{,}741 + 1{,}887\ (BW),\ r = 0.76,\ n = 85.$$

Gonad weight varies seasonally and is closely related to fecundity; therefore, eliminating it from body weight reduced the possibility of autocorrelation. Even without the gonad weight, body weight varies seasonally and to some extent daily as a function of diet; therefore, body weight is not the best predictor of fecundity. The fecundity to ovary weight (OW)

TABLE 3.—Number and percentage of mature and immature female banded drum by 10 mm size categories off North Carolina, April-September 1976. Maturity was judged by gonad index (GI) value.

Standard length (mm)	Immature GI ≤ 1.0	Mature GI > 1.0	Percent mature
<90	1	0	0.0
90-99	0	0	0.0
100-109	4	0	0.0
110-119	4	0	0.0
120-129	6	9	60.0
130-139	1	12	92.3
140-149	1	22	95.7
150-159	0	17	100.0
160-169	1	26	96.3
170-179	0	7	100.0
180-189	0	1	100.0
Total	18	94	

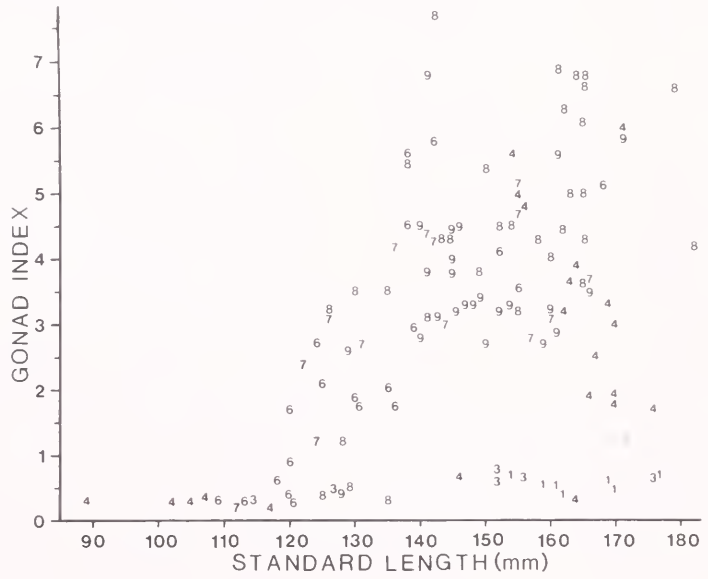

FIGURE 5.—Relationship between famale gonad index and standard length by month for banded drum during January (1)-September (9) 1976 ($n = 124$).

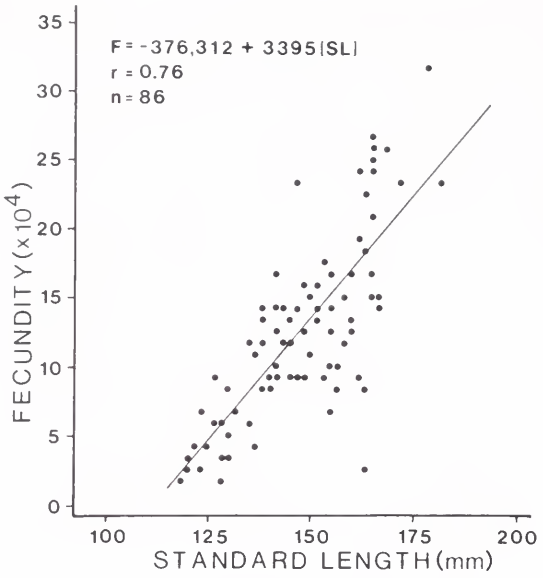

FIGURE 6.—Relationship of fecundity to standard length for banded drum collected in North Carolina from April through September 1976.

relationship was expressed by

$$F = 15{,}490 + 28{,}024\ (OW), r = 0.94, n = 85$$

and had a much higher correlation coefficient than either the length or body weight regressions. To minimize monthly variation (Morse 1980) the most accurate prediction of fecundity was derived from ovary weights only from the peak spawning month, August, expressed by

$$F = 18{,}532 + 28{,}181\ (OW), r = 0.97, n = 31$$

(Fig. 7).

Sex Ratios

Sex was determined for 2,729 banded drum and the overall ratio of males to females varied significantly from 1:1 in favor of females (Table 4). This nonhomogeneity of total sex ratios could not be accounted for by any consistent pattern of seasonal ratio differences. The two largest size groups exhibited sex ratios significantly in favor of females. The disparity between sexes in the size range 100-139 mm SL was accounted for during winter, spring, and summer, while that in the fish ≥140 mm SL was accounted for during fall and winter (Table 4). Contingency table analysis indicated strong dependency between sex and size group ($\chi^2 = 17.84$, df $= 3, P \leq 0.001$), even though differences in the smallest two size groups were nonsignificant (Table 4). As fish grew, the population shifted from more males to more females. There were more total females than males in all seasons except summer; however, the differences were only significant in the fall. The fall divergence from a 1:1 ratio was explained by differences in the 60-99 mm and ≥140 mm SL size groups (Table 4).

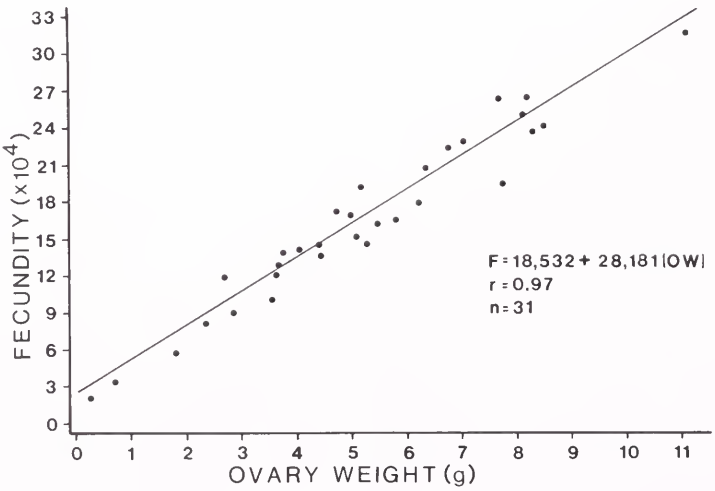

FIGURE 7.—Relationship of fecundity to overy weight during August 1976 for North Carolina banded drum.

TABLE 4.—*Larimus fasciatus* male/female sex ratios by season and size group from North Carolina (September 1975-September 1976) with chi-square values from testing a 1:1 ratio.

Size group (mm SL)	Season				Total	df	X^2
	Fall (Sept.-Nov.)	Winter (Dec.-Feb.)	Spring (Mar.-May)	Summer (June-Aug.)			
≤59	151/144	22/27	104/100	65/34	342/305	3	5.23
60-99	77/103	15/12	492/479	65/64	649/658	3	2.14
100-139	71/67	19/34	87/123	48/74	225/298	3	8.04*
≥140	21/64	14/23	19/22	49/50	103/149	3	8.47*
Total	320/268	70/96	702/724	227/222	1,319/1,410		
df	3	3	3	3			
x^2	9.28*	3.64	7.28	7.63	10.38*		

*$P < 0.05$.

DISCUSSION

The prolonged April-September spawning season of *L. fasciatus* in this study is supported by the few published references to its reproduction. From analysis of larval occurrence in North Carolina, Hildebrand and Cable (1934) proposed a May through October spawning season. Powles (1980) reported a May to October spawning in the South Atlantic Bight also based on larval collections. Gunter (1938) suggested April spawning for banded drum in Louisiana. Standard and Chittenden (in press) found two spawning peaks for *L. fasciatus* off Texas, a minor one in the spring (April-June) and the major one in the fall (September-November). They did not find significant evidence of spawning in July or August.

My data suggested a prolonged spawning effort in North Carolina beginning as early as April, peaking in August, and possibly continuing after September. This major departure from Standard and Chittenden's (in press) biomodel spawning was supported by 1) a steady increase in gonad indices with a single August peak, 2) a single peak mode of ova diameters of 0.48 mm from July through September, 3) continuous recruitment of young-of-the-year through the summer and fall months, and 4) the collection of larvae in all months except March (Powles 1980; K. A. MacPherson footnote 4). Although it is fairly certain that spawning begins in April, at least for larger fish, I did not determine if spawning continued into October because samples of adults were lacking. Although the September gonad index declined, young-of-the-year recruitment in North Carolina in February and larval collections in November, December, January, and February (K. A. MacPherson footnote 4) indicated that spawning may last at least through October. Protracted spawning is also characteristic of many other Sciaenidae (Welsh and Breder 1923; Thomas 1971; Merriner 1976; Warlen 1980).

Maturation at an early age is typical in sciaenids (Schaefer 1965; Meriner 1976; Shlossman and Chittenden 1981) and in short-lived fishes in general which tend toward *r* strategy life histories (Adams 1980). Since *L. fasciatus* is a short-lived sciaenid, rarely completing a fourth year, the small size (120 mm SL) at first maturity, attained shortly after reaching 1 yr of age, is not surprising (Ross 1978). *Larimus fasciatus* off of Texas apparently live only 2 yr and consequently mature earlier (80 mm TL) than North Carolina individuals (Standard and Chittenden in press). In addition to short life and early maturation, *r* strategists' traits are rapid growth, high fecundity (even at early ages), small maximum size, high mortality, and low maximum age (Adams 1980), all of which are related to emphasizing reproductive productivity. Banded drum have all of these characteristics as indicated in this study and by Ross (1978) and Standard and Chittenden (in press).

As banded drum became older their growth rate slows (Ross 1978; Standard and Chittenden in press), as is typical of most fishes, and they can devote relatively more energy toward reproductive activity than at earlier ages. Only the largest females (≥150 mm) appeared to spawn as early as April and continue spawning into September. Although the phenomenon of older fish having a longer spawning season has not been reported in United States east or gulf coasts sciaenids, it does occur in other fishes (Quast 1968; Grimes and Huntsman 1980).

Larimus fasciatus spawns as far north as Cape Hatteras. Although larvae have been collected off Chesapeake Bay (Berrien et al. 1978), there are no records of reproductively active adults north of Cape Hatteras and this species is rare north of Chesapeake Bay (Hildebrand and Schroeder 1928; Johnson 1978); therefore, Cape Hatteras is probably the northern limit of banded drum reproduction. *Larimus fasciatus* in spawning condition were most often collected in the nearshore waters between

Beaufort Inlet and Cape Lookout, larval distributions have not clarified the preferred spawning depth range, since larvae have been collected over a wide range of the continental shelf (Berrien et al. 1978; Powles 1980); there is, however, some tendency toward increased abundance over the inner shelf (Powles 1980). Miller et al. (in press) suggested that onshore transport by currents into estuarine nurseries of offshore spawned larvae is most favorable during the winter off North Carolina south of Cape Hatteras. Several winter spawners with estuarine dependent young spawn along the outer continental shelf (*Leiostomus xanthurus*, Dawson 1958; *Mugil cephalus*, Anderson 1958; *Brevoortia tyrannus*, Nelson et al. 1977; *Micropogonias undulatus*, Warlen 1980); thus, the young could take advantage of the inshore directed currents. A corollary to this theory indicates that summer spawners should reproduce near shore or in the estuary if larvae are to be retained in the more productive shallow waters because net current movement is offshore (Miller et al. in press). In addition to *L. fasciatus*, other fishes also spawn in nearshore or estuarine waters south of Cape Hatteras during the summer (*Cynoscion regalis*, Merriner 1976; *C. nebulosus*, Mahood 1975; *Stellifer lanceolatus* and Bairdiella chrysoura, Powles 1980).

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NOTES

MARKING GROWTH INCREMENTS IN OTOLITHS OF LARVAL AND JUVENILE FISH BY IMMERSION IN TETRACYCLINE TO EXAMINE THE RATE OF INCREMENT FORMATION

Age determination of fishes by counting daily growth increments in their otoliths is becoming a widely used technique in growth and population studies. Daily formation of otolith increments was first reported by Pannella (1971) for three species of temperate fish. Since then a number of workers, using three basic techniques for confirming the periodicity of increment formation, have reported the presence of daily increments in larval or adult otoliths of at least 15 species of marine and freshwater fishes. Laboratory rearing from eggs to larvae of known age was used to confirm daily increments by brothers et al. (1976), Taubert and Coble (1977), Barkman (1978), Tanaka et al. (1981), and Laroche et al. (1982). The change in the mean number of increments over time in fish captured in the wild and held in captivity was used to validate daily increments by Struhsaker and Uchiyama (1976), Wilson and Larkin (1980), and Uchiyama and Struhsaker (1981). The third method makes use of chemical agents to mark the growing margin of calcified structures in order to examine their rate of growth (Harris 1960). Tetracycline is one of the best chemical markers because it is relatively nontoxic and produces a fluorescent mark which is easily viewed in ultraviolet light (Harris 1960; Weber and Ridgway 1962). It has been administered to fish by feeding (Choate 1964; Weber and Ridgway 1967; Trojnar 1973; Odense and Logan 1974) and by injection (Kobayashi et al. 1964 and others below). Tetracycline has been used in two studies to determine the rate of increment formation in otoliths. Wild and Foreman (1980) injected the drug into large juveniles and adult skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *Thunnus albacares*, in a mark-recapture program in the tropical eastern Pacific. They found that otoliths of yellowfin tuna of 40-110 cm FL showed daily average increment formation, but that skipjack tuna of 42-64 cm FL showed <1 increment/d. Campana and Neilson (1982) injected tetracycline into juvenile starry flounders, *Platichthys stellatus*, and found that daily increments were subsequently produced in both field and laboratory conditions. These authors briefly mentioned obtaining similar marking results by immersion, but did not detail their procedure.

This paper presents a technique for marking otolith increments by immersing larval and juvenile fish in a solution of tetracycline in seawater, and reports the rate of increment formation under laboratory conditions for two species from the Great Barrier Reef, Australia: *Hypoatherina tropicalis* (Atherinidae) and *Spratelloides dellicatulus* (Dussumeriidae).

Materials and Methods

The experiments were conducted between July 1980 and February 1982 at One Tree Island Field Station and Lizard Island Research Station, during a field study of the population dynamics of these species.

Achromycin (a brand of tetracycline HCl[1]) was used in all experiments. The concentration that would mark the otoliths but not kill the fish was determined by testing three concentrations (400 mg/l, 250 mg/l, and 40 mg/l) using *H. tropicalis* from 12.8 to 23.0 mm SL. The otoliths of survivors were compared with untreated specimens to assess the effectiveness of the mark.

The appropriate concentration, 250 mg/l, was then used in a series of similar experiments to determine the rate of increment formation (Table 1). The experiment number (I-IV) designates a group of fish collected at the same time. In each experiment, fish were killed at two different times, designated as A or B, to compare the number of increments in fish held for different time periods. In experiment IV, the treatment times also differed, but in all other experiments the treatment time was the same for both groups A and B.

Both species are small (adults <7 cm SL), midwater, reef-associated, schooling fishes which do not undergo a marked metamorphosis between larval and juvenile stages (pers. observ.). Both attain their full complement of fin elements and begin to form scales and adult pigmentation at a standard length of 17-19 mm. Following the convention of Ahlstrom (1968), I consider this to be the size at which larvae become juveniles. *Hypoatherina tropicalis* used in the rate-determination experiments ranged from 12.8 to 27.2 mm SL, with 10 of 21 fish classed as larvae (<17.0 mm SL). *Spratelloides delicatulus* ranged from 15.5 to 22.9 mm SL, with 2 of 29 being larvae (Table 1).

[1]Manufactured by Lederle Labs, a division of Cyanamid Australia Pty. Ltd. References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA.

The fish were collected at night with a light and a dip net, and placed in 25 l aquaria without aeration or running seawater as soon as possible after collection. The aquaria were located outdoors under an awning, and therefore were exposed to the ambient diel light cycle, but not to direct sunlight. The fish were allowed to acclimatize for 12-24 h before treatment. Usually there was mortality during this period, but the proportion was not determined. All dead fish were removed prior to treatment.

The fish were exposed to 250 mg tetracycline/l seawater for 12 h from sunset to sunrise, except in experiment IVB when the immersion period was from sunrise to sunset (Table 1). After an immersion period, the aquarium was flushed with 90% water changes until no visible color remained. The tetracycline-seawater solution is yellow until exposed to sunlight for more than ~3 h, when it turns pink, due to oxidative photolysis. Following the treatment, fish were maintained in clean seawater for 2-6 d by feeding either fresh wild plankton >125 mm diameter once a day (experiment I) or *Artemia salina* nauplii 3-4 times/d (all subsequent experiments). *Artemia* nauplii were more convenient for frequent feedings than fresh wild plankton. Ninety percent of the water in each aquarium was changed each morning by siphoning, to minimize handling the fish. Tank water temperatures were measured over the diel cycle during February 1982 (summer) at One Tree Island. The temperature ranged from 25°C at 0630 h to 30°C at 1800 h. Replacement water, added at 0700 h from the surface of the lagoon, measured 27°C.

Larvae were killed at the end of each experiment by placing them into 70% ethanol. Fish were subsequently measured to the nearest 0.1 mm SL. Their otoliths (both sagittae and lapilli) were removed and mounted whole on glass slides without coverslips, using Protexx.

The following terms are used in this report for the concentric rings seen in otoliths. A growth zone is a wide ring which appears light or hyaline under transmitted light. A discontinuous zone is the narrower ring between two growth zones, often called the opaque zone because it appears dark under transmitted light. A growth increment, or simply an increment, is a growth zone plus a discontinuous zone.

Otoliths were examined at 250-1,000× magnification with a combination of incident ultraviolet light to reveal the fluorescent tetracycline-marked rings, and polarized transmitted light to count the rings. The fluorescence microscope used ultraviolet light from a 50W mercury lamp. Excitation wavelength was limited by a band pass filter (450-490 nm) and a long pass suppression filter (515 nm).

In most cases, one sagitta from each fish was read, although occasionally the lapillus was used if its rings were clearer. The area to be counted was selected by scanning the margin of each otolith to find the place where the greatest number of distinct rings could be seen between the innermost fluorescent increment and the edge. A datum was considered valid only if identical counts were obtained in at least two out of three blind readings. No other otoliths were considered in the analysis. Of 21 *H. tropicalis* otoliths

TABLE 1.—Summary of tetracycline-marking experiments to determine the rate of increment formation in *H. tropicalis* and *S. delicatulus*.

Experiment	N	Standard length (mm) Mean (range)	Treatment period	Date and time of killing	Predicted no. of discontinuous zones	No. of fish with various deviations from the predicted number		
						−1	0	+1−
Hypoatherina tropicalis								
IA	2([1])	14.0 (13.6-14.4)	2130, 8 July to 0830, 9 July 1980	0830, 12 July	2+1		1	1
IB	4	13.7 (12.8-14.7)	2130, 8 July to 0830, 9 July 1980	1730, 14 July	5		2	2
IIA	6([2]1)	20.5 (16.2-27.2)	1830, 31 Oct. to 0630, 1 Nov. 1980	0730, 6 Nov.	4+1		5	
IIB	6	18.9 (16.8-20.7)	1830, 31 Oct. to 0630, 1 Nov. 1980	0600, 7 Nov.	5+1		6	
IIIA	3	16.1 (15.4-17.2)	2000, 6 Nov. to 0700, 7 Nov. 1981	0545, 12 Nov.	4+1		3	
Total	21([2]1)					0	17	3
Spratelloides delicatulus								
IIIA	6	17.5 (15.5-19.1)	2000, 6 Nov. to 0700, 7 Nov. 1981	0545, 12 Nov.	4+1		3	3
IIIB	5([2]2)	17.9 (17.6-18.2)	2000, 6 Nov. to 0700, 7 Nov. 1981	1800, 9 Nov.	2			3
IVA	9	19.9 (18.8-22.8)	1800, 31 Jan. to 0630, 1 Feb. 1982	1800, 6 Feb.	5	5	3	1
IVB	9([2]1)	20.5 (17.9-22.9)	0600 to 1800 31 Jun. 1982	0715, 6 Feb.	4+1	2	6	
Total	29([2]3)					7	12	7

[1]Otoliths of two treated fish were destroyed by poor preservation.
[2]Number of fish discarded because of inconsistency between otolith readings.

examined, 1 (4.8%) was discarded. Of 29 *S. delicatulus*, 3 (10.3%) were discarded (Table 1).

Results and Discussion

Marking Technique

In the experiment to determine an effective tetracycline-marking concentration, all fish ($n = 17$) in 400 mg/l died during the 12-h immersion period. Of 10 fish treated with 250 mg/l, 1 died during treatment, and 1 died during the subsequent holding period. Of 10 fish treated with 50 mg/l, 1 died during treatment.

Otoliths of untreated specimens showed faint fluorescence around the edge and occasionally along cracks and surface irregularities (Fig. 1A); this is a naturally occurring autofluorescence (Campana and Neilson 1982). Otoliths of fish in 50 mg/l were indistinguishable from those of untreated specimens. Otoliths of fish in 250 mg/l showed a strong fluorescent band medial to the edge, in addition to the weak fluorescence at the edge (Fig. 1B, C). This strong band consisted of two growth zones and one discontinuous zone (Fig. 2).

It is not known how long it takes for tetracycline to be incorporated into the growing otoliths when administered by immersion. Campana and Neilson (1982) reported that after injection, 50% of fish showed fluorescent otoliths after 10 h, and 100% after 24 h. If one assumes similar or slightly longer incorporation times in the present study, then the inner fluorescent growth zone was probably formed the day after the immersion period. The subsequent discontinuous zone and growth zone were formed while there was residual tetracycline in the water or fish. Another possible explanation is that the appearance of fluorescence in two growth zones is an artifact of viewing whole otoliths.

The results of this experiment indicate that immersion in a concentration of 250 mg Achromycin/l of seawater for 12 h is adequate to mark one or more growth increments in *H. tropicalis* and *S. delicatulus* larvae and juveniles. The overall mortality rate in experiments I, II, and III (total $n = 37$), was 5.4% during treatment and 2.7% during the holding phase.

To determine whether fluorescent marking would occur if the tetracycline immersion period was during daylight hours, an experiment was conducted using *S. delicatulus* from 17.9 to 22.9 mm SL (experiment IV). The fish were collected and divided between two tanks. One tank received tetracycline from 1800 h to 0630 h, the other from 0600 to 1800 h. Mortality due to treatment was not monitored. After 6 d, the fish were killed and examined. The fluorescent bands medial to the edges were similar in width and intensity to those in previous experiments, and showed no difference between the two treatments. This indicates that tetracycline is incorporated into growing otoliths and produces fluorescent increments equally well during the day and night, regardless of whether the solution is yellow or has oxidized to pink.

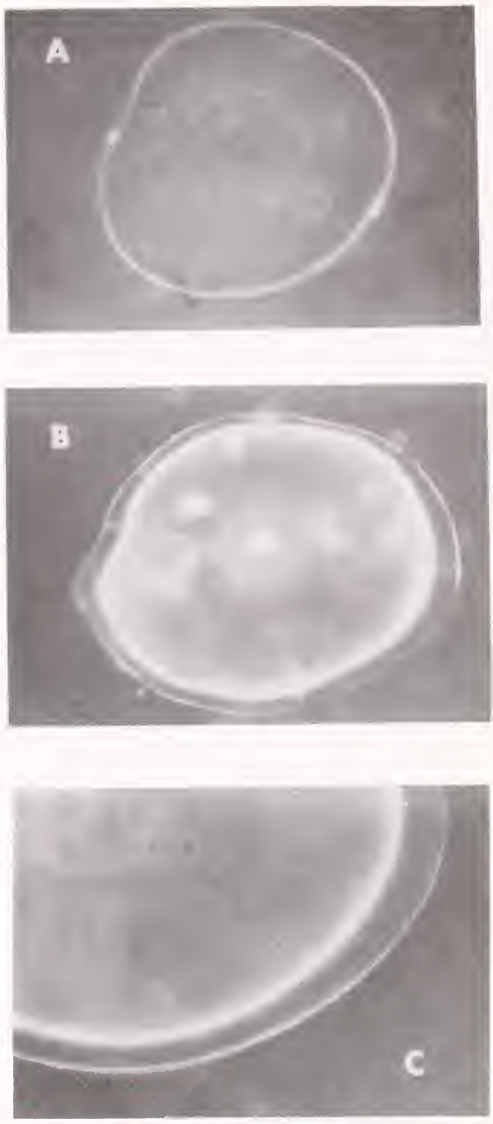

FIGURE 1.—Flourescence photomicrographs of sagittae of larval *Hypoatherina tropicalis*. A. Untreated otoliths, showing autofluorescence around the edge (10.1 mm SL). B. Tetracycline-marked otolith, showing fluorescent band medial to the edge (16.2 mm SL). C. Marked otolith under higher magnificaton (17.6 mm SL).

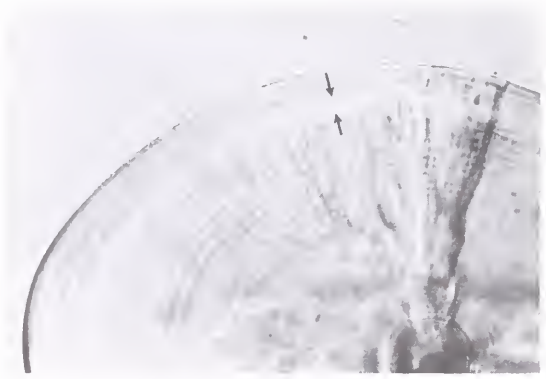

FIGURE 2.—Tetracycline-marked otolith from *H. tropicalis* (17.6 mm SL), photographed with a combination of fluorescent and transmitted polarized light. Arrows indicate the fluorescent band produced by the marking technique. This individual is from experiment IIB, and shows six discontinuous zones between the innermost fluorescent growth zone and the edge. The edge appears to be a growth zone.

In summary, tetracycline can be administered by three techniques: feeding, injection, and immersion. Feeding has apparently not been used in otolith studies. The immersion technique presented here has advantages over injection in some situations. It can be used on fish which are too small or fragile for injection. The fluorescent mark obtained is relatively narrow, covering only two increments, compared with the wider mark resulting from injection (Kobayashi et al. 1964; Campana and Neilson 1982). Therefore, it is distinguishable from edge autofluorescence after a shorter period of time, and allows finer resolution of increment formation, which may be useful in some experimental situations. Also, immersion requires minimum equipment, facilities, and handling of fish.

Rate of Increment Formation

In interpreting the results of my experiments, the number of discontinuous zones between the innermost fluorescent growth zone and the edge was compared with the number predicted if one discontinuous zone formed every day from ca. 0700 to 1000 h. Tanaka et al. (1981) found that growth zones in juvenile *Tilapia nilotica* held under various photoperiods started forming a few hours after lights-on, continued through the dark period, and stopped or slowed down about the time of the following lights-on. The discontinuous zone was formed in the few hours after lights-on. Mugiya et al. (1981) demonstrated that the deposition of calcium in goldfish, *Carassius auratus*, slowed down or stopped at sunrise and resumed in 3 h. Since otoliths are made of a matrix of organic fibers, which are calcified in the growth zones and not calcified in the discontinuous zones (Panella 1980; Watabe et al. 1982), the findings of Mugiya et al. (1981) support Tanaka et al. (1981). Whether this rhythm of increment formation is found in most fish remains to be investigated.

The results for all experiments are presented in Table 1. For fish that were killed between 0545 and 0830 h, the predicted number includes an additional discontinuous zone that should have been forming at the time of death, although this ring was probably not always sufficiently formed to be counted. In these cases, an otolith was considered to show daily increment formation even if the number of discontinuous zones was one less than predicted.

One growth increment was formed each day in 85% of *H. tropicalis* ($n = 20$); the rest had one more than the predicted number of increments. In *S. delicatulus*, 46% ($n = 26$) showed daily formation of growth increments; 27% showed one less, and 27% showed one more, than expected if increments form daily. Thus, the variability in rate of increment formation was greater in *S. delicatulus* than in *H. tropicalis*, but the average rate for *S. delicatulus* was still 1 increment/d.

This apparent difference in the rate of increment formation between species may be partially due to a difference between larvae and juveniles. Almost all (93%) of the *S. delicatulus* treated were juveniles, but only about half (52%) of the *H. tropicalis* were juveniles. However, no conclusion can be drawn from these data because the experiments were not designed to examine this factor, and the numbers are too small to compare larvae with juveniles.

It is possible that tetracycline may affect the rate of increment formation. Some workers have reported that tetracycline inhibits mineralization in scales and bone (Harris 1960; Kobayashi et al. 1964), although others note neither growth promotion, retardation, nor structural weakness in bone as a result of tetracycline administration (Weber and Ridgway 1967). The possibility that the tetracycline treatment interferes with growth of otoliths or fish was not considered in this study, but should be examined before further use is made of this technique.

In conclusion, the rate of increment formation has been examined in only a small number of species under a limited range of conditions. Recent evidence suggests that increment formation may be affected in some species by temperature, food availability and feeding frequency, photoperiod, and developmental stage (Taubert and Coble 1976; Brothers 1978; Pannella 1980; Wild and Foreman 1980; Geffen 1982;

Lough et al. 1982; Neilson and Geen 1982). It is therefore desirable to examine the rate of increment formation under various conditions before using otoliths for age determination (Brothers 1979). The technique presented here is a tool for studying increment formation in otoliths of young fish under laboratory and possibly field conditions. It can be used for reef and nearshore benthic species which can be captured while larvae or juveniles and kept in containers or enclosures.

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TAG-RECAPTURE VALIDATION OF MOLT AND EGG EXTRUSION PREDICTIONS BASED UPON PLEOPOD EXAMINATION IN THE AMERICAN LOBSTER, *HOMARUS AMERICANUS*

Techniques for molt prediction based upon epidermal and setal development in pleopods (Aiken 1973) and for egg extrusion prediction based upon pleopod cement gland development (Waddy and Aiken 1980; Aiken and Waddy 1982) provide opportunities for more comprehensive studies of growth and reproductive potential in natural American lobster, *Homarus americanus*, populations than have previously been possible. These laboratory-developed techniques have only recently been applied to field samples from a number of areas of Atlantic Canada (Robinson 1979; Campbell and Robinson 1983; Ennis 1984). Although the methodologies are fairly straightforward and may be applied in field studies quite readily, in practice the investigator will sometimes be faced with specimens for which predictions can only be made with some degree of uncertainty. A study of Newfoundland lobsters using these techniques has included the tagging of animals from which pleopods were obtained. This paper presents results from observations on recaptured lobsters which validate the predictions that were made at the time of tagging that molting or egg extrusion would or would not occur during the current molting/spawning period.

Materials and Methods

Pleopods were obtained from American lobsters (ranging from 33 mm to 130 mm CL (carapace length)) caught in traps and by scuba divers near Arnold's Cove, Placentia Bay, Newfoundland, between 24 June and 17 July 1981. These were examined for molt and cement gland stages according to the methodologies of Aiken (1973), Waddy and Aiken (1980), and Aiken and Waddy (1982).

It is clear from Aiken (1973) that one can predict with considerable confidence that lobsters with pleopod stages 3.0 and higher just prior to or early in the molting season will molt that year. It is also clear, however, that for animals with pleopod stages 1.0-2.5 one cannot predict with confidence that molting will or will not occur. Molt prediction for these stages is not reliable because of development plateaus that occur during D_0 (i.e., molt stages 1.0-2.5). However, most such plateaus occur at stages 1.5-2.0, and a lobster will rarely remain at stage 2.5 for more than 2 wk. Once an animal has passed beyond stage 2.5, there will be no further plateaus, and proecdysis will proceed at a rate that is regulated by temperature (Aiken 1973). Aiken (1980) also stated that at stage 2.5, the epidermis in the general integument begins to show signs of activity, indicating imminent transition from indecisive D_0 into the irreversible premolt development of D_1. Considering that animals with stage 2.5 pleopods should molt in 48-52 d at 10°C (Aiken 1973) plus the fact that at Arnold's Cove the July-August temperatures on the lobster grounds average in excess of 10°C (mean daily temperatures from 24 June to 31 August averaged 12.1°C in 1981), it appeared more likely that lobsters with stage 2.5 pleopods during the 24 June-17 July sampling at Arnold's Cove would molt. As a working hypothesis, it was decided to predict that lobsters with pleopod stages 2.5 and higher would molt during the 1981 molting season at Arnold's Cove and that those with pleopod stages 0-2.0 would not molt.

Cement glands were initially staged according to the classification scheme of Waddy and Aiken (1980). These stages were subsequently converted to their more recent scheme (Aiken and Waddy 1982). It is clear from these papers that for lobsters with stage 0 or stage 1 cement glands just prior to or early in the spawning season one can confidently predict that egg extrusion will not occur that year, whereas for those with stage 2 or higher cement glands one can confidently predict that egg extrusion will occur.

During the sampling at Arnold's Cove, 356 of the lobsters from which pleopods were removed for molt and cement gland staging were tagged with "sphyrion" tags, which are designed to remain attached through ecdysis (Scarratt and Elson 1965), and released within a few minutes of being taken from the water very close to where they were captured. Observations on 171 of these lobsters recaptured subsequent to the molting/spawning period (mainly during the 1982 fishing season, 20 April-30 June)

provide a basis for validating the molt or egg extrusion predictions.

Results

Molt Predictions

Four of the 11 males (36.4%) and 11 of the 27 females (40.7%) with pleopod stages 0-2.0 molted instead of not molting as was predicted (Table 1). Even some with pleopod stage 0 molted. Of the 16 females which did not molt, 14 extruded eggs, and the 2 females which did not extrude eggs had stage 1 cement glands, indicating that egg extrusion would not occur. Six out of 21 males (28.6%) with pleopod stages 2.5 and 3.0 did not molt, whereas all with pleopod stages ≥3.5 and all females with pleopod stages ≥2.5 did molt (Table 1). Overall, 78.4% of the predictions which could be validated were correct. There was greater success with predicting that molting would occur (89.8% correct predictions) than with predicting it would not (60.5% correct predictions). There was no pleopod stage at and below which none molted; however, at stage 3.5 and higher all molted.

Validations of molt prediction are available for males ranging in size from 73 to 104 mm CL. Except for one animal at 99 mm, it was only for animals smaller than 81 mm that any of the predictions were incorrect. The size range for which validations are available for females is limited (75-82 mm CL).

Egg Extrusion Predictions

All of 17 females with either stage 0 or stage 1 cement glands did not extrude eggs, and all of 7 with stage 3 cement glands did extrude eggs as predicted. However, 2 out of 9 with stage 2 cement glands, which were predicted would lay eggs, did not do so (Table 2). Overall, 93.9% of the predictions which could be validated were correct. The 2 females which failed to extrude eggs as predicted, molted, despite having molt stage 0 pleopods.

TABLE 1.—Summary of molt predictions and subsequent validations for American lobsters sampled and tagged at Arnold's Cove, Newfoundland, 24 June-17 July, 1981.

	Number of molt predictions/validations							
	Males				Females[1]			
Pleopod stage	Yes	Correct	No	Correct	Yes	Correct	No	Correct
0							14	9
1.0			1	1			2	2
1.5			8	5			8	4
2.0			2	1			3	1
2.5	7	4			2	2		
3.0	14	11						
3.5	13	13			1	1		
4.0	11	11			3	3		
4.5	1	1						
5.0	2	2						
5.5	5	5						

[1]This table does not include 69 females which were ovigerous with old eggs at the time of sampling/tagging, all of which subsequently molted

TABLE 2.—Summary of egg extrusion predictions and subsequent validations for female American lobsters sampled and tagged at Arnold's Cove, Newfoundland, 24 June-17 July, 1981. Sixty-nine (69) females which were ovigerous with old eggs at the time of sampling/tagging, all of which subsequently molted, are not included in the table.

	Number of egg extrusion predictions/validations			
Cement gland stage	Yes	Correct	No	Correct
0			8	8
1			9	9
2	9	7		
3	7	7		

Discussion

There have long been problems associated with growth rate and functional maturity determinations in American lobsters. Reliable data on annual proportions molting (or molt frequency) and proportions laying eggs in relation to size are difficult to obtain. Both these parameters are essential in assessing the impact of size limit and/or exploitation rate changes in a lobster fishery on yield per recruit and reproductive potential. Such assessments are important to proper lobster fishery management.

The techniques used here to predict molting and egg extrusion provide new approaches to the study of lobster growth and maturity that have only recently been used in studies of lobster populations. Results of this validation study, however, clearly indicate that caution has to be used in their application.

In the case of molt prediction it appears that the time of sampling in relation to the molting period is critical. The ideal situation would be a very short annual molting period with sampling just prior to the start of molting when all animals going to molt would have well-developed (stage 3 or higher) pleopods. American lobsters reach the northern limit of their range in Newfoundland waters, and it is probably here that their annual molting period is the shortest. In the Arnold's Cove area, molting starts early in July and is virtually completed by early September. In the present study, 5 out of 14 lobsters (all females, Table 1), sampled and tagged between 24 June and 17 July 1981 and had stage 0 pleopods (for which it was pre-

dicted that molting would not occur that year), had molted when recaptured prior to the molting period the following year. For these animals premolt development must have occurred very rapidly during the 1981 molting period. This indicates that periodic sampling throughout the molting period along with a validation study are required in order to use these molt prediction techniques as a basis for estimating annual proportions molting in a lobster population.

The overall success rate with predicting egg extrusion was much greater than with molt prediction (94% cf. 78%). The small number of incorrect predictions may have resulted from loss of eggs rather than failure of the animals to extrude. One of 6 ovigerous females with newly laid eggs that were tagged during the 24 June-17 July sampling period had molted and was nonovigerous when recaptured. While egg extrusion prediction based upon the cement gland staging technique provides a reliable basis for estimating annual proportions laying eggs in a lobster population, it is clear that such estimates should be adjusted, using the kind of information that can be obtained from a validation study before being used in an assessment of reproductive potential in a population.

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COMPARISON OF PHYSIOLOGICAL AND FUNCTIONAL SIZE-MATURITY RELATIONSHIPS IN TWO NEWFOUNDLAND POPULATIONS OF LOBSTERS *HOMARUS AMERICANUS*

Lobster (genus *Homarus*) fisheries are characterized by excessive exploitation rates and small, minimum legal sizes in relation to sizes at maturity (Anonymous 1977, 1979). Under such conditions, widespread recruitment overfishing is a distinct possibility and in eastern Canada appears to be the cause of stock collapses in certain areas (Robinson 1979). Stock-recruitment relationships as such are poorly known for the genus *Homarus*; however, since current levels of landings are well below historical levels in most fisheries, it is reasonable to assume that, within the limits of habitat carrying capacity, increased egg production will result in increased recruitment. It is clear that increasing the minimum legal size and/or reducing exploitation rates will result in increased egg production within a lobster stock; however, detailed knowledge of size-fecundity and size-maturity relationships is required to properly assess the impact of changes in fishery regulatory measures on annual egg production within a given stock.

Size-maturity relationships, based mainly on observations of ovary color and ova size in nonovigerous females for five Newfoundland lobster populations, indicate 100% maturity (physiological) for sizes at which tagging results show that substantially <100% of the nonovigerous females lay eggs in a given spawning season (Ennis 1980). Resorption of the mature ovary near the expected time of oviposition is a common phenomenon in *H. americanus* (Aiken and Waddy 1980a) and presumably is the main reason for failure on the part of physiologically mature females to express their maturity by extruding eggs. Clearly, it is an "expressed" or functional size-maturity relationship that is required to assess the impact of size limit and/or exploitation rate changes in a fishery on annual egg production. Using the pleopod cement gland staging technique described by Aiken and Waddy (1982) as a basis for predicting egg extrusion, such a relationship was derived for two Newfoundland populations. These are compared with physiological size-maturity relationships for the same populations.

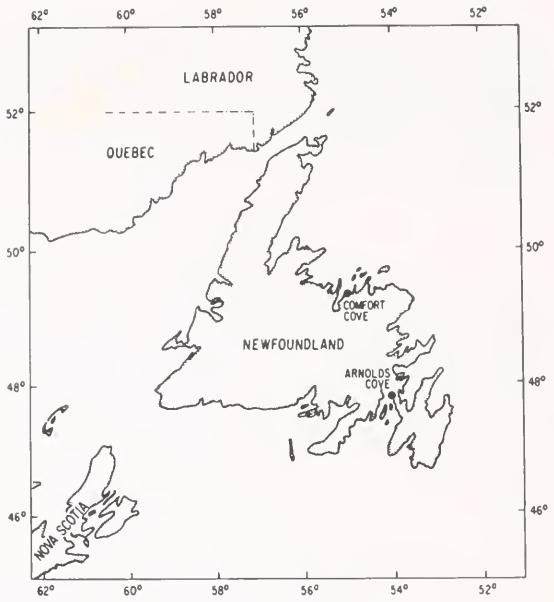

FIGURE 1.—Map of Newfoundland showing location of Arnold's Cove and Comfort Cove.

Materials and Methods

Pleopods were obtained from 172 nonovigerous female lobsters caught between 24 June and 17 July 1981 and 77 caught between 14 and 18 June 1982 near Arnold's Cove, Placentia Bay, and 246 caught between 1 and 7 July 1982 at Comfort Cove, Notre Dame Bay, Newfoundland, (Fig. 1) using traps and by scuba diving. Sizes ranged from 40 to 111 mm CL (carapace length) at Arnold's Cove and from 58 to 113 mm at Comfort Cove. Pleopods were examined for molt stage according to the method of Aiken (1973) and for cement gland development according to the method of Aiken and Waddy (1982) to determine whether molting or egg extrusion would occur during the current molting/spawning period. In this study it was predicted that females with cement glands in stages 0 and 1 would not extrude eggs during the current spawning period whereas those with stage 2 or higher cement glands would (see Aiken and Waddy 1982 for descriptions of cement gland stages). A validation study (Ennis 1983) has demonstrated that egg extrusion prediction based on cement gland staging is quite reliable. Of the predictions that could be validated, 94% were correct. The only incorrect predictions were for females with stage 2 cement glands of which 2 out of 9 (22%) failed to extrude eggs. Accordingly, in the data analyzed here the number of animals with stage 2 cement glands in each size group was reduced by 22% to obtain a more accurate estimate of the number that would actually extrude eggs. Where 22% of the number was < 0.5, nothing was subtracted.

The two Arnold's Cove samples were combined. For each area the numbers examined and numbers functionally mature (i.e., going to extrude eggs during the current season) were grouped by 1 mm CL and subjected to probit analysis. Although good statistical fits were obtained (P values >0.9), the fitted curves did not approximate the data very well at the upper and lower ends. Proportions from the same data were analyzed using the logistic equation

$$Y = \frac{a}{1 + e^{b+cX}}. \qquad (1)$$

An SAS[1] program, which performs this analysis by means of a nonlinear regression procedure using the Marquardt method, was used. Curves were obtained with substantially improved visual fits to the data.

Previously published size-maturity relationships for Arnold's Cove and Comfort Cove lobsters (Ennis 1980) were based mainly on detailed examination of the gonads of nonovigerous females, but ovigerous females in the samples were included as mature animals. For this paper the ovigerous specimens were excluded from these samples and the data

[1]SAS User's Guide: Statistics, 1982 ed. SAS Institute Inc., Cary, N.C., 584 p.

reanalyzed using the above equation. The size maturity relationships thus derived are a more accurate reflection of the proportions of non-ovigerous females whose gonads are developing for extrusion during the upcoming spawning season (i.e., physiologically mature).

Results

The smallest female lobsters with cement glands in stage 2 (or higher), indicating that egg extrusion would occur during the current spawning period, were 73 mm CL at Arnold's Cove and 71 mm at Comfort Cove (Tables 1, 2). All smaller animals had stage 0 or 1 cement glands, indicating that egg extrusion would not occur. The largest female lobsters with cement glands in stage 0 or 1 were 96 mm CL at Arnold's Cove and 88 mm at Comfort Cove. All larger animals had stage 2 (or higher) cement glands.

Functional and physiological size-maturity relationships were derived for each area and plotted together (Figs. 2, 3). Sizes at 50% functionally mature female lobsters from the relationships were 81 mm CL at Arnold's Cove and 80 mm at Comfort Cove. These compare with sizes at 50% physiologically mature female lobsters of 74 mm and 76 mm for Arnold's Cove and Comfort Cove, respectively.

Observations taken from the data indicate that at Arnold's Cove the shift in physiological maturity from none to all occurred over a 9 mm CL size range (71-80 mm) compared with a 25 mm size range (72-97 mm) for functional maturity. The equivalent size ranges for Comfort Cove lobsters were 22 mm CL (64-86 mm) for physiological maturity and 23 mm (70-93 mm) for functional maturity. Examination of the fitted curves shows considerable disparity between proportions of physiologically mature and functionally mature lobsters at given sizes over much of the size range in each area. In order to quantify this disparity, points on the curves were treated as numbers (out of 100) rather than percentages and the difference determined between the two curves at any given size. The greatest disparities were for 73 mm CL lobsters at Arnold's Cove (Fig. 2) and for 70 mm lobsters at Comfort Cove (Fig. 3) where this comparison of the curves indicates that 60% and 41%, respectively, of the physiologically mature animals fail to extrude eggs. This percentage decreases with increasing size in each area. To derive an estimate of this percentage for the population as a whole, the

TABLE 1.—Cement gland stages for female lobsters caught at Arnold's Cove, Newfoundland, 24 June - 17 July 1981 and 14-18 June 1982.

Carapace length (mm)	Cement gland stage					Total
	0	1	2	3	4	
40-69	31					31
70	2	1				3
72	1					1
73	3	1	1	1		6
74	2					2
75	2					2
76	2	3			2	7
77	5		3	3	4	15
78	3	4	3	3	2	15
79	3	6	7	6	9	31
80	3	3	8	4	6	24
81	2	6	9	4	1	22
82	1	1		1	1	4
83	4	2	5	1	1	13
84		1	1	1		3
85	2	2	3	4	1	12
86		2	1	3	1	7
87		1	1	1	3	6
88	1		9		1	11
89	1	1	3	1		6
90			2	1		3
91		1	3			4
92			1			1
93			1	1		2
94			1			1
95				2	1	3
96	1		1	2		4
97			1	1		2
98			2	2		4
100				1		1
102				2		2
107			1			1
109-111				1	1	2

TABLE 2.—Cement gland stages for female lobsters caught at Comfort Cove, Newfoundland, 1-7 July 1982.

Carapace length (mm)	Cement gland stage					Total
	0	1	2	3	4	
58-69	7	1				8
70	2	1				3
71	1	1	1			3
72	3	1				4
73	2		1			3
74	1	2	1			4
75			5			5
76	1	2				3
77			2	1		3
78	1	2	1			4
79	1	1	7			9
80		1	7			8
81		2	7			9
82	3	2	8			13
83	1	4	16	4		25
84		4	15			19
85	1	2	15	1		19
86		4	4	4		12
87	1	2	8	6		17
88		1	13	1		15
89			8	1		9
90			5	5		10
91			4	1		5
92			3	2		5
93			2	4		6
94			1	2	1	4
95			1	1		2
96				4		4
97				1		1
98			2			2
100			1	2		3
101-113				7	2	9

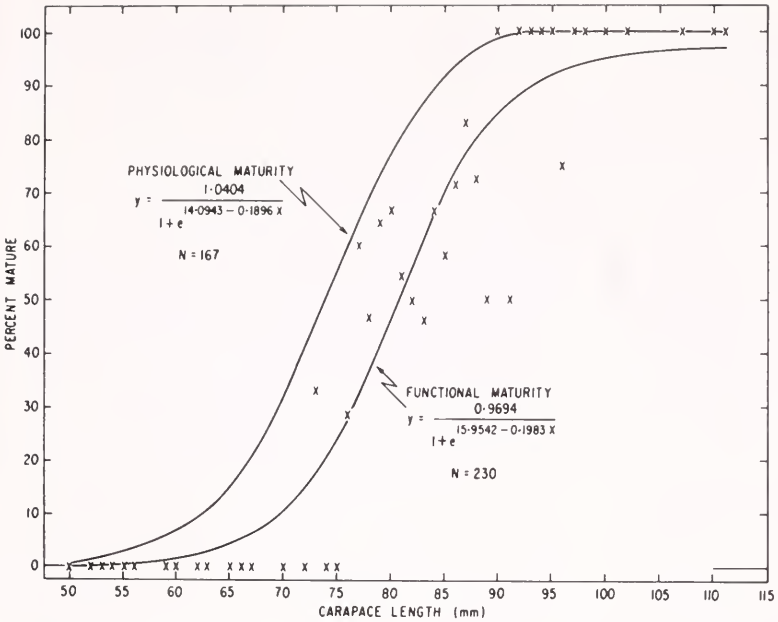

FIGURE 2.—Physiological and functional size-maturity relationships for female lobsters at Arnold's Cove, Newfoundland. Functional maturity data only are provided.

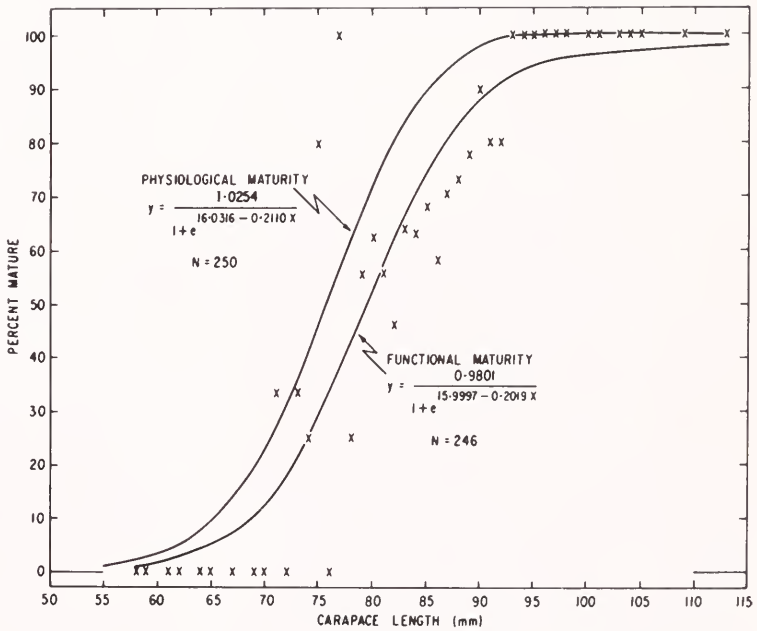

FIGURE 3.—Physiological and functional size-maturity relationships for female lobsters at Comfort Cove, Newfoundland. Functional maturity data only are provided.

above procedure was followed for those sizes between the largest with 100% functionally immature and the smallest with 100% functionally mature (from the data) and the numbers added. The resulting estimates were 25% at Arnold's Cove and 20% at Comfort Cove.

Discussion

This study has demonstrated that failure on the part of physiologically mature female lobsters to "express" their maturity by extruding eggs is quite common in the wild. Resorption of the mature ovary near the expected time of extrusion appears to be the main reason. Resorption occurs when the molting and reproductive cycles conflict (Aiken and Waddy 1976, 1980a, b). These cycles are normally synchronized by temperature and photoperiod regimes so that conflict between them is minimized. However, final ovary maturation is disrupted, if it coincides with middle to late premolt, and the ovary is resorbed prior to the impending molt. Not only would this ensure the conservation of energy, but it might also serve to resynchronize the molt and reproductive cycles (Aiken and Waddy 1980b).

Nonfertilization may also be a cause of resorption. In *Jasus lalandii*, for example, oviposition will not occur in unfertilized females (Heydorn 1969). While oviposition will occur in *H. americanus* even if the female has not successfully mated (Aiken and Waddy 1980a), it is not clear if this is the rule or the exception. Physiologically mature *H. americanus* females which are unfertilized (i.e., empty seminal receptacles) occur in the wild (Krouse 1973; Ennis 1980). In sampling from January to June 1973 at St. Chads, Bonavista Bay, on the northeast coast of Newfoundland, Ennis (1980) found 6 (11.5%) of 52 physiologically mature females to be unfertilized. At Arnold's Cove in August and September 1981, 98 of 100 females $\geq$79 mm CL were fertilized as determined by the presence of spermatophores in seminal receptacles.While nonfertilization may be a contributing factor in some areas, it does not appear to be a major cause of ovary resorption in wild *H. americanus*.

A validation study (Ennis 1983) has demonstrated that the cement gland staging technique enables a reliable prediction of whether a female lobster will extrude eggs during the upcoming spawning season. However, caution has to be exercised in applying a functional size-maturity relationship based on these predictions because there is substantial loss of eggs subsequent to spawning. For example, 2 of 15 females with well-developed (stages 3 and 4) cement glands, indicating extrusion to be imminent, and 1 of 6 females with newly laid eggs (all tagged during the 24 June to 17 July 1981 sampling period at Arnold's Cove) had molted and were nonovigerous when recaptured prior to the 1982 molting/spawning period.

There is also substantial loss of eggs other than through molting. Some of this loss may be the result of eggs not being fertilized. Unfertilized eggs do not attach securely and may be lost soon after oviposition, but in some cases a fair number will remain attached for several months (Aiken and Waddy 1980a, b). However, it is common for fertizlied eggs to be lost as well (Aiken and Waddy 1980a , b). Normal attrition of properly attached (fertilized) eggs over the 9-12 mo incubation period has been estimated at around 36% (Perkins 1971); however, some females lose up to 100% of their eggs. The six ovigerous females referred to above (i.e., tagged during 24 June to 17 July 1981 at Arnold's Cove) had apparently normal clutches of eggs when tagged, but, of the five that had eggs when recaptured, four had normal clutches and one had $<$ 200 eggs remaining. A normal clutch for this particular animal, which was 79 mm CL, would have been about 10,000 eggs (Ennis 1981). Similar observations were made on animals tagged between 1 and 14 August 1981 at Arnold's Cove. Of six females with newly laid, normal-sized clutches of eggs, one had just a few hundred eggs remaining when recaptured. Another female, which had well-developed (stage 4) cement glands, had no eggs but had pleopods covered with cement when recaptured, indicating that eggs had been extruded and subsequently lost (Templeman 1940).

These observations demonstrate that there is substantial loss of eggs subsequent to extrusion over and above that attributed to normal attrition. This loss of eggs should be taken into account in any assessment of the impact of changes in fishery regulatory measures on reproductive potential (i.e., annual egg production) in a population.

Acknowledgments

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CONVERSIONS BETWEEN TOTAL, FORK, AND STANDARD LENGTHS IN 35 SPECIES OF *SEBASTES* FROM CALIFORNIA

In recent years, the rockfishes (Scorpaenidae: *Sebastes*) of the northeastern Pacific Ocean have been investigated extensively. With many institutions studying diverse aspects of their biology and fisheries, a lack of standardized methods has hampered attempts to synthesize the data. A particular problem has been the reporting of different length measurements. To provide the means to convert one of these length measurements to another, we report here the linear regression statistics necessary for conversions in 35 species of *Sebastes*.

Specimens were collected from fishery catches between Cape Blanco, Oreg., and San Diego, Calif., during 1977-82. The sample included five fish for each centimeter of body length throughout the size range of each species. Measurements were taken on a meter board in millimeters on frozen, then thawed, carcasses. Standard length was measured from the anterior tip of the upper jaw to the posterior end of the vertebral column (Hubbs and Lagler 1970:25); fork length was measured from the anterior tip of the longest jaw to the median point of the caudal fin; and the total length was measured from the most anterior tip of the longest jaw to the most posterior part of the tail when the caudal rays are squeezed together (Holt 1959:71). Linear regressions were run on all combinations of the measurements of length. Outliers (± 3.0 standard deviations) from the line were noted by the computer program, then checked for data entry error and corrected when possible. If a data entry error was not found, an outlier was assumed to result from measurement error and the observation was deleted.

Statistics reported for each species are y-intercept (α), slope (β), standard error of estimate ($S_{y\,x}$), correlation coefficient (r), range in length, and the sample size used in the regression (n) (Tables 1-3). Estimates of α imply impossible values for the dependent variable when the independent variable is zero. The impossible results could be caused by random error in estimation of α or nonlinearity for values less than those observed. The high values of r and examination of scattergrams indicate that the length relationships are linear over the observed range of values. The standard precaution of limiting the application of these regressions to the ranges of observed values is advised. To calculate the total length (TL) of *S. alutus*, given a standard length (SL) of 250 mm, the regression values from Table 1, total length on standard length, are used so that

TABLE 1.—Results of linear regressions of standard length versus total length for *Sebastes*. Measurements are in millimeters.

Species of *Sebastes*	*n*	*r*	Standard length		Total length on standard length			Standard length on total length		
			Min	Max	α	β	$S_{y \cdot x}$	α	β	$S_{y \cdot x}$
alutus	49	0.995	232	361	1.454	1 249	3.746	2.056	0.792	2.984
auriculatus	116	1 000	72	426	−1.423	1.240	3.787	1.369	0.806	3.054
aurora	43	0 991	164	324	0.098	1 220	4 709	4.398	0.806	3.827
babcocki	74	0.999	185	532	6.478	1.196	4 833	−4 614	0.834	4.035
carnatus	105	0.999	75	292	3.676	1 201	2.206	−2.866	0.832	1.836
caurinus	113	0 997	111	443	3.873	1 209	5.769	−0.653	0.820	4.568
chlorostictus	107	0.999	107	382	5.316	1.202	3 636	−3.931	0.830	3.023
chrysomelas	60	0.998	77	316	1 007	1 211	3.161	−0.123	0.822	2.605
constellatus	105	0.999	148	365	4.497	1.175	3.119	−3.204	0.849	2.651
crameri	102	0.999	102	394	−0.304	1.266	4.153	0.737	0.788	3.278
diploproa	80	0.999	87	308	1.286	1 242	2.718	−0.740	0.804	2.188
elongatus	108	0.998	107	317	15 238	1.165	3.543	−12.144	0.855	3.036
entomelas	105	0.998	194	435	9 496	1.211	5.679	−6.296	0.822	4.679
flavidus	193	0.997	191	453	0.468	1 247	5.700	1.379	0.798	4.558
goodei	99	1.000	101	449	4 199	1.224	2.870	−3.196	0.816	2.344
hopkinsi	71	0.993	99	251	3 059	1 200	4.788	−0.195	0.822	3.964
jordani	145	0.998	77	260	4.610	1 216	2 903	−3.128	0.819	2.382
levis	31	1.000	190	717	−4.500	1.248	4.907	3.813	0.801	3.932
maliger	42	0.996	174	397	1.463	1 220	5.639	1.120	0.813	4.604
melanops	138	0.999	74	495	7.724	1 221	5.193	−5.596	0.817	4.247
melanostomus	87	0.994	207	421	−0.954	1.244	6.897	4.780	0.794	5.508
miniatus	109	0.994	237	550	9.629	1.229	9 765	−3.095	0.804	7.900
mystinus	163	0.998	102	387	2.930	1 238	5.694	−1.192	0.804	4.588
nebulosus	69	0.995	213	366	4 294	1.196	3.962	−0 731	0.828	3.296
ovalis	83	0.997	181	375	0.550	1 225	4.374	1.329	0 811	3.558
paucispinis	163	0.999	103	649	−5.035	1 262	7.550	4.882	0.790	5.974
pinniger	136	0 997	196	565	11 476	1.239	8.002	−7.447	0.803	6.443
rosaceus	83	0.996	132	263	3 917	1.199	2.867	−1 794	0.828	2.383
rosenblatti	104	0.999	132	428	9.567	1 182	3 653	−7.374	0.844	3.086
ruberrimus	118	0.996	203	565	5.856	1.202	9.465	−1.717	0.826	7.843
rufus	26	0.999	152	447	12.946	1.177	5.963	−10.316	0.848	5.061
saxicola	68	0.999	109	288	3.226	1.242	2 456	−2.252	0.804	1.976
semicinctus	31	0 979	101	147	8 179	1.170	3.617	−1.752	0.820	3.027
serranoides	129	0.995	190	441	8.292	1.209	7.277	−3.542	0.819	5.988
wilsoni	48	0.999	71	126	0.572	1.234	1 071	−0.231	0 808	0.868

TABLE 2.—Results of linear regressions of standard length versus fork length for *Sebastes*. Measurements are in millimeters.

Species of *Sebastes*	*n*	*r*	Standard length		Fork length on standard length			Standard length on fork length		
			Min	Max	α	β	$S_{y \cdot x}$	α	β	$S_{y \cdot x}$
alutus	48	0.996	232	361	−0.281	1.195	3.024	2.492	0.831	2.521
auriculatus	114	0.999	72	426	−0.369	1 228	4 126	0.575	0.813	3.358
aurora	44	0.993	164	324	−3 046	1.201	4.237	6 237	0.821	3.502
babcocki	76	0.999	185	532	9 034	1.153	5.190	−6.860	0 865	4.496
carnatus	104	0.999	75	292	4 601	1.194	2 425	−3.613	0.836	2.030
caurinus	117	0.996	111	448	5 896	1.187	6 764	−2.272	0.836	5.674
chlorostictus	107	0.999	107	382	5 289	1.171	3.719	−3.987	0.852	3.173
chrysomelas	58	0.997	77	226	1.137	1.209	3.209	−0.009	0.822	2.647
constellatus	107	0.999	148	365	3.883	1.152	2.964	−2.774	0.866	2.571
crameri	103	0.999	102	394	1.390	1.205	4.282	−0.565	0.828	3 550
diploproa	82	0.999	87	308	2.092	1.181	2.627	−1 460	0.845	2.223
elongatus	116	0.998	107	317	14 186	1.116	3.469	−11.724	0.892	3 102
entomelas	106	0 997	194	435	16.964	1.124	5.602	−13.326	0.885	4.970
flavidus	198	0.998	191	453	−0.918	1.213	5 367	2.363	0.820	4 412
goodei	99	1.000	101	449	1 515	1.159	3.085	−0.988	0.862	2.660
hopkinsi	72	0.994	99	251	3.011	1.153	4.465	−0.372	0.856	3.847
jordani	154	0.998	77	260	5.645	1.124	2.519	−4 418	0.887	2.238
levis	34	0.999	190	717	0.033	1.177	8.446	0.688	0.848	7.169
maliger	41	0 997	174	397	11.835	1 173	4.867	−8.202	0.848	4 138
melanops	135	0.999	74	495	7.149	1.197	5.042	−5.247	0.834	4 209
melanostomus	86	0.994	207	421	−0.828	1.201	6.853	4.912	0.822	5.670
miniatus	106	0.994	237	550	16.442	1 168	9.200	−9.445	0.847	7.836
mystinus	164	0.998	102	387	0.352	1.192	4.975	0.644	0.836	4.166
nebulosus	71	0.993	213	366	6.934	1.181	4 623	−1.852	0.835	3.888
ovalis	83	0.996	181	375	−3 554	1 187	4.677	5.130	0 836	3.925
paucispinis	162	0.999	103	649	−4.082	1.209	6.819	4.183	0.826	5.636
pinniger	138	0 998	196	565	12.880	1 164	7.440	−9.326	0 855	6.378
rosaceus	83	0.997	132	263	1.399	1.187	2.730	0.225	0 837	2.293
rosenblatti	104	0.999	132	428	9.938	1.147	3.347	−8.023	0.870	2.915
ruberrimus	118	0 996	203	565	6.665	1 181	9.028	−2.664	0.841	7.620

TABLE 2.—*Continued*

Species of *Sebastes*	*n*	*r*	Standard length Min	Standard length Max	Fork length on standard length α	Fork length on standard length β	Fork length on standard length $S_{Y \cdot X}$	Standard length on fork length α	Standard length on fork length β	Standard length on fork length $S_{Y \cdot X}$
rufus	26	0.999	152	447	14 246	1.112	4.416	−12.392	0.898	3 969
saxicola	77	0.999	109	288	3 234	1 200	2.511	−2.315	0.831	2.090
semicinctus	31	0.978	101	147	6.486	1.128	3.562	−0.343	0.849	3.091
serranoides	126	0.995	190	441	4 422	1.184	6.779	−0 672	0.837	5.700
wilsoni	53	0.999	71	126	0.671	1.203	0.884	−0.372	0.830	0.734

TABLE 3.—Results of linear regressions of fork length versus total length for *Sebastes*. Measurements are in millimeters.

Species of *Sebastes*	*n*	*r*	Fork length Min	Fork length Max	Total length on fork length α	Total length on fork length β	Total length on fork length $S_{Y \cdot X}$	Fork length on total length α	Fork length on total length β	Fork length on total length $S_{Y \cdot X}$
alutus	48	0.999	278	430	−0.003	1.050	1.483	1.321	0.949	1.272
auriculatus	113	1.000	90	529	−0.586	1.007	1 637	0.634	0.993	1.626
aurora	43	0.998	198	388	2 293	1.019	2.349	−0.917	0.977	2.300
babcocki	72	1.000	222	635	−1.146	1.032	2.392	1.336	0.968	2.316
carnatus	101	1.000	92	351	−0.759	1.005	0.510	0.768	0.995	0.507
caurinus	107	0.999	135	538	0.629	1.010	3.022	0.005	0.988	2.988
chlorostictus	106	1.000	127	449	−0.723	1.028	1.905	0.858	0.972	1.852
chrysomelas[1]										
constellatus	104	1.000	174	422	−0.134	1.023	1.504	0.301	0.977	1.470
crameri	99	1.000	124	480	−1.700	1.051	2.002	1.756	0.951	1.904
diploproa	80	1.000	106	364	−0.558	1.049	1.704	0.669	0.953	1 625
elongatus	102	1.000	129	360	−0.552	1.047	1.449	0.701	0.954	1.383
entomelas	100	0.999	231	496	−6.845	1.072	3.251	6.954	0.931	3.029
flavidus	191	1.000	226	551	2.358	1.025	2 439	−1.906	0.974	2.377
goodei	96	1.000	122	527	2.468	1.057	2.647	−2.096	0.945	2.503
hopkinsi	70	0.999	115	292	0.002	1.041	1.917	0.428	0.959	1.840
jordani	140	0.999	89	296	−1.872	1 086	1 885	2.036	0.920	1.735
levis	34	1.000	228	855	−3.335	1.055	4 452	3.369	0.947	4 219
maliger	40	0.999	215	480	−8.696	1.034	2.782	9.075	0.965	2 687
melanops	132	1.000	91	599	1.595	1.017	2.099	−1.421	0.983	2.063
melanostomus	82	0.999	247	519	−0.635	1.036	2.181	1.065	0.964	2.103
miniatus	103	0.999	293	654	−7 857	1.054	4 638	8.665	0.946	4.394
mystinus	158	1 000	122	463	2 495	1.039	2.329	−2.164	0.962	2.241
nebulosus	71	1.000	256	498	0.854	1.001	1.423	−0.487	0.998	1.420
ovalis	78	0.999	225	438	3.914	1.033	1.996	−3.311	0.967	1.931
paucispinis	157	1.000	123	781	−0.870	1.045	2.273	0.930	0.956	2.174
pinniger	132	1.000	235	586	−4.107	1.070	2.822	4 108	0.934	2.638
rosaceus	79	0.999	158	316	1.409	1 015	1.173	−1.085	0.984	1.155
rosenblatti	103	1.000	155	497	−0.453	1.030	2.026	0.692	0.970	1.966
ruberrimus	118	1.000	243	680	−0.758	1.018	3.640	1 296	0.981	3.573
rufus	24	1.000	182	517	−2.197	1.057	1 659	2.135	0.946	1.569
saxicola	69	0.999	136	347	−0.669	1.038	2.009	0.921	0.963	1.935
semicinctus	29	0.998	119	174	−0.422	1.050	1.178	1.010	0.949	1.120
serranoides	125	0.999	222	518	1.419	1.029	2.623	−0.862	0.971	2.548
wilsoni	45	1.000	86	151	−1.141	1.035	0.560	1.182	0.966	0.541

[1]No regression was run because total length and fork length are equal.

$$TL = \alpha + \beta\,(SL)$$
$$TL = 1.454 + (1.249)\,(250)$$
$$TL = 313.7 \text{ mm}.$$

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NOTICES

NOAA Technical Reports NMFS published during first 6 months of 1983

Circular

448. Synopsis of biological data on the grunts *Haemulon aurolineatum* and *H. plumieri* (Pisces: Haemulidae). By George H. Darcy. February 1983, iv + 37 p., 33 figs., 26 tables.
449. Synopsis of biological data on the pigfish, *Orthopristis chrysoptera* (Pisces: Haemulidae). By George H. Darcy. March 1983, iv + 23 p., 22 figs., 15 tables.
450. The utility of developmental osteology in taxonomic and systematic studies of teleost larvae: A review. By Jean R. Dunn. June 1983, iii + 19 p., 7 figs., 5 tables.

Special Scientific Report—Fisheries

761. Sea level variations at Monterey, California. By Dale Emil Bretschneider and Douglas R. McLain. January 1983, iii + 50 p., 16 figs., 3 tables, App. A, B.
762. Abundance of pelagic resources off California, 1963-78, as measured by an airborne fish monitoring program. By James L. Squire, Jr. February 1983, v + 75 p., 65 figs., 4 tables.
763. Climatology of surface heat fluxes over the California Current region. By Craig S. Nelson and David M. Husby. February 1983, iii + 155 p., 21 figs., 1 table, App. I, II, III.
764. Demersal fishes and invertebrates trawled in the northeastern Chukchi and western Beaufort Seas, 1976-77. By Kathryn J. Frost and Lloyd F. Lowry. February 1983, iii + 22 p., 4 figs., 6 tables, App. A.
765. Distribution and abundance of larvae of king crab, *Paralithodes camtschatica*, and pandalid shrimp in the Kachemak Bay area, Alaska, 1972 and 1976. By Evan Haynes. April 1983, iii + 64 p., 29 figs., 1 table, App.
766. An atlas of the distribution and abundance of dominant benthic invertebrates in the New York Bight apex with reviews of their life histories. By Janice V. Caracciolo and Frank W. Steimle, Jr. March 1983, v + 58 p., 69 figs., 5 tables.
767. A commercial sampling program for sandworms, *Nereis virens* Sars, and bloodworms, *Glycera dibranchiata* Ehlers, harvested along the Maine coast. By Edwin P. Creaser, Jr., David A. Clifford, Michael J. Hogan, and David B. Sampson. April 1983, iv + 56 p., 16 figs., 30 tables, App. A.
768. Distribution and abundance of east coast bivalve mollusks based on specimens in the National Marine Fisheries Service Woods Hole collection. By Roger B. Theroux and Roland L. Wigley. June 1983, xvi + 172 p., 121 figs., 327 tables.

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Notes

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DEPARTMENT OF COMMERCE
UNITED STATES OF AMERICA

Fishery Bulletin

Vol. 82, No. 2 April 1984

(Continued on back cover)

Seattle, Washington

Fishery Bulletin

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

The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115. Second class postage is paid at Seattle, Wash., and additional offices. POSTMASTER send address changes for subscriptions to Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402.

The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget through 1 April 1985.

Fishery Bulletin

CONTENTS

Vol. 82, No. 2 April 1984

Notes

(Continued on next page)

Seattle, Washington

1984

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Notice

NOAA Technical Reports NMFS published during last 6 months of 1983.

SIZE, AGE, SEXUAL MATURITY, AND SEX RATIO IN OCEAN QUAHOGS, *ARCTICA ISLANDICA* LINNÉ, OFF LONG ISLAND, NEW YORK

JOHN W. ROPES, STEVEN A. MURAWSKI, AND FREDRIC M. SERCHUK[1]

ABSTRACT

Ocean quahogs, *Arctica islandica*, were collected off Long Island, New York, in 1978 for a determination of sexuality and gonadal condition. A microscopic examination of histologically prepared tissues of 133 clams, 19-60 mm in shell length, revealed that 36 were in an undifferentiated condition and could not be sexed. Sexual differentiation was evident in 97 clams; of the latter, 69 were in two types of intermediate development: those with sparse (20) and moderate (49) tubule development. Only 28 clams were fully mature. Age and growth were assessed from acetate peels of shell cross sections. Determinations of sex of these, and of specimens 57-103 mm in shell length collected from the same area in 1980, indicated that the smallest and youngest ocean quahogs were predominantly male, but the largest and oldest were predominantly female.

Ocean quahogs, *Arctica islandica*, like most other bivalves, lack external characteristics for a determination of sex, maturation, and gonadal condition. Sex determination has been made for other bivalves, such as the surf clam, *Spisula solidissima* (Ropes 1979a), from microscopic examinations of gametogenesis in histological preparations of gonadal tissues. Similar examinations were lacking for ocean quahogs. The resource has become an important fishery within the past half-decade (Ropes 1979b; Serchuk and Murawski 1980[2]).

In most bivalves that have been studied, sexual maturity occurs at a young age and small size, but species differences have been observed (Altman and Dittmer 1972). Thompson et al. (1980a, b) found that the ocean quahog is a slow growing, long-lived species which exhibits considerable variability in maturation with respect to size and age. The latter conclusion was based on examinations of 39 specimens, 87% of which were 40 mm or longer in shell length. The samples were collected in April-May, 3-4 mo before the spawning period reported for this species by Loosanoff (1953). It seemed reasonable to assume that mature, older quahogs in the sample would produce large numbers of sex cells, but it was not possible to determine whether most of the undifferentiated gonads in the sample would do likewise. Their contribution to the reproductive potential of the species was an enigma, and our knowledge of maturation was incomplete.

In late July and early August 1978, the National Marine Fisheries Service marked large numbers of ocean quahogs at a location near a site sampled in the study of sexual maturity reported by Thompson et al. (1980b). This was an opportunity to collect specimens for a reexamination of gonadal condition at about the time of maximum ripeness, as Loosanoff (1953) had reported finding many ocean quahogs in the partial spawning condition in mid-August. The time of collection, then, seemed favorable for obtaining sexually mature quahogs with fully developed, ripe gonads that could be clearly separated from immature quahogs with undifferentiated sex cells in the gonads.

METHODS

A commercial clam dredge vessel, MV *Diane Maria*, was chartered for the marking project during 25 July-5 August 1978. The hydraulic clam dredge had a 100-in (2.54 m)-wide knife and was modified by lining the inner surfaces with 1/2-in (12.7 mm) square-mesh hardware cloth to retain small clams. Sample tows were of 4-5 min duration and usually resulted in a dredge filled with clams, shells, and bottom substrata.

[1]Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[2]Serchuk, F. M., and S. A. Murawski. 1980. Evaluation and status of ocean quahogs, *Arctica islandica* (Linnaeus) populations off the Middle Atlantic coast of the United States. Woods Hole Lab. Ref. Doc. 80-32, 4 p. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

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The sample site was 48 km SSE of Shinnecock Inlet, Long Island, N.Y., at lat. 40°21′N, long. 72°24′W, and 53 m deep. This location contained high densities and a wide size range of ocean quahogs and had a low probability of being disturbed by the fishery: criteria important for success in the marking experiment (Murawski et al. 1982). The wide size range of ocean quahogs found at and near the site included more small individuals for a study of maturity than elsewhere in the Middle Atlantic Bight.

Small quahogs (< 65 mm shell length) were sorted from the catch during the marking operation, and the soft bodies were immediately removed from the shells for preservation in Bouin's fixative; shells were saved and coded for reference to corresponding tissues. Slides of the gonadal tissues were prepared for microscopic examination using standard histological techniques. The clam bodies were cut dorsoventrally through the midsection, and the anterior and posterior pieces of each clam were embedded to produce two sections for examination. The 6 μm thick sections were stained in Harris' hematoxylin and eosin. Recognition of gametogenic stages was based on previous studies of bivalve reproduction by Loosanoff (1953); Ropes and Stickney (1965); Ropes (1968a, b; 1971; 1979a); Thompson et al. (1980b); Jones (1981); and Mann (1982).

The shells were processed for observation of internal age/growth lines in acetate peels by methods similar to those reported in Thompson et al. (1980a, b) and reported more fully by Ropes (1982)[3]. A radial section was made from the umbo to ventral margin of left valves, since these contain a single prominent tooth that Thompson et al. (1980a, b) found had growth lines corresponding in number to those in the valve. Proper orientation of the valve for sectioning to retain the umbonal portion and broadest tooth surface in the anterior portion of the valve was a critical procedural step. The sections were made on a low-speed saw and by a 10.2 cm diameter by 0.03 cm thick diamond wafering blade. The cut edges were hand polished on wetable carborundum paper (240, 400, and 600 grits) to remove saw marks, polished to a high luster on a vibrating lap machine charged with aluminum oxide, then etched in a 1% HCl solution for one min. Peels were produced by flooding the etched surfaces with acetone and applying 0.127 mm thick acetate film. After a 15-min drying period, the film was peeled off and sandwiched between glass slides. Peel images were enlarged on a microprojector to 40×. Age/growth lines were counted and the exit location of each at the external edge was marked on the peel for a comparison with the external bands by placing the anterior valve portion on the peel image. This procedure clearly demonstrated correspondence between the number and location of internal lines and external bands. It also delimited sequential increments between external bands for measurement to the nearest 0.1 mm with calipers.

Periodic age/growth phenomena in the shells of ocean quahogs have been called "bands" for increments of darker periostracum deposits on the external shell surfaces and "lines" for those accreted in the shells. The latter have been identified as prismatic microstructures that demark boundaries of growth increments (Ropes et al. in press); the external pigmented bands varied in intensity and width (from 0 to ~2 mm). A slight concentric depression often outlined the shell shape in the bands and corresponded to the location of internal lines. This and the method of marking the acetate peel aided in measuring increments of growth.

After completing the study of the gonadal tissues of small ocean quahogs, it was evident that the sex ratio of larger clams from the same area should be examined. Therefore, squashes of thawed gonadal tissues from 199 marked clams 57-103 mm shell length recaptured in August 1980 were examined microscopically at the laboratory for determination of sex.

RESULTS

Observations of Age

The shells and acetate peels of 137 clams were examined. Bands on the external shell surfaces were not equally distinct for all clams in the sample. The bands were widely separated for small clams, but crowded together at the ventral margin for large clams. A few shells had poorly defined bands, but lines in the peels aided in locating them. Age annuli formed during the earliest ontogeny of ocean quahogs are difficult to detect on the valve surface and must be carefully exposed in the sectioned shell. A quahog 20.0 mm in shell length had three barely detectable bands on the surface of its valves; the two most recent annuli in peels of the valve and hinge tooth were most obvi-

[3]Ropes, J. W. 1982. Procedures for preparing acetate peels of embedded valves of *Arctica islandica* for ageing. Woods Hole Lab. Ref. Doc. 82-18, 8 p. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

ous and the first was confounded by a secondary incomplete line that had formed slightly later (Fig. 1a, b). The formation of secondary lines is not typical at a young age. The formation of a complete line is, however, important in detecting annuli.

Three clams had shell abnormalities related to an injury. An ocean quahog with six bands had a slight depression at the anterior end of the left valve that was not detected as unusual growth lines or increments in the peel of either the valve or tooth; the right valve showed no evidence of an injury (Fig. 2a, b). Another quahog had a deep indentation, and part of the ventral margin was missing in the left valve before band six had been formed, but the right valve showed a slight indentation and darkening as evidence of an injury (Fig. 3a, b). The peel of the left valve showed age lines before and immediately after the site of the injury (Fig. 3c). The sixth annuli in the hinge tooth was very prominent (Fig. 3d). The valve of a quahog with seven bands had definite surface indentations associated with annuli, and the hinge tooth showed regularly spaced growth increments (Fig. 4a, b, c). An injury was not clearly evident. The annuli in peels of all these clams were easily related to bands on the valve surface for measurements of growth.

For 9 clams (47.5-60.4 mm long), all annuli in the peels were counted, but only some bands were measured because those near the ventral margin were too crowded and poorly defined.

The shells of 3 clams (39.7-64.0 mm long) produced a confused pattern of lines in the ventral third of the peels and extensive ridging and poorly defined bands on the external valve surfaces (Fig. 5a, b, c). It was not evident that these clams had been injured, but they were omitted in analyses, since growth appeared to be aberrant. In all, 134 clams, 18.7-60.4 mm long and averaging 38.9 mm (S.D. $\pm$ 8.65), were used.

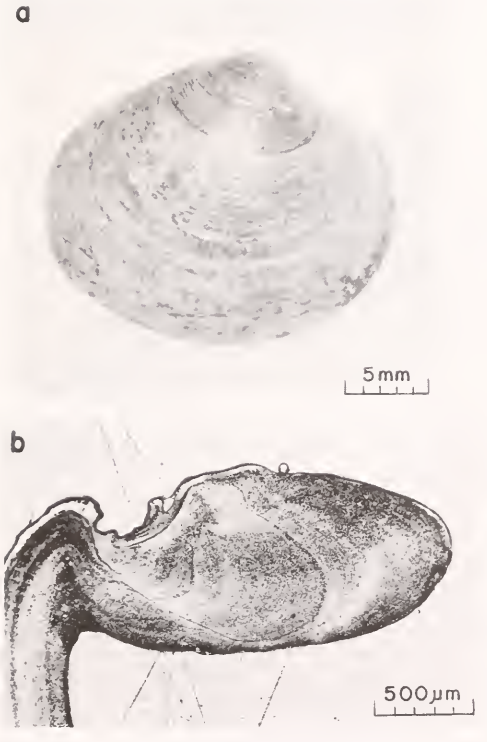

FIGURE 1.—(a) Right valve of a 3-yr-old ocean quahog, *Arctica islandica*, 20.0 mm shell length. (b) Photomicrograph of the acetate peel image of the hinge tooth showing three annuli.

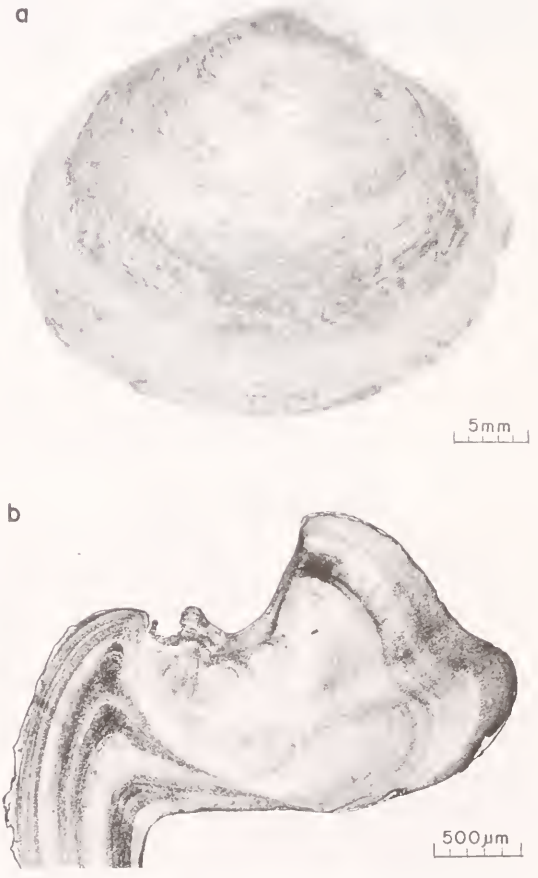

FIGURE 2.—(a) Right valve of a 6-yr-old ocean quahog, *Arctica islandica*, 31.1 mm shell length. (b) Photomicrograph of the acetate peel image of the hinge tooth showing six annuli.

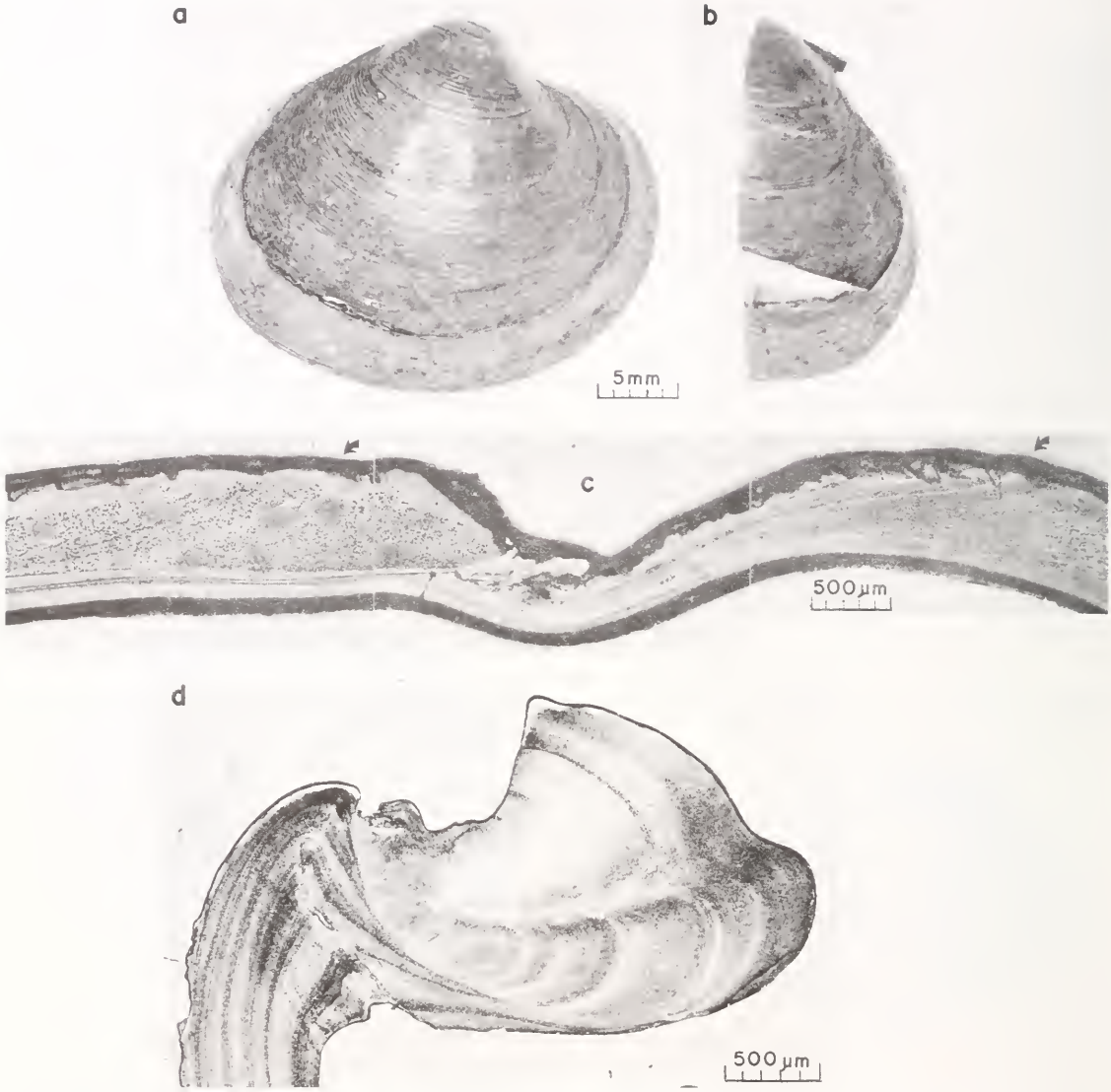

FIGURE 3.—(a) Right valve of a 6-yr-old ocean quahog, *Arctica islandica*, 33.1 mm shell length. (b) Sectioned anterior portion of the left valve showing injury. (c) Three serial photomicrographs of the acetate peel image. Arrows point to annuli formed before and after the injury. (d) Photomicrograph of the acetate peel image of the hinge tooth showing six annuli.

Size measurements at age of the clams are shown in Figure 6. The mean shell length, one standard deviation from the mean, and range are given for clams 3-8 yr old. The bands on the shells and lines in the peels indicated rapid growth through age 8. From age 3 and a mean size of 23.4 mm, the clams increased about 5 mm in shell length each year to age 8 and a mean size of 46.1 mm. Thereafter, growth seemed to decrease in rate. The bands were well separated to age 13. The bands at the ventral margin of 14-yr-old and older clams were too indistinct for accurate measurements, but the growth lines in peels were clearly separated and easily counted. The oldest 14- to 18-yr-old specimens may have been the smallest and slowest growing individuals in their year classes, but mean lengths were not progressively smaller than means for clams 9-13 yr old. Thus, a significant bias was not clearly indicated in the selection of older specimens.

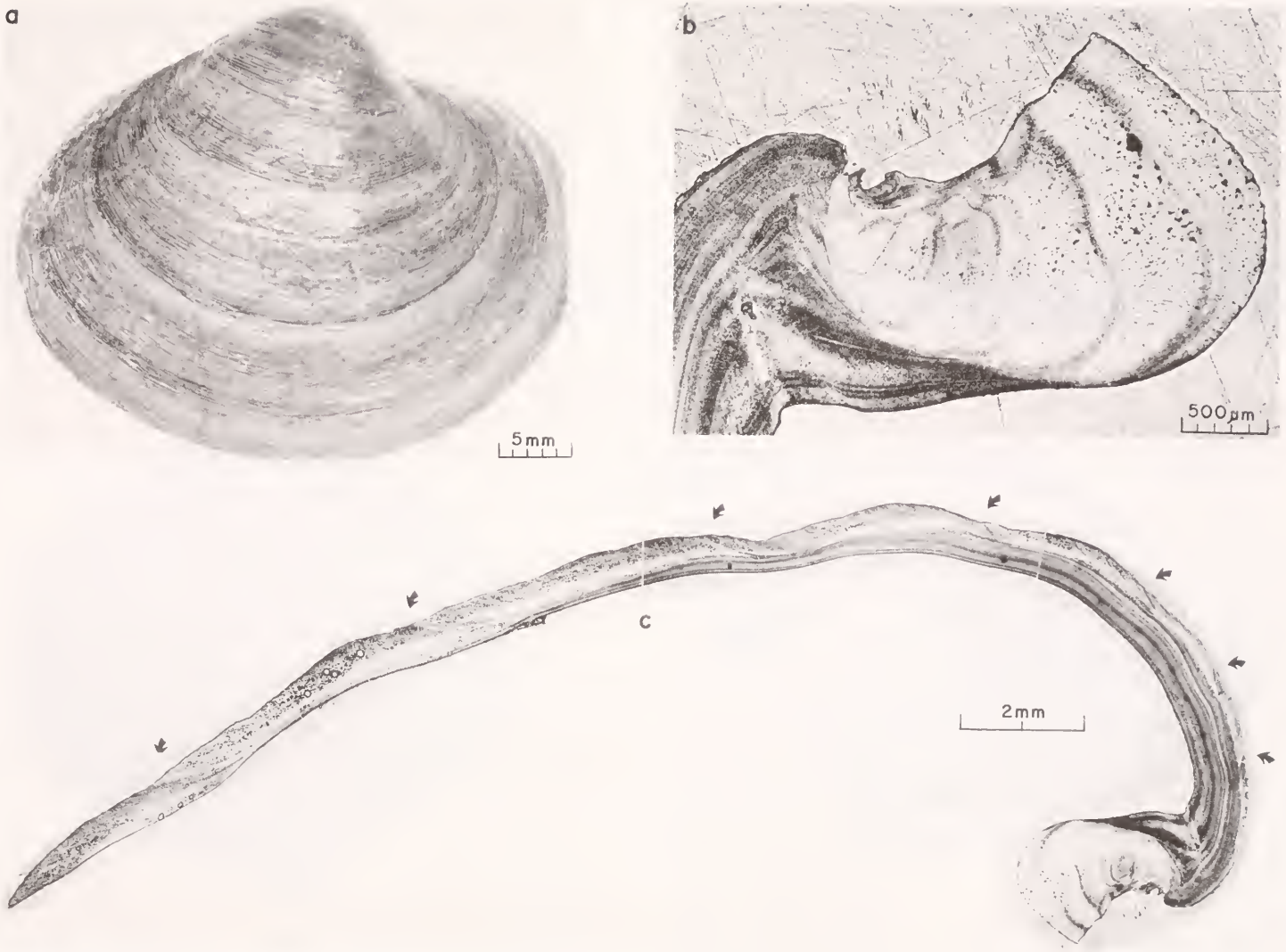

FIGURE 4.—(a) Right valve of a 7-yr-old ocean quahog, *Arctica islandica*, 35.6 mm shell length. (b) Photomicrograph of the acetate peel image of the hinge tooth showing seven annuli. (c) Four serial photomicrographs of the sectioned left valve with arrows pointing to annuli in the valve.

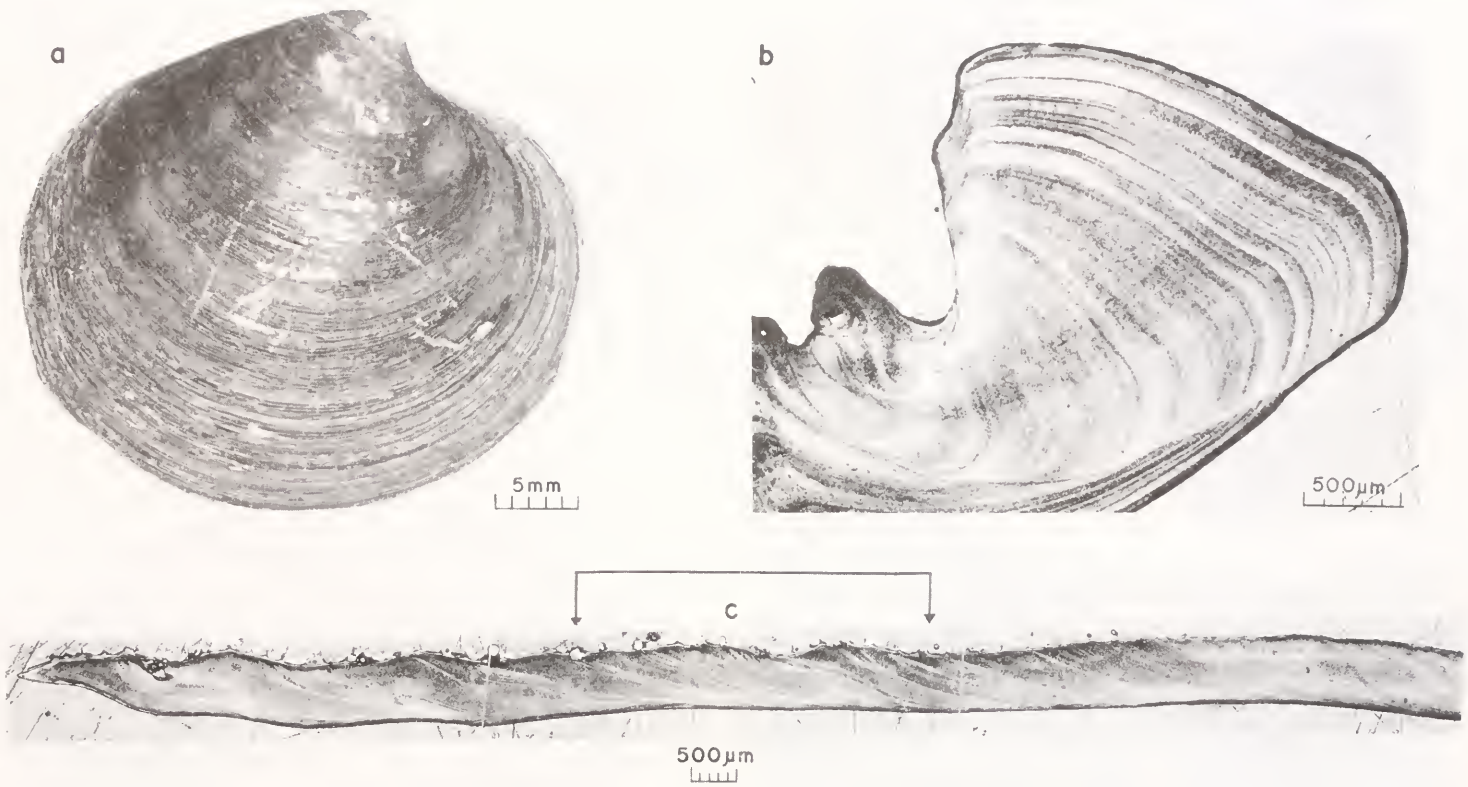

FIGURE 5.—(a) Right valve of a 40.0 mm shell length ocean quahog, *Arctica islandica*. (b) Photomicrograph of the acetate peel image of the hinge tooth. (c) Three serial photomicrographs of the acetate peel image of the sectioned valve at the ventral margin. Brackets show a zone of poorly defined and incomplete growth lines.

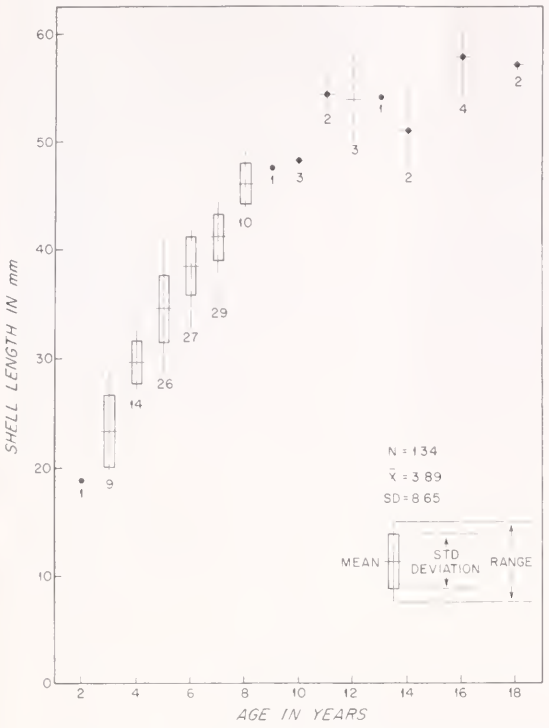

FIGURE 6.—Observed shell lengths at age of ocean quahogs, *Arctica islandica*, off Long Island, N.Y., late July-early August 1978.

Observations of Gonadal Condition

Gametogenesis

Gametogenesis in pelecypod molluscs exhibits similar basic characteristics. Each reproductive cycle begins with the production of the smallest, earliest cells at the basement membrane of follicles or alveoli. These infiltrate the lumina during maturation. Spermiogenesis through meiotic divisions is completed within male gonadal alveoli; oogenesis undergoes mitotic division of the oogonia and growth of the primary oocytes within the female gonadal alveoli. Oocytes may reach metaphase of the first meiotic division in the ducts of spawning females, but are blocked from completing maturation until after spawning and sperm penetration (Raven 1958). Most pelecypods expel the ripe cells into the surrounding environmental water where fertilization and larval development occur. A few pelecypods, and most notably female oysters of the genus *Ostrea*, are exceptions, since the eggs are held in the inhalent cavity during fertilization and initial developmental stages (Yonge 1960). A reproductive cycle corresponds to the initiation and completion of gametogenic stages and spawning. Single annual cycles have been described for many pelecypods, including the ocean quahog, although biannual and continuous cycles have been discribed for others (Sastry 1979). In some species, such as the ocean quahog, successive reproductive cycles begin at or soon after spawning; in others, activation of a cycle is delayed and the gonads are considered to be in a quiescent or resting stage (Sastry 1979). The latter condition frustrates determination of sex, since secondary sexual characteristics are generally lacking in most pelecypods.

Spermiogenesis

Spermatogonia about 5.5 μm in diameter are the initial germinal cells produced by male *Arctica islandica* during a mitotic phase of spermiogenesis. Successive meiotic stages follow and include primary and secondary spermatocytes (~3.7 and 4.0 μm in diameter, respectively), spermatids (~2.2 μm), and flagellated spermatozoa. The respective cells proliferate into the lumina of alveoli. Sperm have conical heads ~4.8 μm long.

Oogenesis

Oogonia are the initial germinal cells produced by female *Arctica islandica* during oogenesis. These are embedded in the basement membrane and are comprised of cytoplasm and a conspicuous nucleus or germinal vesicle with a basophilic nucleolus surrounded by a network of loose chromatin. The distinction between oogonia, spermatogonia, and other cells in the basement membrane is not obvious. Primary oocytes begin protruding from the basement membrane into the lumina of alveoli and retain an attachment with it during the growth stage. The large spherical, vesicular nucleus of primary oocytes is surrounded by a coarse cytoplasm containing granules of the golgi apparatus and acidophilic granules of proteid yolk (Raven 1958; Kennedy and Battle 1964). The nucleolus differentiates into an amphinucleolus with maturation. Mature oocytes appear free in the lumina of alveoli and are often of irregular shape and have a distinct vitelline membrane. Measurements of the diameter of 50 clearly spherical oocytes that were sectioned through the nucleus and amphinucleolus ranged from 49.4 to 65.0 μm and averaged 56.6 μm.

Thirty-six gonadal tissues were in an undif-

ferentiated condition (Table 1, Fig. 7a, b). Gonadal tubules were of small diamater, few in number, and surrounded by an abundant loose vesicular connective tissue. Gonia embedded in the germinal epithelium lacked definite cellular structures for sex determinations. The lumina of tubules were empty.

Sex determinations were possible for 97 quahogs, but in most (69) the gonads appeared to be in an intermediate stage and not fully developed. These latter tissues were separated into two categories: Those with either sparse or moderate tubule development.

Differentiated gonads with sparse tubule development were characterized by a limited number of gametogenic cells, as well as a limited number of tubules. The 16 male tissues examined were producing a few sperm; the 4 female tissues examined were producing a few oocytes. Abundant loose vesicular connective tissue occurred between the widely spaced gonadal tubules. In males, spermatogenic cells at the germinal epithelium were about one layer thick, but were absent in portions of the epithelium (Fig. 8a, b). Some sperm were in close contact with the spermatogenic cells and a few were scattered in the lumina of tubules. In females, the few small oocytes occurred at the germinal epithelium, none were in the tubule lumina, and all were in an early developmental stage (Fig. 8c, d).

For differentiated gonads with moderate tubule development, 39 males examined were producing sperm, while 10 females examined were producing oocytes. The gonadal tubules were more numerous than in gonads of sparse tubule condition, and some exhibited an expanded alveolar condition. Loose vesicular connective tissue clearly separated the tubules. In males, several layers of spermatocytes proliferated from the germinal epithelium with some sperm forming a fringe extending toward the empty lumina; however, portions of the germinal epithelium in some tubules

TABLE 1.—Gonadal condition relative to age, sex, and size of three categories of ocean quahogs, *Arctica islandica*—sexually immature, intermediate, and mature—off Long Island, N.Y., late July-early August 1978. M = male; F = female.

	No. clams (%)							
		Intermediate						
		Tubule development						
	Immature (undifferentiated)	Sparse		Moderate		Mature		Total no.
		M	F	M	F	M	F	
Age (yr)								
2	1(0.8)							1
3	4(3.0)	2(1.5)		2(1.5)				8
4	7(5.3)	5(3.7)		2(1.5)				14
5	11(8.2)	4(3.0)	1(0.8)	9(6.7)		1(0.8)		26
6	9(6.7)	3(2.2)	(1.5)	10(7.5)		2(1.5)	1(0.8)	27
7	3(2.2)	2(1.5)	1(0.8)	12(9.0)	9(6.7)	2(1.5)		29
8	1(0.8)			3(2.2)	1(0.8)	5(3.7)		10
9						1(0.8)		1
10				1(0.8)		2(1.5)		3
11						1(0.8)	1(0.8)	2
12						1(0.8)	2(1.5)	3
13						1(0.8)		1
14						1(0.8)	1(0.8)	2
15								
16							4(3.0)	4
17								
18						2(1.5)		2
Age range	2-8	3-7	5-7	3-10	7-8	5-18	6-16	2-18
Mean	5.03	4.63	6.00	6.08	7.10	9.79	13.22	6.71
Shell length (mm)								
20	2	0	0	0	0	0	0	2
20-29	8	4	0	3	0	0	0	15
30-39	16	9	3	18	2	2	0	50
40-49	10	3	1	18	8	12	1	53
50-59	0	0	0	0	0	5	6	11
>59	0	0	0	0	0	0	2	2
Length range	19-46	21-44	36-42	20-48	39-45	36-58	41-60	19-60
Mean	34.4	33.8	38.4	37.2	41.8	47.1	55.0	39.0
Total no.	36(27.1)	16(12.0)	4(3.0)	39(29.3)	10(7.5)	19(14.3)	9(6.8)	[1]133

[1]The tissues of a 21.1 mm, 3-yr-old clam were too poorly prepared for examination.

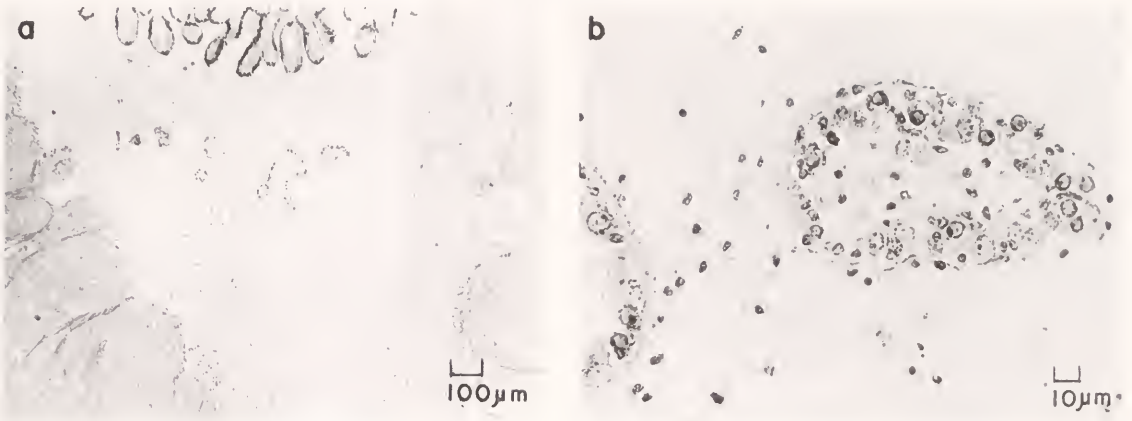

FIGURE 7.—(a) Undifferentiated gonadal tissue section from a 5-yr-old ocean quahog, *Arctica islandica*, 37.2 mm shell length. (b) Enlargement of a gonadal tubule from the same clam.

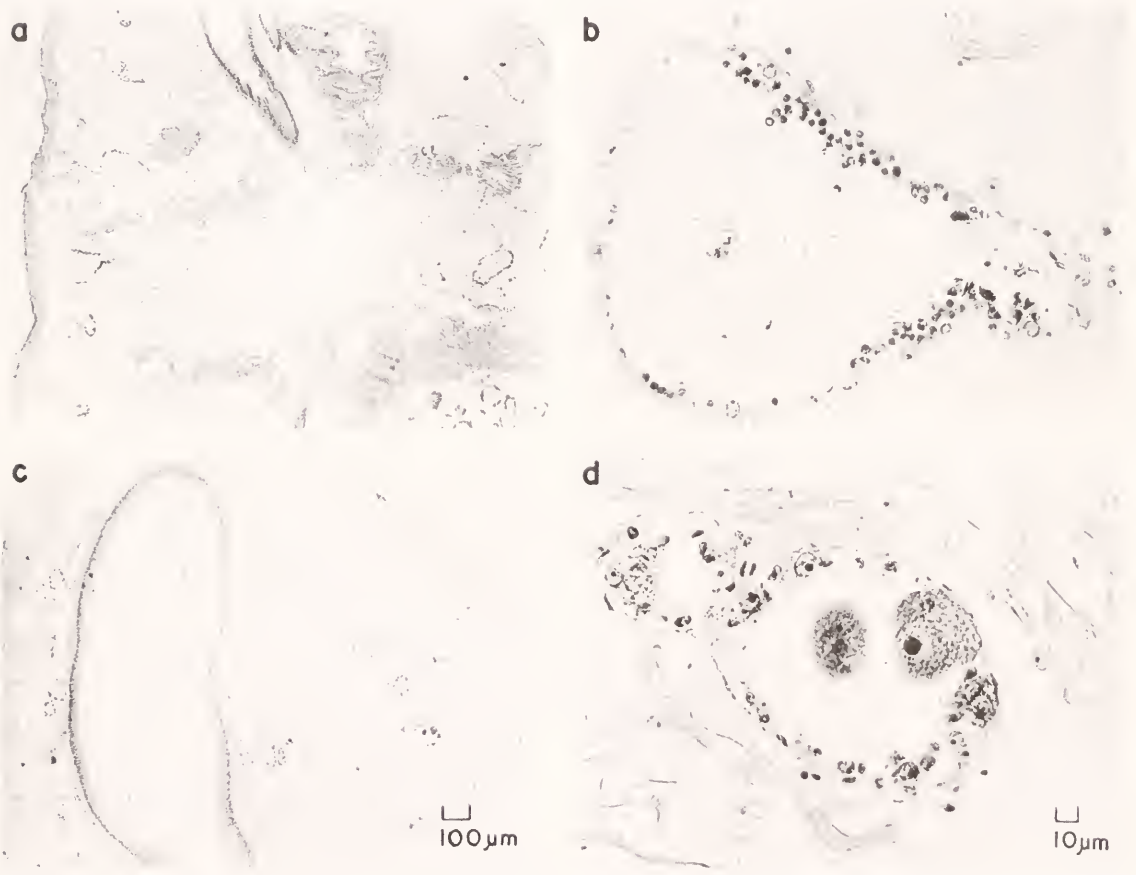

FIGURE 8.—(a) Differentiated gonadal tissue section in the sparse condition from a 3-yr-old male ocean quahog, *Arctica islandica*, 21.0 mm shell length. (b) Enlargement of spermiogenesis in a portion of a gonadal tubule. (c) Differentiated gonadal tissue section in the sparse condition from a 5-yr-old, 37.5 mm shell length, ocean quahog. (d) Enlargement of oogenesis in a gonadal tubule.

again lacked obvious spermatogenic cells (Fig. 9a, b). Oocytes in females were at the same stage of development as seen for females with sparse gonadal tubules, but more were growing from the germinal epithelium and some portions of the germinal epithelium lacked obvious oogenic cells (Fig. 9c, d).

The sexually mature condition was found in 19 males and 9 females. In these quahogs the tubules were greatly expanded and filled the gonadal area; little connective tissue occurred between adjacent tubules. Developmental stages similar to those described for other bivalves by Ropes and Stickney (1965) were recognized. Two males and one female were in an early gonadal condition. Spermiogenesis and oogenesis had cellular characteristics as in gonads of moderate tubule development, but the tubules were more numerous and crowded together. Six males were in a late gonadal condition. Primary and secondary spermatocytes and spermatids were proliferating from the germinal epithelium, filling about half of the tubules and sperm crowded into the lumina. No females were found in the late gonadal condition, but 11 males and 2 females were in an advanced late stage. In males, spermatocytes and spermatids proliferated from the germinal epithelium and sperm predominated in the lumina of the tubules (Fig. 10a, b). In females, oocytes crowded into the lumina of tubules and a few seemed to be attached to the germinal epithelium. No ripe males and only six ripe females with numerous ripe oocytes crowding into the tubules were found (Fig. 10c, d). The potential for developing large numbers of germinal cells was most evident and indicative of full sexual maturity in all of these quahogs.

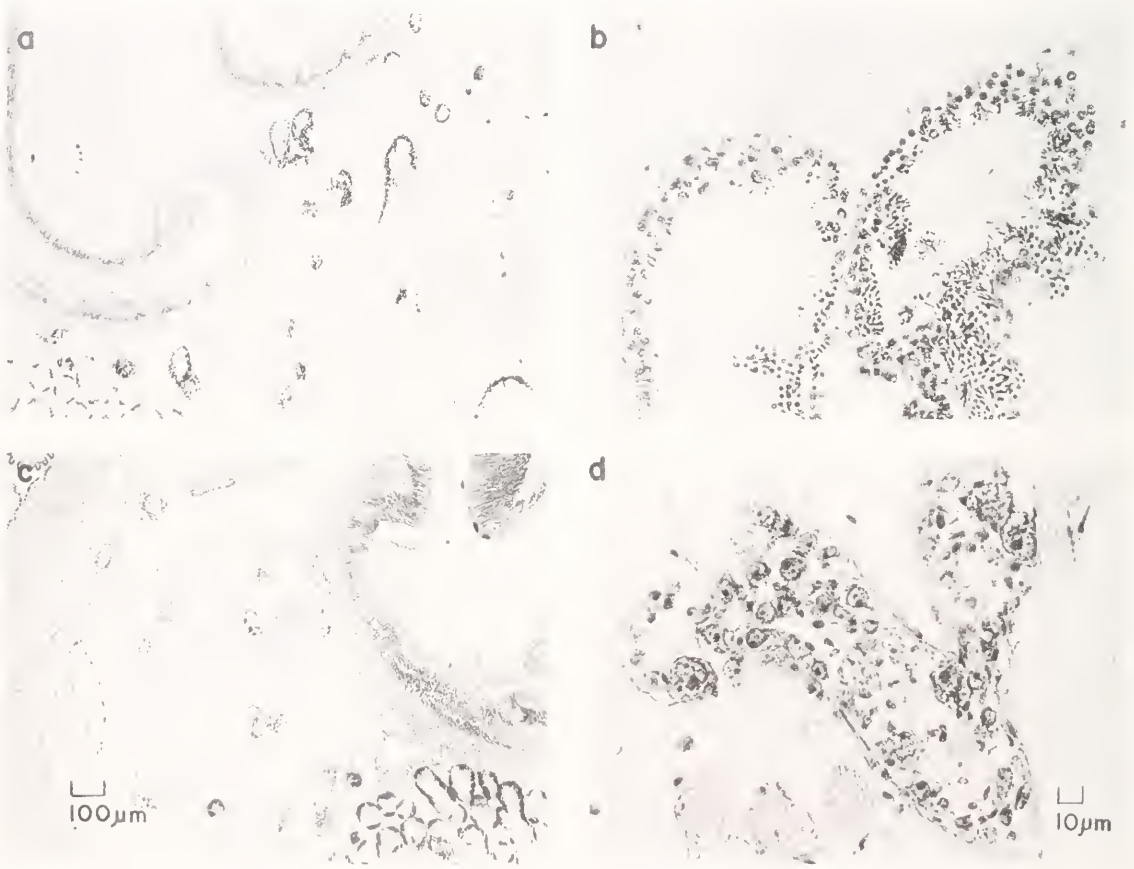

FIGURE 9.—(a) Differentiated gonadal tissue section in the moderate condition from a 7-yr-old ocean quahog, *Arctica islandica*, 42.9 mm shell length. (b) Enlargement of spermiogenesis in a portion of a gonadal tubule. (c) Differentiated gonadal tissue section in the moderate condition from an 8-yr-old female ocean quahog, 43.3 mm shell length. (d) Enlargement of oogenesis in a portion of a gonadal tubule.

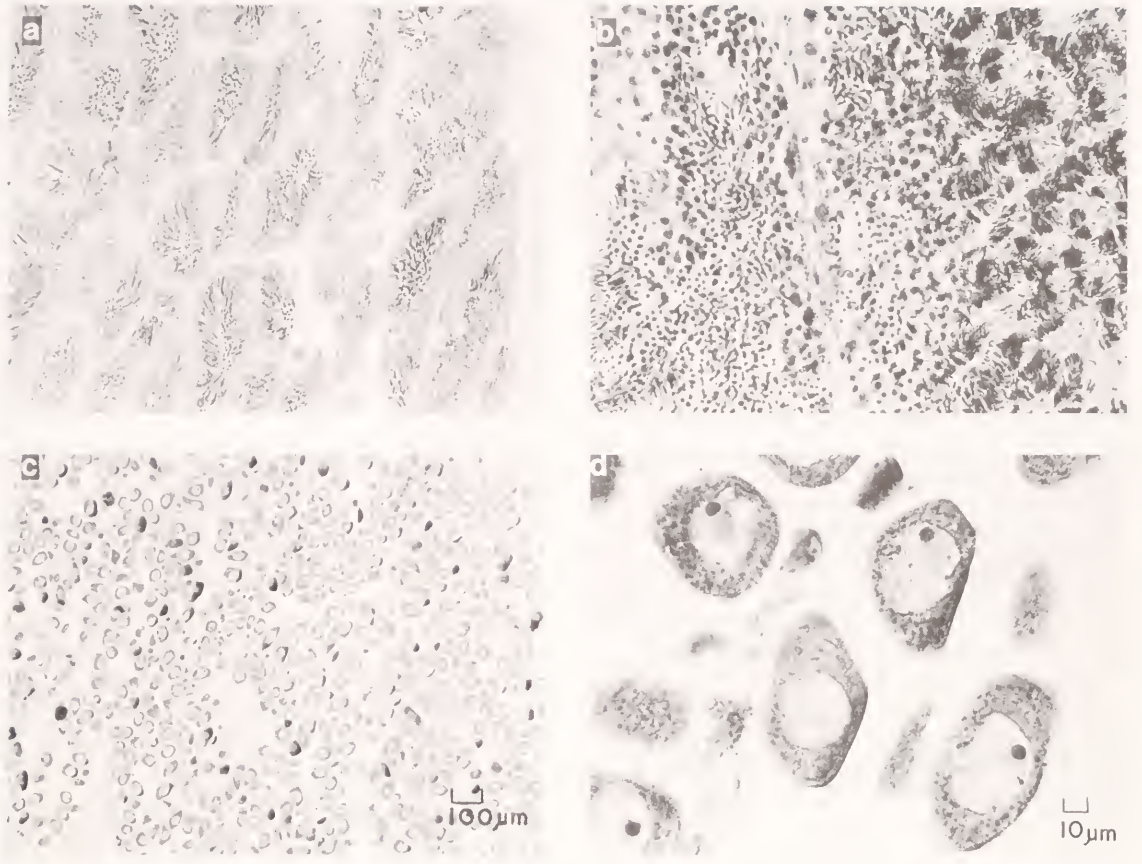

FIGURE 10.—(a) Differentiated gonadal tissue section in the mature condition from an 18-yr-old male ocean quahog, *Arctica islandica*, 57.8 mm shell length. (b) Enlargement of spermiogenesis in a portion of a gonadal tubule. (c) Differentiated gonadal tissue section in the mature condition from a 16-yr-old female quahog, 59.8 mm shell length. (d) Enlargement of ripe oocytes in a tubule.

Gonadal Condition vs. Size and Age

In an analysis of gonadal condition relative to age and size, quahogs in the undifferentiated, immature condition ranged from 2 to 8 yr old, averaged 5.0 yr old, and were from 19 to 46 mm long and averaged 34.4 mm (Table 1). This condition was found in 27% of the gonads in the sample.

For the three types of differentiated gonads, quahogs with sparse tubule development comprised 15% of the sample. Males ranged from 3 to 7 yr old, averaged 4.6 yr old, and were from 21 to 44 mm long and averaged 33.8 mm; females ranged from 5 to 7 yr old, averaged 6.0 yr, and were from 36 to 42 mm long and averaged 38.4 mm. This category contained the smallest and youngest female in the sample: 38 mm long and 5 yr old.

Quahogs with moderate tubule development comprised 37% of the sample. Males ranged from 3 to 10 yr old, averaged 6.1 yr, and were from 20 to 48 mm long and averaged 37.2 mm; females ranged from 7 to 8 yr old, averaged 7.1 yr, and were from 39 to 45 mm long and averaged 41.8 mm. This category contained the smallest and youngest male in the sample, which was 20 mm long and 3 yr old (Fig. 1a, b).

Sexually mature quahogs comprised 21% of the sample. Males ranged from 5 to 18 yr old, averaged 9.8 yr, and were from 36 to 58 mm long and averaged 47.1 mm; females ranged from 6 to 16 yr old, averaged 13.2 yr, and were from 41 to 60 mm long and averaged 55.0 mm. The smallest mature quahog found was a male 36 mm long and 6 yr old, although a 5-yr-old, 41 mm long male was also mature; the smallest and youngest mature female found was 41 mm long and 6 yr old.

None of the gonads contained germinal cells

suggestive of ambisexuality. This is consistent with the conclusion of Loosanoff (1953) that the sexes are separate. The sex ratio, however, was particularly imbalanced in favor of males. In the 69 quahogs considered less than fully mature, 55 were males and 14 were females, while in the 28 sexually mature specimens, 19 were males and 9 were females; the observed ratios were 4:1 and 2:1, respectively. The data were subjected to goodness of fit tests under the hypothesis of a 1:1 ratio between the sexes; results indicated highly significant ($P < 0.01$) and significant ($P < 0.05$) differences, respectively.

Microscopic examinations of gonadal tissue squashes of the 199 clams collected in 1980 revealed an overall sex ratio of 96 males and 103 females. These results were not significantly different from parity (1 male:1.07 female), but by separating the data into 10 mm size groups, a significant difference ($P < 0.05$) in favor of males was indicated in the size group 80-89.9 mm, and a highly signficant difference ($P < 0.01$) in favor of females was indicated in the 100-110 mm size group (Table 2).

Figure 11 shows the combined observations of clam size and sex obtained from the 1978 and 1980 samples. In these samples, males tended to decrease in occurrence relative to females with increasing shell size.

TABLE 2.—Occurrence of male and female ocean quahogs, *Arctica islandica*, within 10 mm size groups off Long Island, N.Y., August 1980.

Size group (mm)	Number	
	Males	Females
50-59	4	0
60-69	44	32
70-79	12	21
80-89	16	5
90-99	19	33
100-109	1	12
Total	96	103

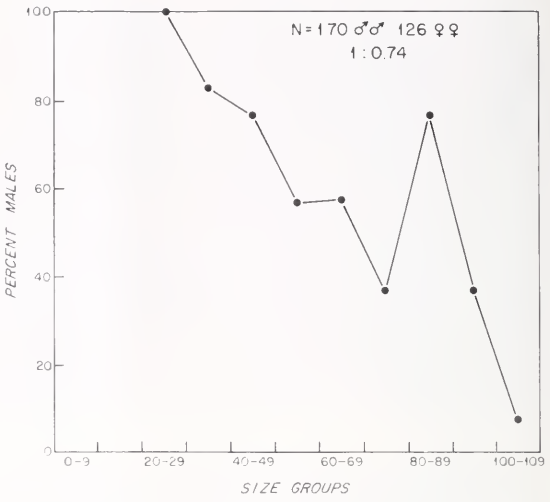

FIGURE 11.—Sex of ocean quahogs, *Arctica islandica*, relative to shell length (mm) in collections off Long Island, N.Y., 1978 and 1980.

DISCUSSION

The time of sampling, sample size, and capture of small quahogs provided a basis for detection of the differentiated and sexually mature stage at younger ages and smaller sizes as compared with the study of Thompson et al. (1980b). In the present study, 5- and 6-yr-old quahogs 41 and 36 mm long, respectively, were considered sexually mature; the youngest mature quahog reported by Thompson et al. (1980b) was a 42 mm male 11 yr old. The intermediate gonadal condition was found to occur at lower ages and smaller sizes than by Thompson et al. (1980b), and slightly smaller sizes were found for sexually mature quahogs. Variability in attainment of sexual maturity at age/size was observed in both studies.

The onset of sexual maturity at young ages has been reported for several bivalves. The bay scallop, *Argopecten irradians*, attains maturity at 1 yr; the hard clam, *Mercenaria mercenaria*, soft clam, *Mya arenaria*, and blue mussel, *Mytilus edulis*, matures at 1-2 yr (Altman and Dittmer 1972). Surf clams, *Spisula solidissima*, from an inshore habitat showed precocious sexuality in a few postlarvae or juveniles; they spawned at 1 yr, but reached full maturity at 2 yr (Ropes 1979a). Sea scallops, *Placopecten magellanicus*, spawned at about 1.5-2 yr after forming the first growth ring (Naidu 1970). In apposition to more mature gonadal conditions, some scallops in his collections were considered undifferentiated and differentiated male and female immature specimens. Lucas (1966) observed precocious sexuality in a scallop (*Chlamys varia*) and two clams (*Glycymeris glycymeris* and *Venus striatula*) from waters off France. The development of the reproductive potential during the early life history of these several bivalves seems consistent with estimates of their life span, which are as short as 2 yr for the bay scallop and as long as 30 yr for the surf clam (Belding 1906; Ropes 1979a). In contrast, the present study revealed that ocean quahogs attain maturity at 5-10 yr of age, and Thompson et al.

(1980a) reported a longevity of about 150 yr. They found that growth was vigorous at old age and that there were no obvious indications of reproductive senility. A small abyssal nuculoid bivalve, *Tindaria callistiformis*, studied by Turekian et al. (1975) seems most exceptional with regard to age and size at sexual maturity. They found a longevity of about 100 yr for a large specimen (8.4 mm shell length) by radiometric techniques and counts of shell growth bands, but gonadal development was not recognized until the clams were about 4 mm long and 50-60 yr old. The attainment of sexual maturity about midway in the life span of *Tindaria* sets it apart from other species that reproduce at a younger age. Nevertheless, all have the potential to reproduce for many years. Reproduction during a long life span of a species may be an evolutionary strategy in response to uncertain larval and juvenile survival (Krebs 1972). Reproduction during a particularly long life span is most obvious for *Arctica islandica*.

For the 69 gonads containing sexually differentiated germinal cells and sparse-to-moderate tubule development, some morphologically ripe sperm were present. In contrast, oogenesis never exceeded an early developmental state. Jones (1981), Loosanoff (1953), von Oertzen (1972), and Mann (1982) reported that mature ocean quahogs spawn each year. Thus, the sperm may be spawned, but the fate of the oocytes remains an enigma. In American oysters, *Crassostrea virginica*, germinal cells remaining in the gonads after spawning are reabsorbed (Galtsoff 1964), but viable, nearly ripe, or ripe germinal cells may be retained by hard clams throughout the fall, winter, and into the following spring (Loosanoff and Davis 1951). Thus, bivalves appear to differ greatly in this respect. No conclusion can be drawn relative to retention of germinal cells after spawning for ocean quahogs which were intermediate between the immature and mature condition in the absence of collected data.

Gonadal development in 28 mature clams suggested that many (46%) were approaching ripeness or were ripe (21%). Later development probably resulted in a spawning which was begun in late August-September. This seems reasonable based on observations by Mann (1982) of the reproductive cycle of *Arctica islandica* from sample locations in Block Island Sound. At the beginning of his study in September 1978, most (69%) were in the partially spent or spent condition and spawning was indicated until mid-November. An exact correspondence of the time and duration of spawning may be a hazardous assumption, since the two sample sites are about 110 km apart and some of the samples taken by Mann (1982) were at shallow depths (36 m).

A disparity in the initiation of gametogenesis was observed between the sexes. Male ocean quahogs began producing germinal cells at a smaller size and younger age than females. This suggests that females require a longer period of development and growth. The later development of female sexuality is a probable explanation for the highly significant difference obtained in tests of the sex ratio of quahogs in the intermediate gonadal condition. The significant difference observed for fully mature quahogs may be due to the small number in the sample (Dixon and Massey 1957), but Jones (1981) observed a similar disparity ($P = 0.008$) for quahogs > 75 mm from offshore New Jersey. In his collections 184 were males and 136 were females, a ratio of 1:0.74. Mann (1982) examined ocean quahogs that were mostly 80-100 mm long and found 185 males and 169 females, a ratio of 1:0.91. These observations suggest that spatial variation may occur in the sex ratio of ocean quahog populations, but that males are more numerous than females.

Pelseneer (1926) investigated the sex ratio of several mollusc species, including bivalves. He found more females among the older individuals of some populations and the converse among younger individuals. Coe (1936) recognized the existence of such disparities in molluscs and proposed the following hypotheses as possible explanations: 1) That males have a shorter longevity than females, because of a differential mortality rate or less resistance to unfavorable environmental conditions; 2) that the development of alternative sexual conditions is environmentally determined; and 3) that sex change may occur. Loosanoff (1953), von Oertzen (1972), Thompson et al. (1980b), and Jones (1981) all considered the species to be strictly dioecious, as did Mann (1982), although he found two hermaphrodites. These are anomalous, "accidental functional hermaphrodites" by the terminology of Coe (1943). Although Sastry (1979) hypothesized that a failure in the genetic sex-differentiating mechanism may produce some hermaphrodites, he found no evidence of a phenotypic or genetic basis for sex determination in pelecypods.

It is unlikely that ocean quahogs are protandric. This condition in a typically hermaphroditic species is characterized by the development of male organs or maturation of their products before

the appearance of corresponding female products. In *Ostrea lurida*, for example, spermatogonia are proliferated first throughout the follicles, but before the sperm mature oogonia have developed into numerous oocytes in the same follicles and the gonad has a definite intersexual character (Coe 1932). More than 90% of the young oysters exhibit the bisexual condition and no strictly male or female specimens occur. Old oysters in the female phase retain sperm balls and spermatogonia, and those in the male phase retain large and small oogonia. The two anomalous ocean quahogs found by Mann (1982) were examples of bilateral hermaphroditism, i.e., the germinal cells for each sex were in separate follicles. None of the investigators of the reproductive cycle in ocean quahogs suggested finding ambisexual conditions (Loosanoff 1953; von Oertzen 1972; Jones 1981; Mann 1982). Thus, the characteristic germinal cell development for protandry is lacking in ocean quahogs.

Sex reversal in some molluscs has been linked to castration from parasites invading the gonads, but evidence of causality was considered inconclusive by Noble and Noble (1961) and Malek and Cheng (1974). Except for the occurrence of the commensal nemertean, *Malacobdella grossa*, in ocean quahogs (Gibson 1967; Jones 1979), parasites in the species have not been reported (Ropes and Lang 1975)[4]. The causality of hermaphroditism in ocean quahogs, then, remains uncertain and evidence is unavailable that sex may be environmentally determined.

The hypothesis that female ocean quahogs may live longer than males has some support from determinations of the sex of specimens recovered from the marking site in August 1980. Based on predicted ages of ocean quahogs at the marking site reported by Murawski et al. (1982), the largest and oldest notched ocean quahogs were predominantly female. Since this may be atypical for the extensive population of ocean quahogs inhabiting the Middle Atlantic Bight, samples from other locations are being examined to determine possible spatial variations.

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FOOD HABITS AND DIETARY OVERLAP OF SOME SHELF ROCKFISHES (GENUS *SEBASTES*) FROM THE NORTHEASTERN PACIFIC OCEAN

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ABSTRACT

Euphausiids were the major food of five co-occurring species of rockfishes (*Sebastes* spp.) along the west coast of North America from Vancouver Island to northern California. Copepods, decapods, cephalopods, amphipods, fishes, and other pelagic prey were also consumed but were less important to the overall diet. Two species, *S. flavidus* and *S. diploproa*, were relatively euryphagous, utilizing a high number of prey taxa. The other species, *S. pinniger*, *S. alutus*, and *S. crameri*, had a more restricted diet comprised mostly of euphausiids. The numerical composition of prey in the diet of all species was similar due to the preponderance of the two dominant euphausiid species. Diet overlaps based on weight composition were high for *S. pinniger*, *S. diploproa*, and *S. alutus* but were moderate for most comparisons involving *S. flavidus* and *S. crameri*.

The diets of *S. flavidus* and *S. pinniger* were examined in more detail to explain some of the variability associated with their food habits. Both species exhibited peak feeding periods at the same time during the day. They consumed about the same mean size of prey, although *S. flavidus* consumed a wider size range of prey. Size of prey and dietary composition did not vary much with size of fish. There were significant seasonal, geographical, and diel differences in food composition for both species, which may be a function of varying food availability.

Factors that allow coexistence of a large number of morphologically similar species have been the focus of numerous studies and continued debate in the ecological literature. Competition and resource partitioning have been reviewed in general by Schoener (1974), and for fishes by Helfman (1978). Potential competition for resources is thought to be most common in three aspects of the ecological niche in fish communities: habitat, food, and time of activity (Tyler 1972; Bray and Ebeling 1975; Ross 1977; Werner 1979; Larson 1980; McPherson 1981).

Rockfishes (*Sebastes* spp.) of the family Scorpaenidae are, a priori, interesting subjects for examining the various modes of resource partitioning. This genus is extremely speciose, with about 100 species reported from the North Pacific Ocean. At least 69 of these species are known to occur in the eastern North Pacific (Chen 1975). In addition to the large number of species, rockfishes also exhibit a high degree of overlap in their geographical distributions, with as many as 50 species occurring in a narrow latitudinal band (lat. 34°-38° N) off central California (Chen 1971). Several of these congeners are morphologically similar and occupy similar habitats, so the potential for resource overlap and competition is high (Larson 1980).

Many of these species are abundant enough and of sufficient size to contribute substantially to commercial trawl landings in the northeastern Pacific (Alverson et al. 1964; Alton 1972; Gabriel and Tyler 1980; Gunderson and Sample 1980). Despite their abundance in the northeastern Pacific, relatively few quantitative studies exist on rockfish feeding habits. Most of the studies to date have dealt with shallow-water, neritic species often taken in recreational fisheries or accessible to in situ observations and sampling by scuba divers (Gotshall et al. 1965; Larson 1972; Hobson and Chess 1976; Love and Ebeling 1978). Descriptions of the diet of offshore species of *Sebastes* generally either lack taxonomic or quantitative detail (Phillips 1964) or encompass limited geographical area or collection times (Pereyra et al. 1969; Lorz et al. 1983). Skalkin (1964) and Somerton et al. (1978)[2] described food habits of rockfishes from the Bering Sea and Gulf of Alaska, far

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[2]Somerton, D., F. Funk, K. Mesmer, L. J. Bledsoe, and K. Thornburgh. 1978. A comparative study of the diets of Pacific ocean perch (*Sebastes alutus*) and walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska. NORFISH Tech. Rep. NPB8, Wash. Sea Grant, 25 p.

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north of our study area which extends from off northern California to off Vancouver Island, British Columbia.

This study represents the first attempt to examine broad geographical and seasonal patterns in food utilization and overlap by several commercially important species of rockfish on the outer continental shelf. The species considered include the yellowtail rockfish, *Sebastes flavidus*; canary rockfish, *S. pinniger*; Pacific ocean perch, *S. alutus*; splitnose rockfish, *S. diploproa*; and the darkblotched rockfish, *S. crameri*, all important members of the demersal shelf rockfish complex (Gabriel and Tyler 1980). In addition, variability in the diet of two of these species, *S. flavidus* and *S. pinniger*, was examined for the purpose of determining the effects of factors such as season, geographic area, time of capture, and predator size.

MATERIALS AND METHODS

Sampling Methods

The food utilization patterns of the five rockfish species were determined by examining stomach contents. Fishes were obtained by two different survey methods (hereafter referred to as the summer and seasonal surveys). As the collection methods differ, they will be discussed separately. The laboratory methods are similar and will be presented together.

Summer Survey Methods

Collections for the summer survey were made during the National Marine Fisheries Service (NMFS) 1980 West Coast Survey which took place from 12 July to 28 September 1980. The purpose of this survey was to assess the distribution and abundance of commercially important rockfishes. The area encompassed by the survey included much of the continental shelf and inner slope (ranging in depth from 55 to 366 m) between Monterey, Calif., (lat. 36°48′ N) and the northern end of Vancouver Island, British Columbia (lat. 50°00′ N). Two commercial stern trawlers, the FV *Mary Lou* and the FV *Pat San Marie*, were utilized for the survey. A Nor'Eastern[3] high-opening bottom trawl with an estimated 13.4 m horizontal and an 8.8 m vertical mouth opening was used on both vessels. The main body was constructed of 127 mm stretched mesh with 89 mm mesh in the cod end. The cod end also contained a 32 mm mesh liner. Half-hour tows were made at random depth-stratified stations chosen by a method described in Gunderson and Sample (1980).

The majority of the stomach samples used in this study were collected in August and September from north of lat. 43°N (Table 1, Fig. 1). Complete station data are given in Brodeur (1983).

Stomachs were removed at sea from a random subsample of the catch of the five target species (Table 1). *Sebastes pinniger* and *S. flavidus* were the primary target species, and stomachs of these species were collected first and the other species sampled as time allowed. Altogether, 480 stomachs were collected during the survey, all from adult fish (>200 mm FL). Fork length (measured to the nearest millimeter) and sex were recorded for all fish sampled, and stomachs were then removed, individually wrapped and labeled, and preserved in a 10% Formalin-seawater mixture. The intestinal tracts of many of the fish were examined at sea but few contained any recognizable food and none were retained. Total elapsed time between bringing the fish on board and preserving the stomachs was <1 h. The oral cavities of all fish were examined for signs of stomach eversion and regurgitation; any fish showing such signs were discarded. Individual fish weights were not recorded at sea but were later calculated using the length-weight relationships of Phillips (1964).

TABLE 1.—Number of rockfish stomachs analyzed from the 1980 National Marine Fisheries Service summer survey. The approximate latitudinal ranges covered by each leg were I, lat. 37°-42°N; II, lat. 43°-46°N; III, lat. 46°-50°N.

Leg	Sampling dates	Species	Number
I	12-20 July	*S. pinniger*	9
		S. flavidus	8
			17
II	4-29 Aug.	*S. pinniger*	85
		S. flavidus	127
		S. alutus	54
		S. diploproa	52
		S. crameri	30
			348
III	4-28 Sept.	*S. pinniger*	36
		S. flavidus	50
		S. alutus	19
		S. diploproa	10
			115
		Total number analyzed	480

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

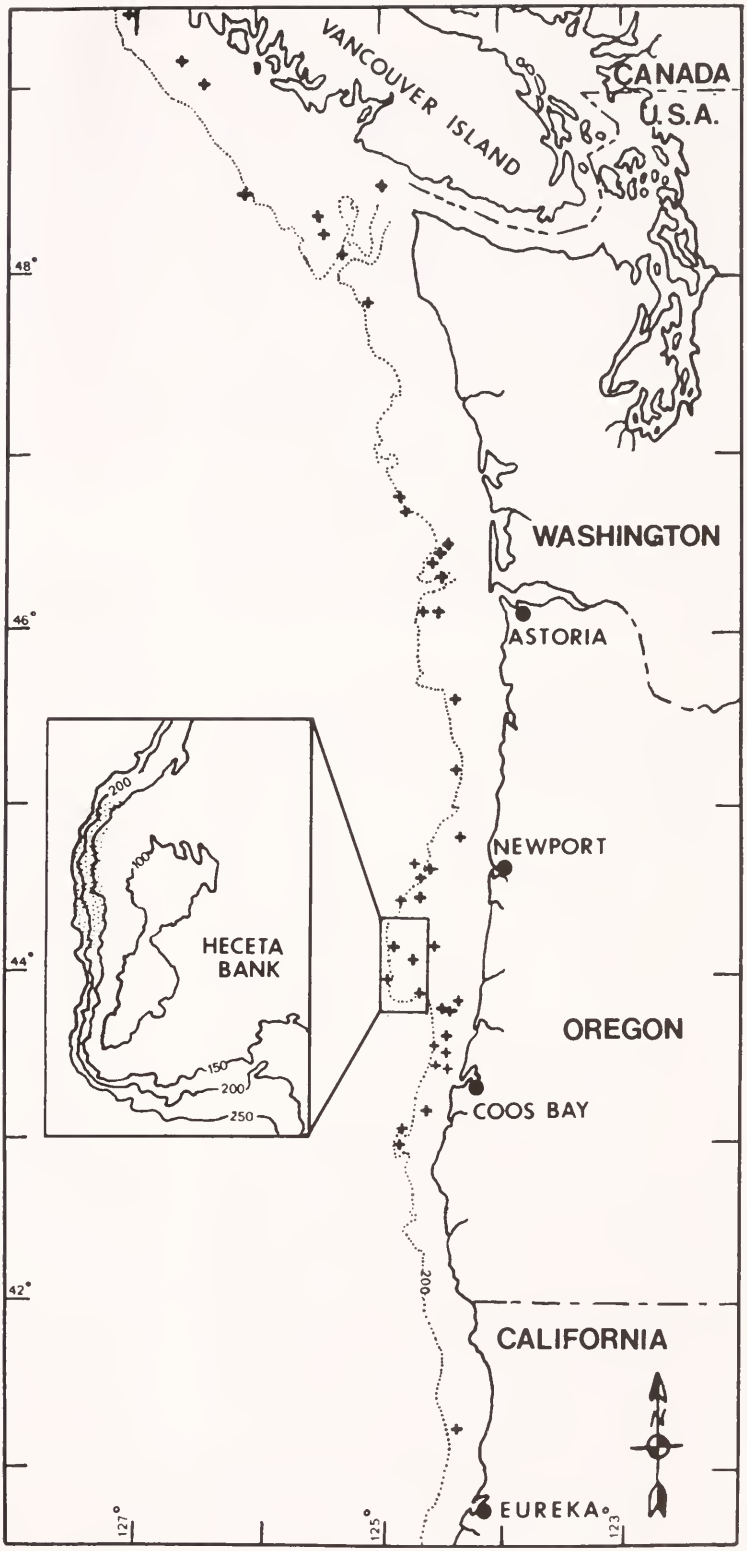

FIGURE 1.—Location of sampling stations from which stomach collections were taken. + sign denotes collections made during the National Marine Fisheries Service's summer survey and the stippled area (inset) shows the sampling area on Heceta Bank of the Oregon Department of Fish and Wildlife's seasonal collections. All depth contours are in meters.

Seasonal Survey Methods

Stomachs for the seasonal study were collected during rockfish surveys conducted by the Oregon Department of Fish and Wildlife (ODFW) on Heceta Bank off the central coast of Oregon. These surveys obtained hydroacoustic and environmental data along with the trawl catches. A total of 317 stomach samples was collected during seven surveys conducted in 1980-81 (Table 2). All surveys used trawling gear similar to that used in the summer surveys.

Locations of the tows were chosen on the basis of high concentrations of fish found during acoustic surveys over the outside edge of Heceta Bank between lat. 44°20′N and 44°00′N between the 128 m and 238 m bathymetric contours (inset, Fig. 1). The duration of tows was variable but averaged < 1 h. No tows were attempted at night because of the lack of acoustical targets near the bottom at this time. Stomachs were collected as described earlier.

TABLE 2.—Number of rockfish stomachs analyzed from the seasonal Oregon Department of Fish and Wildlife collections on Heceta Bank. All dates are in 1980 unless otherwise noted.

Vessel	Cruise	Sampling dates	Species	Number
Ronnie C	I	23-24 April	*S. pinniger*	42
Bay Islander	I	17-18 June	*S. pinniger*	24
Queen Victoria	I	15-16 July	*S. pinniger*	47
			S. flavidus	16
Ronnie C	II	26-28 Sept.	*S. pinniger*	60
			S. flavidus	23
New Life	I	27 Oct.	*S. pinniger*	21
			S. flavidus	2
Ronnie C	III	17-18 Dec.	*S. pinniger*	33
			S. flavidus	25
New Life	II	25 Jan. 1981	*S. pinniger*	11
			S. flavidus	13
			Total number analyzed	317

Analysis of Stomach Contents

The stomachs were opened and their contents transferred to 50% isopropyl alcohol in the laboratory. Contents were examined using a variable power dissecting microscope. Individual stomach fullness was estimated according to a subjective rating ranging from 0 (empty) to 5 (stomach fully distended with food). The condition of the contents was assigned a value from 0 (well-digested, barely identifiable to phylum) to 4 (fresh).

Prey were identified to the lowest possible taxon and enumerated. In stomachs containing many small prey, such as euphausiids, any large or rare prey items were removed first. The remaining contents were then subdivided by means of a Folsom plankton splitter (McEwen et al. 1954), and the contents of one subsample were used to estimate the stomach contents of small prey. The digested state of the contents of many stomachs made precise counts of some prey difficult. Some paired parts of prey animals (e.g., eyes of euphausiids, otoliths of teleosts) were more resistant to digestion and total counts of these parts were halved to yield minimum counts of prey ingested. Total lengths or greatest dimensions of intact prey found in the stomach were measured to the nearest 0.1 mm for the total sample (or a subsample of at least 15 individuals) using a stage ruler or ocular micrometer. All prey were blotted dry with absorbent paper and wet weights of each taxon were recorded to the nearest milligram.

Analysis of Food Habits

The minimum number of stomach samples needed to adequately describe the diet of a species was determined for all five rockfish species, using a cumulative prey species curve. A subset of stomachs of a particular species was randomly chosen and the cumulative number of unique prey taxa were then plotted versus the number of stomachs which produced these taxa. The point on the abscissa where the curve begins to level off is considered the minimum number of stomachs necessary to describe the diet of that species. An example of the cumulative prey curves for the first 28 stomachs of each of the species in this study is shown in Figure 2. Although the curves assume different shapes, all approach an asymptote at sample sizes less than those analyzed.

The contributions of the different prey items to the total diet of the rockfishes were expressed as percent frequency of occurrence, percent numerical composition, and percent gravimetric composition. Breadth and overlap were calculated for the five rockfishes from the summer surveys and for *S. pinniger* and *S. flavidus* from the seasonal surveys, using the pooled p_i's (relative proportion of the total number or biomass of resource i used by each species) for the major taxa. These include all taxa identified to at least generic level that exceeded 0.1% of the total weight or number of all identified foods. Resource breadth was computed for each species using the following formula:

$$B = \frac{1}{\Sigma_i \, p_i^{\,2}}$$

where B equals R (the total number of prey taxa

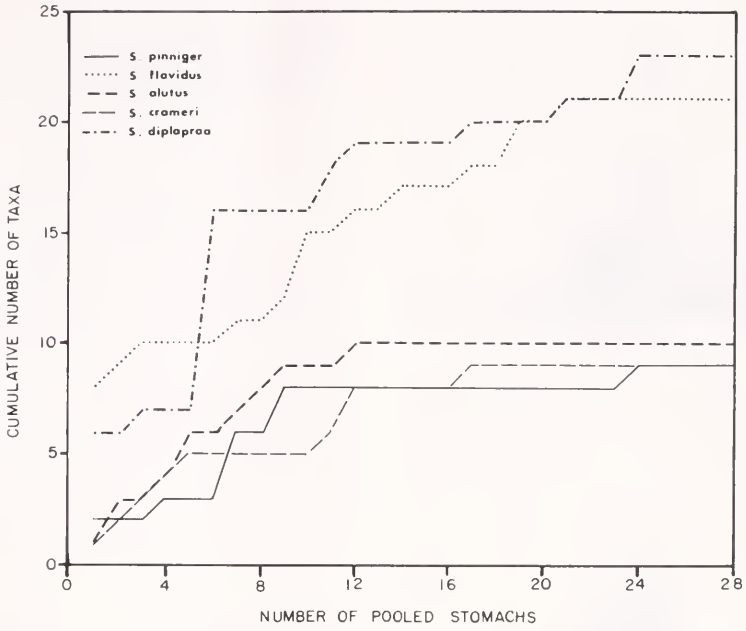

FIGURE 2.—Cumulative prey curves for the first 28 stomachs of each of the 5 rockfish species.

in a food spectrum) when all items are in equal proportion in the diet (Levins 1968). These values were normalized as $B_n = B/R$, which ranges from 0 (most uneven distribution) to 1 (totally even distribution among the prey present). This index assumes equal availabilities of the different prey to all predators.

Several indices of dietary overlap have been proposed and tested with known distributions of prey organisms (see Cailliet and Barry 1979[4]; Linton et al. 1981; Wallace 1981). The coefficient of overlap described by Colwell and Futuyma (1974; identical to Schoener's (1970) index but not expressed as a percentage) was chosen as it was found to be realistic for a wide range of true overlaps (Linton et al. 1981). This coefficient is as follows:

$$C_{ih} = 1.0 - 0.5\,(\Sigma_j\,|\,p_{ij} - p_{hj}\,|)$$

where p_{ij} and p_{hj} are the proportions of prey j found in the diets of species i and h respectively. This coefficient has a minimum of 0 (no overlap of prey) and a maximum of 1 (all items in equal proportions).

Analysis of Diet Variations

The sample sizes of *S. pinniger* and *S. flavidus* were sufficient to permit detailed analyses of their food habits, including seasonal, latitudinal, diel, and predator-size variations.

The 368 specimens of *S. pinniger* and 264 of *S. flavidus* were grouped into 10 mm length categories (Fig. 3). The distribution of *S. pinniger* lengths from the two surveys was similar and no significant differences in the means were found (Student's t-test; $P > 0.05$). Specimens of *S. flavidus* collected during the seasonal survey were significantly larger ($P < 0.001$) than those of the summer survey. *Sebastes pinniger* averaged about 40 mm larger than *S. flavidus* for both surveys combined. Corrections were made for this difference where appropriate in the analyses.

To simplify the analysis of dietary variation in *S. pinniger* and *S. flavidus*, eight major types of prey were selected for comparison, based on their gravimetric importance or frequency of occurrence. Numerical abundances were not used because of the great disparity in prey sizes encountered and the problem of making counts on

[4]Cailliet, G. M., and J. P. Barry. 1979. Comparison of food array overlap measures useful in fish feeding habits analysis. *In* S. J. Lipovsky and C. A. Simenstad (editors), Fish food habits studies, p. 67-79. Proc. 2d Pac. Northwest Tech. Workshop, Wash. Sea Grant.

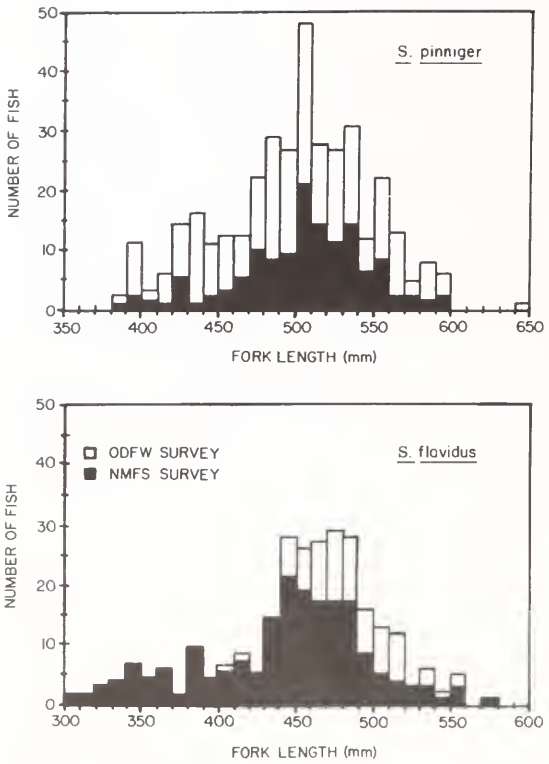

FIGURE 3.—Size distributions of *Sebastes pinniger* and *S. flavidus* from summer (National Marine Fisheries Service) and seasonal (Oregon Department of Fish and Wildlife) surveys.

incomplete animals. These prey categories include the two most important euphausiid species and other major taxonomic groups (Table 3). Other planktonic prey (e.g., copepods, chaetognaths, pteropods) were occasionally present in the diet of one or both species, but their contributions to the overall diets were minor. Cephalopods did not occur in the diet of *S. pinniger*; thus only seven prey categories were used for this species.

TABLE 3.—The major prey categories used in the analysis of diet variations and their respective size ranges found in the stomachs of *S. pinniger* and *S. flavidus*.

Category	Prey size range (mm)	Inclusive taxa or life stages
Euphausia pacifica	8-26	juvenile and adult stages
Thysanoessa spinifera	8-30	juvenile and adult stages
Total euphausiids	8-30	above two and other species, unidentified euphausiids
Decapods	3-87	adult shrimp, crab zoea and megalopae, shrimp mysis
Amphipods	3-30	mostly hyperiid but some gammarid
Cephalopods[1]	18-150+	squid and octopods
Fishes	16-150+	larvae, juvenile and adult stages
Gelatinous zooplankton	10-22	ctenophores, thaliaceans, medusae, and siphonophores

[1]Found in *S. flavidus* stomachs only.

We analyzed four factors that may affect the diet of these two species: season, geographic area, time of day, and size of fish. Each factor was subdivided into four classes to elucidate the general trends within each factor. Stomach content data for all cruises were grouped into four seasons, based on major periods in the hydrographic regime on the continental shelf off Oregon (Huyer et al. 1975; Huyer 1977): spring (March-May), summer (June-August), fall (September-November), and winter (December-February). The collection stations for all cruises were divided into one of four latitudinally defined shelf regions: Northern California-Southern Oregon (lat. 41°00′ to 43°50′N), Heceta Bank-Central Oregon (lat. 43°50′ to 45°00′N), Columbia Region (lat. 45°00′ to 47°00′N), and Northern Washington-Vancouver (lat. 47°00′ to 50°00′N).

For the analysis of diel variation of feeding, the local mean sampling time was adjusted to account for latitudinal, longitudinal, and seasonal differences in daylight. Each collection time was standardized to an equinox day with 12 h between sunrise and sunset, based on solar table values. These adjusted collection times were assigned to one of four time periods: morning (0800-1200 h), early afternoon (1200-1600 h), late afternoon (1600-1800 h), and night (1800-0700 h). Only a small number of *S. pinniger* and *S. flavidus* were collected at night despite extensive nighttime trawling effort on several occasions during the summer survey.

Since the length distributions of the two species were roughly normal (Fig. 3), dividing the length range into four equal size groups would result in disproportionately large sample sizes in the middle size ranges. On the other hand, setting the sample sizes of the four groups equal would result in narrow size ranges around the mode. As neither of these options seemed desirable, compromise groupings were chosen. For *S. pinniger*, we used the following size classes: <45 cm, 45-<50 cm, 50-<55 cm, and >55 cm. Similar size classes were selected for *S. flavidus* but were offset 5 cm to reflect the smaller mean size of this species.

To test whether significant within-factor variation occurred in the diet of each species, contingency tables were constructed comparing the occurrence of food or a particular prey category versus the absence of food or that prey category. A variance test for homogeneity of binominally distributed data (Snedecor and Cochran 1967) was

used for testing differences among the classes within each factor. Any comparisons which exceeded the tabulated 0.05 χ^2 percentage caused a rejection of the null hypothesis of similar diets.

RESULTS

General Food Habits

The results of the stomach content analysis are presented for both surveys and all five species in Tables 4 through 8. Each species will be discussed in detail in this section.

Sebastes flavidus preyed on a diverse assemblage of planktonic and micronektonic prey (Table 4). Dominating the diet in terms of frequency of occurrence (F.O.), percent by number, and, to a lesser extent, percent by weight were euphausiids, principally *Euphausia pacifica* and *Thysanoessa spinifera*. Many species of hyperiid amphipods were represented in the diet, but these were not numerous and did not comprise a major portion of the food on a weight basis. Decapods and cephalopods were moderately important in stomachs examined from both surveys. Copepods and larval decapods occurred only in the stomachs from the summer survey, while gelatinous zooplankton were found only in the seasonal study, and were common during late fall and winter. Fish were an important component on a weight basis; they were mainly mesopelagic species and juvenile stages of predominantly benthic species, although many adult Pacific herring, *Clupea harengus pallasi*, and some smelts were also found. The mean number of taxa and mean number of myctophids per stomach were higher in fish from the seasonal than those from the summer survey.

Sebastes pinniger had a much more limited diet both in number of prey species and major prey categories consumed than *S. flavidus* (Table 5). Euphausiids were again the dominant prey consumed with proportional abundances and weights exceeding 90% of the total in both surveys. Many stomachs were distended with adult euphausiids (>1,000 individuals). Hyperiid and gammarid amphipods were common but did not appear to be important components of the diet. Mesopelagic fishes, including myctophids and stomiatoids, contributed to the biomass consumed during the fall and winter months of the seasonal survey. There was a low number of taxa represented in each stomach, especially in the summer survey.

Because of the advanced stage of digestion of most of the stomach contents (mean digestion score = 1.05), many taxa were not identified to species in the stomachs of *S. alutus*, although many major prey categories were represented (Table 6). Euphausiids were the principal prey by weight and number. Of the remaining prey species, amphipods were relatively common and numerous. The oceanic shrimp, *Sergestes similis*, appeared in a significant number of stomachs and may constitute an important prey item. Remains of fishes were found in only a few stomachs, a noteworthy difference compared with the other four species examined.

Sebastes diploproa utilized a spectrum of prey items as wide as that of *S. flavidus*, but the smaller mean size of this species is reflected in generally smaller prey taken (Table 7). Euphausiids were less important, and amphipods, copepods, and decapods were more important on a numerical and percentage occurrence basis than for the other species. *Sergestes similis* contributed heavily in all respects and was found in almost half the stomachs examined. The small hyperiid amphipod, *Vibilia propinqua*, was common and numerous but contributed little to the bulk of the diet. The mean number of prey found per stomach was second only to the seasonal number of *S. flavidus*.

The diet of *S. crameri* was characterized by very few prey taxa, perhaps because only 30 stomachs were examined (Table 8). Of these, one-third of the stomachs were empty and only about one-third of the total biomass found in these stomachs was identifiable, resulting in very low mean fullness and digestion scores (1.03 and 1.05, respectively). This identifiable fraction was composed of equal numbers of euphausiids, amphipods, and copepods. Euphausiids contributed a greater share to the total biomass, however, and completely dominated the identifiable contents. Few prey taxa were found, overall, in the stomachs of *S. crameri*.

Diet Breadth and Overlap

In order to quantify the relative food resource used by the various species, niche breadth measures were calculated for all species. The principal prey types (proportional biomasses exceeding 1.0% of the total biomass), and niche breadth values (overall and normalized) are given in Table 9 for all species analyzed from the summer surveys and for *S. pinniger* and *S. flavidus* collected during the seasonal surveys.

Sebastes flavidus utilized the greatest number of prey types (R), had the widest niche breadth

TABLE 4.—Summary of yellowtail rockfish, *Sebastes flovidus*, stomach contents from the Oregon Department of Fish and Wildlife's seasonal and the National Marine Fisheries Service's summer samplings. F.O. = frequency of occurrence.

	Seasonal					Summer				
		Number		Weight (g)			Number		Weight (g)	
Prey organism	F.O. (%)	Mean	%	Mean	%	F.O. (%)	Mean	%	Mean	%
Euphausiacea										
Euphausia pacifica (juv.)	36.7	24.5	6.4	0.34	2.3	—	—	—	—	—
Euphausia pacifica (adults)	60.8	120.1	52.2	2.57	28.3	40.5	37.4	51.3	1.90	26.4
Thysanoessa spinifera (juv.)	—	—	—	—	—	6.0	11.5	2.3	0.43	0.9
T. spinifera (adults)	68.3	40.6	19.8	1.32	16.7	23.2	8.8	6.8	0.80	6.4
T. longipes	—	—	—	—	—	0.5	1.0	—	0.01	—
Thysanopoda acutifrons	1.3	1.0	—	0.12	—	—	—	—	—	—
Euphausiid unidentified	49.4	56.3	19.9	1.08	9.9	16.7	61.1	34.7	2.60	14.9
Amphipoda										
Phronima sedentaria	7.6	1.2	—	0.11	0.2	3.2	1.8	0.2	0.06	—
Paraphronima gracilis	1.3	1.0	—	0.01	—	1.1	1.0	—	0.01	—
Parathemisto pacifica	1.3	1.0	—	0.01	—	2.7	1.0	0.1	0.01	—
Hyperia medusarum	2.5	1.0	—	0.01	—	2.7	1.2	0.1	0.01	—
Hyperoche medusarum	2.5	4.0	—	0.02	—	4.9	1.7	0.3	0.89	1.5
Streetsia challengeri	3.8	1.3	—	0.03	—	0.5	1.0	—	0.04	—
Vibilia propinqua	1.3	2.0	—	0.16	—	0.5	1.0	—	0.01	—
Primno macropa	3.8	1.0	—	0.02	—	0.5	2.0	—	0.02	—
Hyperiidea unidentified	1.3	2.0	—	0.02	—	—	—	—	—	—
Rhacotropis sp.	1.3	1.0	—	0.01	—	—	—	—	—	—
Decapoda										
Sergestes similis	7.6	2.5	0.1	0.71	1.0	2.7	2.8	0.2	0.75	0.7
Pandalus jordani	1.3	12.0	0.1	3.70	0.9	1.1	1.0	—	5.19	1.9
Munida quadrispina (juv.)	3.8	9.3	0.2	0.22	0.2	2.7	5.6	0.5	0.12	0.1
Pinnotheridae megalopae	—	—	—	—	—	0.5	1.0	—	0.10	—
Cancer sp. megalopae	—	—	—	—	—	4.3	1.9	0.3	0.02	—
Decapod mysis larvae	—	—	—	—	—	1.6	2.7	0.1	0.04	—
Copepoda										
Calanus pacificus	—	—	—	—	—	0.5	1.0	—	0.01	—
C. marshallae	—	—	—	—	—	1.6	5.7	0.3	0.01	—
Neocalanus sp.	—	—	—	—	—	2.7	4.4	0.4	0.01	—
Euchirella sp.	—	—	—	—	—	0.5	1.0	—	0.02	—
Copepod unidentified	—	—	—	—	—	2.2	4.5	0.3	0.01	—
Cephalopoda										
Abraliopsis felis	1.3	1.0	—	0.93	0.2	—	—	—	—	—
Gonatus sp.	1.3	3.0	—	0.68	0.2	1.1	1.0	—	0.57	—
Loligo opalescens	3.8	1.0	—	21.24	14.9	2.2	1.5	0.1	2.26	1.7
Japatella heathi	—	—	—	—	—	1.6	1.0	—	0.68	0.3
Octopus sp. (juv.)	6.3	2.6	0.1	0.71	0.8	6.5	6.5	0.3	1.33	2.1
Cephalopod unidentified	11.4	1.2	0.1	1.82	3.8	2.2	2.2	0.2	2.34	1.7
Miscellaneous invertebrates										
Sagitta elegans	2.5	2.5	—	0.16	—	0.5	1.0	—	0.03	—
Limacina helicina	1.3	1.0	—	0.01	—	5.4	1.5	0.3	0.04	—
Alciopid polychaete	1.3	1.0	—	0.27	—	—	—	—	—	—
Siphonophora	2.5	5.5	0.1	0.54	0.3	—	—	—	—	—
Ctenophora	1.3	8.0	—	1.56	0.3	—	—	—	—	—
Cnidaria	1.3	1.0	—	0.27	—	—	—	—	—	—
Osteichthyes										
Clupea harengus pallasi	—	—	—	—	—	3.8	1.6	0.1	14.17	18.4
Thaleichthys pacificus	1.3	1.0	—	1.22	0.3	—	—	—	—	—
Spirinchus starksi	2.5	2.0	—	1.65	0.7	0.5	1.0	—	0.28	—
Stenobrachius leucopsarus	1.3	1.0	—	0.84	—	0.5	1.0	—	0.99	0.2
Diaphus theta	2.5	1.0	—	1.97	0.9	0.5	2.0	—	9.96	1.8
Tarletonbeania crenularis	5.1	1.7	0.1	4.94	4.6	—	—	—	—	—
Symbolophorus californiensis	1.3	1.0	—	0.07	—	—	—	—	—	—
Protomyctophum crockeri	1.3	1.0	—	0.14	—	—	—	—	—	—
Myctophidae unidentified	11.4	1.3	0.1	1.37	2.9	0.5	1.0	—	0.71	0.1
Argyropelecus aculeatus	1.3	1.0	—	2.49	0.6	—	—	—	—	—
Chauliodus macouni	1.3	1.0	—	3.81	0.8	—	—	—	—	—
Nectoliparis pelagicus	—	—	—	—	—	1.6	1.3	—	0.22	0.1
Liparididae unidentified	1.3	1.0	—	0.17	—	—	—	—	—	—
Stichaeidae unidentified (juv.)	1.3	2.0	—	0.44	0.1	1.1	1.0	—	0.26	0.1
Sebastes sp. (juv.)	2.5	1.0	—	0.37	0.2	1.1	2.0	—	1.07	0.4
Glyptocephalus zachirus	1.3	1.0	—	0.88	0.2	—	—	—	—	—
Lyopsetta exilis (juv.)	—	—	—	—	—	1.1	1.5	—	0.29	0.1
Psettichthys melanostictus (juv.)	—	—	—	—	—	0.5	1.0	—	0.06	—
Unidentified fish larvae	—	—	—	—	—	1.1	1.0	—	0.14	—
Fish remains	15.2	—	—	1.31	3.7	8.1	—	—	4.19	11.6
Unidentified animal remains	30.4	—	—	0.66	3.7	38.4	—	—	0.64	8.4

TABLE 4.—*Continued.*

Predator characteristics		
Number of stomachs examined	79	185
Number of empty stomachs:	4	38
Mean weight per stomach	5 192 g ± 7 004 (SD)	2.905 g ± 6.032 (SD)
Mean total length	478.35 mm ± 29.06 (SD)	444 86 mm ± 51 43 (SD)
Mean fullness score:	2.87	1.92
Mean digestion score	2 90	1.95
Mean no. prey taxa per fish:	2 81	1.55

TABLE 5.—Summary of canary rockfish, *Sebastes pinniger*, stomach contents from the Oregon Department of Fish and Wildlife's seasonal and the National Marine Fisheries Service's summer samplings. F.O. = frequency of occurrence.

	Seasonal					Summer				
		Number		Weight (g)			Number		Weight (g)	
Prey organism	F.O. (%)	Mean	%	Mean	%	F.O. (%)	Mean	%	Mean	%
Euphausiacea										
Euphausia pacifica (juv.)	21 0	88 1	12 1	0 65	4 8	3 8	12 5	0.4	0.09	0.1
E. pacifica (adults)	54 6	141 3	50.3	3 21	62.0	40.8	124 3	51 6	5.74	43.5
Thysanoessa spinifera	22.3	24 0	3.5	0.59	4.6	14 6	64 7	9 6	7 40	20.1
Thysanopoda sp.	0.4	3 4	—	0 03	—	—	—	—	—	—
Euphausiid unidentified	37 4	139 6	34 0	1 54	20 4	26.1	141 5	37 7	5.79	28.1
Mysidacea										
Inusitatomysis sp.	—	—	—	—	—	0.8	2.0	—	0.02	—
Amphipoda										
Parathemisto pacifica	0 8	2 0	—	0 01	—	4 6	1.2	—	0.01	—
Hyperoche medusarum	—	—	—	—	—	0 8	2.0	—	0.01	—
Phronima sedentaria	0 4	1 0	—	0.03	—	—	—	—	—	—
Streetsia challengeri	0 4	2 0	—	0.03	—	—	—	—	—	—
Hyperiidea unidentified	—	—	—	—	—	1.5	1.0	—	0 01	—
Rhacotropis sp.	0 4	4 0	—	0.05	—	1.5	6.0	0.1	0.07	—
Atylus tridens	0 4	1 0	—	0.01	—	—	—	—	—	—
Anonyx sp.	0.8	1 5	—	0 18	—	—	—	—	—	—
Lysianassidae unidentified	—	—	—	—	—	0.8	1 0	—	0.02	—
Decapoda										
Sergestes similis	2 9	1.7	—	0.09	0.1	1.5	14.0	0.2	1.89	0.6
Pandalus jordani	0 4	1 0	—	1.05	0.1	1.5	1.0	—	1.55	0.4
Crangon sp.	—	—	—	—	—	0.8	1 0	—	0.03	—
Munida quadrispina (juv.)	2.5	5.0	0.1	0.06	—	—	—	—	—	—
Chaetognatha										
Sagitta elegans	0.4	6.0	—	0.07	—	—	—	—	—	—
Osteichthyes										
Stenobrachius leucopsarus	0.8	1.5	—	0.78	0.2	0.8	1 0	—	0.59	0.1
Tarletonbeania crenularis	0.4	1 0	—	1.70	0.3	—	—	—	—	—
Myctophidae unidentified	1.3	1 3	—	1.47	0.6	—	—	—	—	—
Tactostoma macropus	0.4	1.0	—	1.73	0.2	—	—	—	—	—
Argyropelecus aculeatus	0.4	1.0	—	0.21	—	—	—	—	—	—
Ammodytes hexapterus	—	—	—	—	—	3.1	4 5	0.1	0.76	0 4
Sebastes jordani	0.8	1.0	—	19.04	5 6	—	—	—	—	—
Fish remains	8.4	—	—	0.39	1 2	10.8	—	—	3.00	6.0
Unidentified animal remains	12.2	—	—	0.03	0.1	42.3	—	—	0.09	0.7
Predator characteristics										
Number of stomachs examined:		238					130			
Number of empty stomachs:		39					18			
Mean weight per stomach:		2.828 g ± 4.440 (SD)					5.385 g ± 11.297 (SD)			
Mean total length:		491.45 mm ± 51.07 (SD)					504 07 mm ± 50.34 (SD)			
Mean fullness score:		2.02					1.68			
Mean digestion score:		1.89					1.55			
Mean no. prey taxa per fish:		1.27					1.00			

TABLE 6.—Summary of Pacific ocean perch, *Sebastes alutus*, stomach contents from the National Marine Fisheries Service's summer sampling. F.O. = frequency of occurrence.

Prey organism	F.O. (%)	Number of prey Mean	Number of prey %	Weight of prey (g) Mean	Weight of prey (g) %
Euphausiacea					
Euphausia pacifica	52.1	20.5	62.4	1.12	63.1
Thysanoessa spinifera	19.2	7.1	8.0	0.47	9.8
Euphausiid unidentified	20.6	16.9	20.3	0.55	12.2
Amphipoda					
Phronima sedentaria	2.7	2.0	0.3	0.11	0.3
Paraphronima gracilis	1.4	1.0	—	0.02	—
Parathemisto pacifica	6.8	3.2	1.3	0.03	0.2
Vibilia propinqua	1.4	11.0	0.9	0.12	0.2
Primno macropa	2.7	1.0	0.2	0.02	—
Hyperiidea unidentified	6.8	2.4	1.0	0.01	—
Cyphocaris challengeri	2.7	1.0	0.2	0.03	0.1
Copepoda					
Neocalanus plumchrus	4.1	1.3	0.3	0.01	—
Euchaeta sp.	2.7	3.0	0.4	0.01	—
Decapoda					
Sergestes similis	20.6	3.1	3.7	0.34	7.5
Pasiphaea pacifica	1.4	1.0	—	0.03	—
Decapod mysis larvae	1.4	1.0	—	0.01	—
Crustacea remains	2.7	—	—	0.19	0.6
Cephalopoda					
Loligo opalescens	1.4	1.0	—	0.53	0.8
Cephalopod unidentified	6.8	1.4	0.5	0.22	1.6
Osteichthyes remains	5.5	—	—	0.04	0.1
Predator characteristics					
Number of stomachs examined:		73			
Number of empty stomachs:		26			
Mean weight per stomach:		0.923 g ± 1.954 (SD)			
Mean total length:		365.36 mm ± 60.01 (SD)			
Mean fullness score:		1.49			
Mean digestion score:		1.05			
Mean no. prey taxa per fish:		1.68			

TABLE 7.—Summary of splitnose rockfish, *Sebastes diploproa*, stomach contents from the National Marine Fisheries Service's summer sampling. F.O. = frequency of occurrence.

Prey organism	F.O. (%)	Number of prey Mean	Number of prey %	Weight of prey (g) Mean	Weight of prey (g) %
Euphausiacea					
Euphausia pacifica	46.8	26.5	41.2	1.53	42.1
Thysanoessa spinifera	14.5	2.9	1.4	0.16	1.4
Euphausiid remains	29.0	34.9	33.7	1.79	30.6
Amphipoda					
Parathemisto pacifica	1.6	1.0	—	0.01	—
Hyperoche medusarum	3.2	1.0	—	0.01	—
Paraphronima gracilis	3.2	1.0	—	0.02	—
Streetsia challengeri	1.6	1.0	—	0.02	—
Vibilia propinqua	32.3	10.3	11.1	0.10	1.9
Primno macropa	3.2	1.0	—	0.01	—
Hyperiidea unidentified	9.7	1.5	0.4	0.02	0.1
Cyphocaris challengeri	4.8	1.7	0.3	0.02	—
Lysianassidae unidentified	1.6	1.0	—	0.03	—
Gammaridea unidentified	1.6	1.0	—	0.03	—
Isopoda unidentified	1.6	1.0	—	0.02	—
Copepoda					
Neocalanus cristatus	6.5	3.2	0.7	0.02	0.1
Euchaeta elongata	4.8	3.3	0.5	0.03	0.1
Euchirella sp.	3.2	1.5	0.2	0.01	—
Candacia bipinnata	4.8	3.6	0.6	0.01	—
Metridia sp.	3.2	1.0	0.1	0.01	—
Decapoda					
Sergestes similis	46.8	4.4	6.8	0.60	16.5
Pasaphaea pacifica	1.6	1.0	—	0.59	0.6
Benthogenema burkenroadi	1.6	1.0	—	0.12	0.1
Munida quadrispina	1.6	6.0	0.3	0.12	0.1
Cancer sp. megalopae	9.7	1.3	0.4	0.02	0.1
Decapod mysis larvae	1.6	1.0	—	0.01	—
Mollusca					
Pteropoda unidentified	1.6	1.0	—	0.03	—
Gonatus sp.	1.6	1.0	—	0.07	—
Octopus sp. (juv)	1.6	1.0	—	0.17	0.2
Osteichthyes					
Stenobrachius leucopsarus	1.6	1.0	—	0.36	0.3
Myctophidae unidentified	6.5	1.0	0.2	0.13	0.5
Tactostoma macropus	1.6	1.0	—	2.28	2.2
Liparididae unidentified	1.6	1.0	—	0.15	0.1
Fish remains	9.7	—	—	0.38	0.1
Unidentified animal remains	17.7	—	—	0.03	0.3
Predator characteristics					
Number of stomachs examined:		62			
Number of empty stomachs:		15			
Mean weight per stomach:		1.698 g ± 3.449 (SD)			
Mean total length:		264.82 mm ± 41.82 (SD)			
Mean fullness score:		2.50			
Mean digestion score:		1.25			
Mean no. prey taxa per fish:		2.48			

(B), and had the most even distribution among prey types (B_n) of all rockfish examined from the summer survey. *Sebastes diploproa* preyed on fewer taxa than *S. flavidus* but had moderately high overall and normalized food breadth values. *Sebastes pinniger*, *S. crameri*, and *S. alutus* utilized a similar number of distinct prey items and had similar breadth and evenness values with *S. alutus* having a more equitable distribution of prey than the other two.

The seasonal results for the *S. flavidus* and *S. pinniger* were more divergent and represent the extreme values found among the species. Seventeen principal prey types were important in the seasonal diet of *S. flavidus*, contributing toward a high B value. However, the dominance of a few species yielded a low evenness value for this species. *Sebastes pinniger* preyed on few taxa in fairly unequal proportions yielding fairly low niche breadth and evenness values. These low evenness values could be caused by the preponderance of euphausiids found in the guts of both species during the summer months.

The individual overlap coefficients and the mean overlap for each species are presented for both the weight and numerical abundance of prey in Table 10 for the summer surveys. As overlap indices are affected by the level of taxonomic specificity at which the prey have been identified, no unbiased means for testing the significance of these values are available. We adopted the convention that overlap values from 0.00 to 0.29 are considered low, 0.30 to 0.60 considered medium, and those above 0.60 show highly similar diets (Langton 1982).

The coefficients for numerical composition show high values for all possible combinations except those involving *S. crameri*. Very similar proportions of the major euphausiid prey groups resulted in an extremely high overlap value (0.93) between

TABLE 8.—Summary of darkblotched rockfish, *Sebastes crameri*, stomach contents from the National Marine Fisheries Service's summer sampling. F.O. = frequency of occurrence.

Prey organism	F.O. (%)	Number of prey		Weight of prey (g)	
		Mean	%	Mean	%
Euphausiacea					
Euphausia pacifica	13.3	8.0	37.2	0.42	26.2
Thysanoessa spinifera	3.3	1.0	1.2	0.06	0.9
Euphausiid remains	3.3	1.0	1.2	0.01	0.2
Amphipoda					
Parathemisto pacifica	16.7	4.4	25.6	0.01	1.0
Cyphocaris challengeri	6.7	1.0	2.3	0.01	0.3
Lysianassidae unidentified	3.3	1.0	1.2	0.04	0.8
Copepoda					
Neocalanus cristatus	3.3	1.0	1.2	0.01	0.2
Euchaeta elongata	10.0	3.0	10.5	0.01	0.5
Copepod unidentified	16.7	3.0	17.4	0.01	0.8
Decapoda					
Sergestes similis	3.3	1.0	1.2	0.07	1.1
Osteichthyes					
Ammodytes hexapterus	3.3	1.0	1.2	0.28	4.3
Unidentified animal remains	53.3	—	—	0.25	62.5
Predator characteristics					
Number of stomachs examined		30			
Number of empty stomachs		10			
Mean weight per stomach		0.246 g ± 0.389 (SD)			
Mean total length		330.36 mm ± 77.17 (SD)			
Mean fullness score		1.03			
Mean digestion score		1.05			
Mean no. prey taxa per fish		1.26			

pinniger, *S. diploproa*, and *S. alutus* are all relatively high (0.58, 0.56, and 0.61, respectively).

Overlaps between *S. pinniger* and *S. flavidus* for the seasonal cruises are similar to the results of the summer surveys (C_{ih} = 0.80 by number; 0.46 by weight). A possible explanation for the lower values may be changes in availability of both predator and prey (i.e., no *S. flavidus* stomachs were collected during spring and early summer when the euphausiid populations are generally the highest). The variability associated with the different cruises was examined by calculating the overlaps between these two species for the four seasonal cruises that contained at least 10 specimens of each species. The July cruise had the highest overlap of all on a weight basis (C_{ih} = 0.88) and the September cruise had the lowest (C_{ih} = 0.32), while the December and January cruises had intermediate overlaps (C_{ih} = 0.52 and 0.46), suggesting seasonal variations in prey availability for these species.

For comparative purposes, the dietary composition of the five most important prey categories for each of the rockfish species is presented by percent number and percent weight in Figures 4 and 5. Both figures show the importance of euphausiids in all five species. The stomachs of *S. crameri* contained a more equitable distribution of numbers of the major prey groups than the other species of rockfishes, with higher proportions of amphipods and copepods. Some of this difference may be ascribed to the smaller sample size. On a weight basis, *S. flavidus* was unique in that fishes and cephalopods were of greater importance in the

TABLE 9.—Principal prey types making up ~100% of the diet and food breadths of the five species of *Sebastes*. R is the total number of distinct prey items identified to at least genus level and that make up 0.1% (p_i > 0.001) of the identified fraction of the total weight. These prey were used to calculate the overall diet breadth (B) and the evenness of distribution of the prey items in the diet (B_n). The seasonal values for *S. flavidus* and *S. pinniger* are given in parentheses.

Species	Sample size	Principal prey types (p_i's > 0.01)	Pooled species values		
			R	B	B_n
S. flavidus	185 (79)	*Euphausia pacifica*, *Thysanoessa spinifera*, hyperiid amphipods, *Sergestes similis*, *Loligo opalescens*, myctophids, *Clupea harengus pallasi*	12 (17)	3.64 (3.77)	0.303 (0.222)
S. diploproa	62	*E. pacifica*, *T. spinifera*, *S. similis*, *Vibilia propinqua*	8	2.28	0.285
S. pinniger	130 (238)	*E. pacifica*, *T. spinifera*, *Sebastes jordani*	8 (6)	1.86 (1.33)	0.232 (0.222)
S. crameri	30	*E. pacifica*, calanoid copepods, hyperiid amphipods, *Ammodytes hexapterus*	8	1.80	0.225
S. alutus	73	*E. pacifica*, *T. spinifera*, *S. similis*	7	1.73	0.247

S. pinniger and *S. flavidus*, although the diets are not similar for other prey items.

Overlap on the basis of weight, which may be a better measure of the energy obtained from the various food items, indicates high overlap between *S. pinniger* and *S. diploproa* and between *S. alutus* and *S. pinniger*, *S. diploproa*, and *S. crameri*. The rest of the values were < 0.60, including *S. pinniger* with *S. flavidus* (C_{ih} = 0.48). The diet of *S. flavidus* overlaps the least with the other species ($\overline{C}_{ih}$ = 0.42) mainly due to its more piscivorous habits. The mean overlap values of *S.*

TABLE 10.—Overlap matrix for the five species of *Sebastes*. Only those prey that have proportional abundances exceeding 0.1% were used in the analysis. Values above the rules are for proportional weight overlap and values below are for proportional abundance. The mean overlap for each species by weight and number is given in parentheses directly above and below the rules.

	S. pinniger	*S. flavidus*	*S. diploproa*	*S. crameri*	*S. alutus*	
S. pinniger	(0.58) / (0.71)	0.48	0.72	0.47	0.66	
S. flavidus	0.93	(0.42) / (0.70)	0.44	0.30	0.46	WEIGHT
S. diploproa	0.76	0.78	(0.56) / (0.65)	0.48	0.63	
S. crameri	0.40	0.40	0.42	(0.48) / (0.41)	0.69	
S. alutus	0.74	0.70	0.63	0.42	(0.61) / (0.62)	
			NUMBER			

diet of this species than any of the other rockfish. Decapods were of moderate importance to *S. diploproa* and, to a lesser extent, *S. alutus*. Fishes were an important food source by weight for all rockfishes but *S. alutus*.

Seasonal Variation

Differences in the diet of *S. pinniger* and *S. flavidus* are summarized in Table 11 for the four seasons. The spring cruise shows an extreme dominance of one prey item, *Euphausia pacifica*, in the diet of *S. pinniger*. This prey species was found in about three-quarters of the stomachs and made up almost all the prey biomass. Decapod shrimp and fishes were rarely found in the diet at this time. Euphausiids also dominated the diet in the sum-

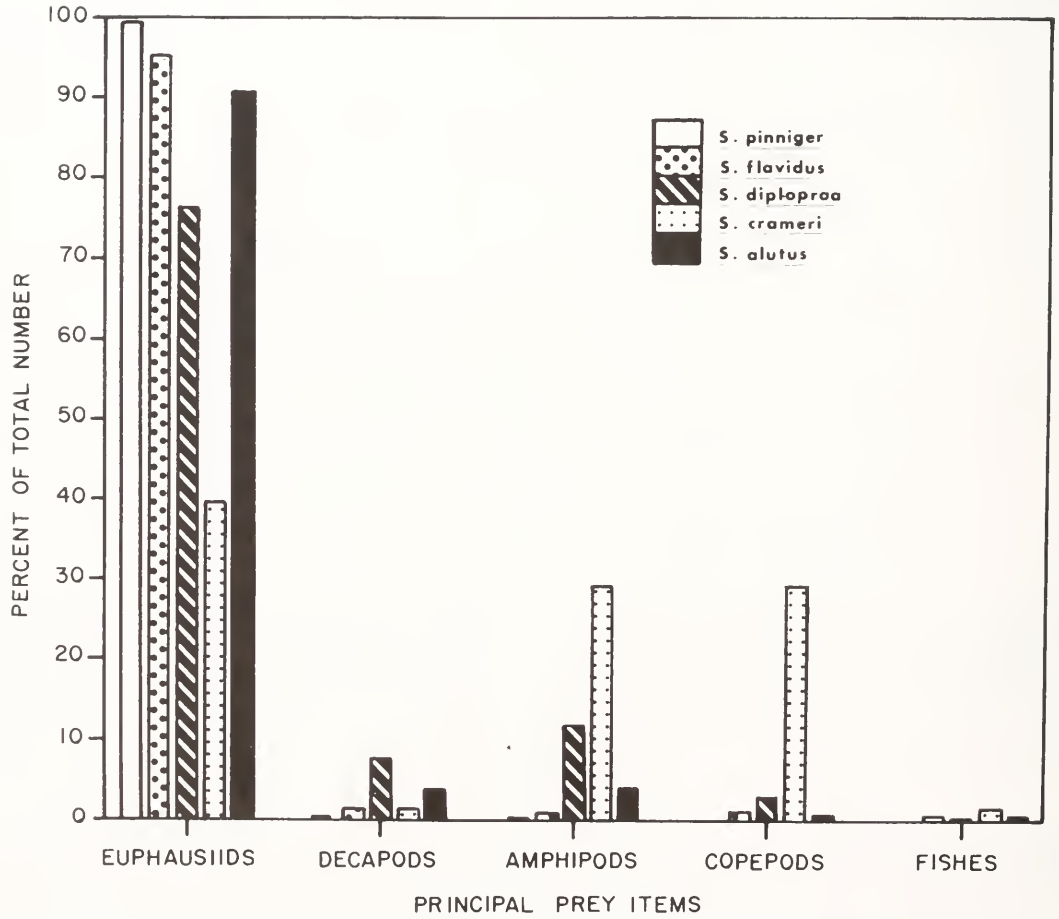

FIGURE 4.—The proportions of the five major prey taxa found in the five rockfish species based on numerical composition.

TABLE 11.—Variation in major prey taxa composition with season for *Sebastes pinniger* and *S. flavidus*. F.O. = frequency of occurrence; % *W* = percent gravimetric composition; + = a prey category was present but made up < 0.1% of the total weight.

Species and season	No. of fish (% empty)	*Euphausia pacifica*		*Thysanoessa spinifera*		Total euphausiids		Decapods		Amphipods		Cephalopods		Fishes		Gelatinous zooplankton	
		F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W
Sebastes pinniger																	
Spring[1] (Mar.-May)	42 (14.3)	73.8	99.6	—	—	73.8	99.6	2.4	+	—	—	—	—	2.4	0.4	—	—
Summer (June-Aug.)	165 (10.9)	61.2	75.1	7.9	0.5	68.5	94.7	3.6	1.1	2.4	+	—	—	6.7	4.2	3.6	+
Fall (Sept.-Nov.)	117 (20.5)	35.9	13.8	32.5	37.8	55.6	84.2	9.4	0.2	12.0	0.1	—	—	17.9	15.1	22.2	0.3
Winter (Dec.-Feb.)	44 (22.7)	50.0	25.9	47.7	12.0	81.8	94.2	—	—	6.8	0.4	—	—	13.6	5.5	4.5	+
Sebastes flavidus																	
Spring[2] (Mar.-May)	0																
Summer (June-Aug.)	151 (16.6)	52.3	37.2	23.2	0.5	58.3	66.7	9.9	0.8	13.2	0.1	15.2	6.5	13.9	25.6	3.3	0.4
Fall (Sept.-Nov.)	75 (22.7)	34.7	6.1	42.7	29.6	54.7	42.2	9.3	13.8	26.7	0.8	6.7	1.8	28.0	40.5	10.7	0.8
Winter (Dec.-Feb.)	38 (0.0)	81.6	19.5	92.1	15.3	94.7	46.7	0.5	0.7	10.5	+	28.9	30.6	52.6	15.4	21.1	6.6

[1]All collections taken during one cruise. All other seasons represent the means of at least two cruises spaced a minimum of 1 mo apart (Tables 1 and 2 give the exact dates and samples collected on each cruise).
[2]No stomachs of *S. flavidus* were collected during this season.

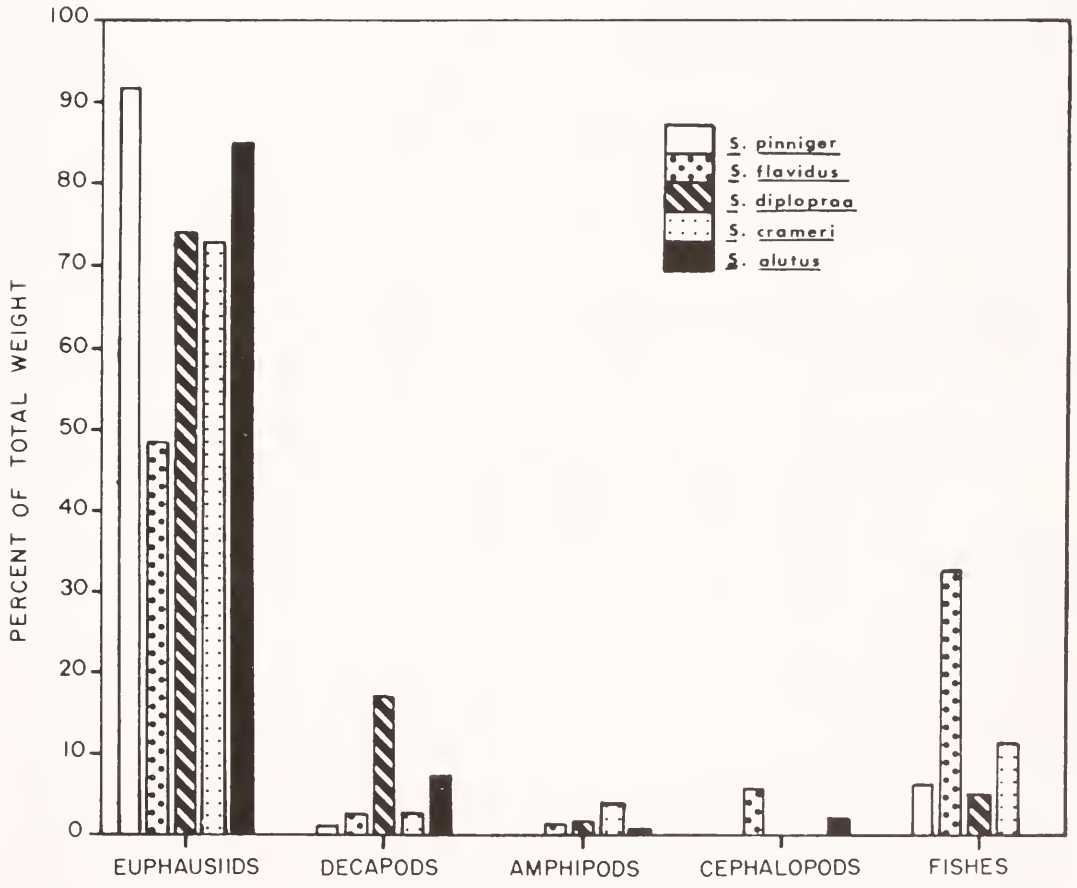

FIGURE 5.—The proportions of the five major prey taxa found in the five rockfish species based on gravimetric composition.

mer but to a lesser degree. *Thysanoessa spinifera* appeared in the stomachs at this time, but *E. pacifica* continued to be the most important euphausiid consumed. Shrimp and fishes were slightly more important but together made up only a minor portion of the diet. A low percentage of empty stomachs occurred in the summer.

The diet of *S. pinniger* in the fall showed substantial shifts in prey composition. Although the frequencies of occurrence were about equal for the two species of euphausiids, *T. spinifera* greatly exceeded *E. pacifica* by weight. Decapods were common but were represented mainly by small shrimp (*Sergestes similis*) and juvenile pelagic crabs (*Munida quadrispina*), which contributed little on a weight basis. Amphipods and gelatinous zooplankton occurred frequently but were not important by weight. Fishes were important by occurrence and weight and consisted mostly of mesopelagic species and several adult *Sebastes jordani* which made a large contribution to the biomass consumed.

Almost one-quarter of the fish collected in the winter had empty stomachs and contained much digested material. *Euphausia pacifica* and *T. spinifera* occurred in about the same number of stomachs, but *E. pacifica* contributed over twice as much of the total weight as *T. spinifera*. Subadult *E. pacifica* were very numerous at this time. The fishes consumed were mostly mesopelagic species.

Sebastes flavidus showed similar trends in food resource utilization among the three seasons from which collections were made (Table 11). Euphausiids, consisting mostly of *E. pacifica*, made up two-thirds of the diet by weight in the summer. Fishes were common and contributed heavily to the total biomass. Cephalopods were next in importance by either occurrence or weight. The diet in the fall showed the same shift in euphausiid species as was apparent for *S. pinniger*, with *T. spinifera* the dominant species. Fishes were almost as important by weight as euphausiids, but their weight total was mostly composed of adult clupeids. Cephalopods were least important in the fall months.

Euphausiids represented about half the diet during the winter, but the remainder was shared mostly by cephalopods and fishes. Both species of euphausiids were commonly found, but *E. pacifica* (mostly subadults) were slightly more important in the overall diet. Cephalopods (mostly adult *Loligo opalescens* and juvenile copepods) did show a substantial increase in weight and occurrence during these months. Fishes were found in over half the stomachs but were mainly juveniles of relatively small myctophids. Gelatinous zooplankton were most common, and decapods were least common, during this season. In contrast to *S. pinniger*, all stomachs of this species contained some food and many stomachs were full during this season.

Geographic Variation

Several trends were evident when comparing the diet of *S. pinniger* between regions (Table 12). The two southernmost regions had similar diets dominated by *E. pacifica* with *T. spinifera* representing only a minor portion of the diet. Meso-

TABLE 12.—Variation in major prey taxa composition with geographic area for *Sebastes pinniger* and *S. flavidus*. F.O. = frequency of occurrence; % *W* = percent gravimetric composition; + = a prey category was present but made up < 0.1% of the total weight.

Area taken	No. of fish (% empty)	*Euphausia pacifica*		*Thysanoessa spinifera*		Total euphausiids		Decapods		Amphipods		Cephalopods		Fishes		Gelatinous zooplankton	
		F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W
Sebastes pinniger																	
Southern Oregon	51 (13.7)	52.9	63.1	9.8	0.6	54.9	93.1	5.8	0.8	7.8	+	—	—	5.8	6.2	5.8	+
Heceta-Central	281 (16.0)	56.9	67.1	19.6	4.4	61.2	91.3	5.3	0.8	3.2	0.1	—	—	11.7	7.6	6.4	0.1
Columbia Region[1]	0																
Washington-Vancouver	36 (16.7)	22.2	4.6	27.8	57.7	36.1	92.8	2.8	+	22.2	0.1	—	—	25.0	6.7	36.1	0.4
Sebastes flavidus																	
Southern Oregon	70 (17.1)	58.6	47.6	30.0	9.2	65.7	84.9	10.0	+	14.3	0.8	24.3	13.7	8.6	0.6	5.7	0.1
Heceta-Central	122 (11.5)	61.5	27.9	49.2	14.1	70.5	50.6	11.4	2.2	18.0	0.3	16.4	16.9	32.8	27.6	13.1	2.3
Columbia Region	22 (13.6)	27.3	3.2	9.1	0.6	36.4	12.1	18.2	1.0	4.6	+	9.1	0.3	45.5	86.5	—	—
Washington-Vancouver	50 (26.0)	28.0	7.3	34.0	12.0	48.0	20.7	12.0	17.2	16.0	0.6	2.0	1.0	26.0	60.5	4.0	+

[1]No stomachs of *S. pinniger* were collected from this region.

pelagic fishes and sergestid shrimps were common but generally contributed little to the diet on a weight basis.

The northernmost region showed reduced occurrences of euphausiids, overall, but they still composed a percent weight equivalent to the two southern areas. This could have resulted from a shift to *T. spinifera*, which is generally larger than *E. pacifica*, as the main euphausiid consumed. Decapods were of lesser importance, but gelatinous zooplankton were very common in the stomachs of fish from this region. This may explain the high abundances of hyperiid amphipods known to be associated with gelatinous zooplankton. Fishes were common, especially juvenile Pacific sand lance, *Ammodytes hexapterus*, a prey species found only in the stomachs collected from this area.

Sebastes flavidus showed a different pattern in food utilization. A general decrease in euphausiid abundance was observed with increasing latitude (Table 12). The euphausiids from the southernmost regions were mostly *E. pacifica*, although many were unidentified. The only other important prey groups in these southern regions were cephalopods (mostly *Loligo opalescens*) and relatively large fishes such as Pacific herring and myctophids (*Diaphus theta*). All other prey groups were common but made little contribution to the diet.

Specimens of *S. flavidus* collected in the northernmost regions consumed substantial amounts of fish (mainly clupeids and myctophids). Euphausiids were relatively unimportant in these regions. As was the case with *S. pinniger*, *T. spinifera* was the dominant euphausiid eaten in the Washington-Vancouver region. Decapods, consisting mostly of *Pandalus jordani*, reached their highest proportion of the diet in the northernmost region.

Diel Variation

Both species showed variation in prey composition with the diel period (Table 13). *Sebastes pinniger* contained high percentages of euphausiids by weight during all four diel periods, with highest percentages occurring in the afternoon periods. Fishes, mostly non-mesopelagic species, were most important on a weight basis during morning and night when they occurred least frequently. Euphausiids were relatively more important by weight in the two afternoon periods. A high proportion of the fishes found in the stomachs during the afternoon periods were mesopelagic species.

Sebastes flavidus exhibited the opposite trends in food consumption with respect to time of day. Euphausiids were found in the highest proportions by weight during the morning and night periods while proportions of fish were substan-

TABLE 13.—Variation in major prey taxa composition with time of day for *Sebastes pinniger* and *S. flavidus*. F.O. = frequency of occurrence; % W = percent gravimetric composition; + = a prey category was present but made up < 0.1% of the total weight.

Time of day (h)	No. of fish (% empty)	*Euphausia pacifica*		*Thysanoessa spinifera*		Total euphausiids		Decapods		Amphipods		Cephalopods		Fishes		Gelatinous zooplankton	
		F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W
Sebastes pinniger																	
Morning (0800-1200)	68 (19.1)	25.0	32.1	19.1	5.7	51.5	83.1	7.3	0.2	13.2	0.1	—	—	8.8	15.9	23.5	0.6
Early aft. (1200-1600)	128 (10.2)	62.5	51.2	21.1	20.5	69.5	95.9	4.7	0.5	6.2	+	—	—	14.1	3.4	7.8	+
Late aft. (1600-1800)	79 (17.7)	50.6	80.2	1.6	1.8	70.9	96.3	3.8	0.7	—	—	—	—	13.9	2.9	5.1	+
Night (1800-0700)	93 (18.3)	52.7	56.8	20.4	5.9	69.9	83.4	4.3	1.4	4.3	0.2	—	—	9.7	14.8	7.5	0.1
Sebastes flavidus																	
Morning (0800-1200)	81 (18.5)	43.2	38.1	35.8	9.1	58.0	76.7	2.5	0.1	3.7	+	6.2	5.3	12.4	17.1	4.9	0.9
Early aft. (1200-1600)	71 (14.5)	54.9	25.5	28.2	7.5	57.7	48.8	14.1	4.4	19.7	0.2	15.5	7.6	25.3	37.4	7.0	1.3
Late aft. (1600-1800)	57 (17.7)	50.9	16.4	43.9	18.5	63.2	46.2	7.0	0.1	22.6	0.3	21.0	6.6	33.3	46.3	7.0	0.3
Night (1800-0700)	55 (12.7)	60.0	31.8	43.6	11.8	69.1	50.6	18.2	4.8	16.4	0.2	21.8	24.9	27.3	15.8	16.4	3.4

tially lower during these periods. Collections taken around late afternoon had equal amounts of fishes and euphausiids, while those taken at night had high occurrences and biomass of cephalopods (mostly *Loligo opalescens*) and gelatinous zooplankton.

The mean fullness score, mean digestion score, mean weight ratio (equal to the weight of stomach contents divided by weight of fish), and the percentage of empty stomachs were plotted for each adjusted collection time for both species. *Sebastes pinniger* had a distinct periodicity in its feeding cycle (Fig. 6). Peak periods of feeding intensity occurred midday and shortly after dusk. One collection (eight stomachs) taken at 0400 h had low values for fullness score and weight ratio but average values for digestion score and percentage of empty stomachs. The fullness and digestion scores (Fig. 6A) follow each other fairly well except that the midday digestion peak was several hours later than the fullness peak. A very distinct peak in the weight ratio at 1200 h and a smaller one shortly after dusk are evident (Fig. 6B).

Sebastes flavidus also appears to show a diel periodicity in its feeding pattern (Fig. 7). The fullness and digestion scores track each other very closely and show distinct peaks of feeding intensity around noon and shortly after dusk, although the number of samples in the latter period was limited (Fig. 7A). The actual mean weight ratio showed similar trends, but the noon peak is somewhat obscured (Fig. 7B). The percentage of empty stomachs was highest in the morning and remained low through the remainder of the day unlike that found for *S. pinniger*.

A high degree of variability in the mean weight ratio was found several times, especially during periods of peak feeding when both totally distended and almost empty stomachs were often found together. The differences in the weight

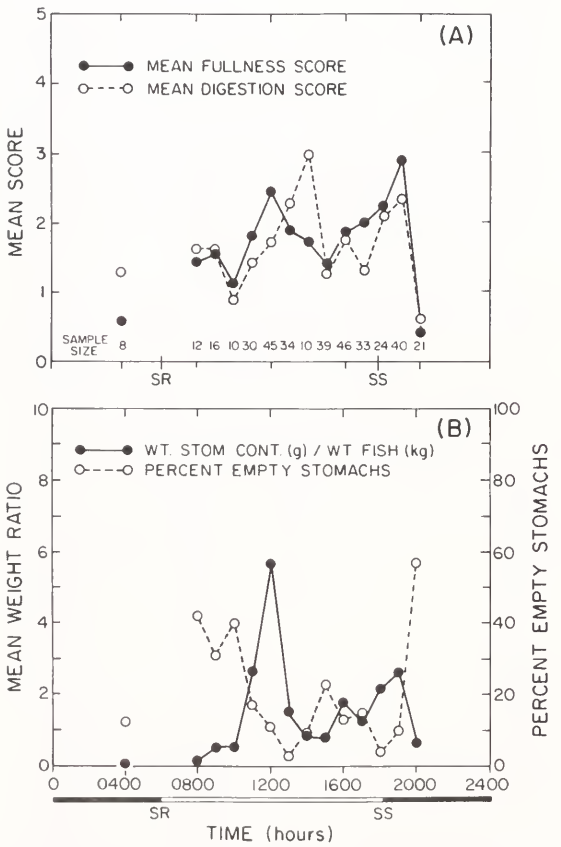

FIGURE 6.—Feeding intensity indices for *Sebastes pinniger* at adjusted times of the day. See text for explanation of indices.

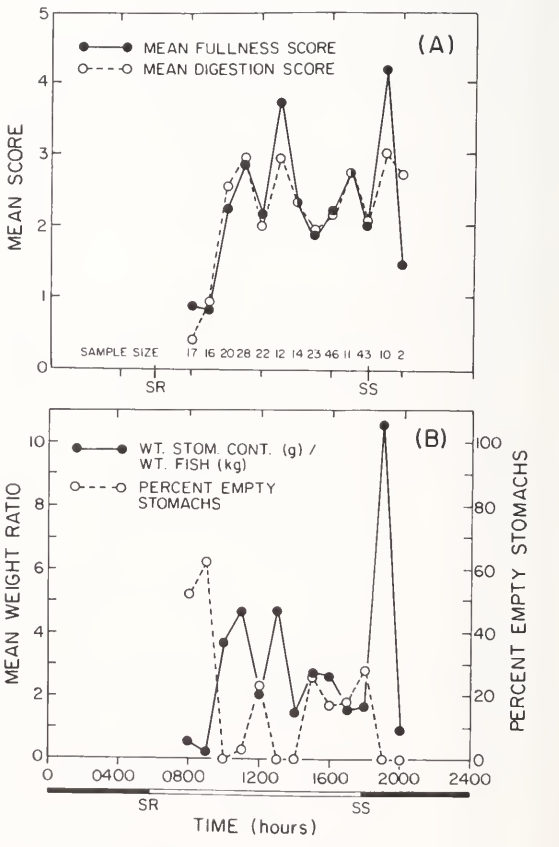

FIGURE 7.—Feeding intensity indices for *Sebastes flavidus* at adjusted times of the day. See text for explanation of indices.

ratios at the individual times were subjected to an analysis of covariance which compared the weight ratios adjusted for fish size (Jenkins and Green 1977). Both *S. pinniger* ($F_{(12,354)} = 5.68$, $P < 0.001$) and *S. flavidus* ($F_{(11,262)} = 6.51$, $P < 0.001$) showed significant differences in the mean weight ratios over the times tested, implying that feeding varied during the diel period. No significant differences ($P > 0.05$) in stomach fullness were associated with size or sex of the predator for either species.

Predator-Size Variation

The proportion of empty *S. pinniger* stomachs as well as the percent frequency of occurrence and percent weight of prey taxa were remarkably invariant among the four predator size classes (Table 14). Only the largest size class (≥55+ cm) shows any substantial variation with a larger proportion by weight of fishes and a commensurate decrease in weight of euphausiids consumed. Much of this fish weight was contributed by a few individual fish of large relative size (mostly adult *S. jordani*); the frequency of occurrence of fishes is only slightly higher for this largest size class.

Few obvious size-related trends were apparent for *S. flavidus*. The two smallest size classes consumed the largest proportion of euphausiids. *Euphausia pacifica* were less important for large fish. Decapods and cephalopods showed similar trends except that the frequencies of occurrence were highest for cephalopods but lowest for decapods in the largest size class. Fishes were consistent in their weight and occurrence proportions except that one size class (40-<45 cm) had much lower proportions than the others. Few trends were apparent for either amphipods or gelatinous zooplankton although both groups were commonly found.

To determine if different sizes of rockfish selected different sizes of prey, all fish that contained measurable prey were grouped into 10 mm length intervals and the means and ranges of their prey were plotted against fish size (Fig. 8). Although some exceptions exist, the majority of the prey of *S. pinniger* are found within a narrow range of prey sizes, a range (15-27 mm) largely determined by adult euphausiids, the dominant prey category (Fig. 8). Fishes of the largest two size classes consumed larger prey on average, and their prey had the largest variation in size due to high numbers of both small and large prey consumed by these fish. No significant relationship was found between length of fish and either overall size of prey or size of euphausiid prey.

Sebastes flavidus showed a much greater range in the sizes of prey consumed with the variation and range in prey length increasing with size of predator (Fig. 8). The mean size of prey eaten did not appreciably increase until the very largest size classes. Although the maximum prey size increases with fish size, the minimum size varies little throughout the length ranges examined. Again for this species, no relationship was found between fish length and overall or euphausiid prey lengths.

The size distribution of prey is shown for both species in Figure 9. The prey-size spectrum of *S. pinniger* was distributed fairly normally with the

TABLE 14.—Variation in major prey taxa composition with size of predator for *Sebastes pinniger* and *S. flavidus*. F.O. = frequency of occurrence; % W = percent gravimetric composition; + = a prey category was present but made up < 0.1% of the total weight.

Size range (cm)	No. of fish (% empty)	*Euphausia pacifica*		*Thysanoessa spinifera*		Total euphausiids		Decapods		Amphipods		Cephalopods		Fishes		Gelatinous zooplankton	
		F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W	F.O.	% W
Sebastes pinniger																	
<45	64 (17.2)	48.4	43.2	21.9	9.7	68.7	91.4	4.7	3.1	6.2	0.3	—	—	14.1	4.8	4.7	0.4
45-<50	102 (17.6)	51.8	46.1	17.6	18.6	67.6	92.5	4.9	0.9	4.9	0.1	—	—	13.7	6.5	5.9	0.1
50-<55	146 (14.4)	47.3	65.6	21.2	12.0	61.1	94.9	5.5	0.2	4.1	+	—	—	11.0	4.7	8.9	0.1
≥55	56 (14.3)	58.9	49.3	12.5	7.6	67.9	83.4	5.4	0.2	7.1	+	—	—	16.1	16.3	14.3	0.2
Sebastes flavidus																	
<40	35 (0.0)	88.6	44.7	57.1	11.7	94.3	61.3	11.4	0.1	14.3	0.1	14.3	2.8	31.4	34.6	2.9	0.1
40-<45	61 (22.9)	45.9	50.2	29.5	12.4	52.5	83.9	13.1	1.2	24.6	0.2	13.1	8.4	9.8	5.8	4.9	0.4
45-<50	126 (21.4)	47.6	22.9	38.1	13.7	57.1	46.8	11.1	3.7	12.0	0.1	12.7	17.4	29.3	29.3	7.9	2.4
≥50	42 (2.4)	47.6	25.8	30.9	8.3	54.7	51.9	7.1	2.6	23.8	0.3	21.4	13.6	45.2	30.3	21.4	0.1

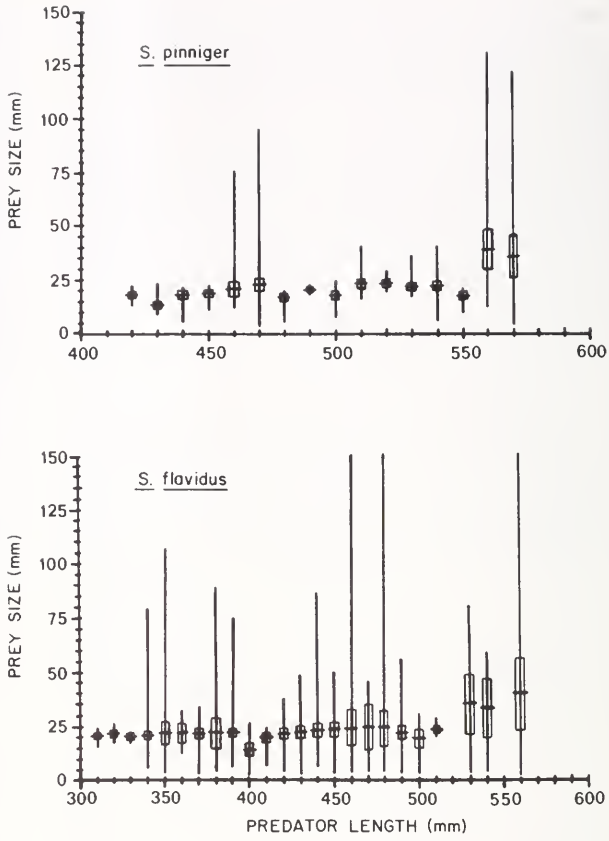

FIGURE 8.—Mean (horizontal lines) ±95% confidence limits (boxes) and ranges (vertical lines) of prey sizes found for each 10 mm interval of *Sebastes pinniger* and *S. flavidus*.

mode coinciding with the mean ($\bar{x}$ = 10.38 mm), although disjunct groups of small and large prey were found (Fig. 9). The prey-size spectrum of *S. flavidus* was slightly skewed toward the larger sized prey with the mean size ($\bar{x}$ = 18.44 mm) less than the mode. A smaller peak also appeared around 25 mm. No significant differences were found in the mean prey sizes utilized by the two species (Student's t-test, $P > 0.05$).

Analysis of Variation

The results of the chi-square analyses for *S. pinniger* showed that none of the factors analyzed had a significant effect on the occurrence of food in the stomachs (Table 15). At least one of the factors was related to the occurrences of all seven prey categories examined. Seasonal effects were the most significant (all $P < 0.01$) and were due to the higher occurrences of hyperiid amphipods, fishes, and gelatinous zooplankton in fall and winter. Area and time of capture showed both highly significant ($P \leq 0.001$) and insignificant effects depending on the prey category, but most comparisons were significant at the 0.05 level. In none of the prey categories examined did the size of the predator have a significant effect on the relative proportions consumed.

For *S. flavidus*, season of capture and size of predator affected the proportion of empty stomachs found (Table 15). Again season had the most significant influence on prey occurrence and was significant in all eight prey categories. Highly significant differences were found in area of capture and size of predator especially in the euphausiid and fish categories. Differences in occurrence of prey with time of capture deviated from expected the least of all the factors analyzed.

DISCUSSION

The five species of rockfishes examined rely heavily, if not exclusively, on pelagic macrozooplankton and micronekton. Although some benthic species appear in the prey lists (e.g., *Lyopsetta exilis*, *Munida quadrispina*, *Psettichthys melan-*

TABLE 15.—Results of chi-square analyses testing for differences in the occurrence of food and specific prey categories within the various factors. All significances are with three degrees of freedom except where noted.

Factor analyzed	Occurrence of food	*Euphausia pacifica*	*Thysanoessa spinifera*	Total euphausiids	Decapods	Amphipods	Cephalopods	Fishes	Gelatinous zooplankton
Sebastes pinniger									
Season	6.59	23.09***	72.48***	11.26**	113.28***	16.76***	—	15.87***	39.96***
Area[1]	0.19	8.61*	5.22	11.42***	0.46	22.44***	—	7.95*	35.66***
Time	4.32	28.18***	53.77***	11.86**	1.37	13.05***	—	1.43	19.21***
Size	0.67	3.12	3.24	6.26	0.04	0.98	—	1.26	4.35
Sebastes flavidus									
Season[1]	9.79**	13.32***	51.33***	10.02**	30.27***	11.15***	6.65*	21.43***	11.67***
Area	5.76	20.83***	15.81***	14.23***	1.21	2.76	11.62**	22.41***	6.43
Time	1.12	3.21	5.42	2.38	10.43*	12.30**	8.25*	9.33*	5.60
Size	17.50***	13.78***	6.35	14.17***	2.02	11.69**	0.94	12.92***	8.86*

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$
[1]Significance with two degrees of freedom.

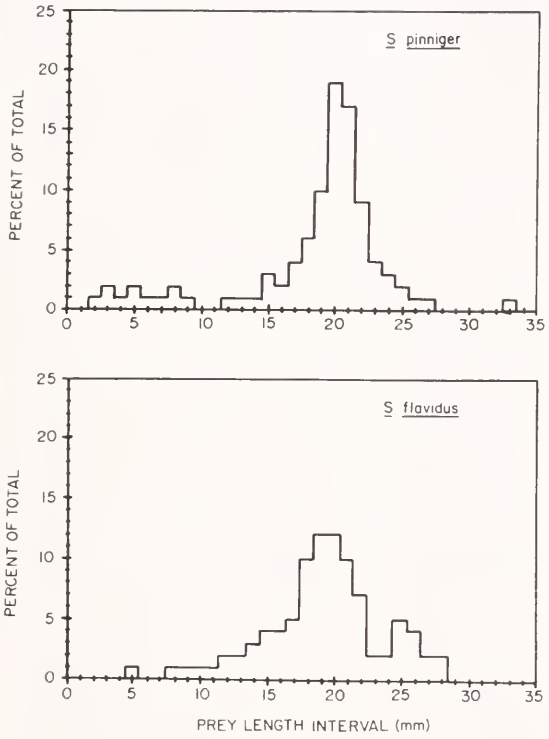

FIGURE 9.—Prey size spectra in percent for *Sebastes pinniger* and *S. flavidus*.

ostictus), they were represented by postlarval or juvenile forms commonly found in the plankton. Several comparatively large nektonic fishes and cephalopods (e.g., *Clupea harengus pallasi*, *Sebastes jordani*, *Loligo opalescens*) were eaten, but their occurrences were relatively rare. Conversely, the virtual absence of many common benthic and epibenthic organisms of appropriate size such as mysids, cumaceans, and gammaridean amphipods further implies that these fish do not normally feed on benthic animals.

These findings concur with the limited number of previous studies dealing with food habits of offshore rockfish. Phillips (1964) reported on the diet of all the species included here except *S. alutus*. Although little taxonomic detail and no quantitative data on prey consumption were given, euphausiids were listed as important forage items for all four species. Fishes were also important prey for several species, especially *S. flavidus*. Skalkin (1964), in a study of *S. alutus* in the Bering Sea, found mostly euphausiids and copepods in the stomachs, but also stated that a few nektobenthic species and "fragments" of benthic echinoderms were present.

The food habits of *S. flavidus* have been described in several studies off Oregon and Washington. Pereyra et al. (1969) found unusually high abundances and volumes of the mesopelagic fish, *Stenobrachius leucopsarus*, in *S. flavidus* stomachs collected near Astoria Canyon and hypothesized that local hydrographic conditions may have aggregated these prey at high densities. Gunderson et al. (1980)[5] reported that *S. flavidus* off the coast of Washington fed mostly on fishes, including some pleuronectid fishes possibly eaten near the bottom along with benthic polychaetes. Lorz et al. (1983) found euphausiids dominating the diet of *S. flavidus* off Washington and Queen Charlotte Sound, with fishes of greater importance in the latter region. Another deepwater species, *S. marinus*, found in the North Atlantic Ocean, also fed chiefly on pelagic prey (Lambert 1960). Euphausiids, hyperiid amphipods, and copepods were the most abundant prey, but mesopelagic fishes were also found in large numbers.

Among the species considered here, two divergent feeding patterns are apparent, assuming that

[5]Gunderson, D. R., G. L. Thomas, P. Cullenberg, D. M. Eggers, and R. Thorne. 1980. Rockfish investigations off the Washington coast. Ann. Rep., prep. for NMFS, Univ. Wash., 68 p.

the same prey items are equally available to all species. These can be seen most clearly in the divergence of the cumulative curves of the number of prey species (Fig. 2). Three species (*S. pinniger*, *S. alutus*, and *S. crameri*) tend to be stenophagous, with very few prey items represented in large volumes of prey organisms. Euphausiids appear to be the most sought after or available prey, and other prey taxa occur in low numbers. These three species show similar low food breadth values.

Sebastes flavidus and *S. diploproa*, on the other hand, have steadily rising prey curves that continue to rise and approach an asymptote beyond the limits of the figure. These curves are characteristic of euryphagous predators which show high overall prey diversity as well as high within-stomach diversity. This high prey diversity can be seen in the greater food breadth values attained by these two species. Although euphausiids predominate in these stomachs, high abundances of other prey, which may be preferred but have lower abundances and availabilities than euphausiids, also occur.

The diet overlap measurements calculated here may be useful in comparing how similar the food habits of two species are but may be of limited use when interpreted in an ecological sense. The interaction of factors that affect or determine the diet of a particular species is complex and may include such factors as temporal and spatial distribution of prey, behavioral adaptations of predator and prey, prey detection capabilities, and feeding morphologies of predators (Hyatt 1979). Caution should be exercised when inferences are made about possible species interactions based on diet overlap measurements alone. Two species may have broadly overlapping diets in terms of prey composition but segregate with respect to prey sizes selected, time of feeding, or habitat utilization (Schoener 1974; Ross 1977; Werner 1979; Macpherson 1981).

Sebastes pinniger and *S. flavidus* are two of the most abundant rockfish species within the geographical confines of this study. They inhabit similar depth ranges, latitudinal ranges, and show broadly overlapping areas of peak abundances according to trawl survey data (Alverson et al. 1964; Richardson and Laroche 1979; Gunderson and Sample 1980). Adams (1980) found that these two species had the highest positive association in trawl catches using presence-absence data of the seven abundant species he examined. Little is known, however, about their small-scale horizontal and vertical distribution. Although they may occupy similar bottom habitat, *S. flavidus* may be more pelagic (Alton 1972).

Seasonal, geographical, and diel variations in the abundance and availability of the important prey of *S. pinniger* and *S. flavidus* could be a major cause of the variations in the diet of these species. These variations may be the result of intrinsic prey population fluctuations with season, behavioral adaptations such as diel and ontogenetic vertical migration, or may stem from the prevailing oceanographic conditions either concentrating, dispersing, or transporting prey so that all prey are not equally available in the limited time and space frame of the individual predator. Current patterns alone are known to vary with season, depth, and geographic area (Huyer et al. 1975; Ingraham and Love 1978) and may affect the availability and concentration of prey.

Quantitative estimates of the seasonal and areal distributions of the total prey spectrum consumed by these rockfishes are limited. Day (1971) sampled macrozooplankton and micronekton from the northern part of the range of this study (lat. 46°45′-50°02′N) using a 0.9 m Isaacs-Kidd midwater trawl in the upper 150 m of the water column during the spring and fall. He found a peak in the biomass of catches at the outer edge of the continental shelf. Euphausiids dominated the catch at most stations, and *E. pacifica* and *T. spinifera* together accounted for 90% of the total abundance of all organisms collected, which is similar to the abundances found in the stomachs of several species examined here. Although the proportional abundance of *E. pacifica* varied greatly relative to *T. spinifera*, *E. pacifica* dominated the catches and was most concentrated during the spring when it comprised the largest proportion of the stomach weights in our study. Mesopelagic fishes were commonly collected in Day's sampling, but mostly at the offshore stations.

Pearcy (1972) reviewed the species composition, vertical and horizontal distribution, and variations in abundance of the macrozooplanktonic and nektonic fauna derived from 8 yr of sampling off Oregon. Annual and seasonal changes in the abundance and distribution of many species could be correlated with changes in oceanographic conditions. Following the cessation of upwelling in fall, surface waters flow predominantly inshore and northward, transporting shrimps and myctophids onto the shelf. We found that shrimp and myctophids became more important in the diets of

S. pinniger and *S. flavidus* at this time. An inshore-offshore peak in the biomass of midwater collections occurred on the edge of the continental slope off the central Oregon coast (lat. 44°39′ N), a zone where oceanic macrozooplankton and micronekton may be concentrated by advection (Pearcy 1976). This is the region where pelagic-feeding rockfishes are often concentrated (Gabriel and Tyler 1980).

The majority of the prey species found in the stomachs of the rockfish species examined are pelagic species that undertake extensive diel vertical migrations and are important components of the biological sound scattering layer in the Northeast Pacific (Pearcy and Laurs 1966; Brinton 1967; Pearcy and Mesecar 1971; Pearcy 1972; Alton and Blackburn 1972). In this study, both of the euphausiid species of interest, *E. pacifica* and *T. spinifera*, have been found to have substantially different daytime and nighttime vertical distributions. According to Alton and Blackburn (1972), catch rates of *T. spinifera* off the coast of Washington were the highest near the bottom during the early evening hours (1800-2000 h) and at the surface a few hours later (2100-2300 h).

The diurnal downward migration of these organisms over the continental shelf may result in a substantial biomass in close proximity to near-bottom predators, such as rockfishes, which feed on pelagic prey during the day. Deeper migration to daytime depths typical of their more open ocean conspecifics is restricted by the shelf, especially in shoaler areas such as Heceta Bank. Isaacs and Schwartzlose (1965) found dense populations of predators, including many rockfishes, on shallow banks off California; these predators presumably take advantage of net inshore transport by currents of oceanic organisms over the bank. Pereyra et al. (1969) reported high incidences of predation on mesopelagic organisms by aggregations of *S. flavidus* residing on the shelf edge near a deep canyon. Vertically migrating mesopelagic organisms may also constitute an important food source for many species of slope fishes (Sedberry and Musick 1978).

Diel vertical distribution patterns of offshore rockfishes are not well documented. Based on acoustic observations, Westrheim (1970) concluded that schools of Pacific ocean perch move off bottom at night. Pereyra et al. (1969) and Love (1981) caught rockfishes that were apparently feeding well off the bottom at night. Lorz et al. (1983) concluded that *S. flavidus* off Washington fed on euphausiids during night or early morning hours, when these euphausiids would be expected to be in surface waters. Similar migrations were seen on Heceta Bank during this study. Figure 10 shows an acoustic 33 kHz transect taken across Heceta Bank during the late morning (about 1023-1050 h PST). Many large "spikes" of fish aggregations were apparent extending over 100 m above bottom. Some of these were probably caused by rockfish ascending in the water column to feed. Figure 11 is a 33 kHz echogram on Heceta Bank made around 1800 h PST. The "haystacks" shown are characteristic of tight aggregations of *S. pinniger* just above bottom (Barss[6]) and may represent feeding aggregations. Also visible in this echogram is more diffuse scattering in the water column (20 m off bottom) probably caused by euphausiids. The tow made concurrently with this trace did yield a large catch of rockfish (97% *S. pinniger*), most of which had stomachs full of fresh euphausiids. This stratification of large sound scatterers below diffuse midwater scattering prey was often observed during the acoustic surveys. Atlantic cod appear to interact with pelagic prey in a similar fashion (Brunel 1965; Pearcy et al. 1979; Falk-Peterson and Hopkins 1981).

The two primary species examined in detail in this study appear to forage mainly during the midday and evening dusk periods, although sampling was limited during nighttime. The similar diel patterns of feeding intensity suggest that temporal partitioning of feeding time is not occurring between *S. pinniger* and *S. flavidus*. The differing utilization patterns of euphausiids and fishes seen for the two species (Table 13) may be related to the vertical positioning of the two species in the water column. *Sebastes flavidus* may feed high in the water column, prey upon adult herring and pelagic juvenile fishes during the daytime, and intercept euphausiids during crepuscular periods, whereas *S. pinniger* may stay nearer the bottom where they may feed almost exclusively on increased daytime aggregations of euphausiids.

The occurrence of a high percentage of empty stomachs and generally low feeding intensity indices in *S. alutus*, which were caught mainly in late afternoon in our study, suggests that this species is more nocturnal in its feeding patterns, assuming that this species has similar regurgita-

[6]W. Barss, fishery biologist, Oregon Department of Fish and Wildlife, Newport, OR 97365, pers. commun. December 1980.

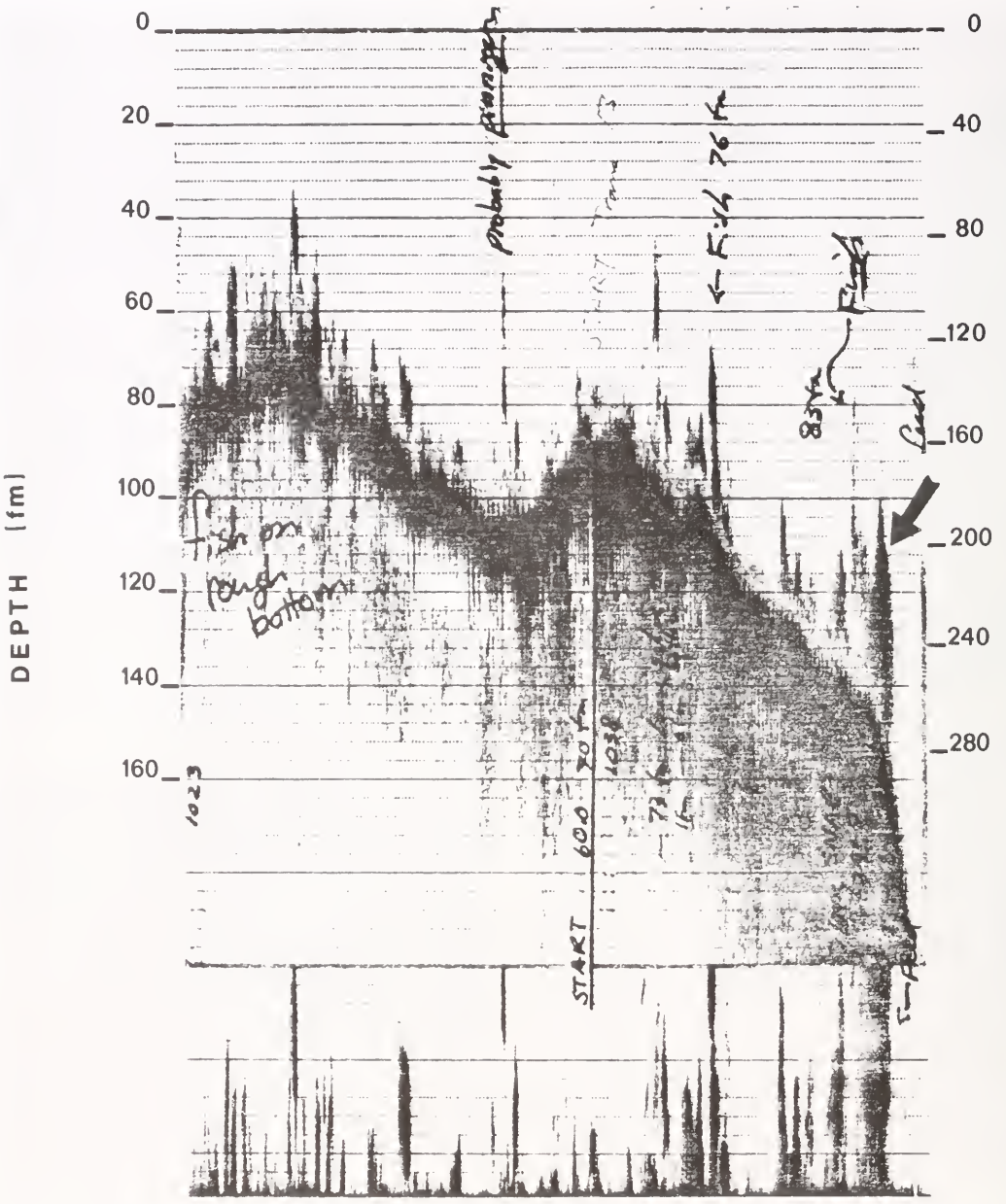

FIGURE 10.—Echo sounder (Krupp-Atlas Elektronik Model 611, 33 kHz) transect across Heceta Bank showing characteristic rough topography and schools of fish in the water column. The larger signal at the extreme right (arrow) is believed to be a large concentration of forage fish, possibly myctophids. The bottom section of the figure shows an expanded version of the layer just above the seabed.

tion and digestion rates as the other species studied. Skalkin (1964) found that the feeding intensity of immature *S. alutus* in the Bering Sea was highest around midday with a smaller peak shortly after dusk as found for *S. pinniger* and *S. flavidus* in this study. He also hypothesized that larger fish may feed higher in the water column at night on euphausiids, but his nighttime sampling was also limited. Similar pelagic feeding by *S. alutus* at night may be occurring in our study area, but these fish would not be available to bottom trawls at this time.

The rockfishes considered here are just a few species in an extensive guild (sensu Root 1967)

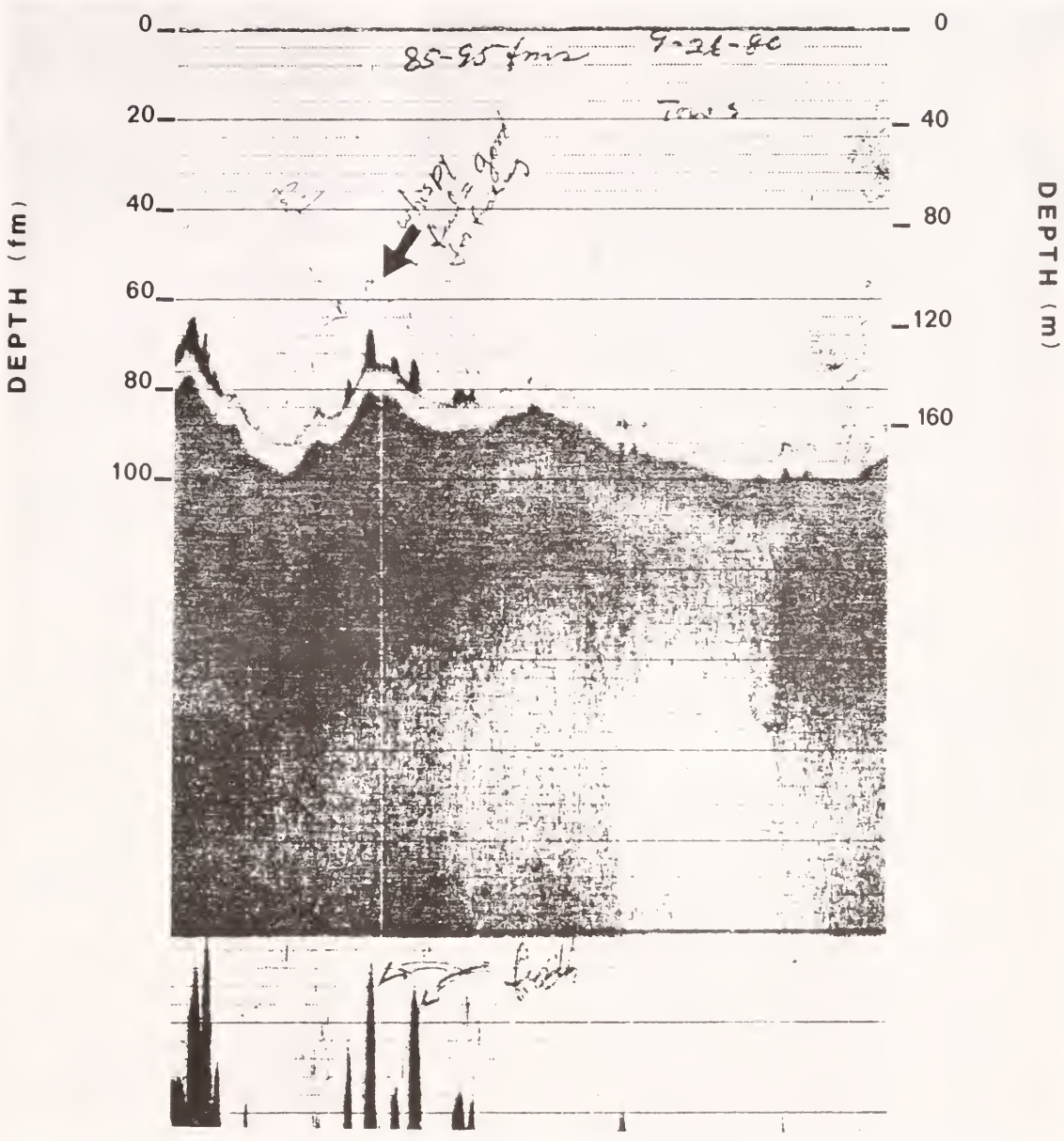

FIGURE 11.—Smoother bottom profile made during a tow showing the "haystacks" of rockfish in close association with the bottom and possibly preying upon the food organisms (arrow) directly above them.

of organisms which feed in varying degrees on euphausiids. Other pelagic predators in this study area known to feed intensively on euphausiids include Pacific hake (Alton and Nelson 1970), myctophids (Tyler and Pearcy 1975), juvenile salmon (Peterson et al. 1982), and squid (Karpov and Cailliet 1978). Standing stocks and production rates of euphausiids in northern latitudes may be of such magnitude that many predators often subsist on them in coexistence rather than compete for other more limited resources. More research is needed on the biology and distribution of these abundant prey species and their importance to fishery resources. In complex, multispecies fisheries such as those utilizing rockfishes, it may be possible to treat several species with similar

life histories and which prey on similar resources as a biological unit for management purposes.

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SPECIES ASSOCIATIONS AND COMMUNITY COMPOSITION OF MIDDLE ATLANTIC BIGHT CONTINENTAL SHELF DEMERSAL FISHES[1]

J. A. Colvocoresses and J. A. Musick[2]

ABSTRACT

Cluster analyses of seasonal NMFS Groundfish Survey bottom trawl catches on the Middle Atlantic Bight continental shelf revealed consistent species associations and faunal zones over a 9-year period. Boundaries between faunal zones tended to follow isotherms and isobaths. During the late winter-early spring, the following faunal zones were found: Northern inner shelf, northern mid-shelf, southern inner- and mid-shelf, and outer shelf-shelf break. Five species groups were identified: A small cryophilic group restricted to the first zone, a cold-water boreal group found in the first two zones, a ubiquitous boreal/resident group containing the major dominants, a warm-temperate group confined to the warmer southern and outer shelf waters, and a group of slope residents confined to the deepest zone. During the fall, five faunal zones were found: Southern inner/mid-shelf, northern inner shelf, northern mid-shelf, outer shelf, and shelf break. Five species associations were largely analogous to those in the spring, with the following exceptions: The cryophilic group was absent, the ubiquitous group contained mixed boreal and warm-temperate elements, and a second outer shelf group was recognized. The most notable change in the distribution of groups from the spring was a general northward shift and a sharply defined inshore movement of the temperate group.

Communities of fishes on the continental shelf have rarely been studied beyond the compilation of species lists for given areas. This is enigmatic when one considers the large amount of survey data that has been collected from much of the world's continental shelf waters in connection with fishery exploration and monitoring. While trawl survey data have traditionally been collected with the primary aim of assessing commercially harvestable stocks, they also provide an excellent base for evaluating the interspecific relationships among trawlable organisms.

The few studies which have previously addressed community structure of open continental shelf fishes have found clearly definable species associations with distributions related to environmental parameters. Demersal fish species assemblages found using objective mathematical measures have been described for the continental shelves in the Gulf of Guinea (Fager and Longhurst 1968), northwest Pacific coast of the United States (Day and Pearcy 1968), and Campeche Bank off Mexico (Sauskan and Ryzhov 1977).

Since 1967 the National Marine Fisheries Service (formerly Bureau of Commercial Fisheries) has conducted a semiannual bottom trawl survey of the continental shelf waters from Nova Scotia to Cape Hatteras (Grosslein 1969). This program has produced a data base which offers a unique opportunity for the analysis of the composition and variability of the fish communities in this region.

In the present study, that portion of these data collected in the Middle Atlantic Bight (Cape Cod to Cape Hatteras) during the cruises from fall 1967 through spring 1976 were analyzed with the aim of defining the composition of fish communities present within this area and how they vary geographically, thermally, and seasonally.

METHODS

Sampling

Groundfish Survey cruises were conducted by the National Marine Fisheries Service during the fall and spring from fall 1967 through spring 1976, aboard either the RV *Albatross IV* or RV *Delaware II*. The survey area extended from the 15-fathom (27 m) contour offshore to 200 fathoms (365 m). A stratified random sampling design was utilized, based on depth and geographical zones (Fig. 1). Catch data from strata 1-12 and 61-76 (Middle Atlantic Bight) were analyzed in the present study. Sampling intensity in each stratum was allocated according to the geographic area of each stratum

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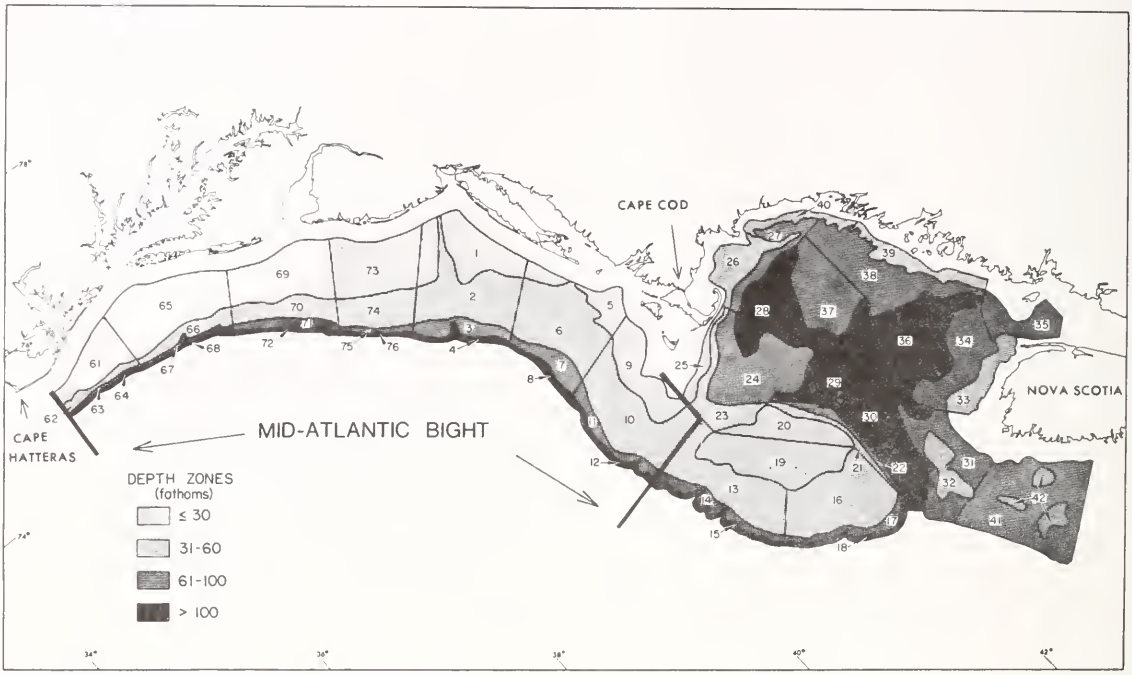


FIGURE 1.—Northwest Atlantic area sampled by NMFS Groundfish Survey. In the present study, data collected from the Middle Atlantic Bight area (strata 1-12, 61-76) between fall 1967 and spring 1976 were examined.

(2-16 stations per stratum). At each station a tow of ½-h duration at a speed of 3.5 kn was made along the bottom. A standard #36 Yankee trawl was utilized except during the spring cruises from 1973 to 1976, when a modified high-opening #41 Yankee trawl was used. The fishes captured were identified, counted, and weighed by species. A bathythermograph cast was made at each station. Further details of sampling design and sample processing may be found in Clark and Brown (1977) and Grosslein (1969).

Analyses

Clustering

Catch data were initially analyzed separately for each of 18 cruises, using numerical classification (clustering). Assemblages of fishes were defined by computing a similarity coefficient, $S_{(j,k)}$, among species from the species-station matrix and subsequently classifying species into clusters or groups (Sneath and Sokal 1973). Stations were clustered in the same manner from the inverted matrix, and species and station (site) groups were compared by nodal analysis (Lambert and Williams 1962). Matrix values entered were counts of individuals, as biomass measurements are overly influenced by the presence of relatively rare but large, motile fishes (which are poorly sampled by trawls) in the collections.

The similarity coefficient used was the Canberra metric (Lance and Williams 1967), which is particularly effective when the organisms under study are contagiously distributed (Clifford and Stephenson 1975) as most fishes are. Also, to further reduce the effects of contagion, the numerical abundance data were transformed [$\log_{10}(x + 1)$] before analysis (Taylor 1953). Species were eliminated from cluster analysis if they occurred at $<5\%$ of the stations occupied during a sampling period. Although this is a more severe data reduction than is commonly employed, examination of the raw matrix and trial runs at various cutoff levels indicated that species occurring below this level showed highly inconsistent distributions.

The clustering strategy used was flexible fusion with beta set at the conventional value of -0.25 (Boesch 1977). Calculations were performed on an IBM 370-115[3] at the Virginia Institute of Marine Science using the Fortran IV program COMPAH

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

(Combinatorial Polythetic Agglomerative Hierarchical Program) developed at the institution. Output was in the form of similarity matrices and computer generated dendrograms.

The choice as to which branches in the dendrograms were to be identified as biologically significant groups was based on the following procedure. Each branch of the dendrogram, composed solely of fusions involving only one entity as at least one-half of each fusion, was considered to constitute a minimal grouping. The distribution of each minimal grouping was then map-plotted, with logarithmic keyed symbols being used for plots of abundances of minimal species groupings. The plot of each grouping was then compared with that of the grouping with which it next fused; if no significant differences in distribution were evident, the fusion was considered to be intragroup. This procedure was repeated until all minimal groupings had been fused into groups showing evident distributional differences. In cases where there was any doubt as to whether two groups should be fused, nodal analysis diagrams were generated and compared for the two cases and the decision producing the "crisper" result (Clifford and Stephenson 1975) utilized. While this method obviously involves some subjectivity in the recognition of groups, it has been pointed out by several authors that all methods of interpreting numerical classifications require a certain degree of subjectivity and that fixed stopping rules are especially inappropriate with fusion strategies which introduce a group size-dependent element into intergroup relative affinities (Boesch 1977; Pielou 1977; Clifford and Stephenson 1975).

Two methods of nodal analysis were performed. The patterns of "constancy" and "fidelity" of species groups to site groups were expressed as relative densities of cells of a two-way table (Stephenson et al. 1972). Constancy is the proportion of the number of occurrences of each species group in the site group to the total number of occurrences possible (Boesch 1977). The index has a value of 1 when all members of a species group occur in all collections in a site group and a value of 0 when a species group does not occur in a given site group. Fidelity is a measure of the degree to which species groups are limited to site groups. The fidelity index used in this study was the constancy of a species group within a site group divided by the average constancy over all site groups. This index is unity when the constancy of a species group in a site group is equivalent to its overall constancy, >1 when its constancy in the site groups is greater than that overall, and between 0 and 1 when its constancy is less than its overall constancy. A chi-square test was applied to the fidelity value of each cell to determine whether it varied significantly ($\alpha = 0.05$) from 1. Fidelity values significantly >1 indicate a positive association of species in a group with a site group, while values significantly <1 suggest a "negative" association. In the present analyses, a highly positive (or strong) association was inferred if the number of occurrences of a given species group within a site group was twice that necessary to produce a fidelity value significantly >1, and a highly negative association was assumed when the number of occurrences was less than half that necessary to produce a fidelity value significantly <1. All nodal diagrams were drawn with the width of the rows and columns proportional to the number of entities in the respective site and species groups.

Species Dominance

Numerically dominant species have been used by ecologists for many years to characterize communities (Thorson 1957), and changes in dominant species often reflect faunal changes. In the present study, we have compared patterns of species dominance among site groups. A species was included in dominance comparisons if it occurred among the five most abundant species in at least 20% of all the stations from a site group.

Faunal Affinities

The faunal affinities of fishes captured were determined by examining published records of their usual ranges of occurrence (Bigelow and Schroeder 1953; Leim and Scott 1966; Struhsaker 1969; Musick 1972). Most warm-temperate species had resident populations south of Cape Hatteras in the "Carolinian" faunal province (Hazel 1970) and had their normal northern range limit somewhere within the Middle Atlantic Bight south of Cape Cod. Boreal species had permanent populations north of Cape Cod, and most had their southern range limit somewhere within the Middle Atlantic Bight north of Cape Hatteras. A few boreal species transcend Hatteras through bathymetric submergence. Certain components of the fauna tended to be residents on the inner shelf (*Scophthalmus aquosus*) or outer shelf (*Paralichthys oblongus*). Many species were resident on the shelf edge and upper slope (Musick 1976).

Pooling of Within-Season Cruises

Size of the data matrix was too large for simultaneous clustering of either of the two multiple-year seasonal data sets. However, the results of the cluster, nodal, and dominance analyses of the individual cruises revealed a high degree of within-season repetition in the composition and distribution of species groups and in the faunal, geographic, and hydrographic attributes of site groups. Major repetitive species groups were recognized for each season, and site groups for each year were referred to generalized seasonal site groups. The validity of these groups was examined by subjecting the pooled seasonal data sets to nodal and dominance analyses based on these groupings and comparing these results to those for the individual cruises.

RESULTS AND DISCUSSION

Thermal Regime

The geographic patterns of bottom-water temperatures were variable among years within both of the sampling seasons, although these differences were minor compared with the seasonal variation within a given year. Variability among years within a season can be attributed to two sources: Climatic differences among years and sampling artifacts (i.e., differences in the dates and duration of the sampling periods, and stochastic differences arising from the location of stations and the temporal sequence in which they were done).

The spring cruises were conducted in March and April, the period during which water temperatures in the Middle Atlantic Bight are at a mini-

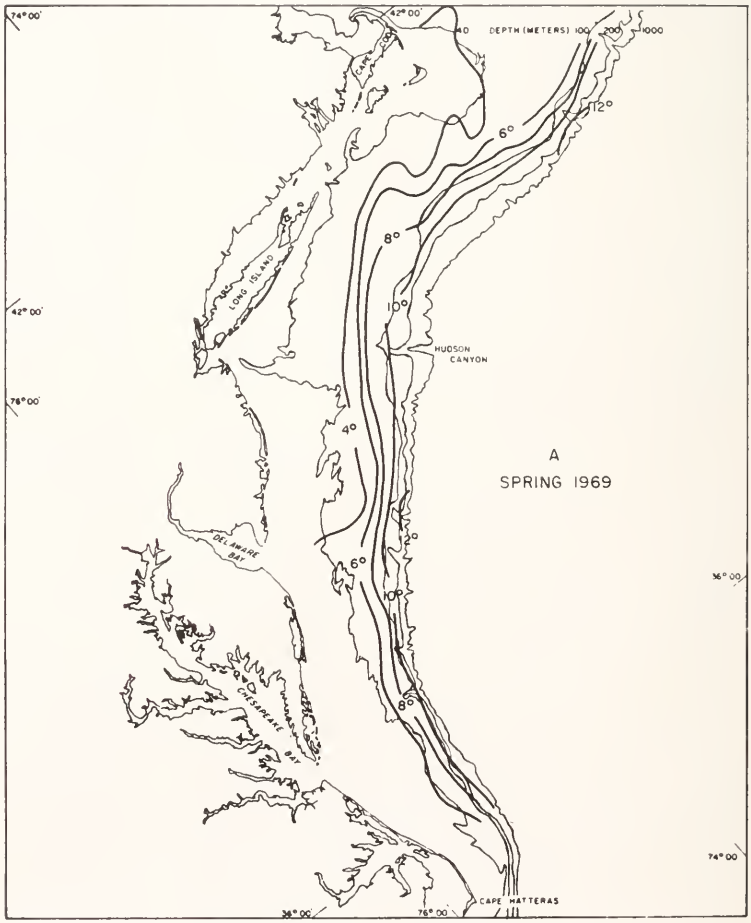
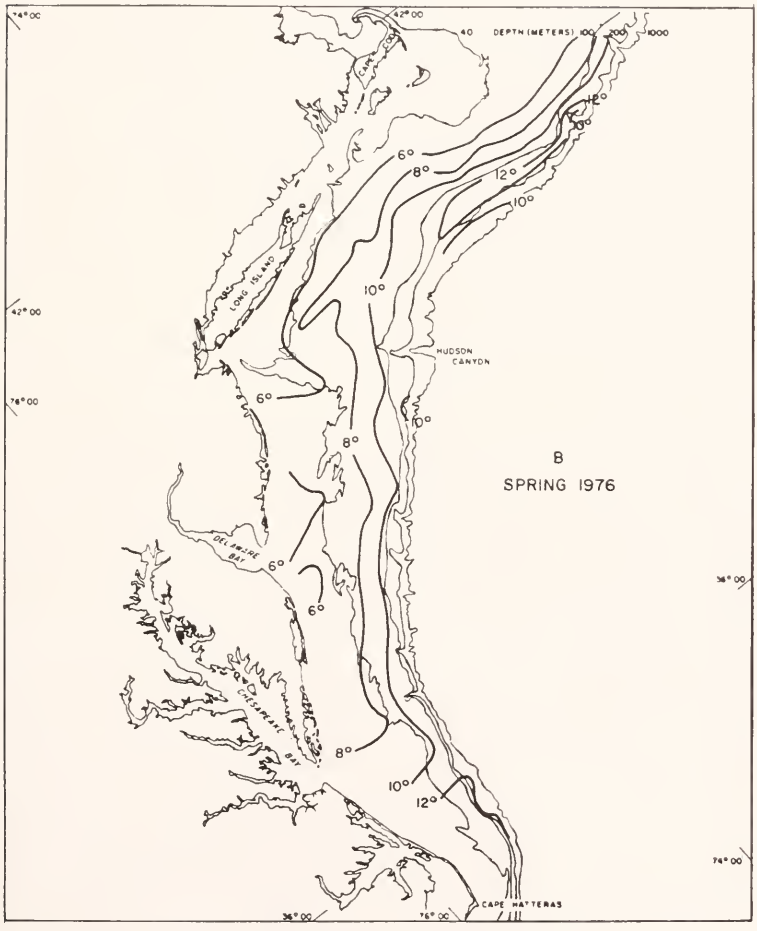


FIGURE 2.—Bottom isotherms for spring 1969 (A) and 1976

mum (Walford and Wicklund 1968), and therefore it is more appropriate to consider these cruises as having sampled the late winter distribution of fishes (Musick and Mercer 1977). There was a definite trend toward warmer temperatures during the study period for this season which cannot be completely attributed to sampling artifacts (Davis 1979). Bottom isotherms extrapolated from the collection data are shown for two cruises representative of the warmer (1976) and cooler (1969) extremes (Fig. 2). During the 1969 cruise, inshore and mid-shelf temperatures were $<4°C$ north of Delaware Bay and between 4° and 6°C between Delaware Bay and Cape Hatteras, with an increasing gradient present along the entire outer shelf. In 1976 temperatures of $<6°C$ were encountered only at northern inshore stations. South of Chesapeake Bay there was a southwardly increasing thermal gradient perpendicular to the shoreline, and the outwardly increasing gradient was distributed across a greater portion of the shelf. Bottom temperatures for the other spring cruises exhibited patterns intermediate between these two (Davis 1979).

Fall sampling cruises were conducted primarily in October. Because of water column turnover, this is the time of maximum temperature for mid-shelf bottom waters in this region (Bigelow 1933); however, coastal waters undergo rapid cooling during the fall (Parr 1933), initiating migrations for many fishes that spend the summer inshore. Bottom isotherms for a typical warm (1973) and cool (1971) fall sampling period are shown in Figure 3. In 1971 a strong thermal gradient was encountered along the mid-shelf from New York to Cape Hatteras. A pocket of cooler water (6°-9°C) was present northward and offshore of this gradient, where turnover was in progress or just beginning.



(B) extrapolated from NMFS Groundfish Survey cruises.

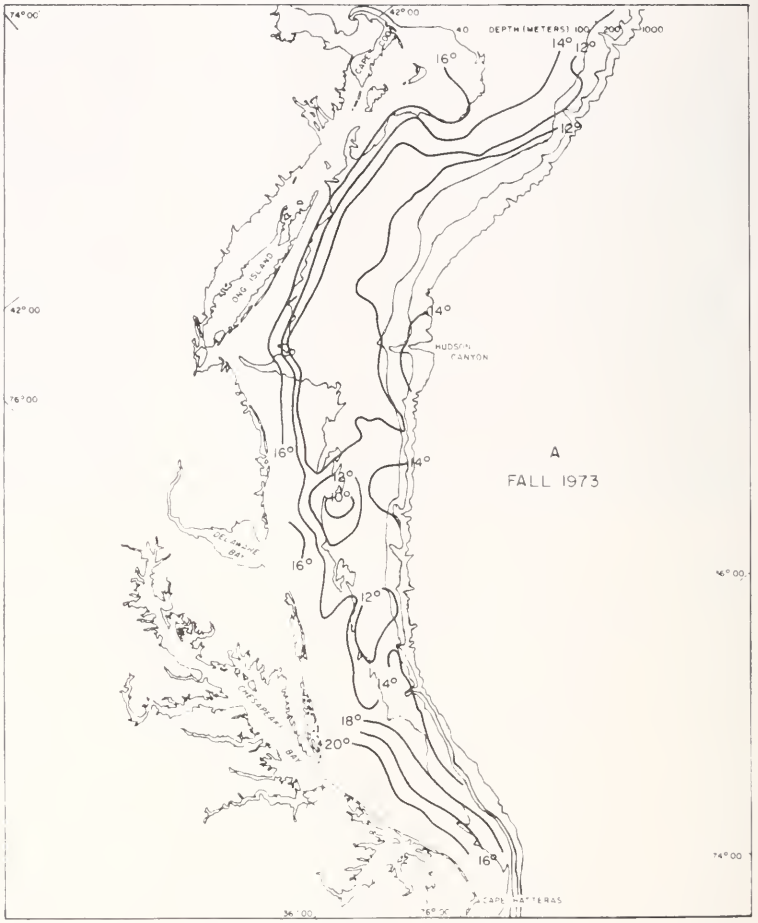


FIGURE 3.—Bottom isotherms for fall 1973 (A) and 1971

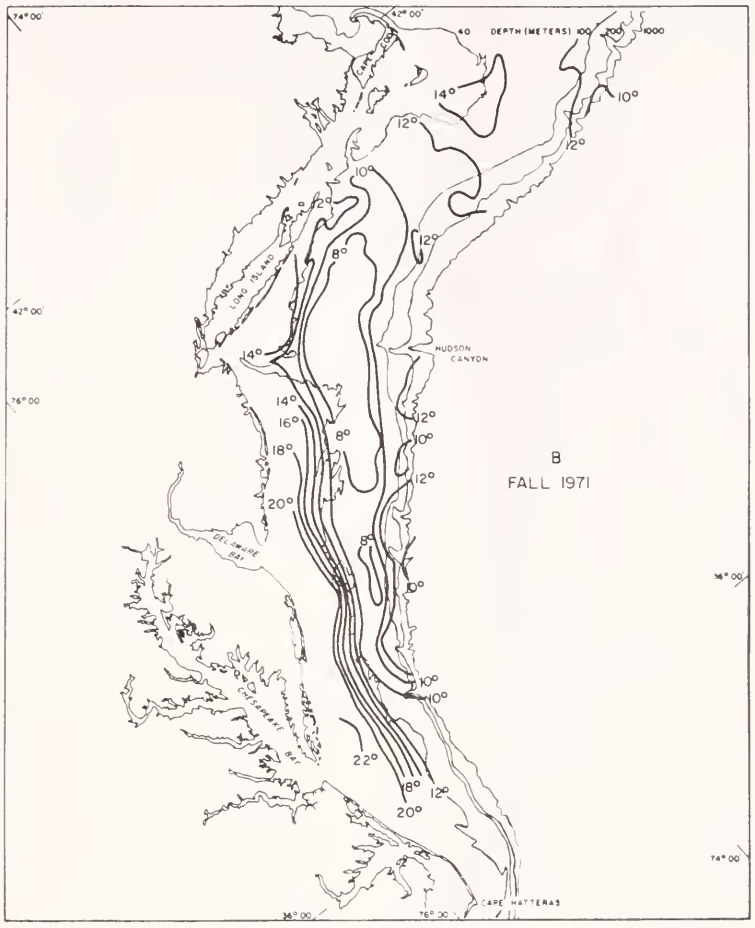
During 1973 bottom-water temperatures were less stratified and 2°-4°C warmer throughout most of the study area. Inshore temperatures exceeded 16°C along the entire Bight, with temperatures above 18°C occurring only south of Chesapeake Bay. The coolest temperatures were found again on the mid-shelf off New Jersey and Long Island, but the "pocket" was much less clearly defined and was composed of waters between 10° and 12°C, indicating that turnover had already occurred. The other fall cruises showed thermal regimes intermediate to those of 1971 and 1973 (Davis 1979).

Site Groups

Spring Cruises

Station groups based on cluster analysis were determined for the nine spring cruises (Colvocoresses and Musick 1979). Most groups were geographically contiguous and tended to be thermally and bathymetrically restricted. Site groups were not precisely comparable from one year to the next, but could, however, be categorized on the basis of faunal similarity, geographic location, bathymetry, and temperature.

During all nine cruises there was a group of site clusters of similar depth and temperature regimes which were contained between the shore and approximately the 8°C isotherm. The geographic extent of these groups varied from year to year, but generally covered the inner- and mid-shelf out to about 70 m from Cape Cod south to between Delaware Bay and Cape Hatteras, depending upon the southward extent of waters cooler than 8°C. These site groups were assigned to site group I (Fig. 4) for the pooled analyses. Adjacent to this group were



(B) extrapolated from NMFS Groundfish Survey cruises.

two other categories of groups: Northern outer shelf groups extending from the cold-water group to the shelf break (150 m) (pooled group II), and southern groups (pooled group III) which occupied the remaining shelf both outward and south of the 8°C isotherm. The boundary between these two categories was generally off the New Jersey coast, at which point there was often considerable overlap. The remaining outermost groups were located along the shelf break at depths of 150-350 m (pooled group IV).

In general, areas of geographic overlap between site groups can be related to variations in the thermal regime. For example, there is considerable overlap between groups I and III on the inner- and mid-shelf south of Delaware Bay. This area showed the greatest temperature variation among years, with group I station clusters predominating in the area in colder years and group III station clusters in warmer years. Hydrographic parameters and basic catch data for each stratum are summarized in Table 1. The hydrographic parameters (depth, temperature) within a site group are much better represented by the mean and standard deviation than by the range of values encountered. At a small percentage of stations only a few species were taken, and in cases where these species occurred within all or several strata, some misclassifications occurred. Because the incidence of these obvious misclassifications was low, they have been ignored rather than introducing an arbitrary system of reclassification. Virtually all extremely variant values of depth and temperature and strong deviation in geographic location within a site group were attributable to stations where only a few ubiquitous species were taken. Figure 5 illustrates temperature-depth envelopes for each site group. In order to reduce dis-

FIGURE 4.—Pooled site groups based on cluster analysis for spring NMFS Groundfish Survey cruises, 1968-76.

tortions introduced by misclassified stations, points which exceeded 2 standard deviations from either mean were not included. As may be seen by a comparison of Figures 4 and 5, groups I and IV are geographically, bathymetrically, and thermally discrete from one another with groups II and III occupying the intermediate area and somewhat overlapping the first two groups in terms of bathymetry and thermal regime. Groups II and III are largely separable on the basis of latitude (as well as faunal composition).

Fall Cruises

Station groups recognized from cluster analysis of the fall cruises (Colvocoresses and Musick 1979) were not as geographically contiguous or as thermally restricted as during the spring cruises, but could still be readily grouped into categories based on faunal attributes. During seven of the nine cruises there was a distinct southern inshore site group between shore and about 60 m extending from Cape Hatteras northward to the region off

TABLE 1.—Hydrographic and average catch parameters by site group for Spring NMFS Groundfish Survey cruises, Middle Atlantic Bight, 1968-76. The 1968-72 cruises used a #36 Yankee trawl, the 1973-76 cruises a #41 Yankee trawl. Numbers in parentheses are retransformed values.

		I		II		III		IV	
Site group		1968-72	1973-76	1968-72	1973-76	1968-72	1973-76	1968-72	1973-76
No. of stations		237	188	92	90	138	53	110	112
Abundance log $(x + 1)$	$\bar{x}$	2.19(154)	2.47(296)	2.40(252)	2.62(416)	2.17(149)	2.35(224)	2.16(144)	2.36(230)
	SD	0.40	0.45	0.54	0.40	0.68	0.67	0 54	0.51
Biomass (kg) log $(x + 1)$	$\bar{x}$	1.70(50)	1.97(95)	1.79(62)	2.14(138)	1.58(38)	1.92(84)	1.56(37)	1.65(45)
	SD	0.40	0.36	0.54	0.43	0.59	0.51	0.57	0.46
No. of species	$\bar{x}$	10.1	12.4	9.7	12.1	8.1	8.8	9 1	13.1
	SD	2.8	3.0	2.9	2.5	2.9	3.3	3 3	4.3
Depth (m)	range	18-101	18-90	24-329	29-152	18-349	27-152	66-379	53-341
	$\bar{x}$	50.0	46.5	117.9	78.9	84 1	75.2	222 1	194.0
	SD	17.3	15.4	46.8	21.9	54 2	33.2	78.3	72.1
Temperature (°C)	range	2-9	3-11	4-14	7-16	5-13	5-14	5-16	5-15
	$\bar{x}$	4.6	6.0	10.0	9 6	8.9	10.2	10 1	11.4
	SD	1.5	1.5	2.1	2.0	2.2	2.1	2.0	1 6

Delaware Bay. This group was generally contained behind a strong thermal gradient and exhibited the warmest bottom temperatures in the study area. These groups were assigned to site group I for the pooled analyses (Fig. 6, Table 2). Extending northward from these groups along the inner shelf was a second, colder site group which tended to be constricted toward shore between northern Long Island and Cape Cod (group II). During 1973 and 1974, when thermal stratification was weaker and inshore water temperatures in the north were higher, there was no distinct break between northern and southern inshore station groups (groups I and II), but instead there were two station groups with members in both northern and southern inshore and mid-shelf waters. One group from each of these years was assignable to each of the two major pooled groups based on faunal similarity; but such assignment, of course, led to the geographical overlap between groups I and II seen off Long Island and Chesapeake Bay in Figure 6.

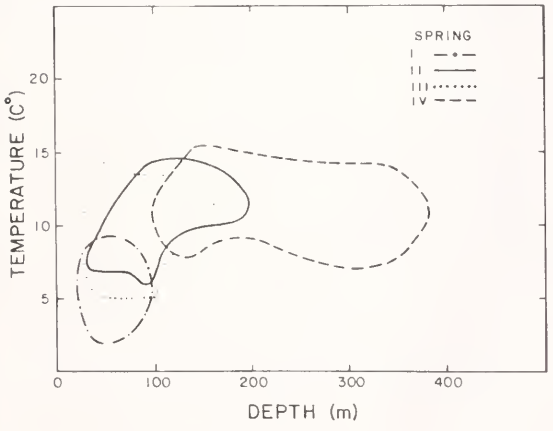


FIGURE 5.—Temperature-depth envelopes for pooled spring site groups, Middle Atlantic Bight area, 1968-76. To avoid distortions introduced by misclassified stations, points falling over two standard deviations from either mean were excluded.

One or two site groups each year occurred on the northern mid-shelf primarily between 35 and 90 m, in the region of the coolest shelf waters (group

TABLE 2.—Hydrographic and average catch parameters by site group for Fall NMFS Groundfish Survey cruises, Middle Atlantic Bight, 1967-75. All cruises used a #36 Yankee trawl. Numbers in parentheses are retransformed values.

Site group		I	II	III	IV	V
No. of stations		114	176	209	382	114
Abundance log $(x + 1)$	$\bar{x}$	2.19(130)	2.30(200)	2.20(249)	2.05(111)	1.92(84)
	SD	0.73	0.59	0.57	0.67	0.54
Biomass (kg) log $(x + 1)$	$\bar{x}$	1.55(36)	1.78(61)	1.73(54)	1.09(11)	0.86(6)
	SD	0.58	0.56	0.59	0.56	0.39
No. of species	$\bar{x}$	8.2	10.8	10.8	6.8	9.3
	SD	3.7	3.6	4.1	2.9	3.7
Depth (m)	range	18-123	20-80	31-192	16-397	71-433
	$\bar{x}$	33.8	42.6	61.5	110.6	249 6
	SD	12.7	12.4	17.1	60.2	77.4
Temperature (°C)	range	8-23	6-25	5-22	6-21	6-18
	$\bar{x}$	16.7	13.4	10.7	11.7	10.4
	SD	3.5	3.5	2.6	2.2	1.9

FIGURE 6.— Pooled site groups based on cluster analysis for fall NMFS Groundfish Survey cruises, 1967-75.

III). The remaining site groups could be classified as outer shelf-shelf break (group IV) or upper slope (group V). The outer shelf-shelf break group displayed a wide depth range and a temperature range very similar to groups II and III, but occurred consistently offshore of those two groups (Fig. 6). The upper slope group had the most restricted temperature range and was bathymetrically discrete from the inner- and mid-shelf groups. The temperature-depth envelopes for the first four site groups (Fig. 7) show a large amount of overlap in the shallower portion of the study area, but much of this overlap is an artifact of combining data across years and over a wide area (i.e., thermal ranges and boundaries between groups varied between years, and bathymetric boundaries varied with latitude).

Species Associations

Between 6 and 11 species clusters were recognized for each cruise (Colvocoresses and Musick 1979). As with the station clusters, although there was some variation in group composition and dis-

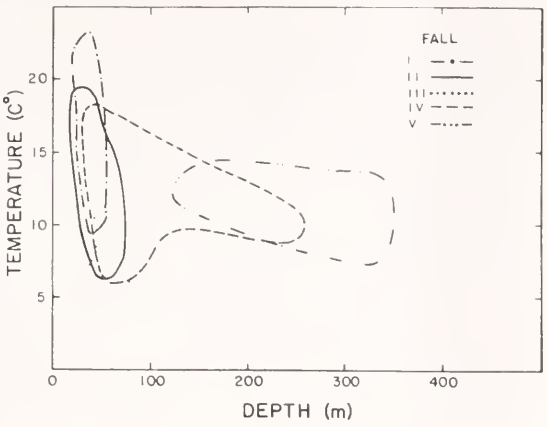
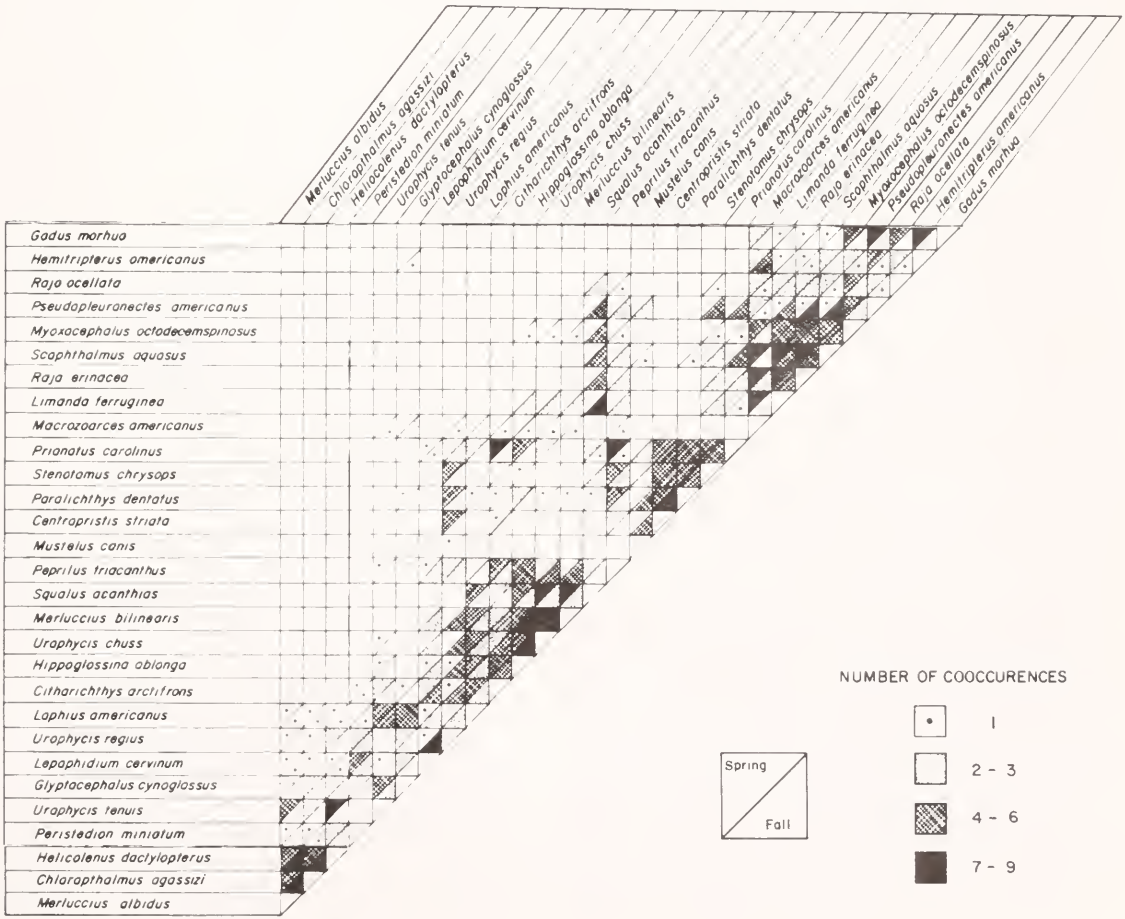


FIGURE 7.—Temperature-depth envelopes for pooled fall site groups, Middle Atlantic Bight area, 1967-75. To avoid distortions introduced by misclassified stations, points falling over two standard deviations from either mean were excluded.

tribution from year to year, the groupings were largely consistent over the 9-yr period of this study. Figure 8 shows the number of times the 30 most commonly occurring and dominant demersal species occurred within the same species group during the spring and fall cruises. The species are arranged so as to be closest to those species they occurred with most often in the clusters, i.e., so that the densest cells fall along the diagonal border of the diagram.

Four strongly recurring species groups are evident from this diagram. *Myoxocephalus octodecemspinosus, Scophthalmus aquosus, Raja erinacea*, and *Limanda ferruginea* frequently appeared in the same group during both seasons. In the spring they were often joined by *Macrozoarces americanus*, a species generally absent from the

FIGURE 8.—Cooccurrences within the same species cluster group for major species, spring and fall NMFS Groundfish Survey cruises, Middle Atlantic Bight area, 1967-76.



clusters in the fall, while *Squalus acanthias* and *Pseudopleuronectes americanus* were common co-group members during the fall cruises. In the spring the latter species regularly occurred in a separate group which included *Gadus morhua* and *Hemitripterus americanus*. Except for *Scophthalmus aquosus*, an inshore resident, all of these species are of boreal faunal affinity and are restricted to cold water (Bigelow and Schroeder 1953; Leim and Scott 1966).

Prionotus carolinus, *Stenotomus chrysops*, *Paralichthys dentatus*, and *Centropristis striata*, all warm-temperate species, were regularly classified in the same group during both seasons. During the fall this group was often joined by *Mustelus canis*, another warm-temperate species which was only rarely taken during the spring cruises. Two other warm-temperate species, *Peprilus triacanthus* and *Urophycis regia*, regularly cooccurred with this group in the spring.

Merluccius bilinearis and *Urophycis chuss* were the two most consistently cooccurring species, appearing in the same group in all but one cruise. These two species formed the core of a third species group which was ubiquitous in the spring and widespread across the deeper portion of the study area in the fall. Both of these boreal species have broader temperature tolerances than the cold-water groups noted above (Musick 1974; Bigelow and Schroeder 1953). Abundances of these two species were greater on the outer shelf and shelf break, and they often clustered with *Paralichthys oblongus* (= *Hippoglossina oblonga*), an outer shelf resident, and, in the fall, with *Citharichthys arctifrons*, a slope resident which also occurs on the outer shelf (Richardson and Joseph 1973) and *Lepophidium cervinum*, another outer shelf resident. The warm-temperate species *Peprilus triacanthus* and *Urophycis regia* were also common group members in the fall, while *Lophius americanus* regularly occurred in this group in the spring.

The fourth clearly defined recurring species group was an upper slope group composed of *Helicolenus dactylopterus*, *Chloropthalmus agassizi*, and *Merluccius albidus*, which appeared consistently during both seasons. *Urophycis tenuis* commonly cooccurred with members of this group during the spring, while in the fall this species was more widely distributed across the outer shelf and tended to appear in small groups with *Lophius americanus* and *Glyptocephalus cynoglossus*.

The major recurring species groups described above are listed for each season in Table 3. The groups are ordered in the same manner as the generalized station groups, that is, from shallowest to deepest (distribution) while still maintaining nearest neighbor intergroup relationships as determined in the clusters. Figures 9 and 10 show the distributional relationships between the major site and species groups as determined by nodal analyses. As noted above, these relationships are more sharply defined during the spring cruises than in the fall, but in both cases the nodal analyses show clear differences in the faunal composition of site groups and the distribution of species groups. The interrelationships seen here are also highly representative of those noted during analyses of the individual cruises.

Dominance

The dominant species for each of the pooled site groups are given in Tables 4 and 5. During the spring *Limanda ferruginea* was the major dominant at the cold-water, inshore site group (I), *Squalus acanthias* and *Merluccius bilinearis* were among the major dominants at all site groups, and *Peprilus triacanthus* was a major dominant at all but the cold-water site group. *Stenotomus chrysops* was a major dominant along the southern outer shelf (group III). In the fall, the southern inshore site group (I) was strongly dominated by three warm-temperate species: *Prionotus carolinus*, *Stenotomus chrysops*, and *Peprilus triacanthus*. These three species persisted as major dominants at the northern inshore site group, but were joined there in roughly equal dominance by three boreal species: *Limanda ferruginea*, *Squalus acanthias*, and *Merluccius bilinearis*. *Peprilus triacanthus* and the latter group were major dominants on the northern mid-shelf (group III). *Peprilus triacanthus* and *Merluccius bilinearis* were also major dominants at the outer shelf stations (group IV), where they were joined by *Urophycis regia*. The shelf-break stations (group V) were dominated by *Merluccius bilinearis*, *Citharichthys arctifrons*, and *Helicolenus dactylopterus*.

There were few major changes in species dominance throughout the study, and Tables 4 and 5 are representative of those for the individual cruises. *Merluccius bilinearis*, *Peprilus triacanthus*, and *Squalus acanthias* were consistently the three most dominant species during both major seasons. Although *Merluccius bilinearis* accounted for only around 10% of the individuals taken, it was the most consistently dominant

TABLE 3.—Major recurrent species groups, NMFS Groundfish Survey, Mid-Atlantic Bight area, 1967-76. Faunal affinity is designated after each species name: Boreal, Bo; warm temperate, WT; inner shelf resident, IS; outer shelf resident, OS; slope resident, Sl.

Spring cruises	Fall cruises
A	A
Gadus morhua Bo	*Centropristes striata* WT
Hemitripterus americanus Bo	*Mustelus canis* WT
Pseudopleuronectes americanus Bo	*Paralichthys dentatus* WT
	Prionotus carolinus WT
B	*Stenotomus chrysops* WT
Limanda ferruginea Bo	B
Macrozoarces americanus Bo	
Myoxocephalus octodecemspinosus Bo	*Limanda ferruginea* Bo
Raja erinacea Bo	*Myoxocephalus octodecemspinosus* Bo
Scopthalmus aquosus IS	*Pseudopleuronectes americanus* Bo
	Raja erinacea Bo
C	*Scophthalmus aquosus* IS
	Squalus acanthias Bo
Lophius americanus Bo	
Merluccius bilinearis Bo	C
Paralichthys oblongus OS	
Squalus acanthias Bo	*Citharichthys arctifrons* OS
Urophycis chuss Bo	*Lepophidium cervinum* OS
	Merluccius bilinearis Bo
D	*Paralichthys oblongus* OS
	Peprilus triacanthus WT
Centropristes striata WT	*Urophycis chuss* Bo
Paralichthys dentatus WT	*Urophycis regia* WT
Peprilus triacanthus WT	
Prionotus carolinus WT	D
Stenotomus chrysops WT	
Urophycis regia WT	*Glyptocephalus cynoglossus* Bo-Sl
	Lophius americanus Bo
E	*Urophycis tenuis* Bo-Sl
Chloropthalmus agassizi Sl	E
Helicolenus dactylopterus Sl	
Merluccius albidus Sl	*Chloropthalmus agassizi* Sl
Urophycis tenuis Bo-Sl	*Helicolenus dactylopterus* Sl
	Merluccius albidus Sl

species, reflecting a very uniform distribution. *Limanda ferruginea* was the only major species to undergo a notable change in dominance, showing a pronounced decline only during the last 2 yr of the study. Parrack[4] has carefully linked the decline of this valuable commercial species to overfishing.

Squalus acanthias and *Peprilus triacanthus*, two of the most dominant species, showed strong seasonal differences in the groups with which they clustered. *Squalus*, a boreal cold-water species, was widespread in the spring and occurred in the ubiquitous group, but during the fall cruises this species was restricted to the cooler waters on the northern shelf and generally clustered with the *Limanda*-dominated cold-water group. *Peprilus triacanthus* generally appeared in the same group as the other warm-temperate species in the spring when it was distributed along the outer shelf, but in the fall this species was widespread across the shelf and tended to be more concentrated in the cooler portions of the study area and usually clustered with the semi-ubiquitous *Merluccius bilinearis-Urophycis chuss* group. *Peprilus triacanthus* is considerably more tolerant of cooler temperatures than the other warm-temperate species encountered in this study (Horn 1970). *Urophycis regia*, another warm-temperate species which inhabits cooler waters (Struhsaker 1969), clustered similarly to *Peprilus triacanthus*, occurring with the warm-temperate group in the spring and with the semi-ubiquitous group in the fall; however, it appeared to have slightly narrower temperature tolerances, as it was more restricted to the southern portion of the outer shelf in spring and tended to be more concentrated in deeper, warmer waters in the fall.

Absolute abundances, both of total catches and of individual species, varied to a much greater extent than did the relative abundances between species throughout the study. Because abundance trends for the fall cruises have been well documented by Clark and Brown (1977) and the change

[4]Parrack, M. L. 1973. Current status of the yellowtail flounder fishery in ICNAF Subarea 5. Int. Comm. Northw. Atl. Fish., Res. Doc. 73/104, Ser. No. 3067, 3 p.

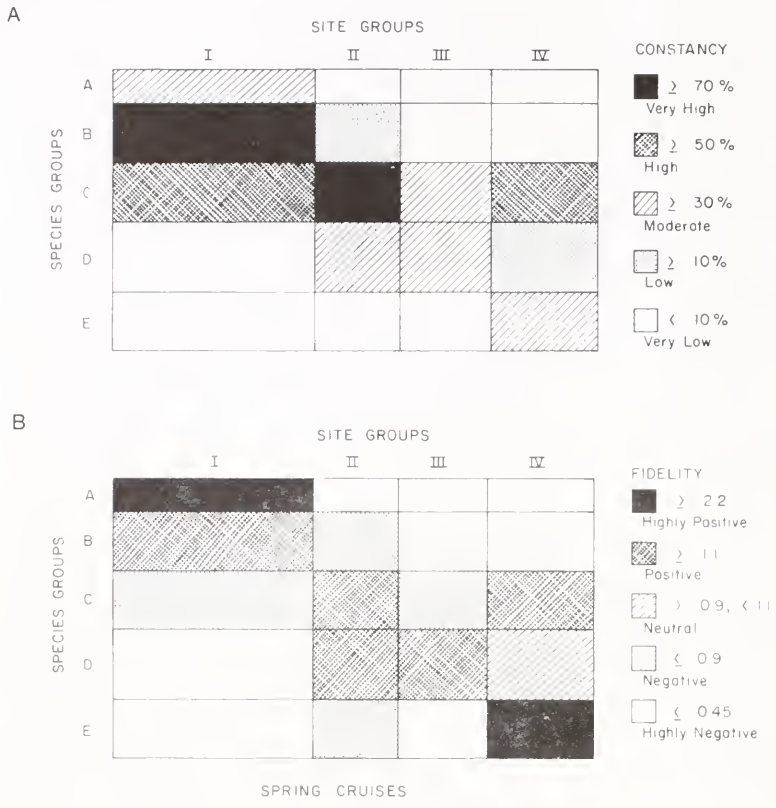


FIGURE 9.—Nodal constancy (A) and fidelity (B) diagrams showing the interrelation between pooled site and species groups, NMFS Groundfish Survey spring cruises, 1968-76.

TABLE 4.—Dominant species by site group for Spring NMFS Groundfish Survey cruises, Mid-Atlantic Bight area, 1968-76. A species was considered dominant if it occurred among the five most abundant species at at least 20% of all stations in the site group. Figures given are percentage of stations within each site group at which a species occurred (%) and the average percentage that the species contributed towards total abundance of nonpelagic fishes ($\bar{x}$%) within the site group. Faunal affinities and species groups are as given in Table 3.

Species	Faunal affinity	Species group	Site group I		II		III		IV	
			%	$\bar{x}$%	%	$\bar{x}$%	%	$\bar{x}$%	%	$\bar{x}$%
Gadus morhua	Bo	A	44	1.4						
Pseudopleuronectes americanus	Bo	A	38	2.2						
Limanda Ferruginea	Bo	B	88	28 5	22	1 4				
Macrozoarces americanus	Bo	B	68	5.2						
Myoxocephalus octodecemspinosus	Bo	B	56	5.0						
Raja erinacea	Bo	B	77	11.9	52	1 5				
Scophthalmus aquosus	IS	B	70	4 7						
Hippoglossina oblonga	OS	C	29	1.1	84	7 6	44	2 4	63	5 2
Lophius americanus	Bo	C			58	0.7			53	1 4
Merluccius bilinearis	Bo	C	79	20 5	97	22 4	66	13.0	90	27 2
Squalus acanthias	Bo	C	73	11.1	87	30.0	82	24 6	58	12 2
Urophycis chuss	Bo	C	54	3.9	84	9 3	25	1 9	74	9.5
Centropristes striata	WT	D					40	4.2		
Paralichthys dentatus	WT	D					47	2 2		
Peprilus triacanthus	WT	D			75	14 8	57	12.3	56	19 4
Prionotus carolinus	WT	D			50	7 1	51	9 8		
Stenotomus chrysops	WT	D			24	2 1	50	15.6		
Urophycis regius	WT	D					48	7.2	35	2.0
Chloropthalmus agassizi	SI	E							31	1.6
Helicolenus dactylopterus	SI	E							59	6.7
Merluccius albidus	SL	E							38	3.1
Urophycis tenuis	Bo-SI	E							38	1.6

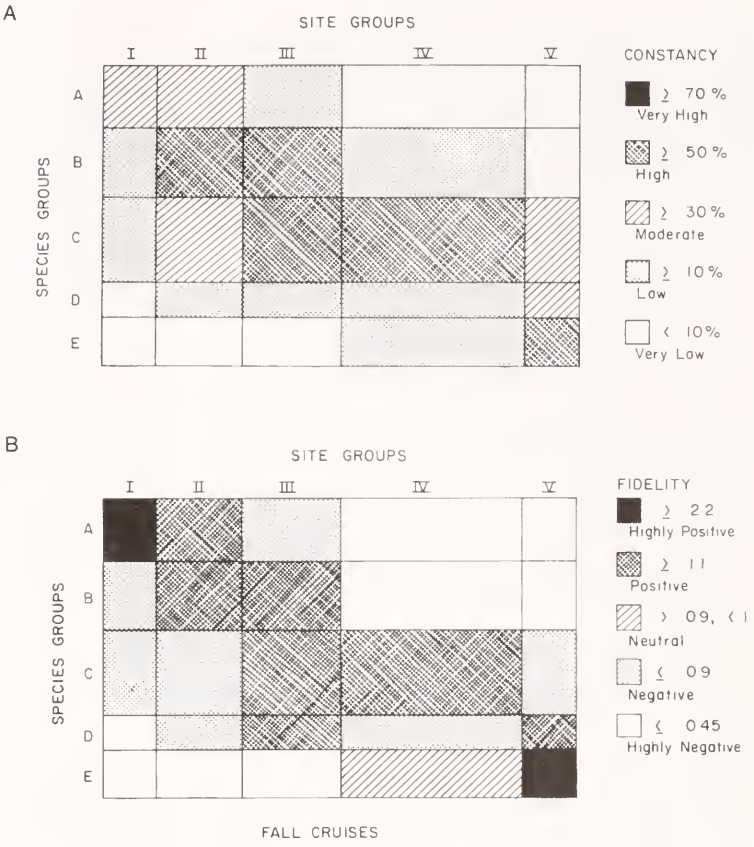


FIGURE 10.—Nodal constancy (A) and fidelity (B) diagrams showing the interrelation between pooled site and species groups, NMFS Groundfish Survey fall cruises, 1967-75.

TABLE 5.—Dominant species by site group for Fall NMFS Groundfish Survey cruises, Mid-Atlantic Bight area, 1967-75. A species was considered dominant if it occurred among the five most abundant species at at least 20% of all stations in the site group. Figures given are percentage of stations within each site group at which a species occurred (%) and the average percentage that the species contributed towards total abundance of nonpelagic fishes ($\bar{x}$%) within the site group. Faunal affinities and species groups are as given in Table 3.

Species	Faunal affinity	Species group	Site group I		II		III		IV		V	
			%	$\bar{x}$%	%	$\bar{x}$%	%	$\bar{x}$%	%	$\bar{x}$%	%	$\bar{x}$%
Centropristes striata	WT	A	50	4.7								
Mustelus canis	WT	A	38	5.7								
Paralichthys dentatus	WT	A	61	6.7	51	13.5						
Prionotus carolinus	WT	A	75	33.3	61	10.1						
Stenotomus chrysops	WT	A	53	17.5	51	13.5	30	2.4				
Limanda ferruginea	Bo	B			65	14.1	79	18.0				
Myoxocephalus octodecemspinosus	Bo	B					52	2.7				
Pseudopleuronectes americanus	Bo	B			69	3.3	47	1.7				
Raja erinacea	Bo	B			64	3.8	58	2.7				
Scophthalmus aquosus	IS	B	52	2.9	62	3.4	25	1.0				
Squalus acanthias	Bo	B			69	16.8	77	11.3	23	5.1		
Citharichthys arctifrons	OS	C					35	2.7	49	6.4	68	11.8
Hippoglossina oblonga	OS	C			59	2.2	70	3.3	53	3.6	34	1.4
Lepophidium cervinum	OS	C							32	2.9	27	2.9
Merluccius bilinearis	Bo	C			67	10.2	92	23.0	80	20.8	58	11.3
Peprilus triacanthus	WT	C	59	15.8	65	11.1	72	19.6	65	26.5	28	5.1
Urophycis chuss	Bo	C			35	2.7	74	8.2	37	4.2	30	2.1
Urophycis regius	WT	C	40	6.5					57	14.8	40	7.9
Lophius americanus	Bo	D							31	2.2	57	3.0
Chlorophthalmus agassizi	SI	E									44	5.9
Helicolenus dactylopterus	SI	E									84	21.2
Merluccius albidus	SI	E									65	7.7

in nets makes a similar analysis of the spring cruises tenuous at best, we will not consider the topic further other than to note that average abundance and biomass were higher in the northern and inshore portion of the study area during both seasons (Tables 1, 2).

CONCLUSIONS

Despite large variation in the abundances of individual species, cluster analyses of 9 yr of survey data have shown clear and consistent patterns of community composition and distribution among demersal fishes of the Middle Atlantic continental shelf. Allowing for thermal variation and misclassification of small catches, persistent site and species clusters have indicated the presence of four relatively constant and well-defined areas of faunal homogeneity in the spring and five more general areas in the fall, and five strongly recurring species associations during both seasons.

The spring site groups can be described approximately as northern inner- and mid-shelf (I), extending from shore out to about 60-80 m from Cape Cod to south of Delaware Bay; northern mid-shelf (II), occupying from around 60-80 m out to about 150 m from Cape Cod to Hudson Canyon; southern outer shelf (III), 60-150 m, from Delaware Bay to Cape Hatteras; and outer shelf-shelf break (IV), >150 m. The southern inner and mid-shelf is a thermally related transition zone between groups I and III. The outer shelf between Delaware Bay and Hudson Canyon was also a transition zone (between groups II and III), but this discontinuity does not appear to be related directly to temperature, but rather to the extent to which the northward migration of the warm-temperate species group has progressed by the time of the survey.

The five spring species groups contained one group specific to this season and four which contained common elements and properties with analogous fall groups. The first group (A) can be characterized as highly cryophilic, being virtually restricted to site group I and containing two members (*Gadus morhua* and *Hemitripterus americanus*) which were relatively absent from the study area during the fall. None of these species were major dominants, even within group I. The second group (B) is also composed of primarily boreal, cold-water species, but in this case is not completely restricted to site group I (although primarily distributed there) and contains the major dominant for that site, *Limanda ferruginea*. The third group (C) may be described as ubiquitous throughout the study area with moderate or better constancy to all site groups (Fig. 9). All members of this group are boreal or resident, and the major dominants, *Merluccius bilinearis* and *Squalus acanthias*, are the nuclear members. The fourth group (D) is composed entirely of warm-temperate members and is restricted to the warmer southern and outer shelf waters (site groups II-IV). *Peprilus triacanthus* and *Stenotomus chrysops* are the major dominants from this group. The last group (E) is composed strictly of weakly dominant slope species mostly confined to the shelf break site group (IV).

The spring warming trend noted during the study period appeared to have no major effect on the composition and distribution of fish communities in the area other than the latitudinal division between the inshore site groupings. The results of the present study are very much in accordance with the conclusions of Taylor et al. (1957) and Colton (1972) who found that while the ranges and distributions of certain species did shift with a changing thermal regime, there were no obvious overall changes in faunal composition. This is understandable when one considers that the average change encountered (about 2°C) is relatively small compared with the temperature tolerances of the species involved and the seasonal and geographic temperature variation encountered.

The five fall site groups can best be described as southern inner- and mid-shelf (I), extending out to about 60 m from Cape Hatteras to Delaware Bay and containing the area of warmest temperatures; northern inner shelf (II), extending northward from group I along a similar depth regime and containing cooler waters; northern mid-shelf (III), extending from group II out to about 90 m and occupying the area of the cold pool; outer shelf (IV), occupying the area between groups I and III and about 150 m; and shelf break (V), >150 m. While, again, with these groups there is some overlap (particularly with groups I and II as discussed above), their definition is fairly good considering the rapidly changing environmental conditions and migratory activity of fish during this period.

The fall species associations, as noted above, have much in common with those noted in the spring. The small cryophilic group is absent, but the terms applied to the other four spring groups may be applied here as well. An exclusively boreal-resident group (B) persists on the northern inner- and mid-shelf, including four members of

the spring cold-water group B, one member of the cryophilic group, and *Squalus acanthias*, a ubiquitous dominant in the spring found only in the northern portion of the study area in the fall. The ubiquitous spring group (C) persists with *Merluccius bilinearis* the major dominant, and two other common members from the spring group, but the fall group is no longer exclusively boreal-resident in faunal affinity and the group is distributed primarily in more northerly and deeper waters. Two warm-temperate species, *Peprilus triacanthus* and *Urophycis regia*, join this group as major dominants, while the other warm-temperate species, dominated by *Prionotus carolinus* and *Stenotomus chrysops*, continue to occur in the same group (A) but show a dramatic change in distribution, occurring on the inner shelf rather than the outer as in the spring. The shelf break group (E) shows the same composition and distribution as in the spring, while the fifth group (D), which did not occur in the spring, is composed of nondominant eurybathyic species which occur sporadically across all but the southern inner site group.

It is obvious that although the two sampling periods included the two extremes of average water temperatures in the study area, the fall (warm extreme) is a much more dynamic period than the spring (cool extreme) for the fish communities in the region. This appears to be related in large part to the much less stable thermal regime encountered in the fall, particularly in shallower portions of the study area. Thermal gradients developed during the warmer months on the inner shelf are much stronger than those encountered on the mid-shelf during the spring, and because cooling waters mix or turn over while warming waters stratify, the fall gradients break down much more quickly than those in the spring. As a result, a fish community in this region may be subjected to rapidly changing environmental temperatures by a number of factors. A relatively small shift of water masses in the vicinity of a strong thermal gradient, migration across a gradient, or rapid cooling and mixing along the gradient all subject these communities to abrupt changes of temperature (Parr 1933), and it is not surprising that the site groupings based on faunal similarities found in the inner portion of the study area during the fall exhibited wide temperature ranges (Fig. 7). Parr (1933) pointed out that the temperature-related distributions of organisms in the vicinity of a strong thermal gradient may be more influenced by the magnitude of short-term temperature changes than by the actual temperatures encountered. This concept may well have application to the formation of the three innermost site groups identified during the fall; for although the groups strongly overlap with respect to the temperature ranges encountered, there is a considerable difference in the strength of the thermal gradients and presumably the short-term temperature variations encountered within each, with group I being primarily sited in the region of the sharpest gradients and group III being located in the most thermally stable area.

The distributional patterns noted in this paper lead to the conclusion that continental shelf demersal fish communities in the Middle Atlantic Bight are largely structured by temperature on the inner- and mid-shelf and by depth on the outer shelf and shelf break. This is not at all unexpected considering the sedimentary and topographical uniformity of the inner- and mid-shelf (Emery and Uchupi 1972) and the large annual variation in bottom-water temperature in the inshore region, with the converse holding true along the outer shelf and shelf break. Scott (1982) found the distributions of a number of groundfish species on the Scotian Shelf to be related to bottom sediment type. Although substrate preference indices were not generated during the present study, comparisons of species group distribution with bottom sediment type maps do not indicate any strong species group-sedimentary relationships. This contrast may be the result of two major differences between the continental shelves in the Middle Atlantic Bight and off Nova Scotia; there is a much more variable sedimentary environment and a considerably smaller annual range of bottom-water temperatures on the Scotian Shelf.

Tyler (1971) examined latitudinal variation in the regular and seasonal components of several nearshore Atlantic marine fish communities, and concluded that the proportion of seasonal and occasional components to regular components varied directly with annual variation in water temperature. The results of the present study are certainly in accord with this conclusion, in that the most highly variable area in terms of annual water temperature variation (the southern inner- and mid-shelf) was also the most variable area in terms of community composition, but it is also evident that Tyler's statement cannot be taken axiomatically. The outer shelf, although very homothermic, was also subject to considerable seasonal variation in community structure because of the changing relationship between the

stable thermal regime on the outer shelf and the highly varying regime in adjacent inshore waters. During the spring, when inshore water temperatures were depressed well below those on the outer shelf, the outer shelf served as a refuge for the warm-temperate species association which occurs largely inshore when water temperatures there become elevated above those on the outer shelf.

It is also interesting to note that while for the most part the communities observed here are structured by species associations that behave as a group in response to environmental variation, two of the most successful species (*Peprilus triacanthus* and *Squalus acanthias*) are those which show the least permanent group affinities. As noted above, the success of *P. triacanthus* may be due in part to the species' very wide thermal tolerance, but *S. acanthias* was one of the more thermally restricted species encountered in the study, being restricted to waters less than 14°C.

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EARLY ZOEAL STAGES OF *PLACETRON WOSNESSENSKII* AND *RHINOLITHODES WOSNESSENSKII* (DECAPODA, ANOMURA, LITHODIDAE) AND REVIEW OF LITHODID LARVAE OF THE NORTHERN NORTH PACIFIC OCEAN

EVAN B. HAYNES[1]

ABSTRACT

Stage I zoeae of *Placetron wosnessenskii*, and Stage I and Stage II zoeae of *Rhinolithodes wosnessenskii*, which were reared in the laboratory, can be distinguished from other described zoeae of Lithodidae: *P. wosnessenskii* have long, blunt spines on posterior margins of abdominal somites 2-5 and sinuate curvature of long, blunt, posterolateral spines on abdominal somite 5; *R. wosnessenskii* zoeae have a spine in the middorsal, posterior portion of the carapace. Zoeae of Lithodidae can be distinguished from zoeae of Pagurinae by body shape, size of the eyes, spines on the carapace, development of uropods, and presence or absence of the anal spine. Stages of lithodid zoeae can be distinguished by eye attachment, number of natatory setae on maxillipeds, and development of pleopods, uropods, and telson. Keys, based on spination of the carapace, rostrum, abdomen, and telson, distinguish between zoeae and glaucothoe of each described species of Lithodidae from the northern North Pacific Ocean.

Crabs of the family Lithodidae constitute a major component of the reptant decapod fauna of the northern North Pacific Ocean. Of about 25 species of Lithodidae in the northern North Pacific Ocean, larvae have been described, at least in part, for eight species: *Dermaturus mandtii* Brandt, *Cryptolithodes typicus* Brandt, *Hapalogaster grebnitzkii* Schalfeew, *H. mertensii* Brandt, *Lithodes aequispina* Benedict, *Paralithodes brevipes* (Milne Edwards and Lucas), *P. camtschatica* (Tilesius), and *P. platypus* Brandt. Most descriptions are scattered in foreign scientific journals, however, and published reviews of the larvae are limited in species and scope. This report describes and illustrates Stage I zoeae of *Placetron wosnessenskii* Schalfeew and Stages I and II zoeae of *Rhinolithodes wosnessenskii* Brandt reared in the laboratory from ovigerous females. I characterize the morphological differences between zoeae of the Lithodidae and subfamily Pagurinae (family Paguridae), compare the morphology of lithodid larvae of the northern North Pacific Ocean, and provide keys for identifying the described larvae to species and stage.

METHODS AND RESULTS

In March 1982, ovigerous females of *Placetron wosnessenskii* and *Rhinolithodes wosnessenskii* were collected near Auke Bay, Alaska, in traps and by divers using scuba. The females were transported to the laboratory and kept in filtered seawater (about 6°C) until the zoeae hatched about 1 wk later. After hatching, about 50 zoeae of each species were transferred to each of four 4 l glass jars containing about 2,500 ml of seawater at 6.1°C. Seawater in the jars was changed about every other day. Zoeae were fed live plankton strained through a 0.333 mm mesh. About 10 ml of live plankton was added to each jar every other day. The live plankton consisted mostly of phytoplankton and barnacle nauplii. A more detailed description of the rearing system and type and duration of illumination is given in Haynes and Ignell (1983).

Zoeae of *Placetron wosnessenskii* hatched at night, and samples of zoeae were taken the following morning. No prezoeae of *P. wosnessenskii* were seen. *Rhinolithodes wosnessenskii* zoeae hatched at night and during the day, and those examined about 10 min after hatching had remnants of prezoeal exuviae attached to the cephalothorax and telson. The remnant exuviae are not described in this paper.

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Although food was seen in the guts of some *Placetron wosnessenskii* zoeae, none molted to Stage II. Zoeae of *Rhinolithodes wosnessenskii* fed actively and molted to Stage II about 20 d after hatching. Failure to change the seawater on schedule prevented rearing the zoeae of *R. wosnessenskii* beyond Stage II.

DESCRIPTION OF ZOEAE

Terminology, methods of measuring zoeae and their appendages, techniques of illustration, and nomenclature of appendages follow Haynes (1979). Carapace length refers to the straight-line distance from posterior margin of eye orbit to middorsal posterior margin of carapace, excluding the middorsal spine. Spines on the telson are numbered from the outermost to innermost (medial) pair. Setation formulae are the number of setae per segment from the distal segment to the proximal segment. For clarity in the illustrations, setules on plumose setae are usually omitted, but

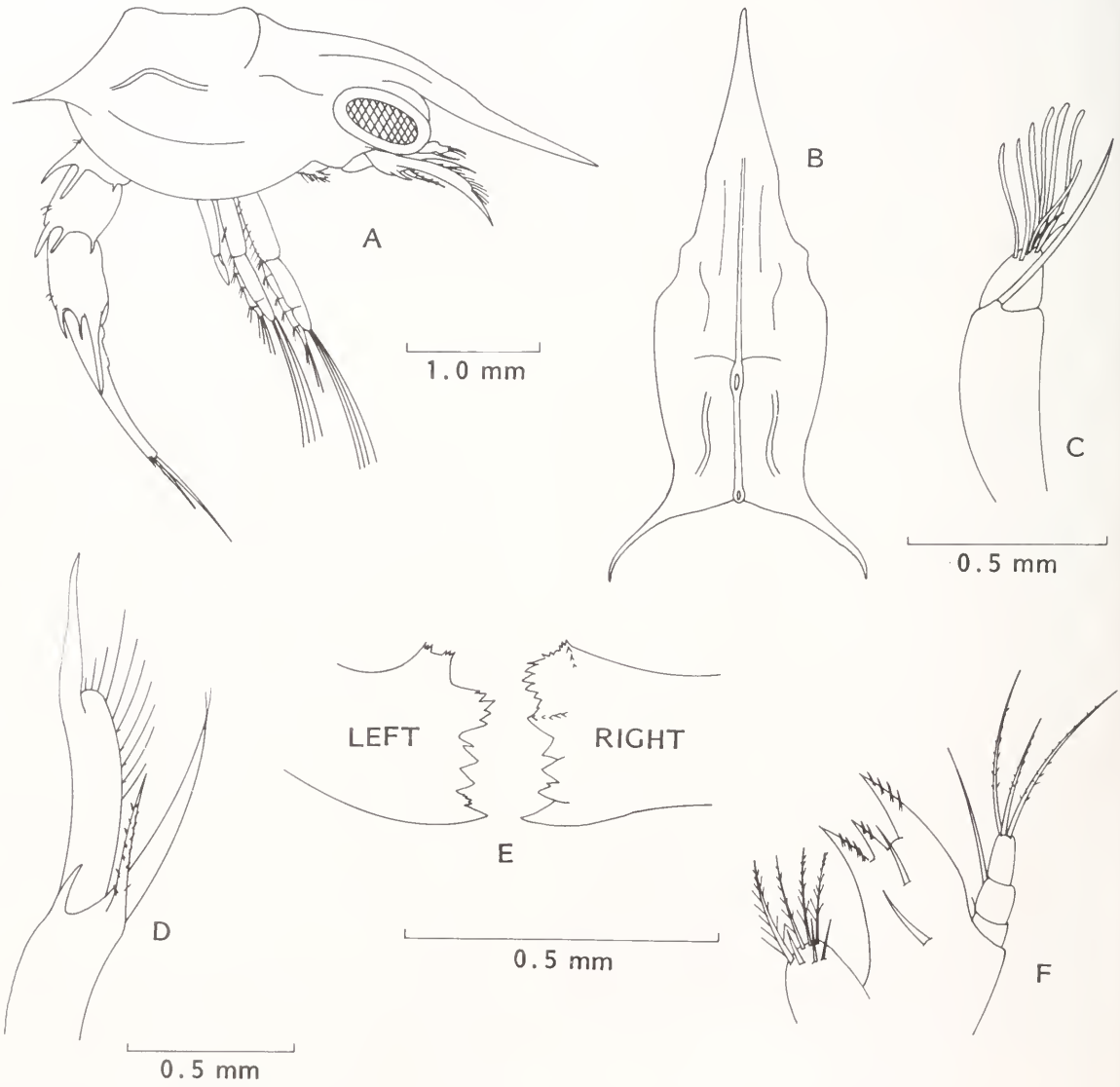
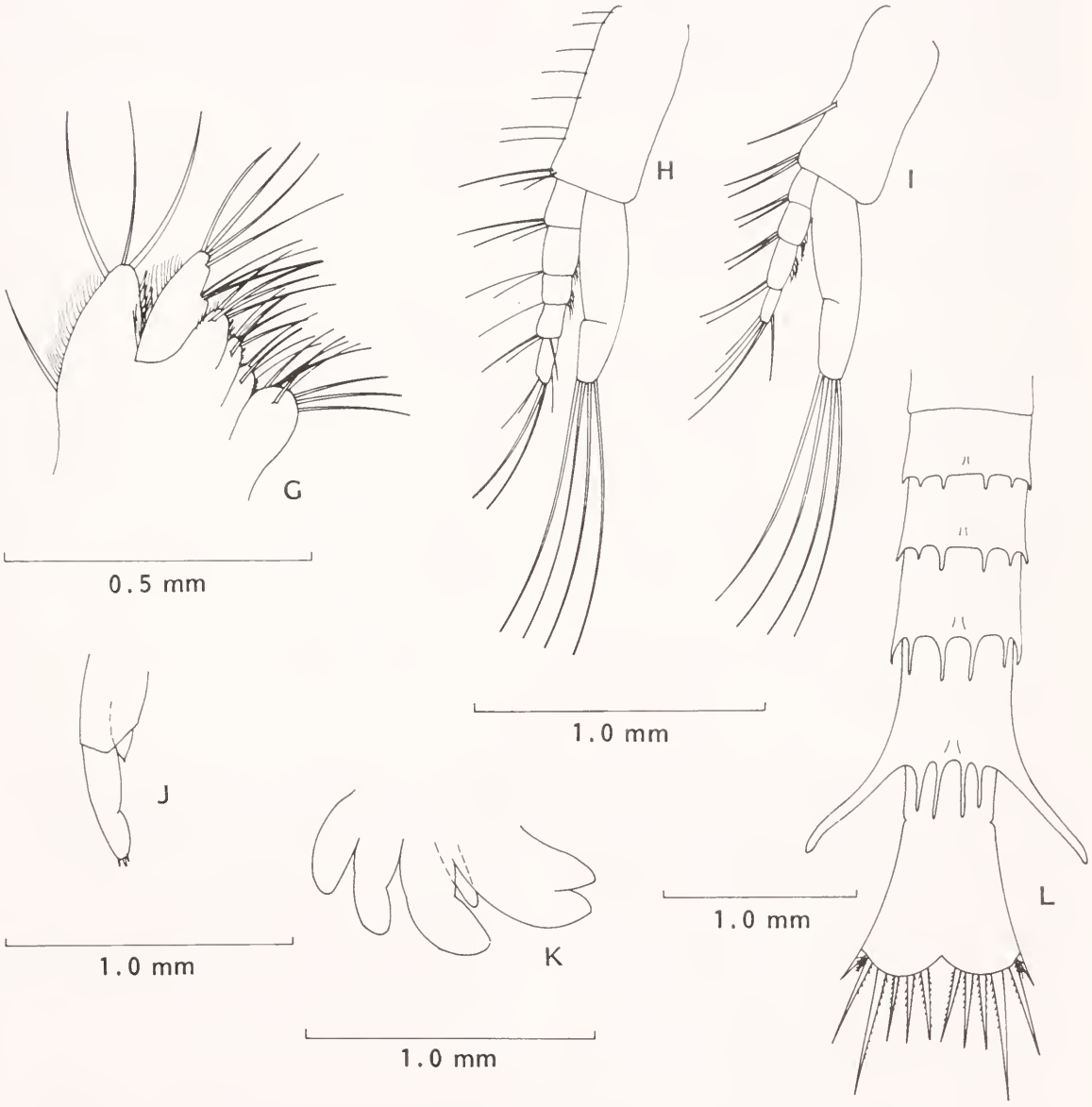


FIGURE 1.—Stage I zoea of *Placetron wosnessenskii*: A, whole animal, right side; B, carapace, dorsal; C, antennule, ventral; D, antenna, ventral; E, mandibles (left and right), posterior; F, maxillule, ventral; G, maxilla, dorsal; H, first maxilliped, lateral;

spinulose setae are shown. Five zoeae were used to verify segmentation and setation; 10 zoeae were used for measurements. Only those morphological characteristics useful for readily identifying each stage are given.

Placetron wosnessenskii — Stage I Zoeae

Mean carapace length, 2.12 mm (range 2.08-2.21 mm, 10 specimens); mean total length, 6.22 mm (range 5.90-6.70 mm, 10 specimens) (Fig. 1A, B). Live zoeae orange throughout except for colorless appendages and posterolateral spines on carapace and abdomen. Carapace with medially curved, long (>1/4 carapace length), posterolateral spines; markedly pronounced lateral ridges and dorsoventral ridge; and two middorsal angular prominences: one near center of carapace and other at posterior edge. No supraorbital spines. Eyes sessile.



I, second maxilliped, lateral; J, third maxilliped, lateral; K, pereopods 1-5, lateral; L, abdomen and telson, dorsal.

Antennule (Fig. 1C).—First antenna (antennule) with unsegmented tubular basal portion (peduncle) and distal conical projection. Peduncle with ventral plumose seta. Conical projection with seven aesthetascs and two simple setae terminally.

Antenna (Fig. 1D).—Second antenna (antenna) with inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum unsegmented, shorter than scale, and tipped with two simple setae. Antennal scale without distal joint, has fringe of 10 heavily plumose setae along terminal inner margin and prominent spine on distal outer margin. Ventral surface of protopodite with spinulose spine at base of flagellum and naked spine at base of antennal scale.

Mandible (Fig. 1E).—Incisor process of right mandible a tooth; left mandible with biserrate incisor process. Anterior margins of each mandible with premolar denticles. Mandibles without subterminal processes or movable premolar denticle (lacinia mobilis).

Maxillule (Fig. 1F).—First maxilla (maxillule) with coxopodite, basipodite, and endopodite. Coxopodite (proximal lobe) unsegmented with four large spinulose spines and three simple spines terminally. Basipodite (median lobe) with three spines terminally (each spine with several spinules) and two simple spines subterminally. Three-segmented endopodite originates from lateral margin of basipodite. Endopodite with three setae terminally, a long distal seta on second segment, and a short distal seta on first segment. Fine hairs on inner and outer margins of exopodite, outer margin of endopodite, both lobes of basipodite, and distal lobe of coxopodite.

Maxilla (Fig. 1G).—Second maxilla (maxilla) with platelike exopodite (scaphognathite). Exopodite with three long plumose setae terminally and a subterminal plumose seta on outer margin; no proximal expansion of exopodite. Endopodite unsegmented, setation formula 3, 1, 3. Basipodite and coxopodite bilobed. Basipodite with four setae on distal lobe and five setae on proximal lobe. Coxopodite with four setae on distal lobe and eight (sometimes seven) setae on proximal lobe. Fine hairs on inner and outer margins of scaphognathite, outer margins of endopodite, and distal margins of basipodite and coxopodite.

First maxilliped (Fig. 1H).—Exopodite partially segmented with four natatory setae. Endopodite slightly longer than exopodite and distinctly five segmented; setation formula 5, 3, 1, 2, 3. Protopodite unsegmented with 10 setae.

Second maxilliped (Fig. 1I).—Similar to first maxilliped except endopodite slightly shorter than exopodite. Endopodite four segmented, setation formula 5, 2, 2, 2. Protopodite with three lateral setae.

Third maxilliped (Fig. 1J).—Exopodite and endopodite undeveloped. Exopodite partially segmented, with three undeveloped setae terminally. Endopodite with undeveloped seta terminally.

Pereopods (Fig. 1K).—Poorly developed, without exopodites. First pereopod bilobed. Fifth pereopod arises medially between first and second pereopods.

Abdomen and telson (Fig. 1A, L).—Abdomen with five somites and telson (somite 6 fused with telson). Somites 2-5 have six bluntly tipped spines on posterior margin and two minute dorsal setae. Outer pair of posterior spines on somite 5 are long (about 1.2 times somite width), blunt, and somewhat sinuate. Telson with medial invagination posteriorly and 6 + 6 spines. Third pair of telsonic spines longest (about 3/4 maximum telson width). All spines jointed with telson. Minute seta between spinal pairs 1 and 2 originates from ventral surface; seta often without setules; spinules on spinal pairs 2-6. No uropods or anal spine.

Rhinolithodes wosnessenskii

Stage I Zoeae

Mean carapace length, 1.29 mm (range 1.21-1.34 mm, 10 specimens); mean total length, 4.45 mm (range 4.02-4.62 mm, 10 specimens) (Fig. 2A, B). Cephalothorax and base of maxillipeds orange; remainder of maxillipeds, most of rostrum, and all of abdomen colorless. Carapace with middorsal angular prominence and spine at middorsal posterior margin; medially curving, long (>1/4 carapace length), posterolateral spines; markedly pronounced lateral ridge. No supraorbital or anal spine. Eyes sessile.

Antennule (Fig. 2C).—Distal conical projection unsegmented from peduncle. Peduncle with ventral plumose seta. Conical projection with seven

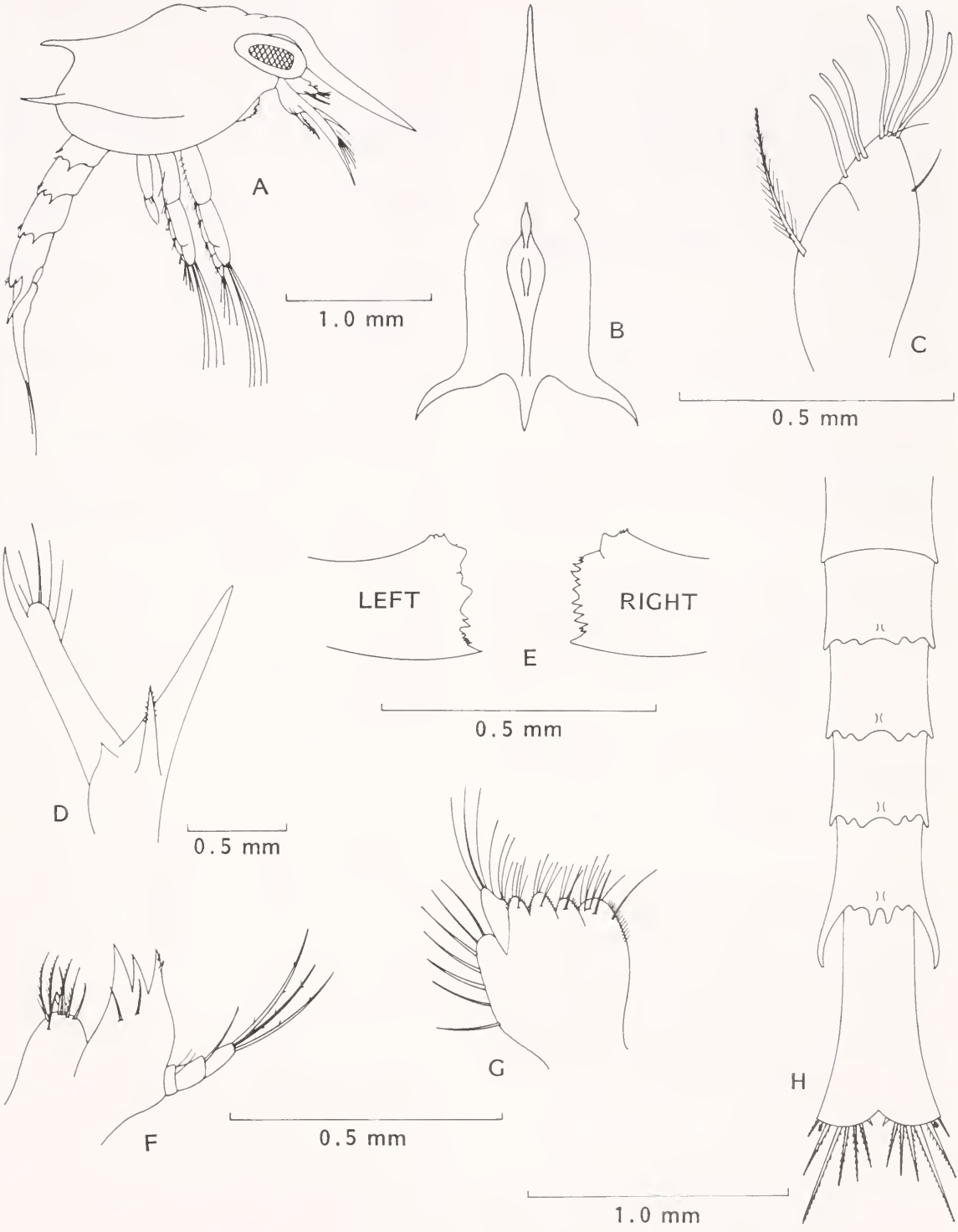


FIGURE 2.—Stage 1 zoea of *Rhinolithodes wosnessenskii*: A, whole animal, right side; B, carapace, dorsal; C, antennule, ventral; D, antenna, ventral; E, mandibles (left and right), posterior; F, maxillule, ventral; G, maxilla, dorsal; H, abdomen and telson, dorsal.

aesthetascs and two simple setae (one terminal and one lateral).

Antenna (Fig. 2D).—Antenna with inner flagellum and outer antennal scale; flagellum without setae and shorter than scale. Antennal scale unjointed distally, fringed with six heavily plumose setae along terminal and inner margins, and prominent spine distally on outer margin. Ventral surface of protopodite with spinulose spine at base of flagellum and smaller naked spine at base of scale.

Mandible (Fig. 2E).—Incisor processes of left and right mandibles a single tooth. Anterior margins of each mandible with premolar denticles. No subterminal processes or movable premolar denticles.

Maxillule (Fig. 2F).—Similar to Stage I *Placetron wosnessenskii* except spines of basipodite less spinulose and proximal segment of endopodite with two simple setae terminally instead of one.

Maxilla (Fig. 2G).—Scaphognathite with seven long plumose setae on outer margin, no proximal expansion, setation formulae of endopodite, basipodite, and coxopodite same as in Stage I *Placetron wosnessenskii*. Fine hairs on margins of basipodite and coxopodite.

Maxillipeds 1-3 and pereopods 1-5.—Nearly identical in shape and number of setae to those of Stage I *Placetron wosnessenskii*.

Pleopods.—Absent.

Abdomen and telson (Fig. 2A, H).—Short blunt spines on abdominal somites 2-5; length of outer pair on somite 5 about 0.8 times maximum width of somite. Telson with medial invagination and 7 + 7 posterior spines. Third pair of telsonic spines longest, about 3/4 maximum telson width; minute seta between spinal pairs 1 and 2 sometimes without setules; spinules on spinal pairs 2-6. No uropods or anal spine.

Stage II Zoeae

Mean carapace length, 1.30 mm (range 1.21-1.34 mm, 10 specimens); mean total length, 4.81 mm (range 4.02-5.03 mm, 10 specimens). No supraorbital spine. Eyes stalked. Characters not mentioned are nearly identical to characters of Stage I.

Antennule.—Distal conical projection segmented from peduncle.

Antenna.—Tip of flagellum may have small spine. Antennal scale with seven plumose setae along terminal and inner margins.

Mandible.—Right mandible with five teeth between incisor and molar processes.

Maxillule.—Basipodite with five terminal spines (four slightly spinulose).

Maxilla.—Scaphognathite with 11 plumose setae on outer margin; no proximal expansion. Setation formulae of endopodite 4, 1, 3.

First and second maxillipeds.—Exopodite with seven natatory setae terminally.

Third maxilliped (Fig. 3).—Exopodite with six plumose setae terminally. Endopodite with two plumose setae terminally.

Pleopods.—May be present as minute buds.

Abdomen and telson.—Identical to Stage I except joint between somite 6 and telson indicated by small indentation in lateral margins.

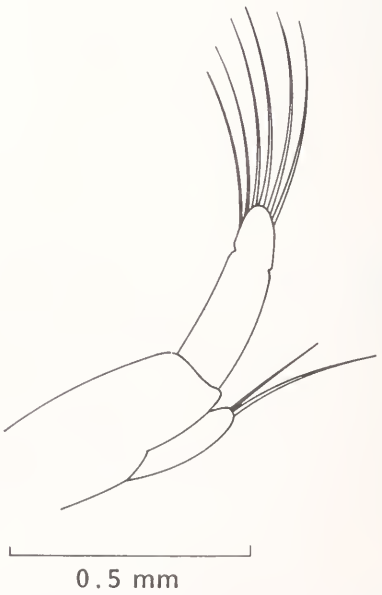


FIGURE 3.—Stage II zoea of *Rhinolithodes wosnessenskii*: third maxilliped, lateral.

DISTINCTION BETWEEN ZOEAE OF LITHODIDAE AND PAGURINAE

Zoeae of the family Lithodidae have long been considered similar morphologically to those of the subfamily Paguriinae (family Paguridae) and differ only in reduction or disappearance of the uropods (Gurney 1942; MacDonald et al. 1957). Recent descriptions of zoeae of *Cryptolithodes typicus*, *Lithodes aequispina*, *L. antarctica*, and *Paralomis granulosa* (Hart 1965; Haynes 1982; Campodonico 1971; Campodonico and Guzman 1981) have extended the range of zoeal characters of the Lithodidae and show that zoeae of the Lithodidae and Paguriinae can be distinguished by size of the eyes and morphology of the carapace and abdominal appendages (Table 1). In general, zoeae of the Lithodidae (except *Cryptolithodes typicus*) are characterized by stoutness, small eyes, posterolateral spines in middle or lower half of carapace, uniramous uropods, and no anal spine. Zoeae of the Paguriinae are characterized by slenderness, large eyes, posterolateral spines in the middle or upper half of the carapace, biramous uropods, and an anal spine. The glaucothoe of the Lithodidae and Paguriinae are readily distinguished from each other by their similarity to the adults (Haynes 1982).

TABLE 1.—Characters useful for distinguishing between zoeae of Lithodidae and zoeae of Paguriinae from the northern North Pacific Ocean. Zoeae of *Cryptolithodes typicus* (Lithodidae) are an exception and are not characterized in this table.

Lithodidae	Paguriinae
1. General appearance, stout	General appearance, slender.
2. Longitudinal diameter of eye less than width of abdomen.	Longitudinal diameter of eye greater than width of abdomen.
3. Posterolateral spines of carapace in middle or lower half of posterior margin.	Posterolateral spines of carapace in middle or upper half of posterior margin.
4. Lateral margins of carapace nearly parallel	Lateral margins of carapace converge posteriorly
5. No anal spine in any stage	Anal spine present until Stage III in some species
6. More than eight pairs of telsonic spines in some species (excluding minute seta).	Never more than eight pairs of telsonic spines (excluding seta).
7. Uropods (when present) uniramous and terminal margin blunt with (usually three or four) short setae.	Uropods biramous; exopodite styliform terminally with usually more than three or four long setae along medial margin.

MORPHOLOGY OF LITHODID LARVAE

Lithodidae of the northern North Pacific Ocean have four zoeal stages and a glaucothoe. Stage I zoeae are characterized by sessile eyes, four natatory setae on maxillipeds 1 and 2; maxilliped 3 is undeveloped and without natatory setae; pleopods and uropods are absent; and the telson and abdominal somite 6 are fused. Beginning in Stage II, the eyes are movable, and maxillipeds have at least six natatory setae. In Stage III, undeveloped pleopods and uropods are present, and the telson and abdominal somite 6 are articulated. In Stage IV, the pleopods are biramous, and the uropods are two segmented and usually have three or four apical setae. Table 2 and the keys are provided for distinguishing described zoeae and glaucothoe of Lithodidae of the northern North Pacific Ocean. Glaucothoe of *H. grebnitzkii*, *P. wosnessenskii*, and *R. wosnessenskii* have not been described.

TABLE 2.—Characters useful for distinguishing between Stages I-IV of lithodid zoeae of the northern North Pacific Ocean. *Paralithodes brevipes* may have only three zoeal stages (Kurata 1956), thus, may not always conform to the descriptions in this table.

Characteristic	Stage I	Stage II	Stage III	Stage IV
Eyes	sessile	movable	movable	movable
Natatory setae				
First maxilliped	4	≥6	≥6	≥6
Second maxilliped	4	≥6	≥6	≥6
Third maxilliped	0	≥6	≥6	≥6
Pleopods	absent	absent	absent or present as buds	present
Uropods	absent	absent	present; unsegmented	present; two segmented
Telson and sixth abdominal somite	fused	fused	articulated	articulated

Described Lithodid Zoeae of the Northern North Pacific Ocean

1a. Carapace without posterolateral spines; uropods absent in all stages; posterior margin of telson without medial invagination ..... *Cryptolithodes typicus*

1b. Carapace with posterolateral spines; uropods present in later stages (usually Stages III and IV); posterior margin of telson with medial invagination 2

2a. Posterolateral spines of carapace short (< 1/4 carapace length) 3

2b. Posterolateral spines of carapace long (> 1/4 carapace length) 5

3a. Posterolateral spines and denticles on abdominal somites 3 and 4 about same length; posterior margins of carapace concave ..... *Hapalogaster grebnitzkii*

3b. Posterolateral spines obviously longer than denticles on abdominal somites

3 and 4; posterior margin of carapace convex 4

4a. Carapace length 1.2-1.4 mm; antennal flagellum and scale (including distal spine) about same length; antennal scale ≤5 times as long as wide ..... *Dermaturus mandtii*

4b. Carapace length 1.4-1.7 mm; antennal flagellum longer than antennal scale (including distal spine); antennal scale about 9 times as long as wide ..... *Paralithodes brevipes*

5a. Carapace with middorsal posterior spine ..... *Rhinolithodes wosnessenskii*

5b. Carapace without middorsal posterior spine 6

6a. Antennal scale with ≤6 markedly short (<1/2 scale width), lightly plumose setae ..... *Hapalogaster mertensii*

6b. Antennal scale with ≥6 long (≥1/2 scale width), heavily plumose setae 7

7a. Posterolateral spines of carapace project somewhat laterally; telson has ≥11 pairs of spines (excluding minute hair); longest (third) pair of telsonic spines fused to telson ..... *Lithodes aequispina*

7b. Posterolateral spines of carapace do not project laterally; telson has ≤8 pairs of spines (excluding minute hair); longest (third) pair of telsonic spines jointed with telson 8

8a. Spines on posterior margins of abdominal somites 2-5 markedly long and tips blunt; posterolateral spine on abdominal somite 5 blunt and sinuate ..... *Placetron wosnessenskii*

8b. Spines on posterior margins of abdominal somites 2-5 typically short and tips pointed; posterolateral spine on abdominal somite 5 pointed and not sinuate 9

9a. Telsonic spines 8 + 8 (excluding minute hair) ..... *Paralithodes platypus*

9b. Telsonic spines 7 + 7 (excluding minute hair) ..... *Paralithodes camtschatica*

Described Lithodid Glaucothoe of the Northern North Pacific Ocean. Glaucothoe of *Hapalogaster grebnitzkii*, *Placetron wosnessenskii*, and *Rhinolithodes wosnessenskii* have not been described.

1a. Dorsal surface of carapace without spines 2

1b. Dorsal surface of carapace with spines 4

2a. Carapace triangular ..... *Cryptolithodes typicus*

2b. Carapace rectangular 3

3a. Lateral margin of carapace with teeth in branchial region but not in hepatic region ..... *Hapalogaster mertensii*

3b. Lateral margin of carapace with teeth in branchial and hepatic regions ..... *Dermaturus mandtii*

4a. Tips of anterolateral spines of rostral complex spinulose; most, if not all, spines on dorsal surface of carapace bifid ..... *Lithodes aequispina*

4b. Tips of anterolateral spines of rostral complex styliform or bifid; most, if not all, spines on dorsal surface of carapace styliform 5

5a. Carapace with 15 pairs of spines on dorsal surface ..... *Paralithodes platypus*

5b. Carapace with <15 pairs of spines on dorsal surface 6

6a. Carapace with 14 pairs of spines on dorsal surface .. *Paralithodes camtschatica*

6b. Carapace with 13 pairs of spines on dorsal surface ..... *Paralithodes brevipes*

Paralithodes brevipes may have three stages; thus, Table 2 may not always be appropriate for distinguishing the stages of this species. Kurata (1956) reared and described the larvae of *P. brevipes* from ovigerous females collected in Japanese waters. In Kurata's description, *P. brevipes* has three zoeal stages instead of the four that characterize the genus, and Stage III zoeae correspond morphologically to Stage IV zoeae of the genus. Makarov (1967), however, found four zoeal stages of *P. brevipes*, including a Stage III zoea, in plankton of the west Kamchatkan coast that correspond morphologically to Stage III zoeae of the genus. Kurata's zoeae may have skipped Stage III of the genus because growing conditions in the laboratory were especially favorable (Makarov 1967).

Only Stage I zoeae of *Placetron wosnessenskii*, and Stages I and II zoeae of *Rhinolithodes wosnessenskii* have been described (this report). Because these zoeal stages are morphologically typical of lithodid species with four zoeal stages, *P. wosnessenskii* and *R. wosnessenskii* likely have the four zoeal stages characterized in Table 2.

Brief descriptions and comparisons of previously described lithodid zoeae follow.

Cryptolithodes typicus.—Based on the description by Hart (1965), *Cryptolithodes typicus* zoeae are markedly different morphologically from other described lithodid zoeae. In *C. typicus* zoeae, the carapace lacks posterolateral spines in all stages, the proximal expansion of the maxilla is present in Stage II, and the telson does not have a medial posterior invagination. In all other lithodid zoeae, the carapace has posterolateral spines in all stages, the proximal expansion of the maxilla is absent until Stage IV, and the telson has a medial posterior invagination. The large eyes of *C. typicus*, however, are typical of zoeae of the Pagurinae, and the absence of posterolateral spines on the carapace is similar to zoeae of some species of the Diogenidae. The shape of the telson, the fused abdominal somite 6 and telson in Stages III and IV, and the absence of uropods in *C. typicus* are characters similar to those of some porcellanid zoeae.

Hapalogaster grebnitzkii, *Dermaturus mandtii*, and *P. brevipes.*—Makarov (1967) briefly described larvae collected off west Kamchatka that he provisionally identified as *Hapalogaster grebnitzkii*, based on distribution of adults. Zoeae of *H. grebnitzkii* are morphologically similar to zoeae of *Dermaturus mandtii* and *Paralithodes brevipes* but can be distinguished by length of the posterolateral spines on abdominal somites 3-5. In zoeae of *H. grebnitzkii*, posterolateral spines on somites 3 and 4 are short (slightly longer than the denticles that fringe the posterior margin), and the posterolateral spines on somite 5 are shorter than the width of somite 5. In zoeae of *D. mandtii* and *P. brevipes*, posterolateral spines on somites 3 and 4 are long (at least twice the length of the denticles), and posterolateral spines on somite 5 are longer than the width of somite 5 (Kurata 1956).

Based on Kurata's (1956) brief descriptions, zoeae of *P. brevipes* can be distinguished from zoeae of *D. mandtii* by size of the carapace and morphology of the antenna. *Paralithodes brevipes* zoeae are slightly larger (carapace length, 1.4-1.7 mm) than *D. mandtii* zoeae (carapace length, 1.2-1.4 mm). The antennal flagellum of *P. brevipes* zoeae is noticeably longer than the antennal scale (including distal spine), and the antennal scale is about nine times as long as wide. The antennal flagellum and antennal scale of *D. mandtii* zoeae are about the same length, and the scale is not more than five times as long as wide.

Hapalogaster mertensii.—Larvae of *Hapalogaster mertensii* were collected from ovigerous females at Fidalgo Island, Wash., and then reared and described by Miller and Coffin (1961). Unfortunately, their description is brief and lacks detail and, therefore, has limited value. Apparently, the only characters useful for distinguishing *H. mertensii* zoeae from zoeae of other lithodid species are size and number of setae on the antennal scale. In zoeal Stages I-III of *H. mertensii*, the antennal scale has six setae and, in Stage IV, four setae. In all stages of *H. mertensii*, the setae are markedly short ($< \frac{1}{2}$ scale width) and lightly plumose. In most other lithodid zoeae, the antennal scale in Stage I has more than six heavily plumose setae that increase in number in later stages, and the setae are as long as, or longer than, the width of the antennal scale.

Lithodes aequispina.—Larvae of *Lithodes aequispina* were reared and described from ovigerous females collected in waters of southeastern Alaska (Haynes 1982). Zoeae of *L. aequispina* are most similar to zoeae of *Paralithodes camtschatica* and *P. platypus* but can be readily distinguished from their zoeae by the number of telsonic spines and the manner in which the third (longest) pair of telsonic spines is attached to the telson. In *L. aequispina*, the telson has ≥ 11 pairs of telsonic spines, and the third pair of spines is fused to the telson. In *P. camtschatica* and *P. platypus* zoeae, the telson has < 8 pairs of telsonic spines, and the third (longest) pair of spines is jointed with the telson.

Paralithodes brevipes, *P. camtschatica*, and *P. platypus.*—Larvae of *Paralithodes brevipes*, *P. camtschatica*, and *P. platypus* have been described (Marukawa 1933; Kurata 1956, 1960, 1964; Hoffman 1958; Sato 1958; Makarov 1967). Zoeae of *P. brevipes* can be distinguished from zoeae of *P. camtschatica* and *P. platypus* by several characters. In *P. brevipes* zoeae, posterolateral spines on the carapace are short and ventrally curved, the dorsal posterolateral margin of the carapace is convex, the rostrum is short (about equal to the length of the antennal flagellum), and the telson has (excluding the hairlike process) six pairs of spines in Stage I and seven pairs of spines in Stages II-IV. In contrast, zoeae of *P. camtschatica* and *P. platypus* have long, posterolateral spines

on the carapace that are not ventrally curved, the dorsal posterolateral margin of the carapace is concave, the rostrum is noticeably longer than the antennal flagellum, and the number of pairs of telsonic spines in all zoeal stages (excluding the hairlike process) is 7 + 7 in *P. camtschatica* and 8 + 8 in *P. platypus*.

Placetron wosnessenskii and *Rhinolithodes wosnessenskii*.—Zoeae of *Placetron wosnessenskii* and *Rhinolithodes wosnessenskii* are readily distinguished from all other described zoeae of the Lithodidae. *Placetron wosnessenskii* zoeae are distinguished by markedly long, blunt spines on the posterior margins of abdominal somites 2-5 and the sinuate curvature of the long, blunt, posterolateral spines on abdominal somite 5. Zoeae of *R. wosnessenskii* have a spine in the middorsal, posterior margin of the carapace.

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SELECTION OF VEGETATED HABITAT BY BROWN SHRIMP, *PENAEUS AZTECUS*, IN A GALVESTON BAY SALT MARSH

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ABSTRACT

Densities of the brown shrimp, *Penaeus aztecus*, in vegetated and nonvegetated habitats of a Galveston West Bay salt marsh were compared. Each of 81 sample pairs taken between 29 March and 23 July 1982 consisted of one sample from *Spartina alterniflora* habitat and another from nonvegetated habitat. Overall a mean density for shrimp of 11.7/m² in vegetation was significantly greater than the mean density of 1.4/m² in nonvegetated habitat ($P < 0.001$, t-test, 81 paired observations). In addition, shrimp densities varied according to a pattern of lower numbers and less apparent attraction to vegetation in the outer bayside part of the marsh to that of highest numbers and greatest attraction in the innermost marsh. Accordingly, respective means for the outer, middle, and inner marsh zones in vegetated/nonvegetated sample pairs were 7.5/2.3, 11.0/1.0, and 16.6/0.6. Simple presence or absence of *S. alterniflora*, area covered by vegetation, and location within the marsh were the primary observed correlates to shrimp density patterns. Mean high water in vegetation was 22.1 cm compared with 41.8 cm for adjacent nonvegetated habitat, making vegetated habitat less accessible during periods of low water. Mechanisms that may have enhanced utilization of vegetated habitat for *P. aztecus* were reticulation in salt marsh macrostructure, relatively low tidal range, and seasonal periods of high water. The nursery function of the salt marsh was confirmed by dominance of small shrimp, with 95% of all individuals being smaller than 50 mm in rostrum through telson length. During April, the maximum mean density of postlarvae under 30 mm was 16.4/m². Recruitment of postlarvae continued throughout the summer.

A 2.8m² drop sampler, used to obtain the data, was found to be 2 to 5 times more effective for estimating densities of *P. aztecus* than trawls or seines. Consequently, our study improved the accuracy of estimates on estuarine shrimp densities, while also providing reliable evidence that *P. aztecus* may select for vegetated marsh habitat.

Estuaries have long been cited in their role as nurseries for penaeid shrimp (Anderson et al. 1949; Kutkuhn 1966; Thayer et al. 1978; Weinstein 1979). Growth and production of penaeids in estuaries have been associated with temperature (St. Amant et al. 1966; Zein-Eldin and Griffith 1966; Aldrich et al. 1968; Pullen and Trent 1969), salinity (Hildebrand and Gunter 1952; Gunter 1961; Barrett and Gillespie 1973; Browder and Moore 1981), and vegetation (Turner 1977; Faller 1979).

In salt marshes, vegetation may function variably to provide food, substrate, and protection for young penaeids. It is well known that *Spartina alterniflora* contributes to a detritus-based food web (Teal 1962; de la Cruz 1965) which at least potentially includes shrimp (Jones 1973). Microalgae and epibenthic biota associated with marshes may also serve in the food web (Haines 1977) and be used as food by foraging shrimp (Trent et al. 1969; Jones 1973). Since dense aquatic vegetation impedes certain predators (Vince et al. 1976; Nelson 1979; Coen et al. 1981; Heck and Thoman 1981), marsh grasses could also furnish protective cover for postlarval and juvenile penaeids. Unfortunately, our understanding of shrimp relationships to vegetation has been impaired by the inherent difficulty of sampling in marine vegetation.

Our aim was to overcome the sampling problem and to obtain accurate data on shrimp densities that could reliably depict differences between estuarine habitats. In the present study, *Penaeus aztecus* densities were compared between adjacent vegetated and nonvegetated habitats within a Galveston West Bay salt marsh. Since our experimental design incorporated paired sampling of habitats and samples with actual as opposed to relative numbers of shrimp, both the resolution

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and reliability of our analyses were improved over previous studies.

METHODS

Study Site

A salt marsh on the West Bay side of Galveston Island was selected as the study site (Fig. 1). The marsh extended into the island for about 2.5 km, allowing tidal circulation throughout numerous coves and bayous. The intertidal marsh was dominated by vegetation, *S. alterniflora*, and the subtidal was not vegetated. Water depth was generally <1 m, but subtidal bottom was always 10 to 20 cm deeper than adjacent intertidal vegetation. Vegetation occurred in irregular patches, creating a reticulated effect on marsh macrostructure, and occupied about 25% of the area (Fig. 2).

Experimental Design

A paired sampling design was employed to compare shrimp densities between marsh habitats. Each sample pair consisted of one sample taken in vegetated habitat and another in adjacent nonvegetated habitat as close as practically possible.

Sampling was scheduled to coincide with the

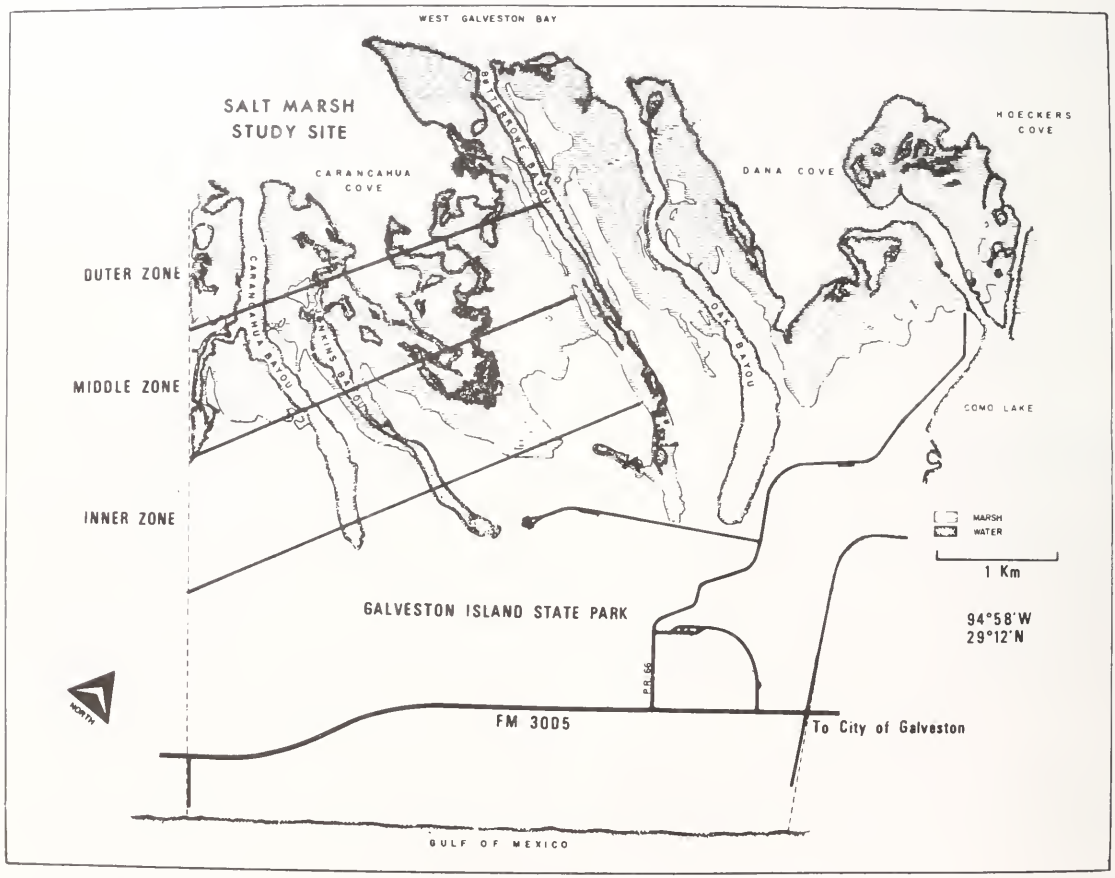

FIGURE 1.—Galveston Island State Park showing the salt marsh study site in Carancahua Cove fronting Galveston West Bay. (Redrawn from Texas Parks and Wildlife Leaflet 4000-42.)

FIGURE 2.—Upper: Reticulation between vegetated and nonvegetated habitats in a salt marsh on Galveston Island. Areal view at about 500 ft altitude. Lower: Stands of intertidal *Spartina alterniflora* and adjacent subtidal nonvegetated bottom in a salt marsh at Galveston Island State Park.

period of maximum seasonal immigration for *P. aztecus* as described by Baxter and Renfro (1967). Accordingly, seven sets of samples were taken between 29 March and 23 July 1982. Each set was obtained over a period of 3 d, and sets were taken biweekly (29 March through 28 May) and monthly (28 May through 23 July). Ordinarily, a set contained 12 sample pairs that were subdivided to sample the inner, middle, and outer marsh zones equally, i.e., during each of three sampling days four vegetated-nonvegetated sample pairs were taken from a single zone. Sample sites within zones were chosen randomly each month from subunits in a grid superimposed on a map of the area. The map and aerial photographs were used to estimate percent coverage of vegetated and nonvegetated habitats within different zones.

A *t*-test of paired observations (Steel and Torrie 1960) provided the primary means for evaluating differences in shrimp density between habitats. Other analyses were performed using Pearson product-moment correlations and ANOVAs across sample sets, and Kendall's nonparametric concordance tests (Tate and Clelland 1957) within sample sets. Analyses across sets incorporated an element of temporal variability that was specifically eliminated in analyses within sets. Data were log transformed for ANOVAs to assure homogeneity of variances.

Procedures

A drop sampler (Fig. 3) was designed to operate in the marsh from the bow of a skiff. The device was an open-ended fiber glass cylinder, reinforced on one end with galvanized metal, that enclosed 2.8 m^2 of marsh bottom. The sampler was deployed endwise and pushed at least 15 cm into the substrate to insure a good seal against leakage. After marsh grass was removed, water was pumped from the sampler and the enclosed bottom was swept with dip nets to capture the entrapped organisms. The water and the contents of the dip nets were placed into a 1 mm square mesh plankton net with a removable cod end bag. When all sample contents were washed, the cod end bag was detached, labelled, and stored in a container with Formalin[4] and Rose Bengal stain.

Two identical sampling cylinders were used to obtain sample pairs. Typically, the first sampler was hoisted above the bow of the skiff and quietly maneuvered into position over either vegetated or barren substrate. The device was released and allowed to free fall to the bottom. After disconnecting the first sampler, the second sampler was hoisted and the operation repeated in the opposing habitat. The sequence of habitats was reversed from pair to pair so that one would not continually precede the other. Sample pairs were always within two sample diameters of each other (3.6 m) and care was taken to not disturb the site until the second sampler was deployed.

Within all samples, the water temperature,

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

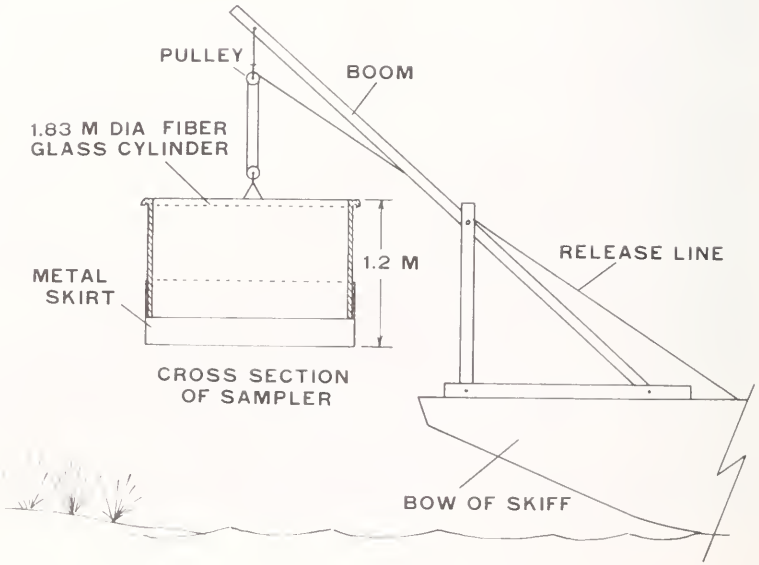

FIGURE 3.—A hand-operated drop sampler used to estimate *Penaeus aztecus* densities in a Galveston West Bay salt marsh.

oxygen (YSI oxygen meter, Model 51 B) and maximum and minimum depth were recorded. Water samples (500 ml) were also procured in order to measure turbidity (HF Instruments, Model DRT-15). In vegetated samples, emergent plant material was cut and removed to measure plant biomass and to facilitate capturing the macrofauna. Tide level was recorded from a permanent station at the beginning and end of each sampling operation. All field work was done during daylight within about 2 h before and after high tide.

In the laboratory, shrimp were identified, sorted, and measured to the nearest millimeter from rostrum tip to end of telson. Shrimp numbers for each millimeter size interval were recorded for each sample. Associated macrofauna from each sample, including fish, crabs, and other shrimp, were identified, measured, and counted. Gut contents of the fish were examined for penaeid shrimp as well as other identifiable material. Plant biomass from each sample was dried in sunlight until weight change was negligible. Sediments and epiphytes were allowed to fall away as the material dried. The resulting dry weight was taken using a Mettler K-7 toploading balance and reported as grams above-ground dry plant biomass. Stem density was calculated by weighing a subsample (about 20% of the total) and counting the number of culms.

Sampler Effectiveness

Since the experimental design assumed no sampling bias, the method was tested for recovery efficiency both in vegetated and nonvegetated habitats. Fifty shrimp, in the size range of 23 to 91 mm, were marked by clipping a uropod and placed into deployed samplers. After a 30-min adjustment period, the usual sampling procedure was followed and recovery was recorded.

Since our density data were compared with other surveys, it was useful to test the effectiveness of the drop sampler in relation to other collecting devices. These included a 1 m beam trawl, a 5.5 m bag seine, and a 3.7 m otter trawl. During the initial test, eight replicate vegetated-nonvegetated sample pairs were taken using the 1 m beam trawl (3.0 m^2) and the drop sampler (2.8 m^2). Later, 10 nonvegetated sample replicates were obtained for each of the following: the drop sampler, a 5.5 m bag seine (110 m^2), and a 3.7 m otter trawl (75 m^2). The data were reported as mean and standard deviation of shrimp density (per m^2) for each sampler. The efficiency for each device was calculated relative to the drop sampler.

RESULTS

A total of 3,277 penaeid shrimp (97% *P. aztecus*) were collected in 81 paired samples taken between 29 March and 23 July 1982. Shrimp densities in the marsh were significantly higher in *S. alterniflora* habitat than adjacent nonvegetated habitat ($P < 0.001$, t-test, 81 paired observations). The magnitude and integrity of the relationship between shrimp density and habitat type held consistently throughout all sampling dates (Table 1, Fig. 4) and zones within the marsh, except for the outer zone during March and April (Table 2). Comparison of marsh zones (Table 2) revealed highest *P. aztecus* densities and greater selection for vegetated habitat in the innermost marsh diminishing toward the outer zone. Shrimp densities in nonvegetated habitat were highest in the outer zone and diminished significantly toward the inner zone (ANOVA, $P < 0.001$).

TABLE 1.—Percent of *Penaeus aztecus* in vegetated (*Spartina alterniflora*) and nonvegetated habitats of a Galveston West Bay salt marsh, 29 March through 23 July 1982.

Sampling period	Shrimp number (n)	Habitat	
		Vegetated (% n)	Nonvegetated (% n)
3/29-4/1	355	94.4	5.6
4/13-15	519	81.7	18.3
4/26-28	802	88.3	11.7
5/11-14	309	90.3	9.7
5/26-28	388	91.8	8.2
6/22-24	237	97.0	3.0
7/21-23	559	90.2	9.8

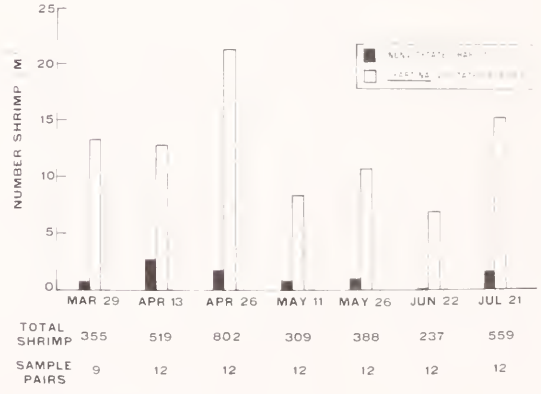

FIGURE 4.—Mean densities of *Penaeus aztecus* compared between vegetated *Spartina alterniflora* habitat and adjacent nonvegetated habitat.

TABLE 2.—Mean number of *Penaeus aztecus* per m^2 by zone in vegetated and nonvegetated salt marsh habitats from Galveston West Bay 29 March through 23 July 1982.

Sampling period	Marsh zone and habitat: Outer Veg/Non[1]	Middle Veg/Non	Inner Veg/Non	Overall Veg/Non
3/29-4/1	[2] 2.7/1.9 8.8/5.5	12.3/2.0	16.7/1.1	12.6/2.8
4/26-28	12.3/6.8	28.5/1.3	22.4/0.4	21.1/2.8
5/11-14	7.2/1.2	9.6/1.3	8.0/0.3	8.3/0.9
5/26-28	12.0/1.5	10.6/0.9	9.2/0.4	10.6/1.0
6/22-24	3.8/0.2	9.7/0.3	7.0/0.2	6.8/0.2
7/21-23	10.9/1.8	13.8/1.9	20.3/1.3	15.0/1.6
Overall	7.5/2.3	11.0/1.0	16.6/0.6	11.7/1.4

[1]Veg = *Spartina alterniflora* habitat; Non = Nonvegetated habitat.
[2]Difference within brackets not significant between vegetated and nonvegetated pairs; for all others, the difference was highly significant ($P < 0.001$, t-test, paired observations).

Penaeus aztecus densities for each 20 mm size interval were more abundant in *Spartina* habitat than adjacent nonvegetated bottom (Fig. 5). Vegetated habitat contained 89 to 96% of all shrimp in size classes under 50 mm and 75 to 78% of larger size classes (Table 3). Those under 30 mm in length comprised 77,% of all shrimp and those under 60 mm made up 98% of the total (Table 3). Size class distributions differed between habitats (Kolmogorov-Smirnov test, $P = 0.02$; Fig. 5), but the very small sample size from nonvegetated habitat decreased the strength of this observation.

The highest *P. aztecus* densities in vegetation and the lowest on nonvegetated bottom were characteristic of the innermost zone (Table 1). The degree of vegetated-nonvegetated differences suggested an apparent selection for vegetated habitat and greater selection in the inner zone compared with the outer zone. The increase in vegetated to nonvegetated shrimp densities coincided with an increase in *S. alterniflora* coverage between the outer and inner marsh (Fig. 6). Areal coverage of vegetation, determined from aerial photographs (Fig. 2), differed by a factor of 3 between the outer and inner marsh, and selection, as measured by the ratio of shrimp density in vegetated habitat to density in nonvegetated habitat, differed by a factor of 9 from outer to inner zones (Fig. 6). In addition, the ratio differed between the middle and inner zone, but shrimp densities within vegetation between those zones (Table 2) did not change significantly (ANOVA, Duncan's multiple range test, 0.05 level). Due to the intertidal nature of vegetated habitat, shrimp were forced into subtidal areas at low tide and redis-

TABLE 3.—Percent abundance among size classes for *Penaeus aztecus* in a Galveston West Bay salt marsh, 29 March through 23 July 1982. n = number of shrimp per size interval; N = total number of shrimp collected.

Size class (mm)	Shrimp abundance: Overall n	Overall % N	Overall Cum. %	Spartina (% n)	Nonvegetated (% n)
<20	1,117	47.7	47.7	89.4	10.6
21-30	683	29.2	76.9	95.6	4.4
31-40	234	10.0	86.9	94.9	5.1
41-50	184	7.8	94.7	88.6	11.4
51-60	86	3.7	98.4	77.9	22.1
61-70	25	1.1	99.5	76.0	24.0
71-80	8	0.3	99.8	75.0	25.0
81-90	4	0.2	100	75.0	25.0
Total (N) = 2,341					

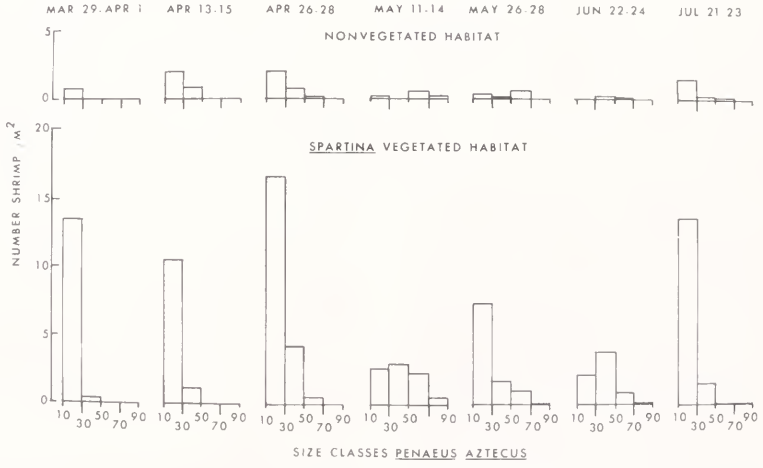

FIGURE 5.—Densities of *Penaeus aztecus* by size class in adjacent vegetated and nonvegetated habitats from Galveston West Bay during 1982. Size class distributions differed between habitats (Kolmogorov-Smirnov test, $P = 0.02$).

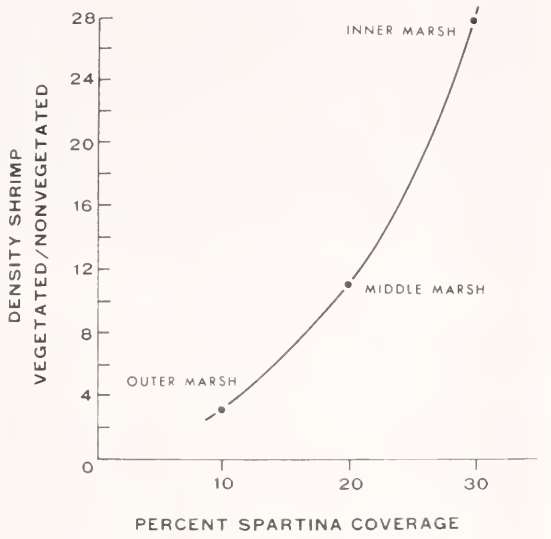

FIGURE 6.—Selection by *Penaeus aztecus* for vegetated habitat compared against percent coverage of *Spartina alterniflora*.

tributed anew on each subsequent flood tide.

Differential predation by fish did not account for shrimp differences between habitats. Of four species preying on shrimp, 328 were in vegetation versus 48 on nonvegetated bottom. Among these, 18 from vegetated (5%) and 3 from nonvegetated (6%) contained shrimp in gut contents. The predators, in order of vegetated/nonvegetated abundance, were *Lagodon rhomboides* (pinfish 246/36), *Fundulus grandis* (gulf killifish 45/0), *Cynoscion nebulosus* (spotted seatrout 22/2), and *Paralichthys lethostigma* (southern flounder 15/10). Only southern flounder contained shrimp in gut contents (3 of 10) from nonvegetated habitat. In vegetated habitat, 8 of 15 southern flounder, 10 of 22 spotted seatrout, 1 of 45 gulf killifish, and 3 of 246 pinfish contained shrimp.

Mean density of *P. aztecus* in vegetation was 11.7/m² overall with a range of 0.7 to 43.2/m² (Table 4). Densities were highest in the innermost marsh ($\bar{x}$ = 16.6/m²; range = 1.8 to 43.2/m²) and lowest in the outer marsh ($\bar{x}$ = 7.5/m²; range = 0.7 to 28.2/m²). The overall variance was less than the overall mean. Among marsh zones, shrimp patchiness in vegetation decreased slightly from the outer to inner marsh (Table 4).

Density of *P. aztecus* in nonvegetated habitat was 1.4/m² with a range of 0 to 18.2/m² (Table 4). Densities on nonvegetated bottom were highest in the outer marsh ($\bar{x}$ = 2.3/m²; range = 0 to 18.2/m²) and lowest in the inner marsh ($\bar{x}$ = 0.6/m²; range = 0 to 2.1/m²). Overall distribution on nonvegetated bottom, as reflected by the variance to mean ratio (coefficient of variation, Table 4), was patchier (more clumped) than on vegetated bottom. Shrimp distributions also were patchier in nonvegetated outer and middle zones, than in the nonvegetated inner zone.

TABLE 4.—Within habitat densities of *Penaeus aztecus* from a salt marsh in Galveston West Bay, 29 March through 23 July 1982. n = number of samples.

Marsh habitat and zone	n	Individuals/m² $\bar{x}$	Median	1 SD	Coeff. var. (%)	Range
With vegetation						
Outer	27	7.5	6.4	6.8	90	0.7-28.2
Middle	26	11.0	11.4	8.9	81	0.4-39.6
Inner	28	16.6	13.8	12.5	75	1.8-43.2
Overall	81	11.7	10.5	9.4	80	0.7-43.2
Without vegetation						
Outer	27	2.3	1.4	3.6	157	0-18.2
Middle	26	1.0	0.7	1.2	120	0- 4.6
Inner	28	0.6	1.0	1.5	56	0- 2.1
Overall	81	1.4	1.1	1.9	136	0-18.2

Stem density and above-ground biomass of *S. alterniflora* were positively correlated (Table 5). The overall range of values was 41 to 784 g/m² for biomass and 33 to 629 stems/m² with respective means of 298 g/m² (1 SD = 175, n = 81) and 234 stems/m² (1 SD = 72, n = 81). Between zones, plant biomass from the outer to inner zone increased from 258 to 348 g/m². The weight per stem increased (larger diameters) from outer to inner marsh. Although the trend suggested a negative relationship between shrimp density and vegetational density and biomass, correlation was not significant over the range examined.

Abiotic Relationships

Water depth between vegetated and nonvegetated sample pairs was significantly different ($P < 0.01$, t-test of 81 paired observations). The mean water depth was 22.1 cm (1 SD = 10.0, n = 81) in

TABLE 5.—Density and biomass of *Spartina alterniflora* from a salt marsh in Galveston West Bay, 29 March through 23 July 1982. n = number of samples.

Biomass and density	n	$\bar{x}$	1 SD	Coeff. var. (%)	Range
Biomass (g/m²)					
Outer zone	27	258	164	64	41-634
Middle zone	26	289	187	65	41-784
Inner zone	28	348	174	50	69-731
Overall	81	298	175	59	41-784
Density (stems/m²)					
Outer zone	28	234	88	38	37-576
Middle zone	26	231	65	28	33-629
Inner zone	28	236	64	27	47-496
Overall	81	234	72	31	33-629

vegetated samples compared with 41.8 cm (1 SD = 11.8, $n = 81$) in nonvegetated samples. Changes in tide level were not large (about 30 cm) but were important relative to sample depths. Since sampling was executed at high tide, tide station measurements were comparable between sampling periods and useful for establishing variability in high-water level. Mean high water during the summer was 12 cm lower than in the spring reflecting seasonally variable tidal inundation (Hicks et al. 1983) and greater accessibility to vegetation (Provost 1976) in the spring.

A weak negative relationship between shrimp density and temperature within a range of 17.0° to 34.0°C was apparent ($r = -0.34$ in vegetation, $P < 0.01$, $n = 57$). Since temperature and oxygen levels were inversely related, the trend, attributed to temperature, also extended to an observed relationship between oxygen concentration and shrimp density. However, oxygen levels were always near saturation (vegetated $\bar{x} = 8.2$ ppm, 1 SD = 1.4, $n = 81$; nonvegetated $\bar{x} = 8.1$ ppm, 1 SD = 1.4, $n = 81$) and unlikely to have influenced shrimp distribution. Shrimp densities did not correlate well with salinities (range of 19 to 35 ppt), turbidities (range of 3.0 to 55 nephelometer turbidity units), or water depths (overall range of 5.5 to 76 cm). In addition, temperature, salinity, oxygen, and turbidity did not differ between habitats (t-test of 81 paired observations for each).

Sampler Performance

Test results suggested that shrimp recovery from the drop sampler was more variable and somewhat less effective in vegetation ($\bar{x} = 91\%$ recovery, 1 SD = 6.6%, $n = 4$) than in habitat without vegetation ($\bar{x} = 97.5\%$ recovery, 1 SD = 2.5%, $n = 4$). However, a t-test between means by habitat revealed no significant difference ($P > 0.1$) and justified combining means (94%, 1 SD = 5.8%, $n = 8$).

Mean shrimp densities on nonvegetated bottom, comparing our 1.8 m diameter drop sampler, a 5.5 m wide bag seine, and a 3.7 m wide otter trawl, were 0.285/m², 0.104/m², and 0.054/m², respectively. Assuming 97.5% recovery and no avoidance with the drop sampler, conservative estimates of efficiency were 33% for the bag seine and 17% for the otter trawl. Clearly, the data from the drop sampler were more accurate (Table 6).

DISCUSSION

Habitat Selection

Significant differences in habitat-related shrimp densities from a Galveston salt marsh (Table 2, Fig. 4) demonstrate that *P. aztecus* may select for *S. alterniflora* habitat. In support, laboratory data of Giles and Zamora (1973) suggest that *P. aztecus* and *P. setiferus* each prefer *S. alterniflora* as opposed to barren substrate. In addition, marsh grass transplanted on a dredge spoil in Galveston Bay increased shrimp numbers (Trent et al. 1969) and elimination of marsh habitat to create waterfront housing diminished shrimp abundance (Mock 1966; Gilmore and Trent 1974; Trent et al. 1976). In other instances, *P. aztecus* has been associated with vegetation including *Ruppia* and *Vallisneria* in Mobile Bay (Loesch 1965), seagrasses in the Laguna Madre (Stokes 1974), and *Juncus*, *Spartina*, and seagrasses in Mississippi Sound (Christmas et al. 1976). The latter reported movement of postlarvae into marsh vegetation during tidal inundation.

The determinants of selection may have less to do with *S. alterniflora* per se than with other characteristics of vegetated habitat. For example, in our case, shrimp numbers were not related to the density or biomass of marsh grass (Table 5) but simply to its presence or absence. Also, attraction to vegetation differed between outer and inner marsh (Table 2). Other studies have shown that

TABLE 6.—Comparative gear efficiencies for sampling *Penaeus aztecus* in a Galveston West Bay salt marsh. Area sampled and number of replicates for each device are as follows: Drop sampler 2.8 m² ($n = 22$); beam trawl 3.0 m² ($n = 12$); bag seine 109 m² ($n = 10$); otter trawl 72 m² ($n = 10$).

Habitat type	$\bar{x}$ Efficiency			
	Drop sampler	Beam trawl	Bag seine	Otter trawl
Spartina vegetation				
(Shrimp count, $\bar{x}$/m² ±SD)	94% (8.9±3.7)	23% (2.2±2.2)	not operable	not operable
Nonvegetated				
(Shrimp count, $\bar{x}$/m² ±SD)	98% (0.30±0.3)	82% (0.25±0.46)	33% (0.10±0.06)	17% (0.05±0.04)

the presence of estuarine macrophytes can be associated with an increase in epifaunal abundance (Heck and Wetstone 1977; Heck and Orth 1980) as well as providing protective cover (Vince et al. 1976; Nelson 1979; Coen et al. 1981; Heck and Thoman 1981). For shrimp selecting vegetated marsh, this may translate into a greater variety and abundance of food and some degree of protection from predation.

Zonal and Areal Relationships

Penaeus aztecus demonstrated a greater degree of attraction to vegetated habitat in the inner than the outer marsh. Accordingly, shrimp densities were higher among vegetation and lower on nonvegetated bottom in the innermost zone compared with the outer zone. This relationship is adequately reflected by comparing ratios of vegetated with nonvegetated shrimp density. Using the ratios, the change in selection from the outer, middle, to inner zone was 3.3:1, 11.0:1, and 27.7:1, respectively. The percent area covered by *S. alterniflora* (Fig. 2) also increased (by a factor of three) from outer to inner marsh, but as vegetational coverage increased arithmetically selection by *P. aztecus* increased geometrically (Fig. 6). This implies that salt marshes with more vegetational coverage have disproportionately greater attractive value to *P. aztecus* than do those with less coverage. On a larger scale, Turner (1977) revealed a positive correlation between extensiveness of estuarine vegetation and offshore shrimp yield. However, the relationship may not be simple; it is likely to depend upon characteristics such as the configuration, accessibility, and quality of vegetational patches within a marsh. For instance, an edge effect has been identified which associates large numbers of shrimp with the nonvegetated zone adjacent to vegetation (Mock 1966; Christmas et al. 1976). Since our *Spartina* habitat was intertidal, and often not inundated during low tides, the nonvegetated subtidal habitat provided a refuge against stranding. We have assumed that it did and that shrimp redistributed accordingly each tidal cycle. It is evident that an increase in the amount of ecotone edge (between habitats) would facilitate movement for the shrimp population. It is also evident that the amount of edge is proportionally related to the degree of reticulation in the marsh (Fig. 2). Thus, reticulation may be an important mechanism for increasing the accessibility of intertidal vegetation to *P. aztecus*.

Shrimp Densities

Density estimates for penaeid shrimp in *S. alterniflora* vegetation have not been reported previously. We found a density range for *P. aztecus* in *Spartina* habitat of 0.7 to 43.2/m^2 with an overall mean, from March through July, of 11.7/m^2 (1 SD = 9.4, n = 81). Comparable densities from adjacent nonvegetated habitat ranged between 0 and 18.2/m^2. All densities were taken when *P. aztecus* numerically dominated the shrimp population. By August, when *P. setiferus* first began to dominate, the combined mean for both species in vegetation increased to 50.8/m^2 (1 SD = 31.6, n = 12) and a single sample attained a density of 118.6 shrimp/m^2. These data may indicate a potential for higher *P. aztecus* densities earlier in the season and suggest that *P. aztecus* were not restricted by lack of space.

To our knowledge, we have provided the first accurate estimates of shrimp density in marsh vegetation, and our densities are among the few available for any estuarine system. Due to method limitations, most researchers have only reported relative abundances of restricted sizes, usually over nonvegetated bottom. The single exception was data by Allen and Hudson (1970), using a suction sampler in seagrasses in Florida Bay. From 43 trials, they reported a mean of 6.2/m^2 ± 3.4 SD for *P. duorarum*.

Estimates of *P. aztecus* densities from nonvegetated bottom in three other Galveston Bay salt marshes were available from the Texas Parks and Wildlife Department (TPWD) from 1976 through 1981 (Benefield 1982, footnote 5.). The data were taken using a marsh net (Renfro 1963) which was relatively effective for capturing shrimp on nonvegetated bottom (Table 6 compares a beam trawl, similar to the marsh net, with other sampling devices). Mean TPWD densities for *P. aztecus* during the latter half of March were 10.4/m^2 for 1976, 5.2/m^2 for 1977, 0.3/m^2 for 1978, 1.3/m^2 for 1979, 8.7/m^2 for 1980, and 5.1/m^2 for 1981 with an overall mean of 5.2/m^2. In our study, on nonvegetated bottom, the March mean for *P. aztecus* was 0.9/m^2 and overall (March through July) the mean was 1.4/m^2. It is evident that our nonvegetated densities for *P. aztecus* were within the range, but low compared with the mean calculated from TPWD data.

These densities of *P. aztecus* may not be strictly

[5]R. L. Benefield, Bay Shrimp Project Leader, Texas Parks and Wildlife Department, Coastal Fisheries Branch, P.O. Box 8, Seabrook, TX 77586, pers. commun. September 1982.

comparable, since sampling was executed during unknown variable tidal stages and the degree of flooding in intertidal vegetation appears to greatly influence shrimp densities on nearby nonvegetated subtidal bottom. Perhaps the only meaningful density estimates are those taken during low tide in nonvegetated habitat or those taken in vegetated habitat at flood tide. In any case, tide stage must be uniform for data to be comparable.

Sampling Integrity

The sampling approach in our investigation provided more realistic density estimates than traditional methods for sampling shrimp in estuaries (Table 6). We agree with Loesch et al. (1976) in concluding that techniques such as the area-swept method using an otter trawl are among the poorest for quantifying *P. aztecus*. Past recognition of this problem stimulated development of the push net (Allen and Inglis 1958), small beam trawl (Renfro 1963; Loesch 1965), and marsh net (Pullen et al. 1968). These samplers improved accuracy on nonvegetated bottom, but were ineffective when vegetation was present and did not solve avoidance problems. Further improvement came for sampling in seagrasses, but not salt marshes, with the invention of a sled-mounted suction sampler (Allen and Hudson 1970) and modification of a drop net technique (Hoese and Jones 1963; Gilmore et al. 1976). Our methodology has been designed to minimize escape, improve recovery from the area sampled (including burrowed shrimp), and to operate in salt marsh habitats. The drop-sampler method proved to be nearly as effective among vegetation as on nonvegetated bottom.

CONCLUSION

We contend that differences in *P. aztecus* densities between vegetated and nonvegetated marsh bottom were due to habitat selection. In support, we refer to Loesch (1965), Trent et al. (1969), and Stokes (1974) who have associated brown shrimp distributions with estuarine vegetation, and a laboratory experiment by Giles and Zamora (1973) demonstrating *P. aztecus* prefer *S. alterniflora* instead of barren substrate. Finally, our fish gut examinations indicate that immediate effects of predation did not account for the density differential.

Since *S. alterniflora* is characteristically intertidal, and not continuously available to shrimp, the adjacent subtidal zone provided an important alternate habitat during low tide. We propose that the amount of edge between habitats facilitated shrimp movement, and the reticulated nature of the salt marsh was an important feature for increasing the amount of edge. In addition, intertidal vegetation was more accessible and its potential for utilization greater during spring and fall high tides. This interaction may in part account for seasonal peaks in *P. aztecus* populations. In our investigation, recruitment began abruptly with equinox tides. The shrimp population during the spring and early summer was dominated entirely by *P. aztecus*.

Our shrimp densities from vegetated habitat were higher than any previously reported including those from seagrass and mangrove systems. The high densities in vegetation were possibly governed by the amount of total marsh, ratio of vegetated to nonvegetated habitat, and size of recruitment. The densities on nonvegetated marsh bottom were probably controlled by the relative accessibility of nearby vegetated habitat. In any case, the observed density differential strongly implies that marsh vegetation provides a vital function for juvenile brown shrimp.

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REPRODUCTION, MOVEMENTS, AND POPULATION DYNAMICS OF THE BANDED DRUM, *LARIMUS FASCIATUS*, IN THE GULF OF MEXICO[1, 2]

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ABSTRACT

Collections of banded drum, *Larimus fasciatus*, were made from 5 to 100 m in the Gulf of Mexico along a cross-shelf transect off Texas during the period October 1977-August 1981. *Larimus fasciatus* mature at 80-130 mm as they approach age I. Spawning occurs during two discrete periods, a major fall period (September-November) and a very minor spring period (April-June), coincident with downcoast alongshore currents (toward Mexico) and onshore surface Ekman transport. Fish first spawning at 12-14 months old produce the predominant fall-spawned groups. Fall-spawned fish spawning at 19-21 months old produce the minor spring-spawned groups, so that temporal reproductive isolation does not exist between spring and fall cohorts. *Larimus fasciatus* in the northwestern Gulf range from <5 to 55 m but are most abundant at 5-16 m. Adults occupy the 13-24 m bathymetric range, while the young recruit in waters of <5-16 m when 2-4 months old. Larger, older, spawning or postspawning individuals may undergo more or less permanent emigration from the northwestern Gulf to the north central area as they approach age I. Apparent mean sizes of fall-spawned fish were 130-150 mm at age I and 155-180 mm at or approaching age II. Von Bertalanffy parameters for fall-spawned fish were 201 and 176 mm for L_∞ and 1.15 and 1.34 for K (annual), respectively. Maximum size is about 180 mm in the northwestern Gulf, but more typically only 160-165 mm. Typical maximum life span (t_L) in the northwestern Gulf is only 1-2 years but may be 2-3 years if the the stock ranges in both the northwestern and north central Gulf. Apparent mean time-specific and cohort-specific total annual mortality rates are 92-100% in the northwestern Gulf but true values probably are 80-90% for a stock that ranges in both the northwestern and north central Gulf. Fecundity, weight, girth, and length relationships are presented.

The banded drum, *Larimus fasciatus*, is a common demersal fish that ranges along the Altantic coast of the United States from Chesapeake Bay to southern Florida and in the Gulf of Mexico (Gulf) from the west coast of Florida to Campeche Bay (Hildebrand and Schroeder 1928; Hildebrand 1954; Briggs 1958). It primarily occurs in nearshore marine waters (Hildebrand and Cable 1934; Powles 1980) and only occasionally enters the lower reaches of estuaries (Gunter 1938; Swingle 1971; Dahlberg 1972). In the northern Gulf this species is most abundant off Louisiana (Gunter 1945; Behre 1950; Hildebrand 1954).

The life history of *L. fasciatus* is poorly known despite its common occurrence. No detailed study describes its life history in the Gulf, although Ross (1978) did so for North Carolina. Life history notes appear in Hildebrand and Cable (1934), Miller and Jorgenson (1969), Christmas and Waller (1973), Chao and Musick (1977), Johnson (1978), and Powles (1980).

This paper describes maturation, spawning periodicity, bathymetric distribution, recruitment, movements, age determination and growth using length frequencies, maximum size, life span, mortality, sex ratios, fecundity, and length-weight, length-girth, and standard-total length relationships of *L. fasciatus* in the northwestern Gulf.

METHODS

Larimus fasciatus were collected in 71 monthly or twice monthly cruises from October 1977 through August 1981 along a transect in the Gulf off Freeport, Tex., (Fig. 1) aboard a chartered shrimp trawler using twin 10.4 m (34-ft) trawls with a 4.4 cm stretched mesh cod end and a tickler chain. Initial stations usually were located at depths of 9, 13, 16, 18, 22, 27, 36, and 47 m. Sampling was expanded to include stations at 5 and 24

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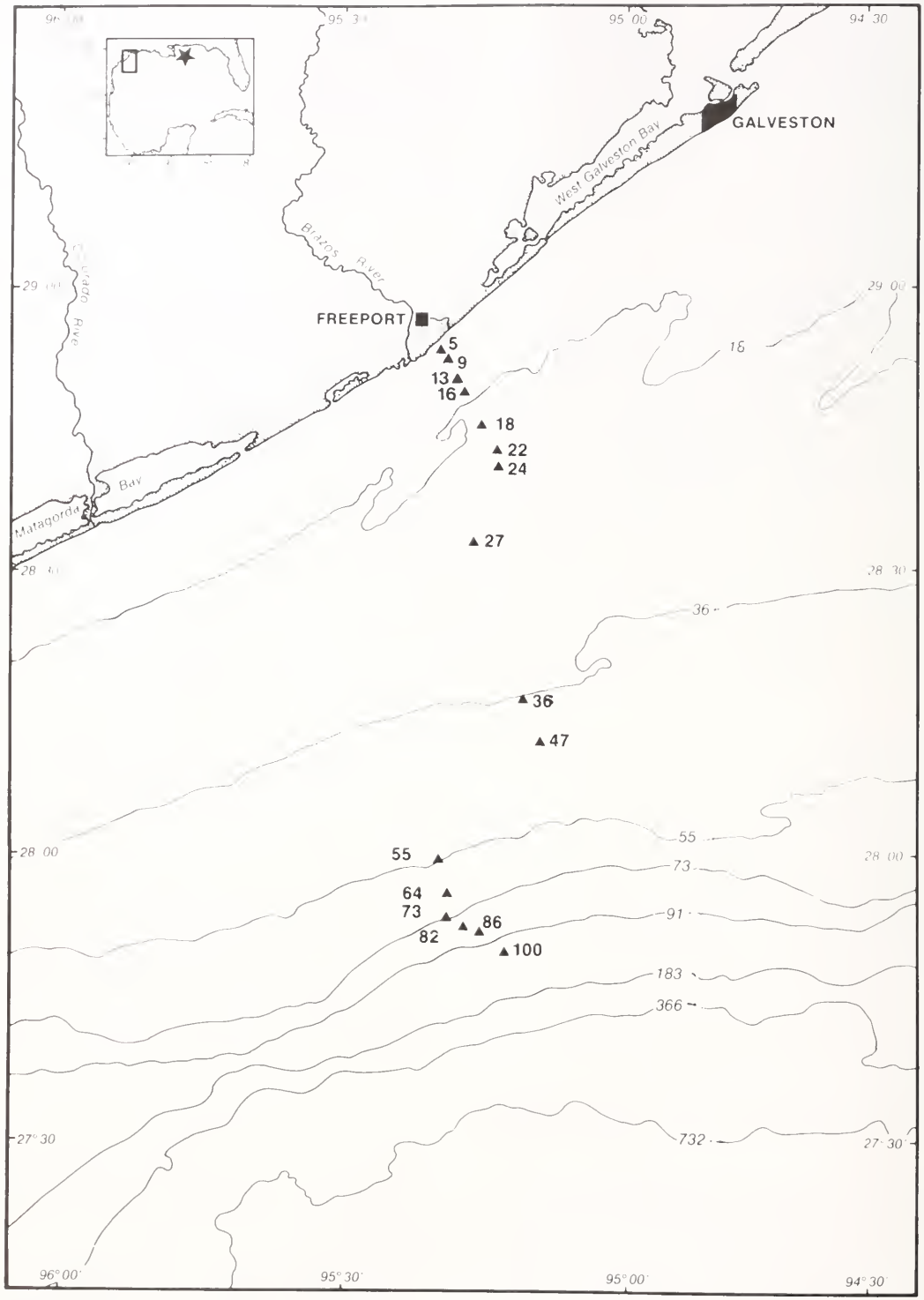


FIGURE 1.—Location of sampling area off Freeport, Tex. Station depths and bathymetric contours are indicated in meters. Starred area in insert indicates where collections were made in the north central Gulf.

m after November 1978 and at 55, 64, 73, 82, 86, and 100 m after May 1979. Collections were made during the day through September 1978; thereafter, a day and a night cruise usually were made each month. Two 10-min tows (bottom time) were made at each depth except that 1 tow was made at most depths prior to October 1978, usually 8 tows were made at 16 m, and usually 24 tows were made at 22 m.

All *L. fasciatus* were culled from the catch, measured to the nearest millimeter total length, fixed in 10% Formalin[5], and later preserved in 70% ethanol. For the period October 1979-April 1981, if available, 300 fish each month were selected for intensive processing using stratified random sampling in which a stratum included an individual spawned group (Standard 1983: app. 1). The following data were taken on the first 200 fish selected: total length (TL), standard length (SL), girth at origin of dorsal fin (G), total weight (TW), gonad weight (GW), sex, and ovary maturity stage. Only sex and ovary maturity stage were recorded for the remaining 100 fish. Maturity stages (Table 1) were assigned to immature and female fish using a slight modification of Kesteven's system (Bagenal and Braum 1971). Gonadosomatic indices (GSI) were calculated for individual females as GSI = 100 GW/TW.

Supplemental collections were made in the north central Gulf from 24 October to 5 November 1982 aboard the FRS *Oregon II* (NMFS) using standard 12.2 m (40-ft) 4-seam semiballoon shrimp trawls at depths of 9-91 m between long. 88°00′ and 89°00′W and at depths of 347-549 m between long. 87°50′ and 88°00′W (Rohr et al.[6]). Total length was measured on all *L. fasciatus* captured to compare with size compositions from the northwestern Gulf.

Age in years was determined by length-frequency analysis, e.g., the Petersen Method (Lagler 1956). Spawned groups (intrayear class cohorts) were specified by the season and year when they hatched, e.g., fall 1980. Descriptions of spawning periodicity (beginnings and ends) using length frequencies assume the following size and age combinations predicted from quadratic regression of total length on age, years pooled, noted below: 15 mm TL at 1 mo, 30 mm at 2 mo, and 45 mm at 3 mo. The same combinations were predicted from regressions for individual fall-spawned groups.

Duration of the spawning period was approximated for fall-spawned groups following Geoghegan and Chittenden (1982) as

$$\frac{\text{Time-specific mean size range early in life}}{\text{Mean growth/day early in life}}.$$

Calculations were based on April-June data, the first months when fall groups appeared fully recruited. Time-specific size range was estimated for each fall group as the mean of the 99% confidence intervals for observations in April-June (Table 2). Growth per day was estimated as the mean of the growth per day values between successive collections in the April-June period (Table 2). This procedure assumes large fish hatch before small ones and that all grow at the same rate (Geoghegan and Chittenden 1982). The latter assumption appears valid because 99% confidence intervals for observations (Table 3) were fairly constant within cruises in the April-June period when sample sizes were large.

Hatching dates used to set time scales to calculate growth of fall-spawned fish were determined by a one-step iteration process. A hatching date of 1 October was assigned to start the process because 1) fish 20-40 mm TL, which we assumed were 1-3 mo old, first appear in November-December, and 2) slopes for regressions of ovary weight on total length (Fig. 2) and mean GSI (Fig. 3) were greatest in September-October. Quadratic regressions of total length on age in days were then used as a simple model to estimate initial x-intercepts for each fall-spawned group. Final hatching dates

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

TABLE 1.—Description of gonad maturity stages assigned to *Larimus fasciatus*.

Stage and name	Description
1 Immature	Gonads barely or not visible, sexes indistinguishable to the naked eye.
2 Maturing Virgin	Ovaries small, thin, confined to posteriodorsal wall of body cavity
3 Early Developing	Ovaries solid, opaque, occupy <30% of body cavity. Individual eggs not visible to naked eye.
4 Late Developing	Ovaries occupy ~30% of body cavity. Individual eggs opaque, distinguishable to naked eye by close examination.
5 Gravid	Ovaries occupy >50% of body cavity. Individual eggs distinct, <50% translucent.
6 Ripe	Ovaries completely fill body cavity, >50% of the eggs translucent.
7 Spawning Spent	Ovaries flaccid, remaining eggs translucent.
8 Resting	Ovaries firm, occupy <30% of body cavity, translucent eggs may persist. Fish large enough to have spawned.

[6]Rohr, B. A., A. J., Kemmerer, and W. H. Fox, Jr. 1983. FRS *Oregon II* Cruise 130, 10-12-11 24 82. Cruise Rep., 22 p. Southeast Fisheries Center Pascagoula Facility, National Marine Fisheries Service, NOAA, P.O. Drawer 1207, Pascagoula, MS 39567-0112.

TABLE 2.—Calculations (see Methods) to estimate duration of fall spawning periods of *Larimus fasciatus* during 1977, 1978, 1979, and 1980. Collection dates, sample sizes, means, and 99% confidence limits for observations were obtained from Table 3.

Group and collection date	*n*	Mean total length	99% confidence limits of observations	Growth increment between first and last date	Time (days)	Growth/Day (mm)
1977 fall-spawned group						
14 Apr. 1978	5	69.0	33.9-104.0	18.5	24	0.77
8 May 1978	37	87.5	63.9-111.1			
Means			58.65 (interval)	18.5	24	0.77
Spawning period = 58.65/0.77 = 76 d						
1978 fall-spawned group						
5 Apr. 1979	197	67.6	39.3-95.9	11.1	15	0.74
20 Apr. 1979	328	78.7	50.6-106.8	16.1	24	0.67
14 May 1979	490	94.8	68.0-121.6	20.5	23	0.89
6 June 1979	65	115.3	85.3-145.3	7.1	15	0.47
21 June 1979	151	122.4	104.0-140.8			
Means			52.64 (interval)	13.7	19	0.69
Spawning period = 52.64/0.69 = 76 d						
1979 fall-spawned group						
1 Apr. 1980	746	72.6	49.3-95.9	7.0	15	0.47
16 Apr. 1980	437	79.6	53.1-106.0	0.1	19	0.01
5 May 1980	1,202	79.7	55.2-104.2	9.1	14	0.65
19 May 1980	239	88.8	59.8-117.8	15.0	14	1.07
2 June 1980	614	103.8	81.3-126.3	12.1	17	0.71
19 June 1980	254	115.9	90.2-141.6			
Means			50.48 (interval)	8.7	16	0.58
Spawning period = 50.48/0.58 = 87 d						
1980 fall-spawned group						
7 Apr. 1981	110	60.0	33.1-86.9	14.2	13	1.09
20 Apr. 1981	69	74.2	45.7-102.7	6.2	14	0.44
4 May 1981	97	80.4	57.0-103.8	9.3	15	0.62
19 May 1981	165	89.7	68.8-110.6	12.8	14	0.91
2 June 1981	128	102.5	77.9-127.1	9.3	13	0.72
15 June 1981	174	111.8	90.4-133.2	10.4	14	0.76
Means			48.57 (interval)			
Spawning period = 48.57/0.76 = 64 d						

TABLE 3.—Growth data (mm TL) by spawned group for *Larimus fasciatus* from the Gulf off Freeport, Tex. Night and day cruises are indicated by night (N) and day (D). Observed size ranges delineate spawned group boundaries used in growth and mortality calculations and indicated in Figure 6. Collection dates with asterisks indicate collections pooled to estimate mean size at age.

Group and collection date		*n*	Observed size range (mm)	Mean length (mm)	s^2	95% confidence limits of the mean	99% confidence limits of observations	Unadjusted growth increment (mm)
1976 fall-spawned group								
1 Oct. 1977	D*	9	120-143	133.6	46.5	128.4-138.8	110.7-156.5	+ 4.9
3 Dec. 1977	D	2	136-141	138.5	12.5	106.7-170.3	86.6-363.6	
1977 fall-spawned group								
21 Mar. 1978	D	10	47-97	62.3	261.3	50.7-73.9	9.8-114.8	+ 6.7
14 Apr. 1978	D	5	62-78	69.0	58.0	59.5-78.5	33.9-104.0	+18.5
8 May 1978	D	37	70-104	87.5	75.0	84.6-90.4	63.9-111.1	+40.0
15 July 1978	D	286	113-141	127.5	26.5	126.9-128.1	114.2-140.8	+20.5
15 Sept. 1978	D*	8	145-152	148.0	8.6	145.5-150.5	137.7-158.3	+ 1.2
1 Dec. 1978	N	14	141-162	149.2	33.3	145.9-152.5	131.8-166.6	+ 5.8
13 Dec. 1978	D	1	155	155.0	—	—	—	+ 1.0
6 June 1979	N	1	156	156.0	—	—	—	+18.0
21 June 1979	D	1	174	174.0	—	—	—	
1978 fall-spawned group								
1 Dec. 1978	N	98	34-99	64.3	220.7	61.3-67.3	25.3-103.3	+ 9.5
13 Dec. 1978	D	51	34-98	73.8	266.6	69.2-78.4	30.1-117.5	− 7.5
24 Feb. 1979	D	19	40-97	66.3	343.8	57.4-75.2	12.9-119.7	+ 1.3
5 Apr. 1979	N	197	45-98	67.6	120.3	66.1-69.1	39.3-95.9	+11.1
20 Apr. 1979	D	328	51-115	78.7	118.7	77.5-79.9	50.6-106.8	+16.1
14 May 1979	N	490	68-134	94.8	108.0	93.9-95.7	68.0-121.6	+20.5
6 June 1979	N	65	78-130	115.3	128.1	112.5-118.1	85.3-145.3	+ 7.1
21 June 1979	D	151	95-140	122.4	51.3	121.3-123.5	104.0-140.8	− 1.4
5 July 1979	N	3	115-131	121.0	76.0	99.3-142.7	34.5-207.5	+ 2.5
19 July 1979	D	83	111-138	123.5	42.7	122.1-124.9	106.3-140.7	+15.6
22 Aug. 1979	D	83	111-155	139.1	54.5	137.5-140.7	119.6-158.6	+ 5.7
22 Sept. 1979	D*	23	132-164	144.8	38.8	142.1-147.5	127.2-162.4	+ 0.8
2 Oct. 1979	N*	59	133-156	145.6	29.8	144.2-147.0	131.1-160.1	− 1.5
16 Oct. 1979	D*	198	127-164	144.1	34.6	143.3-144.9	128.9-159.3	+ 2.0
3 Nov. 1979	N	9	138-158	146.1	43.4	141.0-151.2	124.0-168.2	+ 2.8
15 Nov. 1979	D	7	144-155	148.9	13.8	145.5-152.3	135.1-162.7	+ 2.8

TABLE 3.—*Continued*

Group and collection date		*n*	Observed size range (mm)	Mean length (mm)	s^2	95% confidence limits of the mean	99% confidence limits of observations	Unadjusted growth increment (mm)
1 Dec. 1979	N	3	148-155	151.7	12.3	143.0-160.4	116.9-186.5	
14 Dec. 1979	D	1	163	163.0	—	—	—	+11.3
3 Jan. 1980	N	1	157	157.0	—	—	—	6.0
4 Feb. 1980	N	1	146	146.0	—	—	—	11.0
5 Mar. 1980	N	1	150	150.0	—	—	—	+ 4.0
19 Mar. 1980	D	45	135-163	151.8	29.8	150.2-153.4	137.1-166.5	+ 1.8
16 Apr. 1980	D	8	132-166	150.5	91.4	142.5-158.5	117.0-184.0	− 1.3
19 May 1980	D	2	161-182	171.5	220.5	38.1-304.9	773.8-1,116.8	−21.0
2 June 1980	N	22	146-174	158.5	37.4	155.8-161.2	141.2-175.8	13.0
19 June 1980	D	26	147-180	157.2	50.8	154.3-160.1	137.3-177.1	1.3
7 July 1980	N	45	150-172	159.2	26.1	157.7-160.7	145.4-173.0	+ 2.0
5 Aug. 1980	N*	11	156-175	163.3	31.6	159.5-167.1	145.5-181.1	+ 4.1
7 Sept. 1980	N*	1	177	177.0	—	—	—	−13.7
1979 fall-spawned group								
3 Nov. 1979	N	4	21-41	32.5	70.3	19.2-45.8	−16.5-81.5	
15 Nov. 1979	D	2	36-45	40.5	40.5	−16.7-97.7	−364.6-445.6	− 8.0
1 Dec. 1979	N	24	33-87	55.3	269.6	48.4-62.2	9.2-101.4	+14.8
14 Dec. 1979	D	74	29-88	50.8	146.4	48.0-53.6	18.8-82.8	− 4.5
3 Jan. 1980	N	39	34-110	56.6	313.2	50.9-62.3	8.7-104.5	+ 5.8
16 Jan. 1980	D	246	31-124	54.1	108.8	52.8-55.4	27.2-81.0	− 2.5
4 Feb. 1980	N	581	33-109	58.1	99.2	57.3-58.9	32.4-83.8	+ 4.0
15 Feb. 1980	D	1723	30-97	60.1	77.3	59.7-60.5	37.5-82.7	+ 2.0
5 Mar. 1980	N	507	39-95	61.0	80.5	60.2-61.8	37.9-84.1	+ 0.9
19 Mar. 1980	D	217	47-121	71.9	103.5	70.5-73.3	45.7-98.1	−10.9
1 Apr. 1980	N	746	45-115	72.6	81.7	72.0-73.2	49.3-95.9	+ 0.7
16 Apr. 1980	D	437	44-108	79.6	105.1	78.6-80.6	53.1-106.0	− 7.0
5 May 1980	N	1202	54-114	79.7	90.5	79.2-80.2	55.2-104.2	+ 0.1
19 May 1980	D	239	59-116	88.8	127.1	87.4-90.2	59.8-117.8	+ 9.1
2 June 1980	N	614	72-139	103.8	76.5	103.1-104.5	81.3-126.3	−15.0
19 June 1980	D	254	86-139	115.9	99.6	114.7-117.1	90.2-141.6	−12.1
7 July 1980	N	750	90-149	120.5	84.2	119.8-121.2	96.9-144.1	+ 4.6
21 July 1980	D	142	104-153	124.3	84.6	122.8-125.8	100.6-148.0	− 3.8
5 Aug. 1980	N	794	102-155	130.9	73.0	130.3-131.5	108.9-152.9	+ 6.6
26 Aug. 1980	D	1	157	157.0	—	—	—	+26.1
7 Sept. 1980	N*	116	123-158	146.0	42.1	144.8-147.2	129.0-163.0	−11.0
22 Sept. 1980	D*	12	143-162	151.7	39.2	147.7-155.6	132.3-171.1	+ 5.7
6 Oct. 1980	N*	82	137-168	148.7	36.7	147.4-150.0	132.7-164.7	− 3.0
20 Oct. 1980	D*	5	118-156	141.0	251.0	121.3-160.7	48.5-233.5	− 7.7
3 Nov. 1980	N	27	140-173	152.9	67.1	149.7-156.1	130.1-175.7	+11.9
18 Nov. 1980	D	18	143-157	151.9	14.6	150.0-153.8	140.8-163.0	1.0
1 Dec. 1980	N	4	149-153	151.5	3.7	148.4-154.6	140.3-162.7	0.4
15 Dec. 1980	D	1	147	147.0	—	—	—	− 4.5
7 Jan. 1981	N	7	127-167	143.0	211.7	129.5-156.5	89.1-196.9	− 4.0
2 Feb. 1981	N	1	157	157.0	—	—	—	+14.0
16 Feb. 1981	D	2	130-150	140.0	200.0	12.9-267.1	−760.2-1,040.2	17.0
7 Apr. 1981	N	2	145-146	145.5	0.5	139.1-151.9	100.5-190.5	+ 5.5
20 Apr. 1981	D	3	133-148	141.0	57.0	122.2-159.8	66.1-215.9	4.5
4 May 1981	N	20	148-167	155.8	23.5	153.5-158.1	141.9-169.7	+14.8
2 June 1981	N	5	143-161	153.0	43.5	144.8-161.2	122.6-183.4	− 2.8
15 June 1981	D	11	146-174	159.0	53.2	154.1-163.9	135.9-182.1	+ 6.0
1 July 1981	N	9	143-171	159.0	85.0	151.9-166.1	128.1-189.9	0.0
20 July 1981	D	199	146-176	158.5	40.5	157.6-159.4	142.1-174.9	0.5
1980 spring-spawned group								
3 Aug. 1980	N	7	58-80	65.4	64.0	58.0-72.8	35.7-95.1	
1980 fall-spawned group								
18 Nov. 1980	D	1	68	68.0	—	—	—	−15.4
1 Dec. 1980	N	62	22-108	52.6	267.0	48.4-56.8	15.0-90.2	20.1
15 Dec. 1980	D	2	29-36	32.5	24.5	−12.0-77.0	−282.6-347.6	+19.6
7 Jan. 1981	N	191	31-91	52.1	231.2	49.9-54.3	12.9-91.3	− 2.2
21 Jan. 1981	D	25	33-82	54.3	214.0	48.3-60.3	13.4-95.2	− 7.5
2 Feb. 1981	N	255	21-118	46.8	93.7	45.6-48.0	21.9-71.7	+15.3
16 Feb. 1981	D	49	33-108	62.1	330.2	56.9-67.3	13.4-110.8	− 6.4
2 Mar. 1981	N	32	42-86	55.7	156.5	51.2-60.2	21.4-90.0	+ 0.5
16 Mar. 1981	D	11	43-87	56.2	129.8	48.5-63.9	20.1-92.3	+ 3.8
7 Apr. 1981	N	110	39-87	60.0	105.7	58.1-61.9	33.1-86.9	+14.2
20 Apr. 1981	D	69	56-107	74.2	115.7	71.6-76.8	45.7-102.7	+ 6.2
4 May 1981	N	97	64-107	80.4	79.7	78.6-82.2	57.0-103.8	+ 9.3
19 May 1981	D	165	70-115	89.7	66.0	88.5-90.9	68.8-110.6	+12.8
2 June 1981	N	128	78-129	102.5	91.1	100.8-104.2	77.9-127.1	+ 9.3
15 June 1981	D	174	92-133	111.8	68.8	110.6-113.0	90.4-133.2	+ 8.4
1 July 1981	N	48	106-137	120.2	39.8	118.4-122.0	103.3-137.1	+13.0
20 July 1981	D	152	107-145	133.2	41.8	132.2-134.2	116.5-149.9	+ 8.3
3 Aug. 1981	N	132	120-166	141.5	62.0	140.2-142.8	121.2-161.8	+ 1.8
16 Aug. 1981	D	428	105-170	143.3	49.3	142.6-144.0	125.2-161.4	
1981 spring-spawned group								
15 June 1981	D	2	42-47	44.5	12.5	12.7-76.3	−180.6-269.6	+ 9.5
20 July 1981	D	9	41-72	54.0	110.8	45.9-62.1	18.7-89.3	+14.5
3 Aug. 1981	N	2	58-79	68.5	220.5	−64.9-201.9	−876.8-1,013.8	

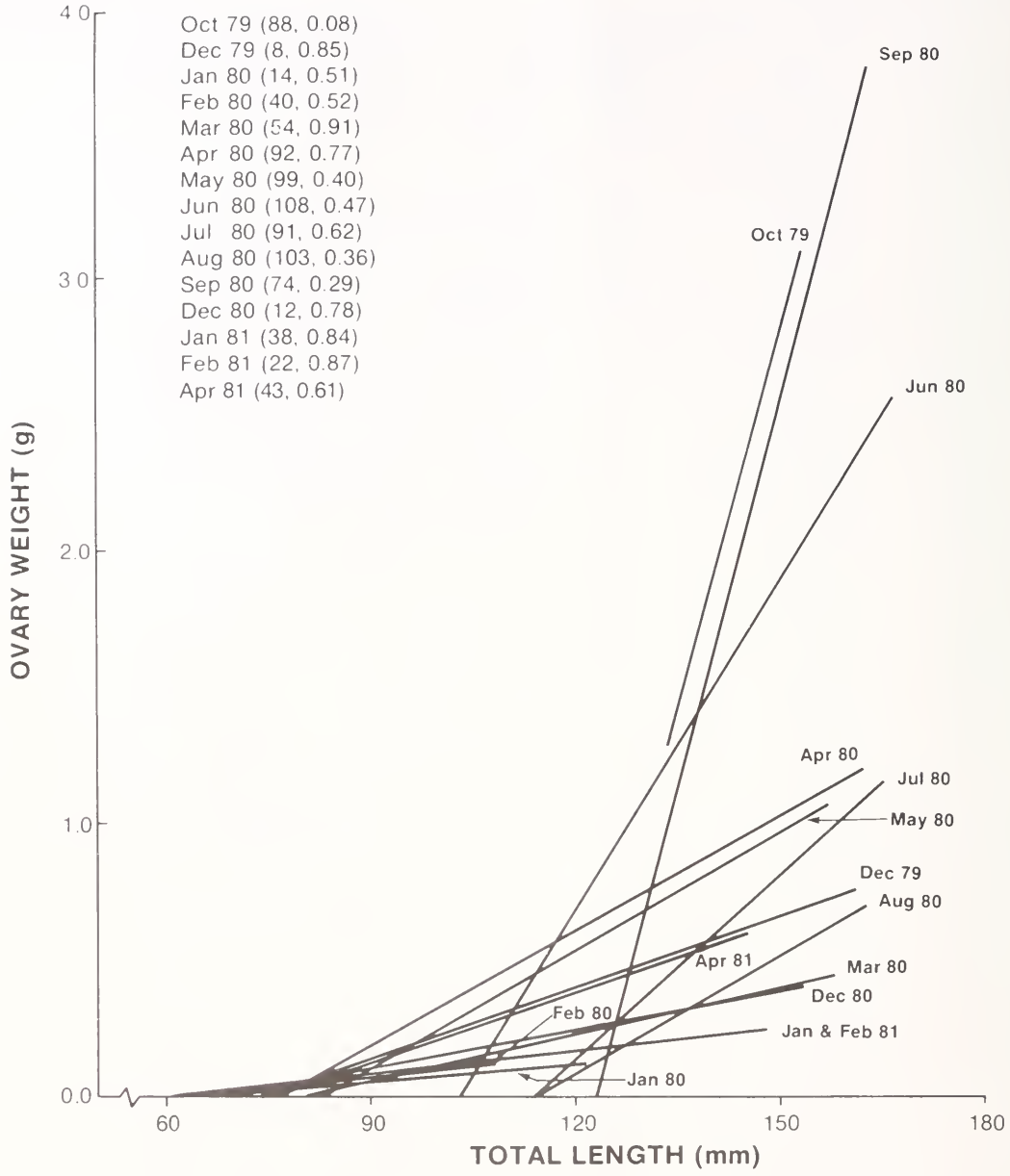


FIGURE 2.—Monthly regressions of ovary weight on total length for *Larimus fasciatus*. Length of each line shows the observed size range. Sample sizes and r^2 values are tabulated for each period. Regressions presented were significant at $\alpha = 0.05$.

were calculated by using initial x-intercepts to readjust the initial x-variable (time) scale, so that each final growth curve passed through the origin (Table 4). Final calculated hatching dates are mean values because regressions predict averages. Rate parameters—e.g., regression coefficients, growth/30 d, and von Bertalanffy K values—fitted to observed size data are the same within rounding error regardless of the hatching dates used, because curves are fitted to the same time dimension between the initial and last collection of a cohort.

Total annual mortality rates ($1 - S$) were calculated on a time-specific and cohort-specific basis from the expression $S = N_t/N_0$ where S = rate of survival, and N_t and N_0 are the numbers of fish at

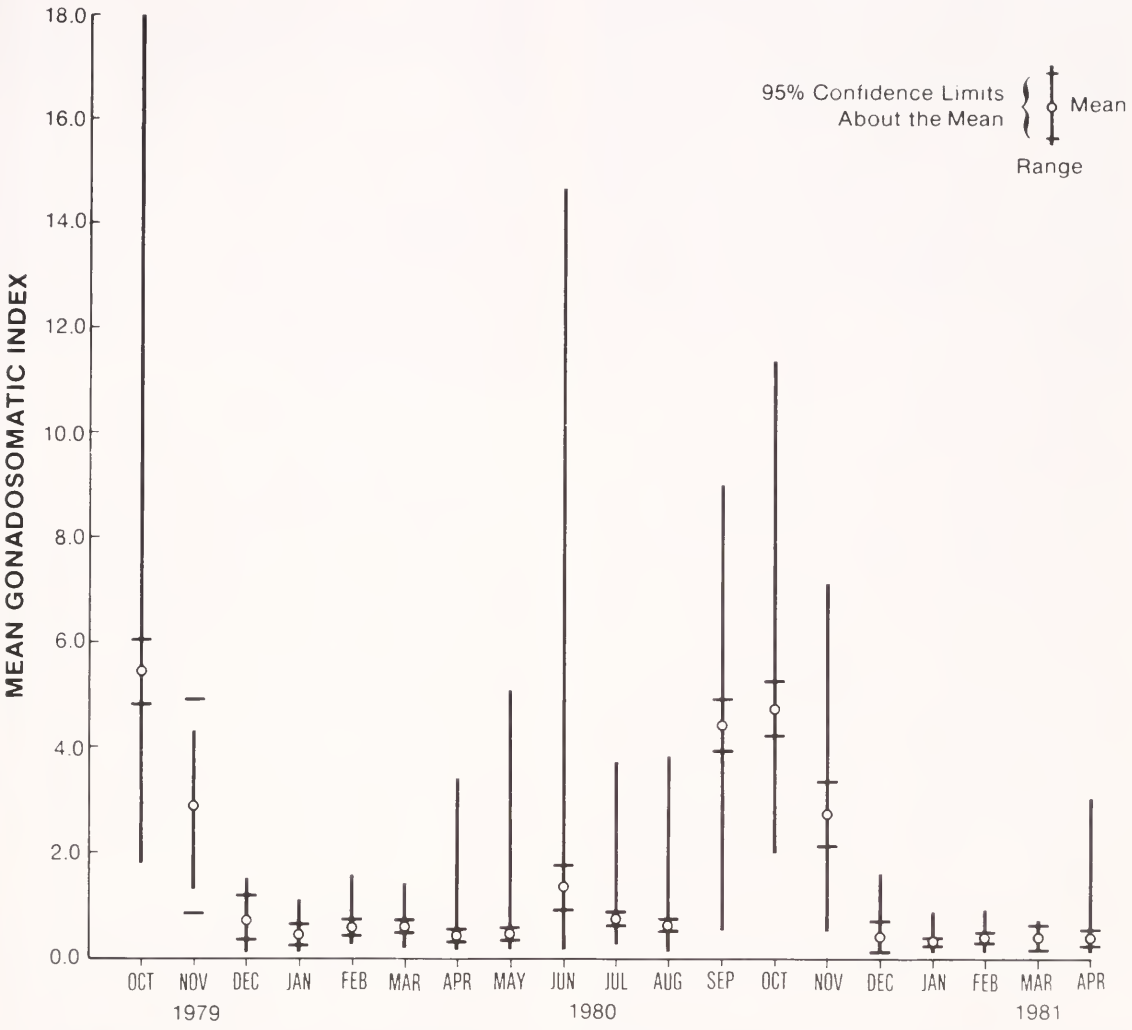


FIGURE 3.—Monthly mean gonadosomatic indices, ranges, and 95% confidence limits about means for female *Larimus fasciatus*, spawned groups pooled, October 1979-April 1981.

TABLE 4.—Summary of iterative process used to calculate final hatching dates and set time scales for growth calculations. Equations describe regressions of observed mean total length (TL) on age in days. Initial age values and growth equations were scaled to a 1 October hatching date. Final fitted regressions are in Figure 7.

Spawned group	Initial growth equation	Initial x-intercept	Final growth equation	Final calculated hatching date
Fall 1978	$y = 28.59 + 0.40825x - 0.00031x^2$	−67	$y = -0.13 + 0.44924x - 0.00031x^2$	27 July 1978
Fall 1978, initial two collections deleted	$y = -8.28 + 0.58365x - 0.00049x^2$	14	$y = -0.21 + 0.56983x - 0.00049x^2$	15 Oct. 1978
Fall 1979	$y = 7.41 + 0.51937x - 0.00045x^2$	−14	$y = 0.13 + 0.53162x - 0.00045x^2$	17 Sept. 1979
Fall 1980	$y = 12.94 + 0.36704x$	−35	$y = 0.09 + 0.36704x$	27 Aug. 1980
Fall 1980, initial two collections deleted	$y = -7.47 + 0.45303x$	16	$y = -0.22 + 0.45303x$	17 Oct. 1980

age each month. Analyses excluded several months in which estimates were not reliable because of incomplete recruitment (2 mo, time-specific; 6 mo, cohort-specific), seeming immigration (1 mo, time-specific), or some stations were not occupied in one cruise (1 mo, cohort-specific). Pooled estimates of S were calculated using Heincke's procedure (Ricker 1975) and were converted to $1 - S$ and Z using relationships in Gulland (1969:59). Observed estimates were compared against theoretical values calculated from the expression $\overline{Z}$ = 4.6/number of years in life span (Royce 1972:238). Typical maximum life span was approximated by the Beverton-Holt yield model parameter t_L (Gulland 1969), and typical maximum size was approximated as a corresponding length (l_L) following Alverson and Carney's (1975) definition that only 0.5-1% of the catch exceeds age t_L. Values of l_L were calculated from the cumulative length frequency for all fish captured in the period October 1977-August 1981. We calculated specific values of t_L from l_L by solving for time in von Bertalanffy (Gulland 1969:40) and quadratic regression equations. Total mortality rates and growth data presented are termed *apparent* because they may be affected by emigration as noted; if so, they overestimate mortality but underestimate sizes at age.

Ovaries were prepared to estimate fecundity (FEC) using procedures similar to Bagenal (1957) and Simpson (1959). Entire ovaries of 60 Early Developing, Late Developing, Gravid, or Ripe fish were removed, split, everted, placed in Gilson's solution for 1-3 mo, and agitated using a magnetic stirrer to enhance separation of ova from connective tissue. Connective tissue was removed and supernatant siphoned off until only ova remained. Eggs were then placed in a beaker, filled to 200 ml with water, and magnetically stirred to be uniformly dispersed. Fecundity was determined for each fish by taking a 2 ml sample from each of three fixed levels in the beaker (at 25, 100, 175 ml) to enumerate eggs. Samples were pooled to calculate a mean/2 ml for each fish because, although significant, differences in mean egg count per level over all fish were small (627, 592, and 598, respectively; n = 60 for each level). Mean counts/2 ml were expanded to determine fecundity as the number of eggs in the total water volume.

Regression relationships were calculated following standard procedures (Helwig and Council 1979; Snedecor and Cochran 1980). Von Bertalanffy growth was calculated using Fabens' (1965) program. All length measurements presented herein are total length unless stated otherwise, and all length frequencies are moving averages of three. Conversions between standard length and total length used regressions presented herein.

We use the verb "recruit" and the noun "recruitment" herein to describe areas in which young *L. fasciatus* descend to the bottom from their pelagic (Johnson 1978) early stages. This usage conforms to Beverton and Holt's (1957) meaning of recruitment, because these bottom areas are exploited, and to Ricker's (1975) meaning, because fish also then enter the exploited phase of life.

RESULTS

Maturation and Spawning Periodicity

Larimus fasciatus from the northwestern Gulf mature at 80-130 mm as they approach age I. Gonad development was distinct at 80-150 mm when most females entered the Early Developing stage (Fig. 4). All fish in Late Developing and later stages were >130 mm. These data are supported by regressions of ovary weight on length (Fig. 2) in which extrapolated x-intercepts were 75-125 mm during the April-October period when spawning occurs. Age compositions and sizes presented later indicate *L. fasciatus* mature to first spawn at 12-14 mo.

Little somatic growth seemingly occurs after *L. fasciatus* enter late stages of gonad development. Mean lengths of fish were 146 mm in the Late Developing stage, 147 mm when Gravid, 149 mm when Ripe and Spawning/Spent, and 150 mm when Resting (Fig. 4). Maximum and minimum sizes also remained constant through these stages.

Larimus fasciatus spawn within a broad period from April through November. Fish in Ripe or Gravid stages occurred throughout this period (Fig. 5), slopes and elevations of regressions of ovary weight on length generally were highest (Fig. 2), and GSI maximums usually were high (Fig. 3). Gonad analyses are supported by 1) recurrent collections of fish 20-40 mm from November through February each year in the period 1978-81 which probably were 1-3 mo old and indicate spawning from September through November (Fig. 6), and 2) collections of distinct groups of fish 40-80 mm in the period mid-June through August in 1980 and 1981 which probably were 3-5 mo old and indicate spawning from April through June.

Little or no spawning of *L. fasciatus* occurs from

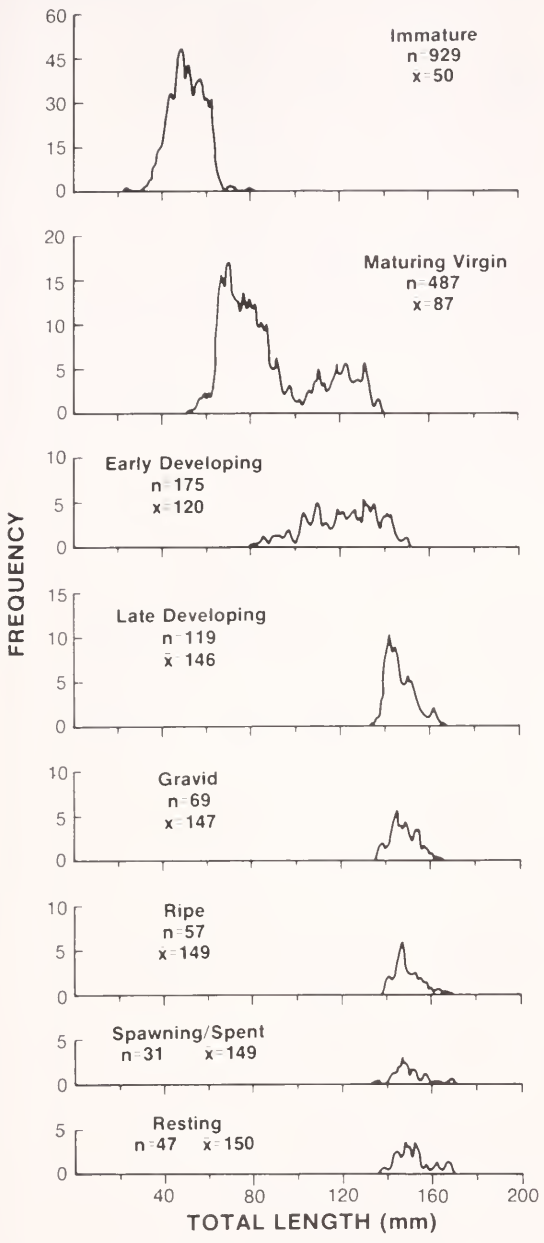


FIGURE 4.—Length frequencies of immature and female *Larimus fasciatus* by gonad maturity stage. See Table 1 for maturity stage criteria.

December through March. Almost all fish were in the Immature, Maturing Virgin, Early Developing, or Resting stages in that period (Fig. 5). Few were in the Late Developing stage then and none were Gravid or Ripe. In addition, mean and maximum GSI values were lowest during the December-March period (Fig. 3) as were the slopes and elevations of regressions of ovary weight on length (Fig. 2). Gonad analyses are supported by the absence of fish 20-80 mm from late February to mid-June each year (Fig. 6) with the exception of fall-spawned fish whose growth in late winter and spring is clearly followed.

Although *L. fasciatus* spawn within a broad time period, spawning primarily occurs during what we interpret as two discrete periods, a major fall period (September-November) and a very minor spring period (April-June). Mean and/or maximum GSI values were highest in the periods May-June and September-November, and these peaks were separated by troughs in the periods July-August and December-April (Fig. 3). Although few fish were Ripe in August, nearly all were in Late Developing, Gravid, Ripe, and Spawning/Spent stages from September through November (Fig. 5); few were in Immature, Maturing Virgin, or Early Developing stages then. Fall-spawned fish greatly predominated each year and formed length-frequency modes easily followed through the spring and summer after their recruitment in fall and winter (Fig. 6). A minor spring spawn is indicated by distinct, but not abundant, groups of fish 40-80 mm in the periods August 1980 and June-August 1981 (Fig. 6) and by the occurrence of a few (14) Gravid and Ripe stage fish from April through June and Late Developing fish in March (Fig. 5). No recently recruited spring-spawned fish were evident after August (Fig. 6), but they may be represented by the few intermediate-sized fish from an unclear spawned group in January and March 1980 and February 1981.

Little or no spawning of *L. fasciatus* occurs in July and August. No fish 20-40 mm (1-3 mo old) were captured from July through October (Fig. 6). Only two fish were Gravid or Ripe during July and August and few were in the Late Developing stage then (Fig. 5).

Calculated hatching dates agree with the major fall-spawning period—September-November—indicated by gonad and length-frequency analyses. Depending on data points included, calculated hatching dates were 27 July or 15 October 1978, 17 September 1979, and 27 August or 17 October 1980 (Table 4). Hatching dates of 15 October and 17 October seem most realistic for 1978 and 1980. The earlier dates for those years are based on regressions fitted to all collections. The earliest two collections in those years, however, probably contribute upwardly biased size data

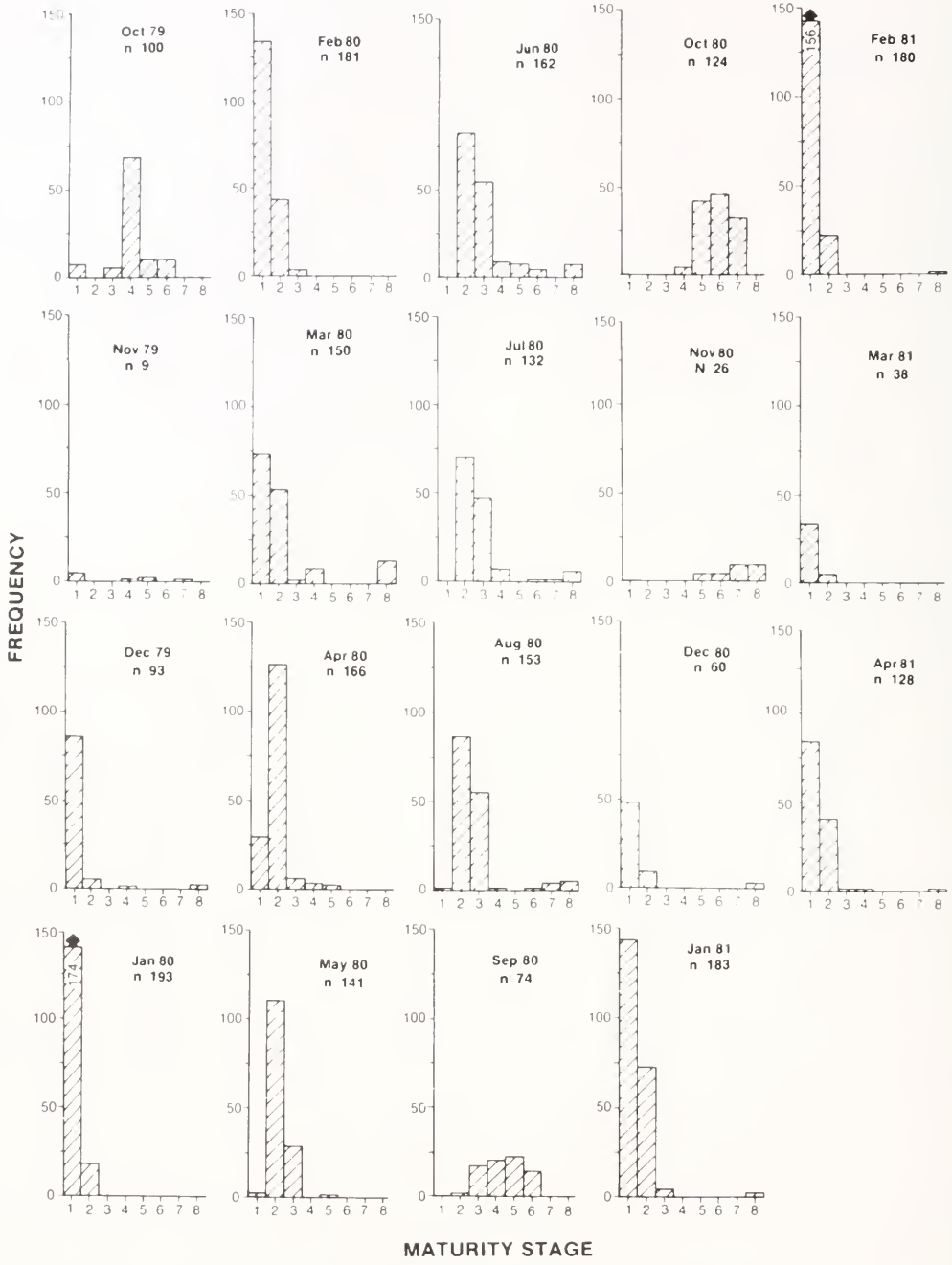


FIGURE 5.—Monthly gonad maturity stages of immature and female *Larimus fasciatus*. Maturity stages (see Table 1) are 1 - Immature, 2 - Maturing Virgin, 3 - Early Developing, 4 - Late Developing, 5 - Gravid, 6 - Ripe, 7 - Spawning/Spent, and 8 - Resting.

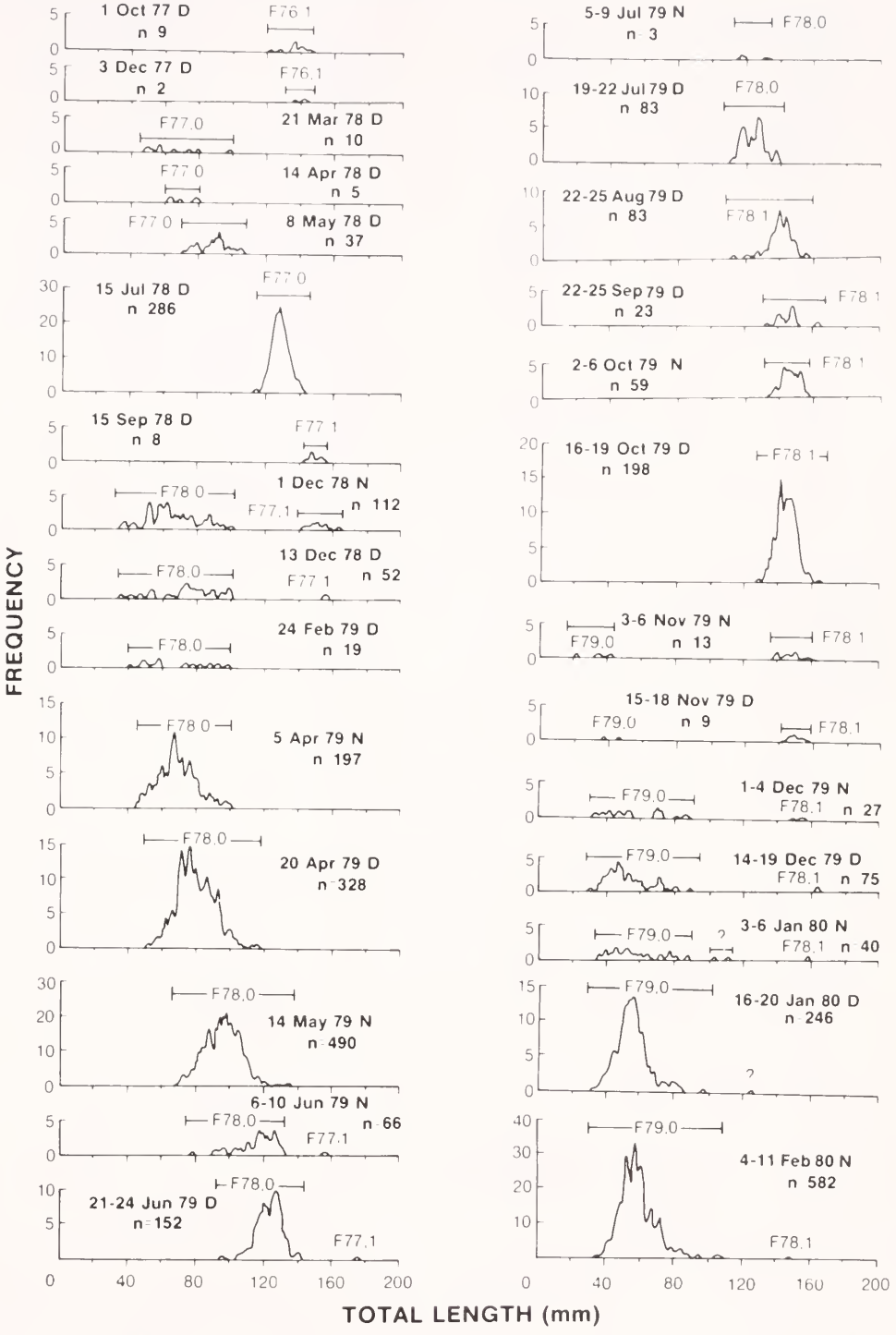


FIGURE 6.—Monthly length frequencies of *Larimus fasciatus* off Freeport, Tex. Day and night cruises are indicated by D and N. Bars in each panel depict size range of indicated spawned group; further detail is in Table 3. The letter and first two digits within a bar indicate spawned groups; the last digit is age in years, e.g., F77, 1

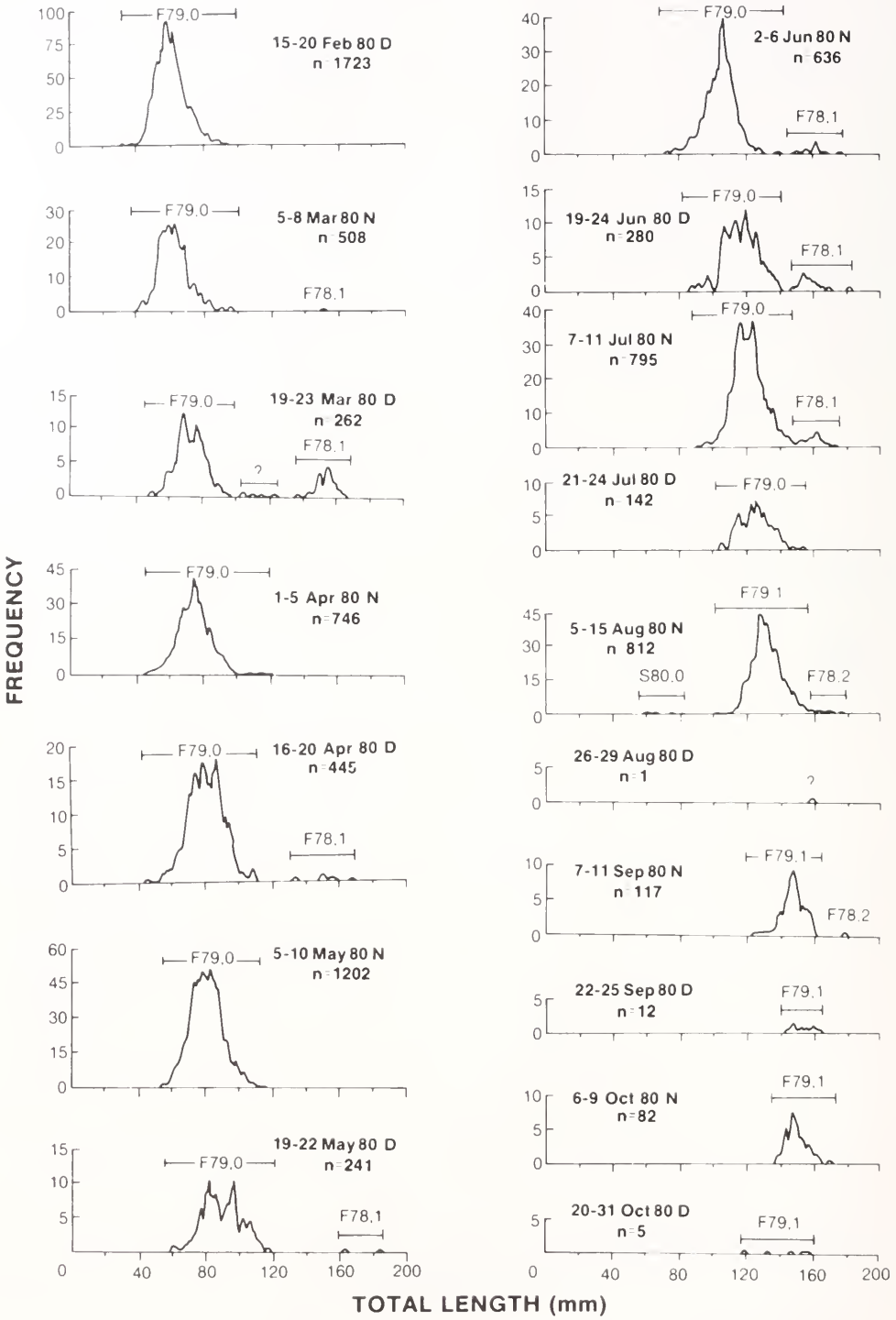


FIGURE 6.—*Continued*—represents the fall 1977-spawned group when age I. Age designation for each cohort changed in August to simplify reference between Figures 6 and 10 D; true ages in August only approach those indicated.

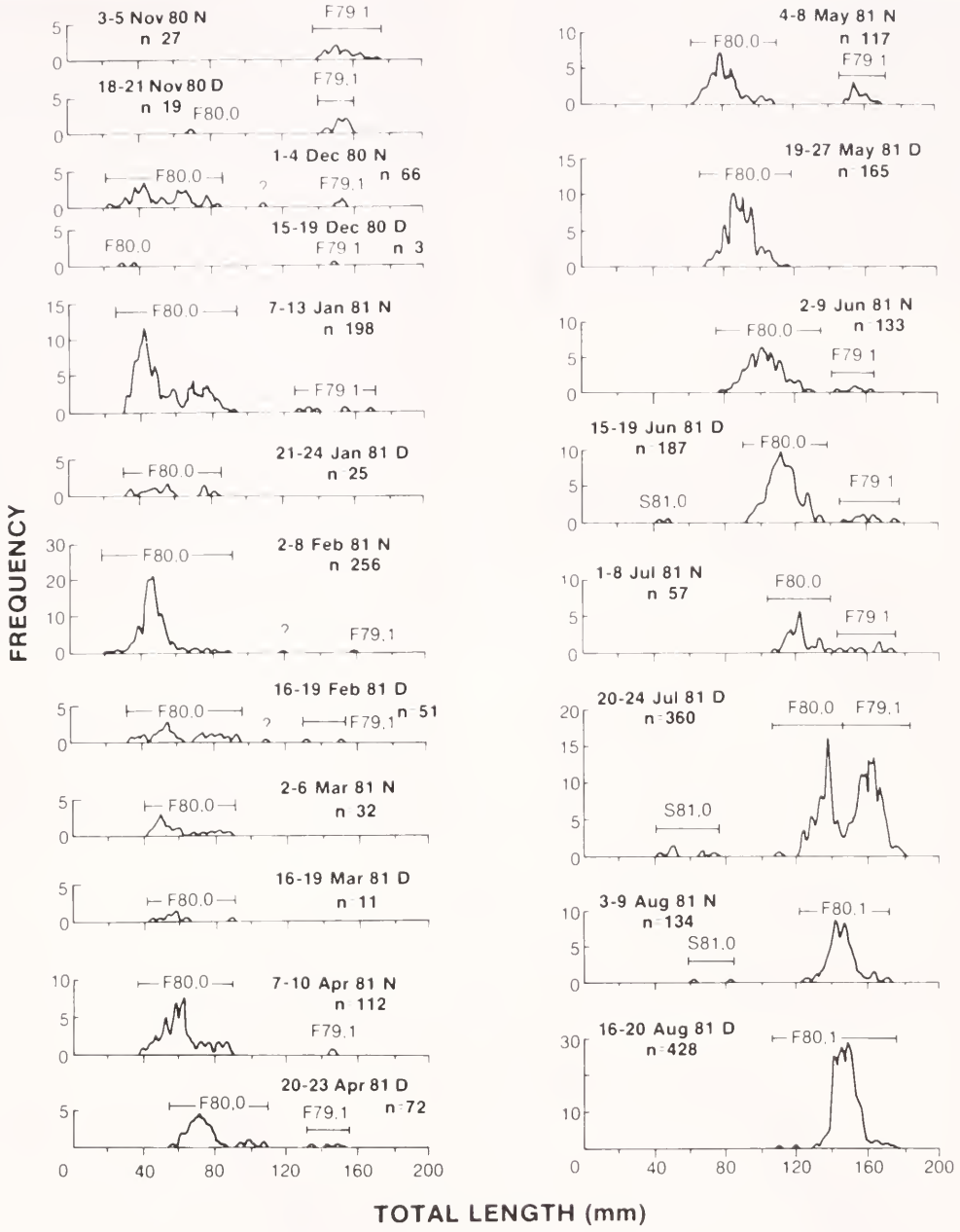
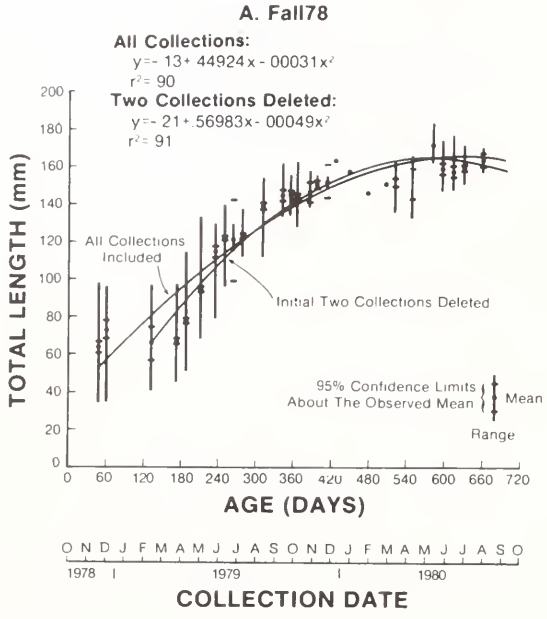


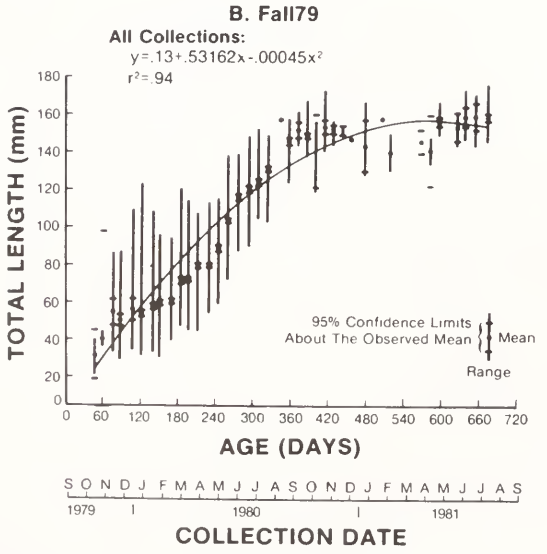
FIGURE 6.—*Continued.*

that reflect gear selection for large fish or incomplete recruitment of smaller fish; mean sizes in those collections were as large as or larger than means in subsequent collections and seem to be outliers (Fig. 7A, C). Coefficients of determination were higher when the earliest two collections were excluded (Fig. 7A, C).

The period of successful spawning spans 60-90 d within the major September through November interval. Based on mean 99% confidence limits for observations and growth per day in each April-June period, calculated durations of fall spawning periods were 76 d in 1977, 76 in 1978, 87 in 1979, and 64 in 1980 (Table 2). These estimates fall within and agree with the broad 90-d duration of the fall-spawning period indicated by gonad maturity and weight data.

The predominant fall-spawned groups are produced by fish that first spawn when 12-14 mo old and the minor spring-spawned groups by fish 19-21 mo old. Fall-spawned fish apparently do not spawn when 5-7 mo old in their first spring, because GSI values for fall 1979 and fall 1980 fish remained low during their initial springs (Fig. 8B, C). Peaks in GSI values from September through November in 1979 and 1980 were formed by fall 1978 and fall 1979 fish, first spawning at 12-14 mo of age (Fig. 8A, B). Peaks in GSI values from April through June in 1980 and 1981 were formed by fall 1978 and fall 1979 fish that spawned when 19-21 mo old (Fig. 8A, B). We were not able to determine age when spring-spawned groups spawn, because these fish were clearly identifiable only until 3-5 mo old (see section on Age Determination and Growth).





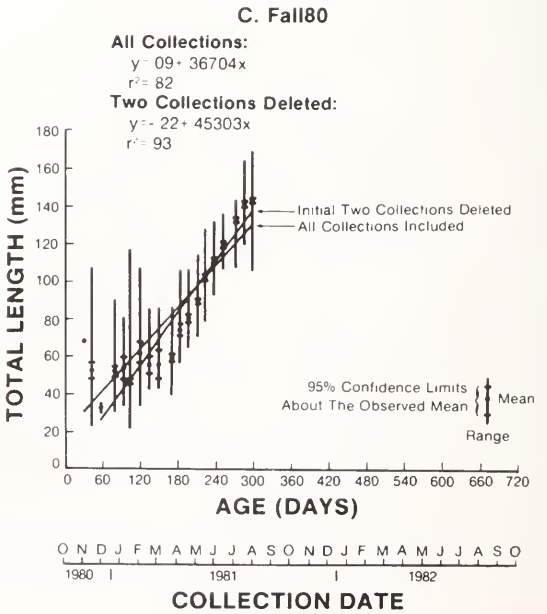


FIGURE 7.—Mean observed and predicted sizes at age (days) for the 1978 (A), 1979 (B), and 1980 (C) fall-spawned groups of *Larimus fasciatus*. Mean sizes at age were regressed on age scaled to calculated hatching dates of 27 July and 15 October 1978, 17 September 1979, and 27 August and 17 October 1980. Observed mean lengths and their confidence limits are from Table 3. Regressions were significant at $\alpha = 0.001$.

Bathymetric Distribution, Recruitment, and Movements

The bathymetric distribution of *L. fasciatus* in the northwestern Gulf off Freeport extends from <5 to 55 m. This species was most abundant at 5 m, the shallowest depth occupied (Fig. 9). Abundance declined sharply between 5 and 18 m and remained low from 18 to 36 m. Only one specimen was collected deeper than 36 m.

Young-of-the-year *L. fasciatus* in the northwestern Gulf recruit in waters < 5-16 m when 2-4 mo old. Fall-spawned young 30-100 mm recruited almost exclusively in 5-16 m from November through April (Fig. 10A, B). Only four young-of-the-year specimens at 18-22 m were collected deeper than 16 m. Similarly, spring-spawned young 60-80 mm recruited only at 5-16 m in the period August-October (Fig. 10D).

Greatest recruitment of fall-spawned *L. fasciatus* occurred in the shallowest depths sampled. Recent fall-spawned recruits were most abundant by far at 5 m in November-April (Fig. 10A, B). Abundance then sharply declined with depth and was very low deeper than 16 m in that period.

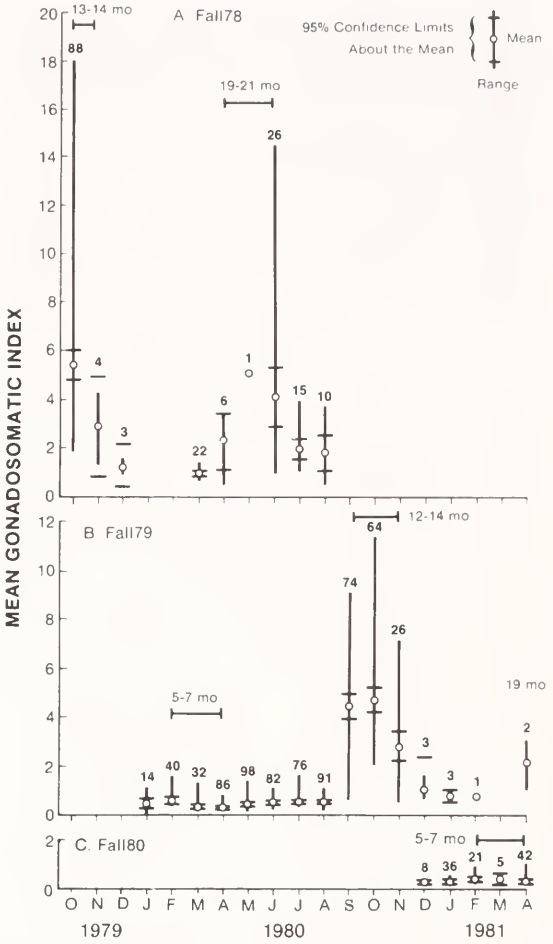


FIGURE 8.—Monthly mean gonadosomatic indices, sample sizes, ranges, and 95% confidence limits about means for the 1978 (A), 1979 (B), and 1980 (C) fall-spawned groups of *Larimus fasciatus*. Age in months is indicated for each spring and fall spawning period.

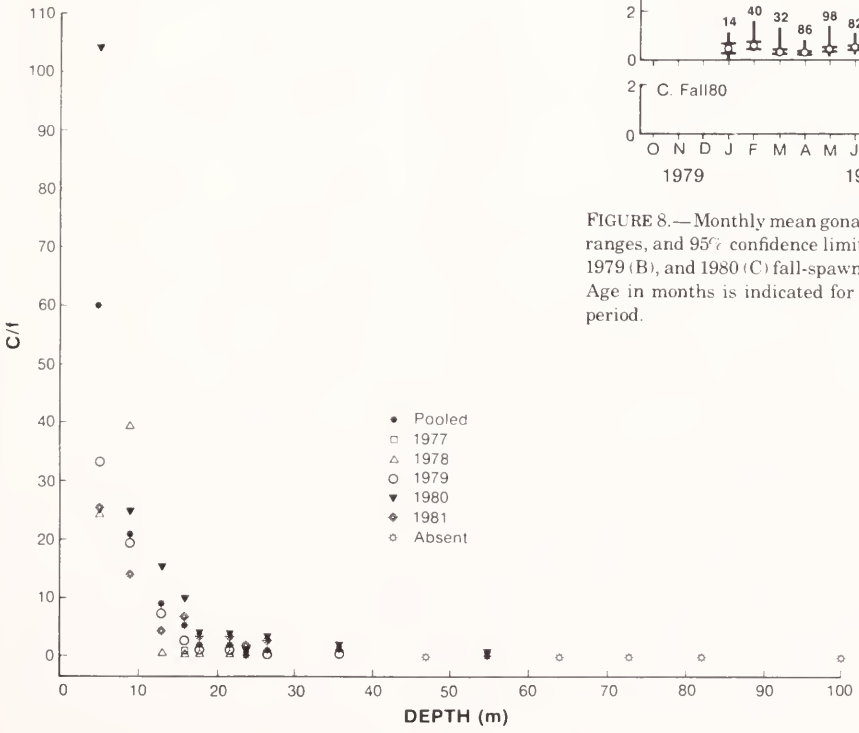


FIGURE 9.—Catch/effort (mean number of individuals per 10 min tow) by depth for *Larimus fasciatus* off Freeport, Tex., each year and pooled, October 1977-August 1981.

Fall-spawned *L. fasciatus* gradually disperse toward deeper water in late spring or summer. The distribution of young-of-the-year in May-July was similar to that in November-April (Fig. 10C). Fish approaching age I showed a clear offshore shift in distribution by August-October when abundance greatly declined at 5-13 m, became highest at 16-22 m, and was as high at 24-27 m as at 5-13 m (Fig. 10D). Fish approaching age I became distributed to 36 m, a depth they previously did not occupy, in August-October.

Larger *L. fasciatus* lead the offshore dispersal as they approach age I. Size compositions of the young-of-the-year were uniform with depth in November-April (Fig. 10A, B). They became skewed toward the right in May-July and show a gradient of increasing size with depth in August-October which suggests larger, presumably older, fish move offshore first.

Adult fall-spawned *L. fasciatus* in the northwestern Gulf occupy the 13-24 m bathymetric range from November through April while

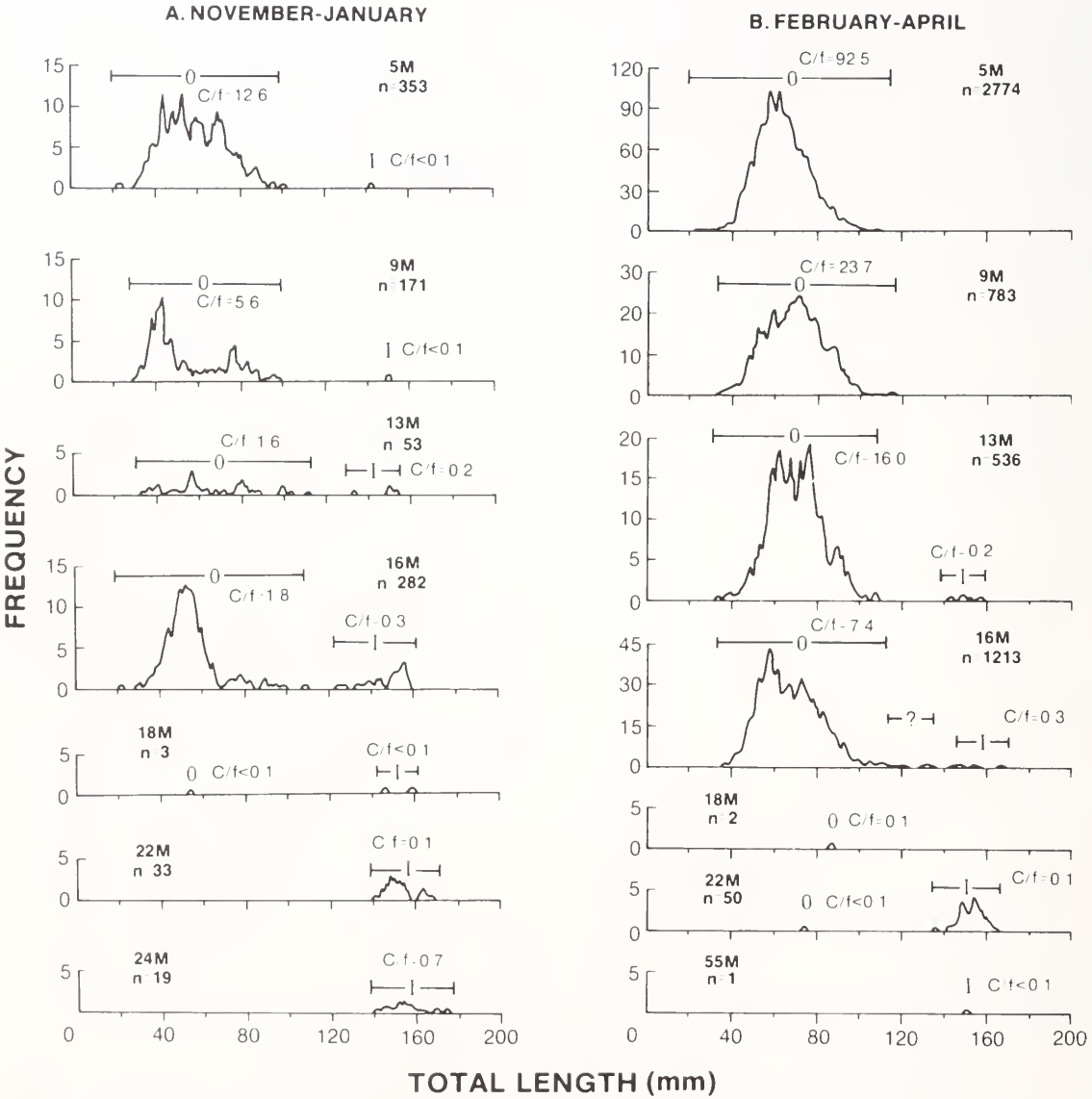


FIGURE 10.—Length frequencies and catch per effort (mean number of individuals per 10 min tow) by depth for *Larimus fasciatus* off Freeport, Tex.: A) November-January, B) February-April, C) May-July, and D) August-October. Data in each panel were pooled over the

young-of-the-year recruit inshore. Newly age I and older fish were most abundant at 13-24 m in November-April (Fig. 10A, B). Few were captured at 5-9 m then.

Age Determination and Growth

Few spawned groups of *L. fasciatus* exist at any one time in the northwestern Gulf and only one normally predominates. No more than three spawned groups were present at any time (Fig. 6). This maximum occurred only in August 1980 and June-July 1981 when spring-spawned fish recruited to join two fall-spawned groups. These were the only occasions when spring-spawned fish were clearly identifiable and their abundance was

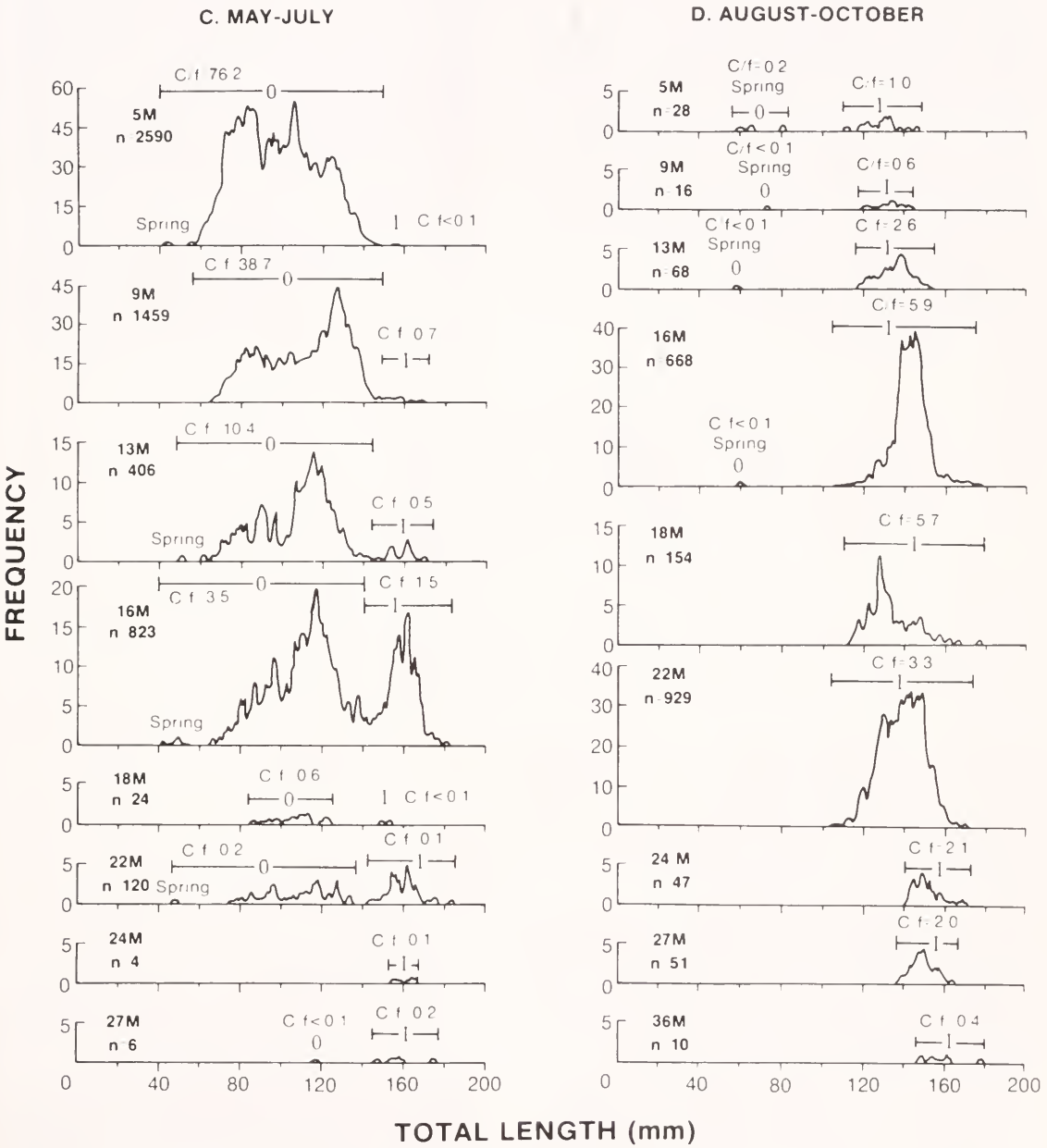


FIGURE 10.—*Continued*—period October 1977-August 1981 because length frequencies were similar each year. Designated ages are for fall-spawned fish except where noted. Age design· ·n for each cohort changed in August.

negligible even then. Although two fall-spawned groups, represented by young-of-the-year and age I fish, often were captured, only one predominated in any month except in July 1981 when fish approaching age II were abundant but disappeared thereafter. Once fully recruited, each fall-spawned group predominated to age I and then nearly disappeared as the next fall group began to recruit.

Larimus fasciatus is not abundant after 12 mo of age in the northwestern Gulf and reaches only 21-23 mo there. Fall-spawned fish were abundant after 12 mo of age (Fig. 6) only in July 1981 when they approached age II. Fall-spawned groups disappeared at 15-23 mo of age (Table 5, Fig. 6). The few spring-spawned fish captured were identifiable only until 3-5 mo of age (Table 5, Fig. 6). Fish of intermediate size between clearly defined fall-spawned groups in January and March 1980 and February 1981 could have been spring-spawned, but their identity is not clear.

Slightly larger *L. fasciatus* occur in the north central Gulf than in the northwestern area. (Harding 1949), moreover, do not and cannot resolve this situation because of the original problem: the underlying length frequency is not absolutely clear. However, the 48 mm range of sizes (139-187 mm) for fish in the north central Gulf is only slightly larger than a 35 mm range (130-165 mm) that tightly brackets most fish in the northwestern Gulf where only one fall group predominated (Fig. 11). Moreover, sizes in the north central Gulf in the period October-November were only slightly larger than and greatly overlap those for northwestern Gulf fish which were just age I. These facts suggest only one or at most two spawned groups predominated in the north central Gulf, fish just age I and age II. This interpretation is supported by our findings noted later that 1) the largest fish we captured in the northwestern Gulf (182 mm) was only 20 mo old, 2) von Bertalanffy predictions indicated mean sizes of 164 and 181 mm at age II in the northwestern Gulf depending upon variation between fall-spawned groups, and 3) the observed size range was 143-176

TABLE 5.—Periods of time, sizes, and age when spawned groups of *Larimus fasciatus* were last captured.

Spawned group	Period last captured	Size (mm TL)	Age (mo)	Comments
Fall 1976	Early December 1977	136-141	15-16	Very few ever captured
Fall 1977	Late June 1979	174	21-22	Few ever captured.
Fall 1978	Early September 1980	177	22-23	Few captured after October 1979
Fall 1979	Mid-July 1981	146-176	22-23	Few captured after October 1980, except for late July 1981.
Spring 1980	Early August 1980	58-80	3-4	Collected only in August 1980.
Fall 1980	Mid-August 1981	105-170	10-11	Still dominant in last collection.
Spring 1981	Early August 1981	58-79	3-4	Very few ever collected

Maximum and mean sizes were greater in the north central Gulf (max. = 187 mm, $\bar{x}$ = 160 mm) than in the northwestern area (max. = 173, $\bar{x}$ = 146) during the period October and November, ignoring the seven recently hatched recruits captured in the latter area (Fig. 11).

Only one or two spawned groups of *L. fasciatus* apparently predominate in the north central Gulf, probably fish that became age I and age II in the fall. We are not able to confidently identify modal groups to assign ages and, particularly, delineate sizes where age groups overlap in that area (Fig. 11), because we made only one cruise there, not the time-intensive series that permits confident age designations for the northwestern Gulf. Analyses such as linear transformation of cumulative percentage frequencies using probability paper

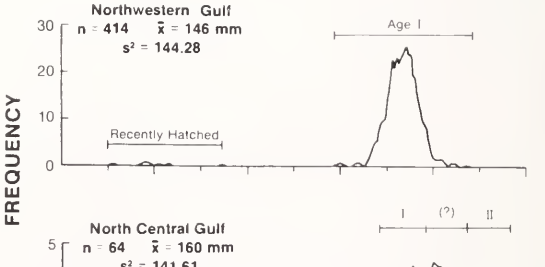


FIGURE 11.—Length frequencies and age designations for all *Larimus fasciatus* captured in the period October-November in the northwestern (1977-80) and north central (1982) Gulf of Mexico. Means, n, and s^2 ignore seven recent recruits (<70 mm) in the northwestern Gulf.

mm in July for the abundant fall 1979-spawned group as it approached age II in the northwestern Gulf. We have assumed fish in the north central Gulf were produced in the major fall-spawning period, not the minor spring one, and that differences in size compositions do not reflect only possible intra-Gulf differences and greater size at age in the north central Gulf. Comprehensive collections in that area are needed to resolve the latter assumption.

Apparent growth of *L. fasciatus* in the northwestern Gulf was similar between fall-spawned groups, mean sizes being 130-150 mm at age I and 155-180 mm at or approaching age II. Observed mean sizes and ranges at age I, based on pooled data from September and October (Table 3), were 134 mm (120-143) for fall 1976 fish, 148 mm (145-152) for fall 1977 fish, 145 mm (127-164) for fall 1978 fish, and 147 mm (118-168) for fall 1979 fish. These sizes at age I agree with quadratic regression predictions of 142 and 134 mm (Fig. 7) and von Bertalanffy model predictions of 137 and 131 mm for fall 1978 and fall 1979 fish, respectively. Observed mean size and ranges at or approaching age II (Table 3) was 159 mm (150-172) in July 1980 for fall 1978 fish, 159 mm (143-176) in July 1981 for fall 1979 fish, and 164 mm (156-177) in August-September 1980 for fall 1978 fish. These values are only slightly larger than a quadratic regression prediction of 155 mm at age II for fall 1978 fish (Fig. 7A), and are the same as or a little smaller than von Bertalanffy model predictions of 164 and 181 mm at age II for fall 1979 and fall 1978 fish, respectively.

Fitted von Bertalanffy equations based on hatching dates of 15 October for fall 1978 fish and 17 September for fall 1979 fish were

$$\text{Fall 1978: } l_t = 201\,(1 - e^{-0.003162(t-1.574)})$$

$$\text{Fall 1979: } l_t = 176\,(1 - e^{-0.003670(t+4.696)})$$

where l_t = length in millimeters, and t = time in days. Annual K values were 1.15 and 1.34, respectively. Respective annual t_0 values (0.00431 and −0.01287) were small which may reflect our forcing the curve through the origin.

Apparent growth of fall-spawned *L. fasciatus* follows an S-shaped intrayear pattern and is greatest in the spring and summer. Observed mean sizes at age showed a clearly S-shaped pattern (Fig. 7). Adjusted growth increments were small early in life (Fig. 12) and may reflect cool-water temperatures then, gear selection for larger young, or a pattern of incomplete recruitment in which smaller, younger fish gradually recruit to join early recruits that are slightly larger and older. Growth increments for age 0 fish were greatest in March-June, peaking in early June (26.7 and 32.1 mm/30 d). Growth increments decreased as maturation occurred from July through September, became small after spawning in October-January, and increased slightly in June-August as the fish approached age II.

Apparent sizes of *L. fasciatus* at or approaching age I in the northwestern Gulf reached a plateau in August-September and for many months later. Mean sizes of fish at or approaching age I remained constant then, and 99% confidence limits for observations generally remained uniform at 130-160 mm (Table 3, Fig. 6). This pattern suggests an exodus of larger individuals and/or cessation of growth coincident with gonad maturation (see section on Maturation and Spawning Periodicity).

Maximum Size, Life Span, and Mortality

The maximum size *L. fasciatus* reach in the northwestern Gulf is about 180 mm, but more typically individuals reach only 160-165 mm. The largest of the 13,676 fish we collected there was 182 mm; 99% were <161 mm and 99.5% were <164 mm (Fig. 13), these sizes being estimates of l_L.

Typical maximum life span of *L. fasciatus* appears to be only 1-2 yr in the northwestern Gulf. A value of t_L = 1-2 yr is reasonable for that area because 1) fish average 155-180 mm at or approaching age II and 130-150 mm at age I with the upper 99% confidence limits for observations at age I generally being 160-165 mm (Table 3), 2) l_L values of 161 and 164 mm predict t_L values of 1.3-2.0 yr (Table 6), 3) the largest specimen was 20 mo old when collected in May 1980, and 4) *L. fasciatus* disappeared off Texas at 15-23 mo of age (Table 5),

TABLE 6.—Values of t_L (yr) for *Larimus fasciatus* calculated from l_L (mm TL) using quadratic and von Bertalanffy equations scaled to hatching dates of 15 October for fall 1978 and 17 September for fall 1979 fish. The apex of the parabola for fall 1979 fish was 157 mm so that t_L values could not be calculated for that cohort.

Spawned group	l_L	t_L calculated from: Quadratic regression	t_L calculated from: von Bertalanffy equation
Fall 1978	161	1.33	1.40
Fall 1978	164	1.44	1.47
Fall 1979	161	—	1.83
Fall 1979	164	—	1.99

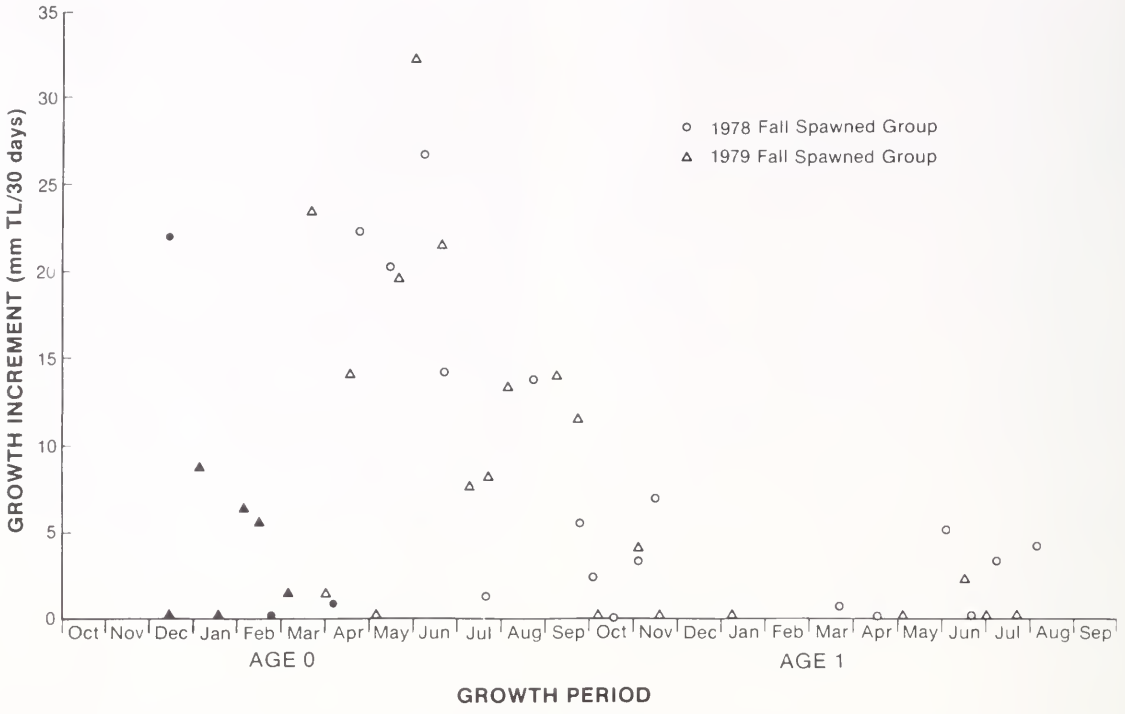


FIGURE 12.—Monthly growth increments for 1978 and 1979 fall-spawned *Larimus fasciatus*. Unadjusted growth increments (Table 3) were converted to growth/30 d, omitting collections of five or less fish. Negative growth is rounded to zero. Values denoted by darkened symbols may reflect incomplete recruitment, gear selection for larger young, or cool-water temperatures early in life.

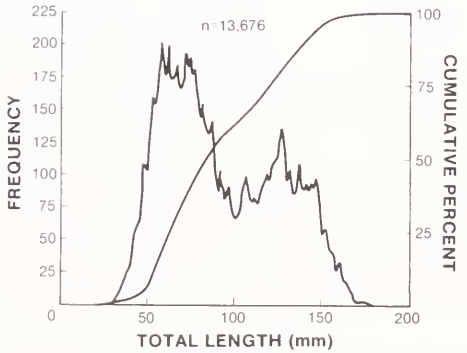


FIGURE 13.—Length frequencies and cumulative percentage of all *Larimus fasciatus* collected off Freeport, Tex., October 1977-August 1981.

and few ever approached age II except in July 1981 as previously noted. The latter instance suggests larger, older specimens of *L. fasciatus* may occur elsewhere; if so, our estimate of t_L may be too low for a stock that also ranges outside the northwestern Gulf.

Larimus fasciatus from fall-spawned groups have an *apparent* total annual mortality rate of 90-100% in the northwestern Gulf, mean time and cohort-specific values being 92-100%. Time-specific values of $1 - S$ were 100% in 17 of the 38 mo in which fish were collected (Fig. 6) because only one fall-spawned group was present and N_t was zero in the ratio N_t/N_0. Time-specific mortality estimates for the 18 remaining months gave ratios whose percentage values ranged from 89.93 to 99.96%; 14 exceeded 94%. Pooled estimates using Heincke's procedure were 97.18-100% depending on the spawned groups compared (Table 7). By pooling the Heincke numerators and denominators from each comparison an average time-specific $1 - S$ was 98.24%, or 96.86% if data from July 1981 are included. Cohort-specific values of $1 - S$ were 100% in 12 of the 24 mo for fall 1978 fish and in 2 of the 12 mo for fall 1979 fish because N_t was zero. Cohort-specific estimates for the remaining 6 mo in the fall 1978 cohort ranged from 97.83 to 99.81% except in June and July 1980 when estimates were 64.84 and 55.05%. Estimates for the remaining 7 mo in fall 1979 cohort ranged

TABLE 7.—Pooled time-specific and cohort-specific mortality estimates for *Larimus fasciatus* using Heincke's procedure (Ricker 1975). Symbols represent: N_0, youngest spawned group in Heincke's estimate; S, annual survival rate; $1 - S$, annual mortality rate; and Z, instantaneous mortality rate.

N_0	S	$1 - S$	Z
Time-specific			
Fall 1977	0	1.0000	∞
Fall 1978	0.0083	0.9917	4.79
Fall 1979	0.0180	0.9820	4.02
Fall 1980	0.0282	0.9718	3.57
Heincke's Pooled	0.0176	0.9824	4.04
Cohort-specific			
Fall 1978	0.0810	0.9190	2.51
Fall 1979	0.0317	0.9683	3.45

from 94.44 to 99.84% except in July 1981 when it was 74.43%. The low estimates in June and July reflect the unusual instance previously noted of immigration by fish approaching age II. Pooled cohort-specific estimates of $1 - S$ using Heincke's procedure were 91.90% for fall 1978 fish and 96.83% for fall 1979 fish (Table 7).

Sex Ratio and Fecundity

Male and female *L. fasciatus* appear equally abundant. The observed sex ratio of 1.00 males to 1.02 females among 2,502 mature or maturing fish examined in the period October 1979-April 1981 did not differ significantly from 1:1 ($\chi^2 = 0.19$; df = 1; $\alpha = 0.05$).

Mean fecundity of *L. fasciatus* in Gravid and Ripe stages was 70,453 eggs. Observed fecundity ranged from 32,333 to 143,800 eggs/female. Untransformed and log-log transformed linear regressions of fecundity on total length and total weight and related statistics are presented in Table 8; the former regression is depicted in Figure 14. The untransformed regression is a better fit ($100r^2$ being 29.7 vs. 27.1 for length and 35.1 vs. 28.4 for weight), but the transformed regression permits extrapolation over a broader size range. Fecundity statistics were based only on Gravid and Ripe fish, because residual plots for untransformed data indicated a relationship between fecundity and maturity stage (Fig. 15): maximum fecundity occurred in the Gravid and Ripe stages.

Weight, Girth, and Length Relationships

Total weight-total length, girth-total length, and standard length-total length regressions are presented in Table 8 with related statistics. Total length-total weight regressions for males and females were not significantly different in slope ($F = 0.35$, df = 1, 1936, $\alpha = 0.05$) or in elevation ($F = 1.62$, df = 1, 1936, $\alpha = 0.05$) so one pooled equation is presented for them. Total length-total weight regressions for males and females pooled and for immatures, males, and females pooled were significantly different in slope ($F = 44.87$, df = 1, 4808, $\alpha = 0.05$), but one equation that pools all sizes may be useful and is presented. Calculated slopes significantly exceeded $\beta = 3.0$ at $\alpha = 0.05$ for both length-weight relationships (males and females pooled, $t = 53.06$; immatures, males, and females pooled, $t = 60.41$).

DISCUSSION

Spawning Periodicity

We found that the broad April to November period within which *L. fasciatus* spawns generally agrees with many studies, including Hildebrand and Cable (1934), Miller (1965), Christmas and Waller (1973), and Ross (1978). However, our interpretation is new that little or no spawning oc-

TABLE 8.—Fecundity, total weight-total length, girth-total length, and standard length-total length regressions for *Larimus fasciatus* with supporting statistics. All regressions were significant at $\alpha = 0.01$; r is from Ricker's (1973) GM regression. Measures are grams and millimeters. See Methods for symbols.

Equation	n	TL range	$100r^2$	Residual MS	Corrected total SSx	Corrected total SSy	$\bar{x}$	$\bar{y}$	GM r
FEC = −295.307 + 2,498.36 TL	40	136-163	29.7	$4,966 \times 10^5$	1,280.00	2.686×10^7	146.4	70,453	4,581.2
$\log_{10}$FEC = −5.5049 + 4.7689 $\log_{10}$TL	40	136-163	27.1	0.0178	0.0111	0.9280	2.17	4.82	9.1573
FEC = −32,999 + 2,223.57 TW	40	136-163	35.1	4.588×10^5	1,906.00	2.686×10^7	46.5	70,453	3,753.7
$\log_{10}$FEC = −2.6564 + 1.3013 $\log_{10}$TW	40	136-163	28.4	0.0175	0.1554	0.9280	1.67	4.82	2.4435
$\log_{10}$ TW = −5.5981 + 3.3481 $\log_{10}$ TL (males + females)	1,938	52-179	99.3	0.0015	34.42	388.67	2.03	1.20	3.3605
$\log_{10}$ TW = −5.4761 + 3.2883 $\log_{10}$ TL (males + females + immatures)	2,874	22-179	99.4	0.0025	108.91	1,184.74	1.92	0.84	3.2983
G = −1.21 + 0.77 TL	2,871	22-179	99.2	7.75	2,628,914 (G)		92.09	69.35	0.77
TL = 2.35 + 1.29 G	2,871	22-179	99.2	13.09	4,439,633 (TL)		69.35	92.09	1.30
SL = −5.63 + 0.83 TL	2,875	22-179	99.8	2.23	3,066,599 (SL)		92.08	70.76	0.83
TL = 6.96 + 1.20 SL	2,875	22-179	99.8	3.24	4,446,964 (TL)		70.76	92.08	1.20

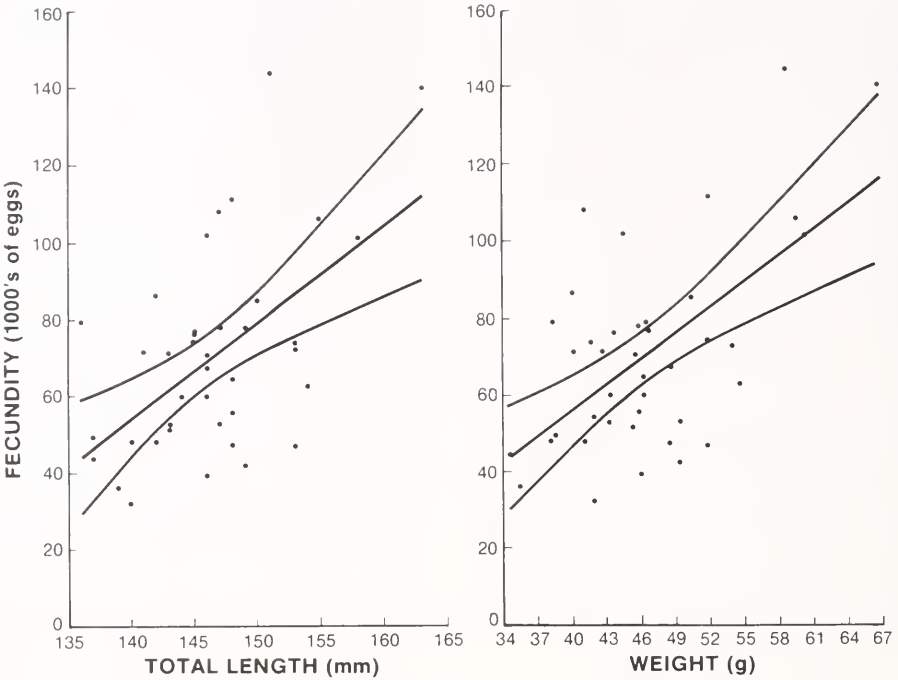


FIGURE 14.—Regressions of fecundity on total length and total weight with 95% confidence limits for $\bar{y}_x$ for *Larimus fasciatus*.

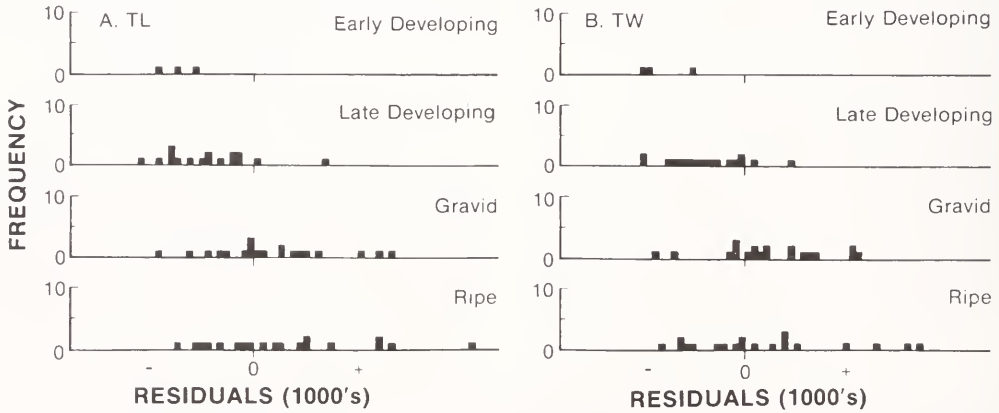


FIGURE 15.—Residual plots of maturity stages of *Larimus fasciatus* for relationship between fecundity and total length (A) and total weight (B) regressions.

curs in July and August and that spawning primarily occurs in two discrete periods, a major fall peak in September-November and a minor spring peak in April-June. The existence of distinct spring and fall spawning periods is supported by 1) Hoese's (1965) collection of larval fish only in June (11.5-25 mm SL modal length) and October (14-39 mm SL modal length) off Port Aransas, Tex., 2) Ross's (1978) collection off North Carolina of presumably fall-spawned fish in February (79 mm modal TL = 60 mm SL) and what must be spring-spawned fish in July (75 mm modal TL = 57 mm SL), 3) Powles's (1980) collections of larval fish in the periods April-May and August-September but not in June-July between Cape Canaveral and Cape Fear, and 4) collections of

larval fish in the periods April-June and August-October between Cape Lookout and Chesapeake Bay (Berrien pers. commun. footnote 7 in Powles 1980). This bimodal pattern, moreover, is similar to findings of distinct spring- and fall-spawning periods in other Gulf fishes such as *Cynoscion arenarius* (Shlossman and Chittenden 1981), *C. nothus* (DeVries and Chittenden 1982), and *Peprilus burti* (Murphy 1981). Murphy and Chittenden[7] integrated biological findings with hydrographic data of Kelly and Randall[8] and suggested hydrographic reasons for this pattern in *P. burti* and *C. nothus*, which probably apply also to *L. fasciatus* and many other species: spawning is timed to coincide with the periodicity of downcoast alongshore currents (toward Mexico) and onshore Ekman transport at the surface. These phenomena probably transport pelagic eggs and larvae inshore and "downstream" to nurseries in the northwestern Gulf from spawning grounds located "upstream" in or toward the north central Gulf. Current transport mechanisms reverse in the summer (a variable period but about mid-June-early August) and would carry pelagic eggs and larvae offshore, which presumably is unfavorable to survival in many species, or toward the north central Gulf. If spawning is substantial, and successful, during summer, our length-frequency data and those for the other species cited indicate summer-spawned individuals do not subsequently appear in the northwestern Gulf. Presumably, their existence would be reflected as unimodal, or at least not clearly bimodal, length frequencies when adequate data become available for the north central Gulf.

Our finding that the few spring-spawned fish disappeared after August at 3-5 mo of age agrees with Hildebrand and Cable (1934) who collected what must have been spring-spawned fish in July ($\bar{x}$ = 34 mm, range 3-70 mm ?L) and August ($\bar{x}$ = 54 mm, range 3-77 mm ?L) off North Carolina and noted they were absent later. Because the magnitude of spring spawning appears so small, for practical stock assessment purposes, our data could just as well be interpreted as one long period with little or no spawning from April to August. It seems more meaningful, however, to regard the spawning of *L. fasciatus* as occurring during two discrete periods because Murphy and Chittenden (footnote 7) suggested a hydrographic basis for that pattern.

Our findings are new that fall-spawned groups spawn in both spring and fall periods and that spring spawning is the product of fish about 20 mo old. Shlossman and Chittenden (1981) noted that temporal isolation of spawned groups in *C. arenarius* implied reproductive isolation and might indicate separate populations. The temporally separate spawned groups in *L. fasciatus*, however, are not reproductively isolated and apparently do not form separate populations because the same spawned group spawns in both periods. This simplifies management, because separate data may not be necessary for both spawning periods, especially considering that one is very small.

Shlossman and Chittenden (1981) and DeVries and Chittenden (1982) noted that the existence of two spawned groups in *C. arenarius* and *C. nothus* might buffer population stability as a multiple year class structure does in longer lived species. In *L. fasciatus*, however, the contribution that spring-spawned groups make to total population size is probably too small to buffer fluctuations at any reasonably "normal" stock size.

Bathymetric Distribution

Larimus fasciatus primarily is restricted to the inner continental shelf. Our finding, that they range from < 5 to 55 m but are most common from 5 to 16 m, agrees with Hildebrand (1954), Miller (1965), Burns (1970), Milstein and Thomas (1976), and Wenner et al. (1979a, b). Franks et al. (1972) captured most specimens in 37-55 m off Mississippi which supports Chittenden and McEachran's (1976) suggestion that the white shrimp community, of which *L. fasciatus* is a member, penetrates into deeper water in the north central Gulf than it does in the northwestern area. However, Springer and Bullis (1956) collected fish at 106 m off both Mississippi and Texas.

Age Determination and Growth

Little literature exists on age determination and growth in *L. fasciatus*. We determined age by length-frequency analysis because our data came from a long-term set of cruises close enough together in time that modes were easily followed.

[7]Murphy, M. D., and M. E. Chittenden, Jr. Unpubl. manuscr. Reproduction, movements, and population dynamics of the gulf butterfish, *Peprilus burti*. 66 p. Marine Research Laboratory, Florida Department of Natural Resources, 100 Eighth Avenue, S.E., St. Petersburg, FL 33701.

[8]Kelley, F. J., Jr., and R. E. Randall. 1980. Physical oceanography. *In* R. W. Hann, Jr. and R. E. Randall (editors), Evaluation of brine disposal from the Bryan Mound site of the Strategic Petroleum Reserve Program, p. (1-1)-(1-93). National Technical Information Service, Springfield, VA 22150 (DOE/P010114-1).

Moreover, we observed so little overlap of lengths from different spawned groups that few individuals could have been incorrectly aged and basic conclusions on apparent growth and mortality would be little affected by such error. As Geoghegan and Chittenden (1982) found for *Stenotomus caprinus*, length-frequency analysis can be a superior method to age *L. fasciatus* because 1) little spawning occurs in other than one major discrete period each year, 2) length frequencies within spawned groups are reasonably described by a normal distribution, 3) growth of large and small fish within a spawned group appears uniform since the variance was generally constant between cruises, and 4) life span is short so age determination need be applied only to a few ages, the ideal situation for using length frequencies (Lagler 1956; Tesch 1971). Ross (1978) successfully used scales and otoliths to determine age of North Carolina fish, but we were not able to do so in limited trials and did not pursue these methods further because it seemed unnecessary.

Larimus fasciatus reach slightly larger sizes at age off North Carolina than apparent sizes we found in the northwestern Gulf. Von Bertalanffy predictions of size at age off North Carolina (Ross 1978) were 153 mm (121.3 mm SL) at age I, 188 mm (151.1 mm SL) at age II, and 209 mm (168.0 mm SL) at age III compared with quadratic and von Bertalanffy predictions of 130-150 mm at age I and 155-180 mm at or approaching age II for the northwestern Gulf. Our finding that growth is greatest in the spring and summer agrees with Ross (1978).

Maximum Size, Life Span, and Mortality

The largest *L. fasciatus* we found in the northwestern Gulf (182 mm) is smaller than most maximum sizes reported from the north central Gulf (Louisiana: 208 mm by Hildebrand 1954, 195 mm ?L by Dunham 1972, and Mississippi: 202 mm by Franks et al. 1972, 189 mm by Christmas and Waller 1973, 187 mm in our data), and much smaller than those reported from the Atlantic coast of the United States (New York to Florida: 220 mm by Wilk and Silverman 1976, Chesapeake Bay: 215 mm ?L by Hildebrand and Schroeder 1928, off North Carolina: 205 mm ?L by Hildebrand and Schroeder 1928, 206 mm ?L by Hildebrand and Cable 1934, and 225 mm = 182 mm SL by Ross 1978). The largest record is a 271 mm specimen collected off Mississippi (Franks 1970). The larger size off the Atlantic coast of the United States may reflect greater longevity there, especially from about Cape Lookout or Cape Hatteras north where zoogeographic change in population dynamics may occur (White and Chittenden 1977). Ross (1978) collected age III fish off North Carolina, but the oldest fish we collected only approached age II.

The appearance of larger *L. fasciatus* in the north central Gulf than in the northwestern area follows a pattern apparent in a variety of species (Murphy and Chittenden footnote 7) including *C. nothus, P. burti, S. caprinus, Brevoortia patronus*, and *Micropogonias undulatus*. These authors suggested this could reflect 1) small but fundamental percentage composition and population dynamics differences between these areas, 2) greater biomass at all ages in the north central Gulf, not necessarily population dynamics differences, so that greater numbers of large fish might be captured there even if percentage compositions did not vary, and/or 3) probable permanent emigration from the northwestern to the north central Gulf by larger, older, spawning or postspawning fish as they approach age I. They suggested the last explanation applied to *C. nothus, P. burti*, and probably other fishes, and that it would be manifested as between area population dynamics differences. The following findings also suggest that *L. fasciatus* too more or less permanently emigrates from the northwestern to the north central Gulf as spawning and age I approaches 1) the plateaus in length formed in August and seeming cessation of somatic growth in later stages of gonad development, and 2) the appearance in the northwestern Gulf in July 1981 of an abundant fall-spawned group approaching age II. This older spawned group, and parallel spawned groups in other years, was absent or rare in all other months even though our data were based on 71 cruises and 3,390 tows over 4 yr.

Because larger, older *L. fasciatus* probably emigrate to the north central Gulf, the typical maximum life span of 1-2 yr we observed for the northwestern area may be a little low for a stock that ranges over both areas. With the exception of the very large specimen that Franks (1970) found, the largest individuals reported from the north central Gulf are only 189-208 mm as noted. This is not much larger than our largest specimen (182 mm) from the northwestern area, which was 20 mo old. Moreover, these maximums are similar to von Bertalanffy predictions of mean sizes at age II (165-185 mm) or at age III (175-195 mm) that we found, and sizes of 188 and 204 mm Ross (1978)

found at ages II and III, respectively. Therefore, a t_L value of 2-3 yr may be realistic for a stock that ranges over the north central and northwestern Gulf. We assume in suggesting this, that differences in size compositions do not reflect only possible intra-Gulf growth differences and greater size at age in the north central Gulf.

The mean *apparent* time-specific and cohort-specific total annual mortality rates we observed for the northwestern Gulf (92-100%) agree with theoretical estimates (Royce 1972:238) of 90-100% if maximum life span typically is only 1-2 yr as we found for that area. Because larger, older *L. fasciatus* probably emigrate to the north central Gulf, our observed mortality estimates are probably too high for a stock that ranges over both areas. Theoretical values of 80-90% based on a 2-3 yr typical maximum life span may be more realistic, a magnitude which agrees with the lowest values tenable for other sympatric species such as *C. arenarius* (Shlossman and Chittenden 1981), *C. nothus* (DeVries and Chittenden 1982), *S. caprinus* (Geoghegan and Chittenden 1982), and *P. burti* (Murphy 1981). Even values of 80-90% are higher than the three lowest mortality rates we found for the northwestern Gulf (55-74%) and rates of 57 and 81% that Ross (1978) reported off North Carolina; the latter range of values is theoretically appropriate as an average over life spans of 3-5 yr, although present data suggest 4-5 yr is too large a value of t_L for the Gulf.

General

Population dynamics of *L. fasciatus* are similar to those reported from the northwestern Gulf for *M. undulatus* (White and Chittenden 1977), *C. arenarius* (Shlossman and Chittenden 1981), *C. nothus* (DeVries and Chittenden 1982), *S. caprinus* (Geoghegan and Chittenden 1982), *P. burti* (Murphy 1981; Murphy and Chittenden footnote 7), and in *Centropristis philadelphica* ignoring its hermaphroditism (Ross and Chittenden[9]). Our findings support the suggestions that 1) groundfishes of the white and brown shrimp communities in the Gulf have evolved a common pattern of population dynamics characterized by small size, early age at maturity, short life spans, high mortality rates, and rapid turnover of biomass (Chittenden and McEachran 1976; Chittenden 1977), and 2) more or less permanent spawning or post-spawning emigration may occur from the northwestern Gulf to the north central area as fish approach age I (Murphy and Chittenden footnote 7). Because typical maximum life spans may be closer to 2-3 yr than 1-2 yr, these fishes may be a little more sensitive to growth overfishing than Chittenden's (1977) simulations, based on a 2 yr life span, suggest for *M. undulatus*.

[9]Ross, J. L., and M. E. Chittenden, Jr. Unpubl. manuscr. Reproduction, movements, and population dynamics of the rock sea bass, *Centropristis philadelphica*, in the northwestern Gulf of Mexico. 50 p. North Carolina Division of Marine Fisheries, North Carolina Marine Resources Center, Manteo, NC 27954.

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IMPLICATIONS OF INVESTING UNDER DIFFERENT ECONOMIC CONDITIONS ON THE PROFITABILITY OF GULF OF MEXICO SHRIMP VESSELS OPERATING OUT OF TEXAS[1]

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ABSTRACT

Due to the inflationary trend in recent years coupled with fluctuating shrimp prices, the shrimp business has become a highly uncertain undertaking. The financial performance of a sample of the Gulf of Mexico shrimping fleet, operating out of the Texas coast, was examined over a 10-year period (1971-80). The results indicate that investments made in the early part of the 1970's performed better than those made in the latter part. Periods of low inflationary levels appeared to be more favorable to investments in the shrimp fishery than periods of high inflationary levels.

In terms of economic profits, steel vessels generally did better than wooden ones. Medium-sized vessels (18.6-20.0 m in overall length) were the most efficient vessels to operate in the Gulf of Mexico.

The Gulf of Mexico supplies a major share of the shrimp landed by commercial shrimp producers in the United States. From 1977 to 1981, Gulf shrimp landings accounted for 62% of the U.S. total. In 1981, 161 million kg of commercial shrimp valued at $463.4 million are landed in the United States. The Gulf of Mexico accounted for 76% of these landings and 87% of the value. Although the Gulf shrimp fishery is the most valuable in the United States, individual harvesters within the industry are not without their financial problems.

Of late, the high variability in shrimp landings and prices has created short-run uncertainty among shrimp producers (Caillouet and Patella 1978; Warren and Griffin 1980). Coupled with this, operating costs have been significantly increasing over the years, to the extent that, it has become quite difficult for fishermen to stay in business (Griffin et al. 1978).

There have been several costs and returns and/or investment analyses conducted on fishing vessels in recent years (Gates and D'Eugenio 1975; Noetzel 1977; Jones et al. 1979; Roberts and Saas 1979; Prochaska and Cato 1981); however, none have been concerned with the effect of inflation on investing in a fishing vessel. This paper uses the period 1971-80 to draw conclusions about the effect of low, medium, and high inflationary periods on return to investment. The study further examines the implication of unstable shrimp prices and rising costs of operations on the profitability of the shrimp industry in the Gulf of Mexico. Finally, the performance of wooden and steel hulled vessels in various size classes is compared.

METHODS

Data Description

The data used in this study are an accumulation of 5 yr of data collection, which have been reported in previous publications (U.S. Department of Commerce 1971-1980, 1971-1981; Griffin et al. 1974, 1976; Griffin and Nichols 1976; Warren and Griffin 1978). Although data were collected for other Gulf states, only data for vessels operating out of Texas are used in this study, since it is the only state for which data were available for all 5 yr that data were collected.

In the original studies, data were collected by personal interview in ports from Galveston to Port Isabel for 1971, 1973, 1974, 1975, and 1977 and estimated for the remaining years. Additional information was obtained from officials of various lending institutions which engage in shrimp vessel financing, from boat builders, and from the National Marine Fisheries Service.

Cost

The variable cost items for which data were gathered included ice, fuel, nets, supplies, repairs

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and maintenance, crew shares, payroll taxes, and packing charges. Fuel consumption by vessel class, for which primary data were unavailable, was estimated according to the following relationship:

$$Y_i = \frac{\Sigma \left(X_{ij} N_{ij}\right)}{\Sigma N_{ij}}$$

where Y_i = estimated number of gallons (1 gal = 3.79 l) used per year by vessel class i.
X_{ij} = actual number of gallons (1 gal = 3.79 l) used in year j by vessel class i.
N_{ij} = number of vessels in vessel class i in year j.

The nets, supplies, and repairs and maintenance variables were similarly adjusted like Y_i to account for unequal numbers of vessels in the sampling years. These variables were deflated into real terms, using the industrial price index, and the weighted average was determined. From the weighted average of the 5 yr for which data were available, adjusted nominal values were determined for the other years. Crew shares were estimated at 33% of value of catch. Packing charge was set at $0.10 per pound (0.454 kg) of shrimp landings.

Fixed costs include insurance, depreciation, interest, and opportunity cost. Reported data were used to determine fixed charges for overhead items, while charges relating directly to investment—depreciation, insurance, and interest—were calculated in nominal dollars for new vessels. Overhead values for years that data were not available were calculated using the industrial price index in the same manner as with variable cost.

Insurance charges were set at 4% of new vessel cost. The standard straight-line formula was used to determine depreciation. In this study the terminal value of the vessel was calculated in two ways: 1) at 100% of original cost, and 2) at salvage value at the end of 1980. The market rates, which prevailed over the years, were employed in deriving the cost and returns budget.

Revenue

Catch relationships were estimated for years for which no data were available by utilizing the following formulation:

$$EC_{ij} = WC_i \, (TL/TL_j)$$

where $WC_i = \frac{\sum_j N_{ij} \cdot RC_{ij}}{\sum_j N_{ij}}$ and

$RC_{ij} = AC_{ij}/(TL_i/TL)$.
EC_{ij} = estimated catch by vessel class i for year j where j = 1971, 1972, ..., 1980.
TL_j = Texas landings for year j, = 1971, 1972, ..., 1980.
TL = average Texas landings for the 1971-80 period.
RC_{ij} = real catch of vessel class i in year j for the 5 yr vessel data were available.
AC_{ij} = actual catch of vessel class i for year j for the 5 yr vessel data were available.
N_{ij} = number of vessels of class i for year j for the 5 yr vessel data were available.

Exvessel[3] prices per pound of shrimp were adjusted according to the formula given below using the average value from the National Marine Fisheries Service data for Texas and that from the survey to generate exvessel prices for those 5 yr that data were not collected.

$$AP_{ij} = (A_i - B) + TP_j$$

where AP_{ij} = adjusted exvessel price per pound (0.454 kg) of shrimp for vessel i in year j.
TP_j = Texas prices as reported by the National Marine Fisheries Service for year j, where j = 1971, ..., 1980.
AI = average exvessel price per pound (0.454 kg) of shrimp for vessel i over the 5 yr data were available.
B = average exvessel price per pound (0.454 kg) of shrimp

[3]It is recognized that exvessel price of shrimp is greatly influenced by seasonal fluctuation in local supply as well as the size composition of catch (Caillouet and Patella 1981). However, this study implicitly accounts for such trends by employing primary data collected for 1971, 1973, 1974, 1975, and 1977. Therefore, the price represents a weighted average between the various shrimp sizes.

reported by the National Marine Fisheries Service.

Analyses

A computer program referred to as a budget generator was devised to organize and assimilate the data for various analyses. The program allowed data reports to be produced according to the desired vessel classifications, interest rate, percent financed, number of years financed, number of loan payments per year, depreciation method, crew share agreement, rate of packing charges, payroll tax rate, discount rate, and planning horizon. The program reported results in the form of annual costs and returns budgets and projected cash flow budgets.

The following analysis first examines a detailed annual income and cash flow statement for a vessel purchased new in 1971. This detailed annual income and cash flow is then compared for the same vessel operated under identical conditions, but purchased in 1977 and 1979. Next, six different types of vessels (three wood and three steel; Table 1) are compared by examining their net returns during the three different periods of investment. Finally, investment performance is analyzed through net present value (NPV).

In all the above analyses three investment periods (1971, 1977, 1979) are considered. A given vessel is assumed to be operated under identical conditions regardless of the investment period. Since the actual sale price of the vessel at the end of the investment period is determined by the economic environment at that time, a comparison is made between the effects of selling the vessel at a salvage value of 35 and 100% of the original price.

TABLE 1.—Number and types of Gulf of Mexico shrimp vessels surveyed operating out of Texas ports.

Vessel type[1]	1971	1973	1974	1975	1977
Wooden, 17.1-18.5 m	1	1	3	3	1
Wooden, 18.6-20.0 m	1	9	8	4	1
Wooden, 20.1-21.5 m	1	26	24	26	4
Steel, 18.6-20.0 m	0	14	19	21	17
Steel, 20.1-21.5 m	3	13	41	41	18
Steel 21.6-23.0 m	2	4	10	5	2

[1]Coast Guard registered length.

RESULTS

Detailed Annual Budgets and Cash Flow

Tables 2 and 3 represent detailed annual income and cash flow budgets for a newly financed 1971 steel vessel, 20.1-21.5 m in overall length. Over the 10-yr study period, annual revenue doubled although it decreased by 18.9% in 1974 and by 7.4% in 1980. The decrease could be attributed, in part, to the decrease in exvessel price for shrimp from $4.23/kg to $3.62 in 1974 and from $8.38 to $7.06 in 1980. Another contributing factor was poor landings recorded in those periods (Fig. 1).

TABLE 2.—Annual income statement for a steel vessel, 20.1-21.5 m. long, operating out of Texas ports, 1971 to 1980.

	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980[1]	1980[2]
Revenues	78,100	95,798	99,903	80,978	99,498	132,799	142,272	155,733	164,638	152,479	152,479
Variable costs											
Ice	1,502	2,062	2,052	1,656	1,903	2,169	2,859	4,371	4,002	4,105	4,105
Fuel	6,515	6,515	9,523	20,549	21,551	22,052	23,055	25,060	40,095	47,613	47,613
Nets, supplies, groceries	8,348	8,186	9,220	11,263	12,559	13,357	14,287	15,334	17,319	20,028	20,028
Repair and maintenance	5,563	5,455	6,144	7,505	8,369	8,901	9,521	10,219	11,541	13,347	13,347
Crew shares	25,773	31,613	32,968	26,723	32,834	43,824	46,950	51,392	54,331	50,318	50,318
Packing	2,580	2,899	2,440	2,679	3,003	3,178	3,891	3,586	2,873	3,143	3,143
Total	50,281	56,730	62,347	70,375	80,219	93,481	100,563	109,962	130,161	138,554	138,554
Fixed costs											
Depreciation	9,084	9,084	9,084	9,084	9,084	9,084	9,084	9,084	9,084	9,084	9,084
Insurance	5,191	5,191	5,191	5,191	5,191	5,191	5,191	5,191	5,191	5,191	5,191
Interest (vessel loan)[3]	6,910	6,412	5,879	5,308	4,697	4,042	3,340	2,589	1,785	923	923
Overhead	3,423	3,357	3,781	4,619	5,150	5,477	5,859	6,288	7,102	8,213	8,213
Total	24,608	24,044	23,935	24,202	24,122	23,794	23,474	23,152	23,162	23,411	23,411
Total operating costs	74,889	80,774	86,282	94,576	104,341	117,275	124,037	133,114	153,323	161,965	161,965
Net revenue	3,211	15,024	13,621	−13,599	−4,843	15,524	18,235	22,619	11,315	−9,487	−9,487
Net return after tax[4]	266	9,405	8,158	−17,106	−8,672	8,916	11,140	14,377	5,100	−15,383	45,273
Current equity	33,611	39,101	42,531	28,724	19,718	32,096	41,324	43,328	39,530	43,282	73,609
Required return to equity	3,946	4,391	4,636	3,326	2,686	4,250	4,992	5,273	5,190	5,376	9,142
Economic profit	−3,680	5,014	3,522	−20,433	−11,357	4,667	6,148	9,104	−90	−20,758	36,130

[1]Vessel sold for salvage value.
[2]Vessel sold for original purchase price.
[3]Vessel was purchased for $129,767; 75% financed at 7.1% interest.
[4]The difference between net revenue and net return after taxes includes owner's salary, social security tax for owner, and income tax.

TABLE 3.—Annual cash flow statement for a steel vessel, 20.1-21.5 m. long, operating out of Texas ports, 1971 to 1980.

	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980[1]	1980[2]
Revenues											
Beginning cash balance	0	2,339	13,319	22,518	5,883	0	5,192	14,835	26,964	29,011	29,011
Receipt from shrimp	78,100	95,798	99,903	80,978	99,498	132,799	142,272	155,733	164,638	152,479	152,479
Capital receipts	0	0	0	0	0	0	0	0	0	38,930	129,767
Total cash inflow	78,100	98,137	113,222	103,496	105,381	132,799	147,463	170,568	191,602	220,420	311,257
Operating expenses											
Fuel	6,515	6,515	9,523	20,549	21,551	22,052	23,055	25,060	40,095	47,613	47,613
Other variable expenses	43,766	50,216	52,824	49,826	58,669	71,429	77,507	84,901	90,065	90,942	90,942
Fixed cash expenses	11,559	14,165	14,436	13,317	14,169	20,205	18,145	19,722	18,510	19,300	49,481
Total	61,840	70,896	76,783	83,692	94,389	113,686	118,707	129,683	148,670	157,855	188,036
Long- and short-term debt											
Long-term debt (principle)	7,011	7,509	8,042	8,613	9,224	9,879	10,581	11,332	12,136	12,998	12,998
Long-term debt (interest)	6,910	6,412	5,879	5,308	4,697	4,042	3,340	2,589	1,785	923	923
Total cash outflow	75,761	84,817	90,704	97,613	108,310	127,607	132,628	143,604	162,591	171,776	201,957
Cash situation											
Net cash balance	2,339	10,980	9,199	−16,635	−8,812	8,121	9,643	12,129	2,047	19,633	80,288
Cash available	2,339	13,320	22,518	5,883	−2,929	5,192	14,835	26,964	29,011	48,644	109,300
Ending cash balance	2,339	13,320	22,518	5,883	0	5,192	14,835	26,964	29,011	48,644	109,300
Net present value 0.1174										22,572	42,560

[1]Vessel sold for salvage value
[2]Vessel sold for original price.

FIGURE 1.—Total Texas landings and value of landings for a typical steel vessel 20.1 to 21.5 m long by year.

There was no significant variation in total fixed costs during the 10 yr for two reasons: Depreciation and insurance charges were set at fixed levels, but while overhead charges increased gradually over the years, interest payments on vessel loans decreased by about the same margin. The highest total fixed cost incurred was $24,608 in 1971 and the lowest was $23,152 in 1978 (Table 2).

Total variable costs, on the other hand, increased by 175.5% over the 10-yr period. The highest increase of 18.4% occurred in 1979, and it was in direct response to an increase in fuel charges from $25,060 in 1978 to $40,095 in 1979 (Table 3). Expenditure on fuel showed a tremendous increase in 1974 by 115.7%; both of these increases were due to the sharp rise in fuel prices (Fig. 2).

In response to an increase in variable costs and relatively constant fixed costs, total operating

FIGURE 2.—Price of fuel and shrimp for a steel vessel 20.1 to 21.5 m long by year operating out of Texas ports.

costs more than doubled over the period 1971-80, from $74,889 to $161,965 (Table 2). The highest net revenue before taxes recorded was $22,619 in 1978. Losses were recorded in 1974, 1975, and 1980, and this could be due to the effects of inflation and poor harvest recorded in those years.

Terminal value has a critical effect on profitability. Decreased landings led to a substantial economic loss of $20,758 in 1980 (Table 2), when vessels were salvaged at 35% of their original values. Increasing the terminal value to 100% of cost resulted in a positive economic profit of $36,130, the highest obtained (Table 2). It was further observed that the net present value for the investment project increased by 72.5% when vessels were salvaged at their original costs rather than at the 35% level of their original values.

Investment in Different Time Periods

Tables 2 and 3 present the results of investing in a shrimp vessel in 1971. Considerable investment has been made in new shrimp vessels since 1977. Table 4 shows the annual increase and cash flow statements for purchasing the same steel vessel in 1977. Since the level of operations is held constant, revenue and variable costs are the same; fixed costs, however, changed dramatically.

In 1971, the value of the 20.1-21.5 m steel vessel was $129,767. In 1977, that same vessel cost $222,084, a 71.1% increase in price. The loan payment in 1971 was a little over $11,600/yr assuming a 10 yr note, but increased to $24,074/yr. If the vessel was purchased in 1971, profits were made in 1977 and 1978; for the vessel purchased in 1977, losses were incurred over the entire investment period. Losses were particularly substantial if the vessel was sold for salvage value at the end of 1980.

The cash flow statement shows that cash available was very low for 1977-79. There was about $35,000 difference in cash available in 1980, depending on whether the vessel had been sold for salvage value or for its original purchase price. For the vessel purchased in 1971, the net cash increase in 1977 was $9,643; and only $2,223 for the vessel purchased in 1977. In 1979 under the 1971 scenario, cash available would have increased $2,047; here it declined $6,252. Despite poor economic conditions, NPV was positive for both vessel sale prices, implying vessels would have had a greater return on investment than bonds purchased in 1977.

Table 5 shows the results of purchasing a vessel in 1979. The price of the vessel went up by about 26.8% since 1977, and substantial losses were incurred. The NPV is negative if the vessel is sold for its salvage value and positive if it is sold for 100% of its original purchase price. Short-term borrowing occurred when the vessel was purchased in 1979. In fact, the vessel owner had to borrow more than he was paying in principal on his original purchase note.

Economic Performance by Size and Construction

Figures 3 through 8 show variations in net revenue for the various vessel types used in the analysis. These variations follow a general pattern. For vessels purchased in 1971, net revenue peaked in 1972 and 1978 and dropped to minimum levels in 1974 and 1980. A major reason for this trend is that

TABLE 4.—Summarized annual income and cash flow statements for steel vessels, 20.1-21.5 m long, operating out of Texas ports, 1977 to 1980.

	1977	1978	1979	1980[1]	1980[2]
Income statement					
Value of landings	142,272	155,733	164,638	152,479	152,479
Total variable cost	100,562	109,961	130,160	138,555	138,555
Total fixed cost[3]	43,497	43,011	42,838	42,883	42,883
Net revenue	−1,787	2,761	−8,359	−28,959	−28,959
Economic profit[4]	−8,628	−5,006	−15,587	−43,663	−158
Cash flow statement					
Total cash inflow	142,272	157,956	172,165	313,654	375,838
Total cash outflow	140,049	150,429	170,890	180,396	187,041
Net cash balance	2,223	5,304	−6,252	131,983	187,522
Cash available	2,223	7,527	1,275	133,258	188,797
Net present value			-	12,759	47,954

[1]Salvage value set at 35% of original cost.
[2]Vessel sold for original purchase price.
[3]Vessel was purchased for $222,084; 75% financed at 7.93% interest.
[4]Economic profit is the net revenue adjusted for any changes in the value of operating inventories and capital items.

TABLE 5.—Summarized annual income and cash flow statements for steel vessels, 20.1-21.5 m long, operating out of Texas ports, 1979 to 1980.

	1979	1980[1]	1980[2]
Income statement			
Value of landings	164,638	152,479	152,479
Total variable cost	130,160	138,555	138,555
Total fixed cost[3]	61,449	63,668	63,668
Net revenue	−26,971	−49,745	−49,745
Economic profit[4]	−34,528	−68,559	−45,932
Cash flow statement			
Total cash inflow	164,638	383,999	421,689
Total cash outflow	184,132	215,631	218,132
Net cash balance	−19,493	187,861	223,049
Cash available	−19,493	168,368	203,556
Net present value		−9,355	18,140

[1]Vessel sold for salvage value.
[2]Vessel sold for original purchase price.
[3]Vessel was purchased for $269,210; 75% financed at 12.25% interest.
[4]Economic profit is the net revenue adjusted for any changes in the value of operating inventories and capital items.

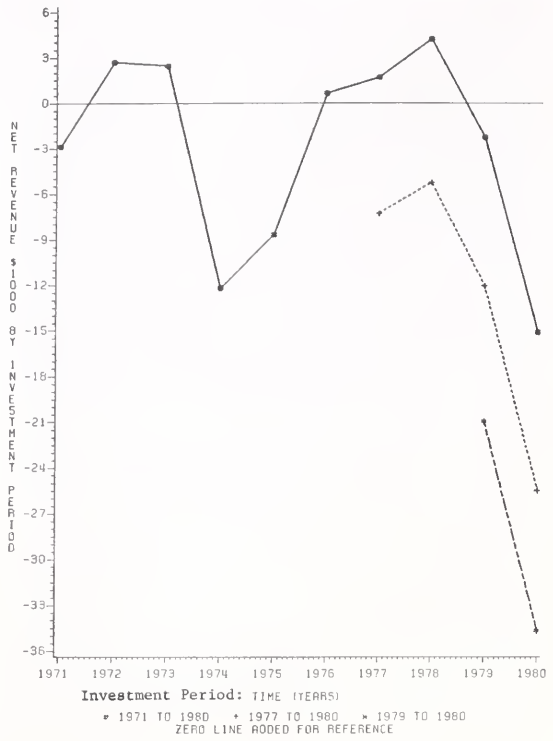

FIGURE 3.—Net revenue for a wooden vessel 17.1 to 18.5 m long operating out of Texas ports by investment period.

while tremendous increases in the value of landings were recorded in 1972 and 1978, 1974 and 1980 were the only periods in which the value of landings actually decreased. It can further be shown that fuel charges increased dramatically in 1974 and 1980 (Fig. 2), making those years particularly bad ones for Texas shrimp producers in terms of net revenue.

In general, steel vessels performed better economically than wooden vessels irrespective of the investment period. This may be attributed to the durability of steel vessels and their ability to operate under more adverse weather conditions than wooden vessels. The performance of 18.6-20.0 m steel vessels was particularly outstanding (Fig. 6) while the same size wooden types performed very poorly, recording losses throughout the study period (Fig. 4). As explained earlier, steel vessels are more durable and can spend more days offshore fishing than wooden vessels. Besides, steel vessels generally call for less maintenance and repair costs and attract a better quality crew than wooden ones. With the exception of the 17.1-18.5 and 18.6-20.0 m wooden vessels, which recorded losses over most of the period, all the other vessels performed satisfactorily.

Variation in Net Present Value

Evaluating the investments based on the net present value criterion, the 18.6-20.0 m steel vessels would be ranked as the best investments in the Gulf shrimp fishery (Table 6). Compared with the other vessel types, they consistently showed the highest net present values under all investment conditions examined. At the other end of the continuum lie the 18.6-20.0 m wooden vessels, which showed the poorest net present values under each investment condition, actually showing negative net present values and implying that investing in 18.6-20.0 m wooden vessels is not a feasible endeavor (Table 6).

With the exception of 18.6-20.0 m wooden vessels, 1971 investments showed the highest net present values, followed by those made in 1977. Investments made in 1979 were the least feasible; this may be attributed to unusually high capital

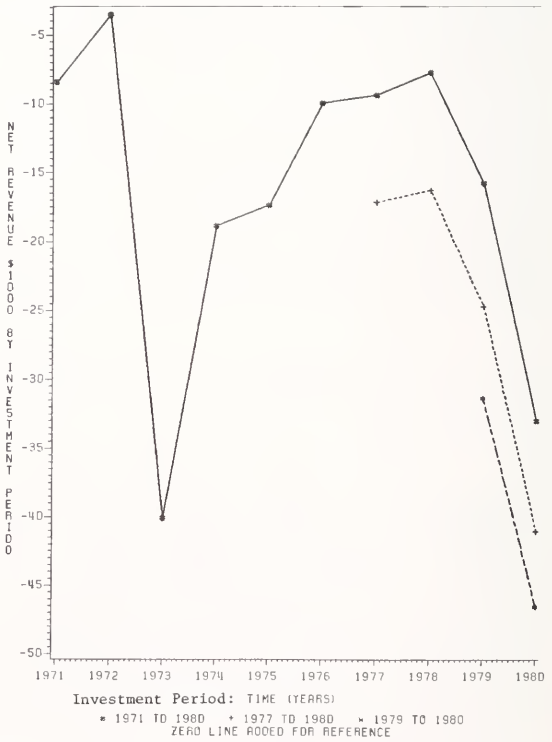

FIGURE 4.—Net revenue for a wooden vessel 18.6 to 20.0 m long operating out of Texas ports by investment period.

and high vessel costs, resulting in higher annual principal and interest payments.

SUMMARY AND CONCLUSIONS

Due to the inflationary trend in recent years, investments made in the early part of the last decade performed better than those made in the latter part. Steel vessels generally showed higher economic profits than wooden ones, and medium-sized vessels (18.6-20.0 m in overall length) were the most efficient vessels to operate in the Gulf of Mexico.

Shrimp production in the Gulf of Mexico has significant seasonal variations—periods of low shrimp landings and periods of abundant catch. Although the general trend in real prices was upward, high variability has created short-run uncertainty for shrimp producers. In general, after-tax net revenue was lowest in 1974; 1978 was the most favorable year of operation.

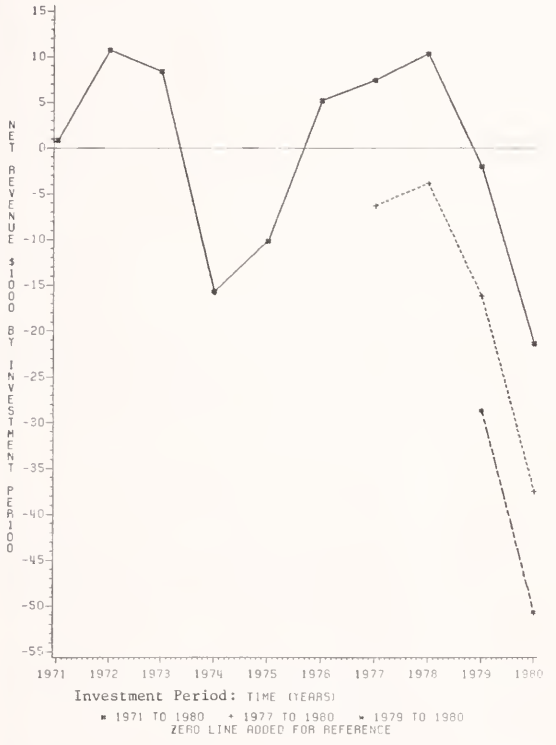

FIGURE 5.—Net revenue for a wooden vessel 20.1 to 21.5 m long operating out of Texas ports by investment period.

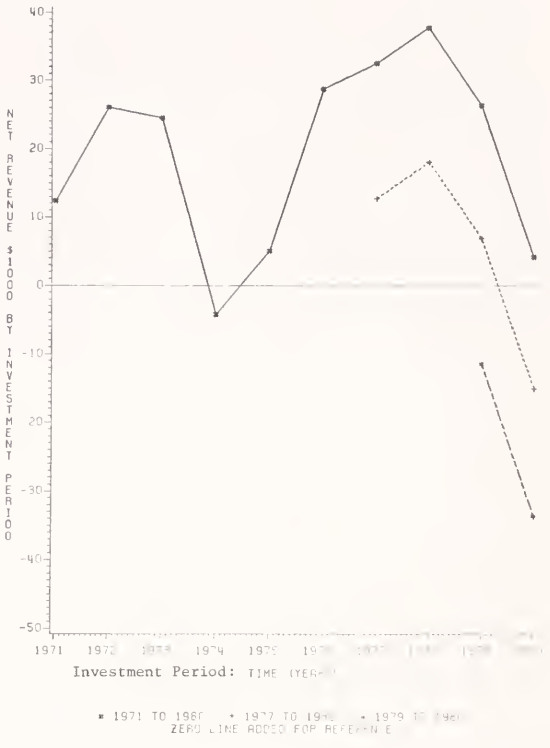

FIGURE 6.—Net revenue for a steel vessel 18.6 to 20.0 m long operating out of Texas ports by investment period.

Vessel terminal value plays a major role in determining overall returns to investment. The NPV for the investment increased when the terminal value rose from 35 to 100% of the original vessel cost (Table 6). Based on the net present value criterion, the 18.6-20.0 m steel vessels once again proved to be the most feasible investment. Inves-

TABLE 6.—Net present value for each investment period, salvage value, and vessel type for vessels operating out of Texas ports.

Investment period:	1971 to 1980		1977 to 1980		1979 to 1980	
Salvage value:	35%	100%	35%	100%	35%	100%
Vessel type						
Wooden, 17.1-18.5 m	−14,303	4,113	−16,166	2,019	−17,766	4,122
Wooden, 18.6-20.0 m	−70,622	−37,348	−49,898	−30,731	−32,431	−17,612
Wooden, 20.1-21.5 m	4,993	23,089	−18,368	6,834	−27,829	−9,667
Steel, 18.6-20.0 m	89,154	106,585	51,483	84,543	16,250	44,462
Steel, 20.1-21.5 m	22,572	42,560	12,759	47,954	−9,355	18,140
Steel, 21.6-23.0 m	13,385	35,352	−18,161	19,655	−27,528	1,212

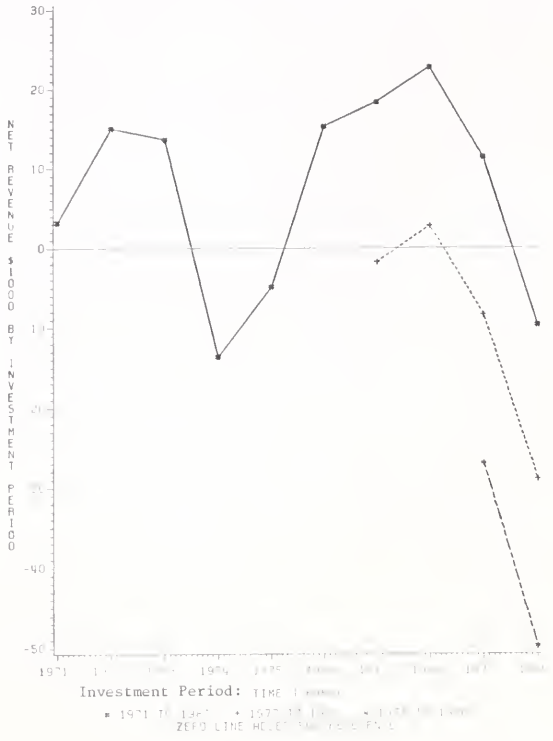

FIGURE 7.—Net revenue for a steel vessel 20.1 to 21.5 m long operating out of Texas ports by investment period.

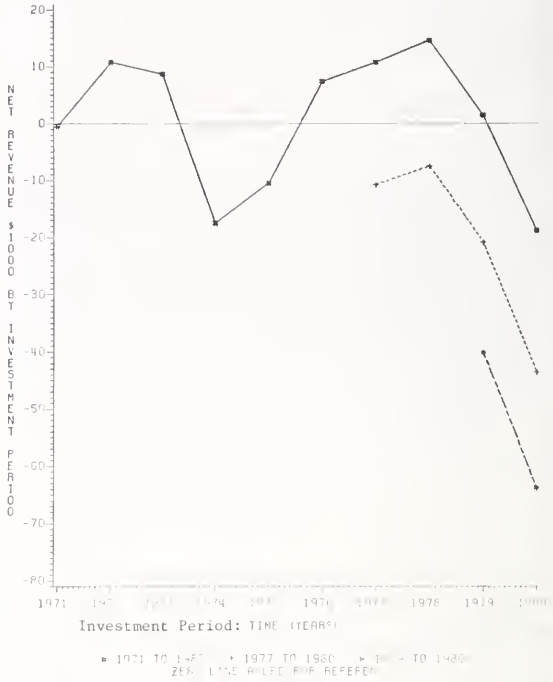

FIGURE 8.—Net revenue for a steel vessel 21.6 to 23.0 m long operating out of Texas ports by investment period.

tors should, however, bear in mind that based on this sample data similar-sized vessels built of wood are not feasible ventures.

It can be inferred from this study that in high inflationary periods, shrimp producers should avoid newly financed vessels. The resultant increases in costs of equity and debt capital are such that economic profit is eliminated. Investing in used vessels may be a viable alternative.

Results from this study further indicate that the economic performance of steel vessels is far superior to that of wooden vessels. Steel vessels can withstand adverse weather conditions much better than wooden ones and as a result, can spend longer days in offshore fishing. Steel vessels showed higher landings per trip than similar-sized wooden vessels. Therefore, the extra expense to purchase steel vessels may prove a worthy investment.

ACKNOWLEDGMENTS

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QUANTITATIVE AND QUALITATIVE BACTERIOLOGY OF ELASMOBRANCH FISH FROM THE GULF OF MEXICO[1]

JOHN D. BUCK[2]

ABSTRACT

Twelve species of elasmobranch fish (8 sharks, 2 rays, 1 skate, and 1 guitarfish) taken from the Gulf of Mexico off Sarasota, Florida, were studied. Numbers of bacteria on skin were recorded, as were types of bacteria occurring on skin, gills, teeth, and in intestinal contents. Comparative observations were made on eight species of osteichthyan fish and seawater. Counts/cm² of elasmobranch skin varied greatly both among genera and within a given species. In general, skin displayed relatively high counts which could be of significance in subsequent flesh spoilage. One brief study of spoilage of nurse shark meat at 5°C and room temperature (24°-26°C) showed that, after 7 days, species of *Pseudomonas*, *Vibrio*, and *Micrococcus* were dominant at the lower temperature while *Micrococcus* and *Proteus vulgaris* were recovered at 24°-26°C. Various types of bacteria found in or on the several areas of elasmobranch fish examined were compared with the little information available in the literature. Overall, Gram negative bacteria, particularly the genera *Pseudomonas* and *Vibrio*, were most common although several species of Gram positive bacteria were found also. *Planococcus* isolates from skin may represent important organisms because they have been implicated in shrimp spoilage. Three genera of hemolytic bacteria (*Proteus*, *Staphylococcus*, *Streptococcus*) were recovered from teeth of several elasmobranchs and may present a hazard to bite victims. Also, a variety of enteric bacteria potentially pathogenic to humans was found in intestinal contents; therefore, caution is suggested in handling shark material.

Considerable information is available on the normal and spoilage microflora of marine fish (e.g., Shewan 1961, 1971; Horsley 1977). However, the bacteriology of the elasmobranchs (sharks, skates, rays) is less understood despite a widespread present commercial fishery in local areas (Riedel 1961; McCormick et al. 1963) and its future potential (Juhl 1973; U.S. Department of Commerce 1982). Venkataramen and Sreenivasan (1955) studied the bacterial flora of skin of one shark caught off India; Johnson et al. (1968) characterized the intestinal microflora of five species of sharks obtained in the Indian Ocean; and Yap (1979) reported on skin isolates of two sharks freshly caught off Australia. Liston (1957) studied the bacteria associated with slime and gills of fresh North Sea skate. Spoilage bacteria in shark flesh were noted by Wood (1950) in Australia and Velankar and Kamasastri (1955) in India. Although the number of shark attacks on humans worldwide is statistically small (Baldridge 1974; Coppleson 1975), there are no substantive data on the potential bacteriological hazard of shark bites other than brief notations of hemolytic bacteria being recovered from the teeth of sharks (Davies 1960; Davies and Campbell 1962).

Consequently, this study was initiated to characterize the numbers and types of bacteria associated with a wide variety of elasmobranch fish common to the Gulf of Mexico. Comparative data were recorded for water and osteichthyan fish caught in the same area. These results will have relevance to the potential spoilage of elasmobranch meat and the pathobiology of shark bites.

METHODS

Sampling Sites

All fish were obtained from the Gulf of Mexico within several kilometers off Sarasota, Fla., or in the contiguous waters of Sarasota Bay. Small elasmobranchs were caught by use of a long, monofilament gill net set from the surface to a depth of about 1 m. Larger sharks were caught using baited longlines farther offshore. The one sand tiger shark, *Odontaspis taurus*, studied was obtained from the Mystic Marinelife Aquarium (Mystic, Conn.) and had been dead and refrigerated for 4 h. This shark, caught off the coast of New Jersey 3 d previously, was maintained in chlorinated brine water at the aquarium for 2 d

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prior to death. Only teeth and intestinal contents were sampled. For comparative bacteriological studies, several osteichthyan fish were caught by rod and reel or retrieved from the gill net mentioned above. Some elasmobranchs were occasionally maintained in large concrete or fiberglass tanks containing seawater piped from Sarasota Bay. All fish examined from tanks were either alive or had been dead for less than 1 h. Fish caught in the Gulf of Mexico were either iced if dead or kept in a wet hold until examined, which was routinely less than 1 h. In one case (see below) sharks were dead for 3 h before sampling. Water samples were collected from either Sarasota Bay or the tanks containing fish.

Quantitative Analysis

Swabbing was compared initially with two other methods involving the use of membrane filters in a quantitative sampling of elasmobranch skin. In the swabbing technique, a sterile aluminum foil template containing a 3.1 × 3.1 cm square opening (9.6 cm^2) was placed on the skin, on the side of each fish just posterior to the gills. A sterile polyester-tip swab (Falcon No. 2069[3]) was used over the exposed area in all directions, and the tip was broken off in a screw-capped tube containing 10 ml of sterile seawater. Decimal dilutions of this were prepared in 9 ml of sterile seawater and 0.1 ml volumes spread (Buck and Cleverdon 1960) on Bacto-Marine Agar (Difco Laboratories, Detroit, Mich.). One procedure with membrane filters involved placing sterile 0.45 μm gridded membranes (Millipore No. HAWGO47SO) on shark skin and pressing them down by rolling a sterile glass rod across the membrane. The membrane was then placed grid uppermost on the surface of an agar plate. The second membrane filter technique was similar to the first except that the membrane, after exposure to the skin, was placed in a sterile plastic screw-cap centrifuge tube with sterile seawater and agitated on a vortex mixer for 30 s. Decimal dilutions and platings were then made as indicated above. All plates were incubated at room temperature (24°-26°C) for 3-5 d. Counts/cm^2 of skin were calculated.

Qualitative Analysis

In addition to skin, other body areas including teeth, gills, and intestinal contents were sampled by use of a swab. The upper third of plates of eosin-methylene blue, tryptic-soy, brain heart infusion, and marine agar (all Difco) was swabbed, and the remaining two portions of the plate were streaked sequentially with a sterile wire loop to isolate colonies. Plates were incubated at room temperature (24°-26°C) and 37°C for 1-5 d and colonies were selected based on differences in morphology.

Qualitative changes in the bacterial flora on shark flesh were assessed as a function of time and temperature. Pieces of nurse shark, *Ginglymostoma cirratum*, flesh (about 2 cm^2) were cut aseptically from one area of one side of the fish after the skin had been removed. These pieces were placed in sterile petri dishes and incubated at room temperature (24°-26°C) and 5°C. Initially and after 3, 4, 5, and 7 d incubation, the surface of the flesh was sampled using a sterile loop, which was used to directly inoculate agar plates to obtain well-isolated colonies.

Tank and bay samples were collected at a depth of about 30 cm in sterile bottles. One ml volumes were diluted in 9 ml of sterile seawater and additional decimal dilutions prepared in a similar manner. Spread plates (see above) were made on marine agar. Representatives of various colonial types were selected and identified after incubation for 3-5 d at room temperature.

All isolates were maintained on slants of either marine agar or tryptic-soy agar. Gram reactions were recorded by both conventional staining and the KOH technique (Buck 1982). Gram negative enteric bacteria were identified using either the Enterotube II (Roche Diagnostics, Nutley, N.J.) or API 20E (Analytab Products, Plainview, N.Y.) systems. Hemolysis was detected on tryptic-soy agar containing 5% horse blood. Other bacteria were characterized using the methods of Shewan et al. (1960) and Oliver (1982).

RESULTS AND DISCUSSION

Quantitative Analysis

Counts by the swab technique averaged 115% higher than those obtained by membrane filters applied directly to agar plates (two experiments) and 910% higher than counts by agitating the membrane in seawater followed by dilution and plating (three experiments). All subsequent counts of skin bacteria on both elasmobranch and osteichthyan fish were made using the swab

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

technique (Yap 1979), although this technique has inherent weaknesses (Horsley 1977), especially in examining shark skin, because it is abrasive and essentially three-dimensional. Nonetheless, counts obtained by swabbing a known area were always higher than those achieved by pressing a membrane filter on the skin, probably because the membrane did not recover bacteria associated with the lower portion of the denticles. The fibrous texture of the swab, while prone to some shredding unless care was used, may have allowed penetration into the skin. Perhaps an agar-coated slide or "paddle" which could be pressed onto shark skin would be more effective, although such a procedure might be unwieldy in the field.

Table 1 shows the number of bacteria recovered from the skin of various elasmobranch and osteichthyan fish. Elasmobranch skin showed a very wide range of counts both among genera and within a given species. Data in Table 1 indicated that there was no obvious correlation between bacterial counts on tank-held and freshly caught elasmobranchs, although bacterial counts on skin of three tank-held Atlantic sharpnose sharks were about two orders of magnitude lower than counts for one specimen of the same species caught in a gill net. Three of the highest counts on shark skin noted in Table 1 (bonnethead, 410,000/cm^2; blacktip, 530,000/cm^2; blacknose, 330,000/cm^2) were from fish which had been dead for 3 h. This suggests that bacteria rapidly colonize skin of dead sharks. Yap (1979) reported varying counts on skin of freshly caught shark which depended on the area of the fish sampled. His counts (310-1,900/cm^2) were, in general, lower than those reported herein, and were estimated from broth dilutions and not plates. The shark skin sampled here displayed relatively high bacterial counts which are of considerable significance if the sharks are to be used for food. Large numbers of bacteria could be deposited onto flesh which subsequently may undergo more rapid spoilage if not adequately washed and/or refrigerated. With the exception of the bighead searobin, *Prionotus tribulus*, the counts on osteichthyan fish were quite similar and within the range reported in other studies (Horsley 1977).

TABLE 1.—Number of bacteria on fish skin (Bacto-marine agar).

Taxon	Source	No./cm^2
Elasmobranchs		
Florida smoothhound, *Mustelus norrisi*	Gill netted	[1]120
		[1]840
Nurse shark, *Ginglymostoma cirratum*	Gill netted	[1]8,200
Atlantic sharpnose shark, *Rhizoprionodon terraenovae*	Gill netted	[1]2,300
		220,000
		[1]1,000
		[1]1,000
Bonnethead or shovelhead shark, *Sphyrna tiburo*	Gill netted	400,000
		42,000
		1,100
		410,000
Brown or sandbar shark, *Carcharhinus plumbeus*	Longline caught	2,300
Blacktip shark, *Carcharhinus limbatus*	Gill netted	530,000
Blacknose shark, *Carcharhinus acronotus*	Gill netted	330,000
Tiger shark, *Galeocerdo cuvieri*	Longline caught	240
Atlantic guitarfish, *Rhinobatos lentiginosus*	Gill netted	[1]260
		[1]460
Clearnose skate, *Raja eglanteria*	Gill netted	[1]100,000
		80,000
Southern stingray, *Dasyatis americana*	Gill netted	[1]6,700
Cownose ray, *Rhinoptera bonasus*	Gill netted	50,000
Osteichthyes		
Gulf menhaden, *Brevoortia patronus*	Gill netted	23,000
Southern flounder, *Paralichthys lethostigma*	Rod caught	26,000
Spanish mackerel, *Scomberomorus maculatus*	Gill netted	15,000
Ladyfish, *Elops saurus*	Gill netted	19,000
Searobin, *Prionotus tribulus*	Gill netted	100
Black drum, *Pogonias cromis*	Gill netted	15,000
Permit, *Trachinotus falcatus*	Gill netted	7,100
Atlantic spadefish, *Chaetodipterus faber*	Gill netted	14,000

[1]Tank held.

Qualitative Analysis

Table 2 shows the number of isolates and genera of bacteria recovered from elasmobranch and osteichthyan fish and from waters where the fish were taken or held. The Gram negative bacteria, especially *Pseudomonas, Vibrio*, and *Cytophaga*, accounted for 89% of the 111 isolates from skin. In other studies, pigmented Gram positive isolates of *Micrococcus, Bacillus*, and *Corynebacterium* were the most common (30 strains) on the skin of one shark (*Carcharhinus* sp.) caught off India; only 5 cultures of Gram negative *Achromobacter, Flavobacterium*, and *Vibrio* were recovered (Venkataraman and Sreenivasan 1955). *Pseudomonas* (40%), Micrococcaceae (30%), and *Moraxella* (15%) were dominant on skin of a freshly caught shark off Australia (Yap 1979). The data here for skin (Table 2) show a similar percentage for *Pseudomonas* but considerably fewer isolates of *Moraxella* and Gram positive cocci.

Table 2 shows that for Gulf of Mexico sharks, fewer genera were recovered from intestines than from other areas, but that the Gram negative genera were predominant and species of *Photobacterium, Pseudomonas*, and *Vibrio* accounted for 57% of the isolates. Gram positive bacteria (one

TABLE 2.—Number of isolates and percentage of bacterial genera recovered from elasmobranch and osteichthyan fish and water of the Gulf of Mexico.

	Elasmobranchs								All elasmobranch samples		Osteichthyes skin		Water	
	Skin		Gills		Teeth		Intestines							
Genus	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Gram negative														
Aeromonas	1	1			2	3			3	1			2	4
Acinetobacter	4	4	2	10	6	8	1	7	13	6	3	7		
Alcaligenes	2	2	1	5					3	1	2	5	4	8
Cytophaga	11	10	1	5	1	1	1	7	14	6	1	2		
Flavobacterium	1	1			4	5	1	7	6	3	1	2		
Flexibacter	1	1							1	1				
Moraxella	4	4			1	1			5	2	2	5	3	6
Photobacterium	4	4	4	18	5	7	4	29	17	8			6	12
Pseudomonas	35	32	1	5	10	13	2	14	48	22	8	18	15	30
Vibrio	30	27	10	46	17	23	2	14	59	27	16	36	15	30
Xanthomonas	6	5	1	5	2	3			9	4	4	9	2	4
Gram positive														
Arthrobacter	4	4			3	4	1	7	8	4			1	2
Bacillus					4	5	1	7	5	2	4	9	1	2
coryneforms	1	1	1	5	1	1			3	1	2	5	1	2
Micrococcus-Staphylococcus	4	4	1	5	8	11			13	6	2	5	1	2
Planococcus	3	3			2	3			5	2				
Streptococcus					9	12	1	7	10	5				
Total	111		22		75		14		222		45		51	

isolate each of *Arthrobacter, Bacillus*, and *Streptococcus*) represented 21% of the total. In a study of intestinal material from five species of sharks caught in the Indian Ocean, 10 isolates of *Bacillus* were found, and 1 each of *Corynebacterium, Alcaligenes, Vibrio, Spirillum*, and *Xanthomonas*; one animal showed no bacteria (Johnson et al. 1968).

No data are available in the literature on bacterial types recovered from shark gills, although the gills and skin of North Sea skates have been studied (Liston 1957). Gram negative bacteria were dominant with *Pseudomonas* most common on both skin and gills. Qualitative observations of skin agreed with the present data (Table 2), but skate gills showed a much higher percentage of *Pseudomonas* (60%) compared with this study (5%). The other Gram negative bacteria from skate gills were also found in this study (Table 2).

Hemolytic bacteria were isolated from the teeth of sharks in the present study. *Streptococcus* spp. were recovered from teeth of shovelhead, *Sphyrna tiburo*, and sand tiger, *Odontaspis taurus*, sharks; *Staphylococcus* spp. were found on the teeth of a cownose ray, *Rhinoptera bonasus*; and *Providencia rettgeri* was recovered from teeth of two shovelhead sharks. All of these bacteria were from sharks taken in the Gulf of Mexico except for the sand tiger shark which was caught off New Jersey and had been in captivity for only 3 d. In addition, several hemolytic species of *Vibrio* have been isolated recently from the teeth of a white shark, *Carcharodon carcharias*, caught off Block Island, R.I. (Buck et al. unpubl. data[4]).

Hemolytic bacteria were found in the mouths of sharks from South African waters, and it was suggested that bacterial infections of bites could have been a contributing factor in the deaths of victims (Davies 1960). The hemolytic bacterium recovered from teeth of *Carcharhinus zambezensis* (*leucas*?) was described as a "Paracolon bacillus" (Davies and Campbell 1962).

The present observations not only confirm the occurrence of hemolytic organisms on teeth of sharks in nature but also extend these types to include bacteria not reported previously from sharks and the number of species of sharks which harbor them. They suggest that shark bites could possibly introduce potentially pathogenic bacteria into the tissues of victims.

A variety of enteric bacteria was found associated with the intestinal contents and occasionally the teeth of elasmobranchs; none were recovered from the gills or skin. These data are presented in Table 3. Three cultures only, all *Shigella* species, were isolated from bony fish. One was found in pinfish, *Lagodon rhomboides*, intestine, and two strains were isolated from a black drum, *Pogonias cromis*—one on the gills and the other from intestinal contents.

[4]Buck, J. D., S. Spotte, and J. J. Gadbaw, Jr. Manuscr. in prep. Bacteriology of the teeth from "Jaws": Medical implications for shark-bite victims.

Enterobacteria are found frequently on osteichthyan fish, but there are no reports in the literature on their occurrence in (on) elasmobranchs. If waters contain domestic wastes, then the fish will almost certainly be contaminated also (Shewan 1971; Horsley 1977). Coliform counts in Sarasota Bay are generally low, although counts of 1,800/100 ml have been recorded in one bayou receiving treated sewage effluent (Buck, unpubl. data[5]). Areas north (Tamplin et al. 1982) and south (Peterson and Yokel 1983) of Sarasota Bay have shown the presence of potentially pathogenic enteric bacteria. Consequently, the elasmobranch fish studied here may well have been in contact with sources of enterobacteria. The enteric bacteria encountered on the teeth and in the intestines of several elasmobranchs probably reflected feeding habits and originated on smaller prey which had passed through waters receiving human and/or animal excretions. Enteric bacteria do not multiply in passage through rainbow trout but temperature may be an important factor (Lesel and Peringer 1981; Lesel and LeGac 1983). The internal temperature of some sharks (Lamnidae) (Carey et al. 1981; Smigh and Rhodes 1983) is significantly warmer than the surrounding water. In subtropical areas, increased water temperature and that of the interior tissues of elasmobranchs might provide an environment that encourages bacterial multiplication, including potential pathogens. While none of the enterobacteria, except perhaps *Shigella* species, recovered from intestines and teeth of elasmobranchs represent primary pathogens, members of the other genera are commonly found as secondary or opportunistic pathogens in humans. Thus, caution should be exercised when handling dead shark material, particularly internal organs such as the digestive tract.

The genera *Vibrio* and *Pseudomonas* were predominant bacteria in combined data for all elasmobranch samples (Table 2). When isolates for tank-held and open-water fish were compared, these two genera were the most common in each group. The occurrence of other microbes did not vary more than 6% for any genus of bacteria between tank-held and freshly caught elasmobranchs, except for *Photobacterium* species which represented 11% of the isolates from the former and 3% of the latter.

The bacterial flora of osteichthyan fish and seawater consisted largely of Gram negative bacteria (82% and 94%, respectively), with *Vibrio* and *Pseudomonas* predominating. No substantial differences in generic composition were noted between Sarasota Bay water and fish holding tanks. Fewer numbers of several other Gram negative forms were found; these results agree with those of others (e.g., Shewan 1961). Small populations of Gram positive bacteria (*Arthrobacter, Bacillus*, cocci) were noted and probably represented terrestrial influence because the fish were taken from nearshore waters. This assumption may require reevaluation because there may be a widespread distribution of Gram positive bacteria in seawater (Gunn et al. 1982).

The microflora of spoiling shark muscle (no species indicated) from Australia have been studied, and the genus *Corynebacterium* was the dominant organism; *Pseudomonas* species and Gram positive cocci were also found in large numbers (Wood 1950). Few coryneforms were isolated in the present study, although *Pseudomonas* and Gram positive organisms were commonly recovered. In the brief study here of nurse shark flesh, the dominant bacteria found initially were species of *Vibrio* and *Pseudomonas*. After 7 d of incubation at 5°C, the flora were composed principally of *Pseudomonas*, *Vibrio*, and *Micrococcus*. When flesh was held at room temperature (24°-26°C), Gram positive cocci and *Proteus vulgaris* were

[5]J. D. Buck, University of Connecticut Marine Research Laboratory, Noank, Conn., unpubl. data, 1982.

TABLE 3.—Enterobacteriaceae isolated from elasmobranch fish.

Taxon	Bacteria
Nurse shark, *Ginglymostoma cirratum*[1]	*Proteus vulgaris*
Intestine	*Escherichia coli*
Shovelhead shark, *Sphyrna tiburo*	
Intestine	*Enterobacter agglomerans*
	Escherichia coli
	Shigella sp
Teeth	*Citrobacter freundii*
	Providencia rettgeri
	Providencia sp.
Sandbar shark, *Carcharhinus plumbeus*	
Intestine	*Shigella* sp
Teeth	*Proteus vulgaris*
	Providencia rettgeri
Blacktip shark, *Carcharhinus limbatus*	
Intestine	*Escherichia coli*
	Providencia alcalifaciens
	Shigella sp.
Teeth	*Escherichia coli*
	Proteus vulgaris
Sand tiger shark, *Odontaspis taurus*[1]	
Intestine	*Citrobacter freundii*
	Morganella morganii
	Proteus vulgaris
Cownose ray, *Rhinoptera bonasus*	
Intestine	*Shigella* sp.
Teeth	*Serratia liquefaciens*
Clearnose skate, *Raja eglantera*[1]	
Intestine	*Escherichia coli*

[1]Tank held.

predominant after 7 d. The latter is capable of hydrolyzing urea, and several species of *Micrococcus* are urease-positive (Buchanan and Gibbons 1974); hence, both of these groups are potential contributors to shark tissue spoilage. This enrichment of Gram positive types in elasmobranch spoilage was noted by Wood (1950).

Bacteria were found in 12 samples of shark muscle (*Scoliodon* sp.) allowed to spoil at 27°-30°C (Velankar and Kamasastri 1955). No coryneforms and only one *Micrococcus* isolate were found; all others were unidentified Gram negative nonpigmented rods.

The spoilage of iced abdominal wall muscle of Australian school shark, *Galeorhinus australis*, was studied by Yap (1979). *Pseudomonas* and *Moraxella* (45% and 20%, respectively) were the dominant bacteria recovered after 10 d although the Gram positive cocci represented 15% of the total.

The data presented here for the flesh spoilage experiment, albeit limited, confirm the observations of Wood (1950) and Yap (1979), but none of these parallel the findings of Velenkar and Kamasastri (1955) which also concerned sharks from subtropical waters. Perhaps the local marine microflora or experimental conditions influenced their observations.

Although the number of isolations was relatively small, the genus *Planococcus* was found associated with elasmobranch skin and teeth in this study. All the cultures recovered were yellow-pigmented and were probably *Planococcus citreus*, the only accepted species (Buchanan and Gibbons 1974). This proteolytic bacterium has been implicated in shrimp spoilage (Alvarez 1982) and may be a significant spoilage organism of elasmobranch flesh.

CONCLUSIONS

The observations reported here have shown that elasmobranch fish contain a large and diverse bacterial flora. Because there is little information on the microbiology of sharks, skates, and rays, assessing the relative significance of the data is difficult. In many cases, counts of bacteria on the skin were an order of magnitude higher than those noted on osteichthyan fish caught in the same waters. In other samples, counts were two orders of magnitude lower. Considerable variation was seen in individual species of elasmobranchs. Types of bacteria recovered from different areas of fresh fish and during one controlled spoilage experiment on flesh did not correlate well in all respects with results of other studies which in some instances were limited to one or a few fish or different species than those considered here. Also, little information was provided in the literature on cultural conditions and other variables which could affect development of various bacteria reported. The data here substantiate the occurrence of certain potential spoilage bacteria on skin and include the genus *Planococcus* which has been implicated in shrimp spoilage. The present study also confirms and extends other observations on the occurrence of hemolytic bacteria on shark teeth. In addition, potentially pathogenic enterobacteria were recovered from teeth and intestinal contents of several elasmobranch species. It is hoped that future studies will include larger numbers of additional shark species for a clearer assessment of the role of bacteria in both spoilage and public health aspects of a valuable and underutilized marine resource.

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DISTRIBUTION AND FEEDING OF THE HORSESHOE CRAB, *LIMULUS POLYPHEMUS*, ON THE CONTINENTAL SHELF OFF NEW JERSEY[1]

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ABSTRACT

The horseshoe crab, *Limulus polyphemus*, population was assessed during hydraulic dredge surveys of the surf clam resource in the inshore 5.5 km (3 nautical miles) of the continental shelf off New Jersey from 1976 through 1979. Frequency of occurrence and abundance was higher off the southern half of the state, which may be a function of its proximity to Delaware Bay, a principal spawning site. Horseshoe crabs consumed various benthic organisms, primarily bivalves, arthropods, and polychaetes. Surf clams, *Spisula solidissima*, were important in the diet of *Limulus*; individual valves ranged in length from <1 mm to about 35 mm. In the laboratory, horseshoe crab predation was observed on surf clams as long as 46 mm.

This report describes the distribution of the horseshoe crab, *Limulus polyphemus*, on the inshore continental shelf off New Jersey, and the diets of a sample of these animals. Previous studies of the horseshoe crab on the continental shelf are limited to distributional records (Wolff 1977; Shuster 1979) or tagging studies conducted close to estuarine spawning areas (Baptist et al. 1957; Rudloe 1980), although crabs have been found at depths as great as 200 m according to National Marine Fisheries Service surveys (J. W. Ropes[4]).

Since the early 1960's, an intensive surf clam, *Spisula solidissima*, fishery has developed along the New Jersey coast (Ropes 1982). The junior author (Haskin) and his colleagues have inventoried the surf clam resource in the New Jersey waters, to 5.5 km (3 nmi) offshore yearly since 1972. All macroinvertebrates, including *L. polyphemus*, captured in hydraulic dredge hauls from 1976 through 1979 were counted. Since a percentage of the horseshoe crab population migrates from the continental shelf to estuaries and back again (Shuster 1982), we analyzed both temporal and spatial variability. Separating these effects was difficult because the sampling program was designed primarily to inventory a sessile clam resource, rather than a migratory one. However, the data, based on over 1,100 stations, still represent the most systematic survey of *L. polyphemus* distribution on the inshore continental shelf, and since exploitation of these crabs for biomedical research and bait is increasing (Pearson and Weary 1980), our study provides baseline information should future population assessment studies be warranted.

Information on the feeding biology of horseshoe crabs is limited (Lockwood 1870; Fowler 1908; Shuster 1950; Smith and Chin 1951; Smith 1953; Smith et al. 1955; Botton 1981). In this study, stomach contents from 36 horseshoe crabs from the continental shelf were examined to supplement a more intensive study of the food habits of animals from Delaware Bay (Botton 1982); in August 1980, predation by crabs on surf clams about 4 cm long was examined in the laboratory.

MATERIALS AND METHODS

Population Survey

Stations were sampled with a hydraulic dredge (Meyer et al. 1981), adjusted to retain surf clams >88 mm. This gear retained both adult and subadult horseshoe crabs. Catch data, as number of animals per tow, were normalized for dredge width and tow time. The standard tow (ST) is defined as a 5-min haul using a 152 cm knife (width of dredge).

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This standard tow covered an area of about 418 m^2.

The New Jersey coastline from Cape May to Shark River Inlet was subdivided into 19 areas (Table 1). Stations were located by 3-point sextant fixes and/or loran C, and grouped in intervals of 0-1.8 km (0-1 nmi) (0-0.9 and 0.9-1.8 km north of Beach Haven Inlet), 1.8-3.7 km (1-2 nmi) and 3.7-5.5 km (2-3 nmi) based on distance from land. Inlets were used as latitudinal break points (Fig. 1). Because of the reduced sampling effort from 1.8 km offshore, these areas were larger than areas inshore of 1.8 km.

For statistical analysis, all tows on the same day in a given area were considered replicates. The Analysis of Variance (ANOVA) for the number of crabs per tow had three sources of variation: Area, time nested within area, and replicate tow nested within time within area. Because each year's design was unbalanced, a pseudo-F procedure (Hicks 1973) tested the significance of the area effect. Data were log-transformed to stabilize the variances. When areas were sampled more than once in a given year, we tested differences between sample dates using a completely randomized one-way classification ANOVA. If the F-test was significant, a Student-Neumann-Keuls procedure for unequal group sizes tested for differences between the means for each sample date (Zar 1974).

TABLE 1.—Description of areas of the New Jersey coast surveyed from 1976 to 1979.

Distance offshore (km)	Area	Southern boundary	Northern boundary
0-1.8	1	Cape May Inlet	Hereford Inlet
	2	Hereford Inlet	Stone Harbor
	3	Stone Harbor	Townsends Inlet
	4	Townsends Inlet	Corson Inlet
	5	Corson Inlet	Great Egg Harbor Inlet
	6	Great Egg Harbor Inlet	Absecon Inlet
	7	Absecon Inlet	Beach Haven Inlet
	8	Beach Haven Inlet[1]	Barnegat Inlet
	9	Beach Haven Inlet[2]	Barnegat Inlet
	10	Barnegat Inlet	Shark River Inlet
	11	Barnegat Inlet[2]	Shark River Inlet
1.8-3.7	12	Cape May Inlet	Townsends Inlet
	13	Townsends Inlet	Absecon Inlet
	14	Absecon Inlet	Beach Haven Inlet
	15	Beach Haven Inlet	Shark River Inlet
3.7-5.5	16	Cape May Inlet	Townsends Inlet
	17	Townsends Inlet	Absecon Inlet
	18	Absecon Inlet	Beach Haven Inlet
	19	Beach Haven Inlet	Shark River Inlet

[1]0-0.9 km
[2]0.9-1.8 km.

Stomach Contents

Thirty-six adult *L. polyphemus* were collected between 10 July and 25 August 1978 for analysis of stomach contents. The results are grouped for three locations: Stone Harbor (1 station, 5 individuals), Atlantic City (12 stations, 24 individuals), and Point Pleasant (3 stations, 7 individuals) (Fig. 1).

Complete digestive tracts were removed from crabs aboard ship or shortly after returning to the laboratory, fixed in 10% Formalin[5] seawater, and later transferred into 70% ethanol until examination. Food, much of which was entangled with mucus, was sorted under a 10× stereoscope. The number of bivalves was determined by counting the number of umbones and dividing by 2. Shells were measured by ocular micrometer or vernier caliper.

RESULTS

Population Surveys

1976 Survey

Sampling commenced in mid-July and was most extensive in late August and early September; no areas north of Beach Haven Inlet were sampled. Horseshoe crabs were present in over 90% of all hauls in the first 1.8 km between Hereford Inlet and Townsends Inlet, and from 1.8 to 3.7 km between Cape May and Townsends Inlet (Table 2). More than 10 animals/ST were dredged from 1.8 to 3.7 km offshore between Cape May and Absecon

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

TABLE 2.—1976 *Limulus polyphemus* survey results. Area means are expressed as the number of crabs per standard tow, as defined in the text. CV = coefficient of variation. Data were log transformed prior to Analysis of Variance. Area locations are shown in Table 1.

Distance offshore	Area	*N* stations	% with crabs	Mean	CV	Maximum
0-1.8 km	1	27	85.2	7.7	0.81	25.7
	2	12	66.7	4.1	1.27	10.7
	3	21	90.5	6.0	0.65	15.0
	4	7	71.4	11.2	1.14	35.3
	5	9	88.9	4.8	1.05	15.0
	6	8	62.5	2.4	1.01	5.4
	7	10	70.0	7.2	1.01	20.0
1.8-3.7 km	12	31	90.3	14.6	0.69	47.1
	13	28	78.6	12.5	2.36	145.7
	14	10	80.0	3.0	0.68	6.0
3.7-5.5 km	16	18	83.3	6.6	0.97	26.8
	17	16	62.5	25.4	2.72	277.4
	18	7	42.9	1.1	1.30	3.2

Analysis of Variance:

Source	df	SS	MS	*F*	*P*
Total	202	259.94			
Area	12	40.08	3.34	1.12	ns
Time (area)	38	80.77	2.13	2.32	0.05
Station (time (area))	152	139.09	0.92		

FIGURE 1.—Map of the New Jersey coast. Filled circles show the locations of stations from which *Limulus polyphemus* stomach contents were obtained.

Inlets, and in several areas from 0 to 1.8 km and 3.7 to 5.5 km between these two inlets. Two hundred seventy-seven crabs were found in a single dredge tow, 5.4 km off Townsends Inlet.

In 1976, both time within area and station within time within area were greater sources of variability than area itself (Table 2). The inshore 1.8 km from Cape May to Hereford Inlets was sampled on 10 and 30 July and again on 4-5 September. The mean number of crabs collected per standard tow on each date was 8.3, 9.3, and 2.1, respectively ($F = 2.86$, $0.10 < P < 0.05$). There were no significant differences between sampling dates within any other individual areas.

1977 Survey

Most sampling in southern New Jersey was done in June and July, but the areas north of Beach Haven Inlet were sampled in August. Thus, temporal variability was confounded with geographic variability. Areas north of Beach Haven Inlet were

relatively depauperate; the area effect was significant at $P < 0.07$ (ANOVA); the time within area effect was significant at $P < 0.05$ (Table 3).

Limulus polyphemus occurred in 70% to 100% of all tows between Cape May and Absecon Inlet (Table 3). Crabs were most numerous from 0 to 1.8 km offshore between Cape May and Hereford Inlets. When sampled on 15 June (23 stations), there was an average of 15.52 crabs/ST, but in late August-early September (9 stations), only 2.17 crabs/ST ($F = 5.006$, $P < 0.05$). Abundance from 1.8 to 3.7 km between Cape May and Townsends Inlets declined over the same time, from 13.08 to 3.3 crabs/ST ($F = 4.805$, $P < 0.05$). From 1.8 to 3.7 km offshore, between Townsends Inlet and Absecon Inlet, crabs declined between early July ($\bar{x} = 25.33$, $n = 6$), late July-early August ($\bar{x} = 3.95$, $n = 14$), and late August ($\bar{x} = 7.6$, $n = 5$), but the differences were marginally significant ($F = 3.03$, $0.10 < P > 0.05$).

Horseshoe crabs were encountered in every tow in the first 1.8 km from Beach Haven Inlet to Barnegat Inlet, although the average abundance was only 5 crabs/ST. No other area north of Atlantic City contained over 4 crabs/ST and an onshore-offshore gradient was particularly evident between Beach Haven Inlet and Shark River Inlet. From 1.8 to 3.7 km offshore, crabs were found in only 40% of the tows, and from 3.7 to 5.5 km, no crabs were present at seven stations.

TABLE 3.—1977 *Limulus polyphemus* survey results. Area means are expressed as the number of crabs per standard tow, as defined in the text. CV = coefficient of variation. Data were log transformed prior to Analysis of Variance. Area locations are shown in Table 1.

Distance offshore	Area	*N* stations	% with crabs	Mean	CV	Maximum
0-1.8 km	1	34	94.1	11.3	1.41	87.0
	2	10	70.0	2.8	1.29	12.0
	3	16	93.8	7.0	0.83	20.6
	4	17	100.0	6.1	0.68	14.2
	5	8	100.0	5.9	0.64	12.0
	6	8	75.0	2.9	0.89	7.0
	7	8	75.0	2.0	0.82	4.0
	8	12	100.0	6.0	0.79	19.6
	9	4	100.0	4.4	0.28	6.0
	10	25	60.0	2.2	1.62	13.9
	11	4	75.0	2.6	1.22	7.1
1.8-3.7 km	12	25	84.0	5.5	1.61	44.0
	13	25	92.0	9.8	1.96	97.0
	14	7	100.0	4.1	0.79	10.0
	15A[1]	9	44.0	1.6	1.34	5.4
	15B[2]	6	33.3	0.9	1.93	4.3
3.7-5.5 km	16	26	96.1	9.6	0.76	22.4
	17	9	77.8	7.6	1.44	33.0
	18	9	44.4	3.0	1.82	16.6
	19	7	0.0	0.0	—	0.0

Analysis of Variance:

Source	df	SS	MS	*F*	*P*
Total	261	258.36			
Area	19	76.05	4.00	1.79	0.07
Time (area)	32	50.07	1.56	2.48	0.05
Station (time (area))	210	132.23	0.63		

[1]Beach Haven Inlet to Barnegat Inlet.
[2]Barnegat Inlet to Shark River Inlet.

1978 Survey

As in 1977, the areas north of Beach Haven Inlet were sampled late in the summer. Stations south of Atlantic City had many more horseshoe crabs than ones farther north, and from Beach Haven Inlet northward, few animals were encountered offshore of 1.8 km (Table 4). Area and time within area effects were significant (ANOVA, $P < 0.01$; Table 4).

Temporal variability within an area was difficult to analyze, because for most areas, either the survey was completed in a single weekend, there were low densities on all dates (north of Beach Haven), or there were small sample sizes on one or more cruises. Between Cape May and Townsends Inlet, from 3.7 to 5.5 km offshore, there were significantly more crabs on 20 July ($\bar{x} = 12.64$, $n = 11$) than on 24 June ($\bar{x} = 3.11$, $n = 9$) ($F = 26.998$, $P < 0.001$).

1979 Survey

In contrast to 1977 and 1978, sampling of the Beach Haven Inlet to Shark River Inlet region

TABLE 4.—1978 *Limulus polyphemus* survey results. Area means are expressed as the number of crabs per standard tow, as defined in the text. CV = coefficient of variation. Data were log transformed prior to Analysis of Variance. Area locations are shown in Table 1.

Distance offshore	Area	*N* stations	% with crabs	Mean	CV	Maximum
0-1.8 km	1	32	96.9	16.7	0.79	54.0
	2	10	90.0	12.2	0.71	24.0
	3	21	90.5	10.4	0.70	28.0
	4	14	100.0	13.4	0.46	24.0
	5	10	100.0	4.0	0.64	8.0
	6	14	50.0	2.4	2.19	20.0
	7	22	54.5	0.8	1.47	5.2
	8	13	46.2	0.9	1.28	3.0
	9	11	72.7	3.6	0.94	9.0
	10	25	64.0	2.2	1.05	6.4
	11	8	37.5	1.9	2.18	11.8
1.8-3.7 km	12	15	86.7	13.7	2.67	150.0
	13	20	85.0	3.5	1.26	20.0
	14	12	58.3	1.2	1.26	5.0
	15	12	41.7	1.0	1.90	6.4
3.7-5.5 km	16	20	90.0	8.4	0.75	20.0
	17	13	84.6	3.3	0.74	7.0
	18	9	55.6	2.3	1.56	11.0
	19	5	0.0	0.0	—	0.0

Analysis of Variance:

Source	df	SS	MS	*F*	*P*
Total	281	347.91			
Area	18	165.30	9.18	4.38	0.01
Time (area)	35	38.72	1.11	1.76	0.01
Station (time (area))	228	143.89	0.63		

took place early in the summer, thus enabling a comparison of the southern and northern parts of the coast without a confounding effect of time. Both area (ANOVA, $P < 0.01$) and time ($P < 0.01$) effects were significant, and percent occurrence and abundance were low from Beach Haven Inlet northward, where horseshoe crabs were particularly scarce offshore of 1.8 km (Table 5). The inner 0.9 km from Barnegat Inlet to Shark River Inlet had significantly more *L. polyphemus* on 24 June ($\bar{x} = 5.48$, $n = 12$) than 17 August ($\bar{x} = 0.07$, $n = 10$) ($F = 11.913$, $P < 0.005$). From 3.7 to 5.5 km offshore between Townsends Inlet and Absecon Inlet, the density in late July ($\bar{x} = 3.24$, $n = 8$) was significantly higher than the density found on 17 May or 26 June ($\bar{x} = 0.88$, $n = 6$ and $\bar{x} = 1.4$, $n = 3$, respectively) ($F = 6.646$, $P < 0.005$). Stations on 28 August and 16 November, also contained fewer crabs ($\bar{x} = 0.19$, $n = 4$ and $\bar{x} = 0.44$, $n = 2$, respectively).

Stomach Contents

Stone Harbor individuals were collected on 24 July 1978, from a station, 13.4 m depth and 3.7 km offshore, which contained 150 *L. polyphemus*. Their digestive tracts were packed ($\bar{x} = 383.2$, range 88-791 individuals/crab) with blue mussels, *Mytilus edulis*; there were only traces of other food (three other bivalves, four brachyuran crabs, two foraminifera, and polychaete setae). The mean length of 38 whole valves was 6.3 mm, with a range from 4.2 to 9.0 mm. Virtually all remaining umbones were estimated to be from mussels in that range.

Crabs in the Atlantic City series ate a variety of food, primarily bivalves, annelids, and arthropods (Table 6). The surf clam, *Spisula solidissima*, was an important prey item, ranking first in frequency of occurrence and third in total abundance. Valves <1 mm in length were found, as were portions of a 35-40 mm shell length individual; about 62% of the valves were >4 mm. Other important bivalves were *Tellina* sp. and *Siliqua costata*. Twelve polychaete taxa were identified, of which *Nereis* sp. was the most frequently occurring, while the most abundant were unidentified Spionidae. Fifteen digestive tracts contained one or more specimens of brachyuran crabs, which in several cases were identified as young rock crabs, *Cancer irroratus*.

Stomachs of the seven horseshoe crabs from the Point Pleasant series contained little food. Only four bivalves (one *S. solidissima* and three *M. edulis*), a gastropod (*Nassarius trivittatus*), and a brachyuran were identified. Polychaete setae were

TABLE 5.—1979 *Limulus polyphemus* survey results. Area means are expressed as the number of crabs per standard tow, as defined in the text. CV = coefficient of variation. Data were log transformed prior to Analysis of Variance. Area locations are shown in Table 1.

Distance offshore	Area	*N* stations	% with crabs	Mean	CV	Maximum
0-1.8 km	1	30	96.7	20.2	1.20	107.8
	2	11	100.0	9.6	0.70	18.3
	3	21	100.0	15.5	0.63	33.3
	4	20	100.0	20.6	0.96	92.5
	5	9	100.0	9.4	0.67	19.2
	6	19	68.4	3.8	1.13	14.2
	7	20	55.0	1.4	1.15	5.1
	8	20	55.0	1.7	1.38	7.5
	9	11	63.6	2.0	1.49	10.3
	10	22	45.5	3.0	1.50	13.3
	11	4	25.0	0.2	2.00	0.7
1.8-3.7 km	12	23	95.7	7.9	1.25	41.7
	13	20	70.0	2.9	1.92	25.0
	14	19	73.7	2.4	0.94	8.3
	15	8	50.0	1.5	1.48	5.1
3.7-5.5 km	16	15	100.0	7.8	1.05	32.5
	17	26	73.1	2.6	1.55	20.0
	18	16	43.8	1.3	1.52	6.2
	19	3	0.0	0.0	—	0.0

Analysis of Variance:

Source	dt	SS	MS	*F*	*P*
Total	312	401.42			
Area	18	206.37	11.46	4.74	0.01
Time (area)	47	62.30	1.33	2.46	0.01
Station (time (area))	247	132.76	0.54		

TABLE 6.—Ranking of food items by total abundance and frequency of occurrence, from 24 *Limulus polyphemus* collected in the Atlantic City series, summer 1978.

Item	Number of specimens	Rank	Number of occurrences	Rank
Foraminifera	136	1	9	5
Unidentified bivalve	65	2	13	2
Spisula	48	3	14	1
Tellina	42	4	10	4
Brachyura	16	5	11	3
Siliqua	16	5	6	6
Spionidae	15	6	3	9
Nematoda	10	7	4	8
Cancer	9	8	4	8
Fecal pellets	9	8	9	5
Plant material	9	8	9	5
Gemma	8	9	5	7
Glycera	7	10	3	9
Polychaete setae	6	11	6	6
Ensis	6	11	5	7
Polynoidae	6	11	3	9
Mytilus	4	12	4	8
Nereis	4	12	4	8
Cirripedia	3	13	3	9
Spiophanes	3	13	2	10
Ampharetidae	2	14	2	1
Anomia	2	14	2	10
Capitellidae	2	14	2	10
Isopoda	2	14	2	10
Mulinia	2	14	2	10
Nemertea	2	14	2	10
Ostracoda	2	14	2	10
Turbellaria	2	14	2	10
Unidentified gastropod	2	14	2	10
Unidentified oligochaete	2	14	1	11
(Tie-17 items)	1	15	1	11

noted in two samples and unidentified shells in three. The most numerous item was Foraminifera (n = 21), and no other item was found more than three times.

In a laboratory experiment, a 20.3 cm (prosomal width) male horseshoe crab ate one 40.6 mm surf clam; the same crab consumed two clams, 43.8 and 42.4 mm, several days later (see Botton 1982 for procedural details). A 27.9 cm female ate two clams, 46.0 and 36.2 mm. Clams of this size are manipulated by the walking legs so that the ventral shell margin is held against the gnathobases. The chitinous gnathobases chip the ventral margin, eventually resulting in the fracture of one of the valves. Cracking of the valves continues until the crab is able to remove the meat from the shell using the pincer-tipped walking legs or the chelicerae. Ingestion of the shell of 4 cm *S. solidissima* is apparently incidental.

DISCUSSION

A latitudinal gradient in horseshoe crab abundance along the New Jersey coast during the spring and summer months was recognized as a decrease in abundance with distance north from Delaware Bay, and an onshore-offshore gradient was apparent in northern New Jersey. The transition between areas of high and low density takes place between Great Egg Harbor Inlet (Ocean City) and Absecon Inlet (Atlantic City). Horseshoe crabs were more abundant inshore in the late spring and early summer than in the late summer and fall.

Why are adult *L. polyphemus* concentrated in southern New Jersey, at least during the spring and summer? Since Delaware Bay, in southern New Jersey, contains the largest spawning population of horseshoe crabs in North America (Shuster 1982), we believe that the distribution on the New Jersey continental shelf may be related to the migration of deep-water crabs to those beaches for reproduction. However, horseshoe crabs spawn elsewhere in New Jersey and are widely distributed on the middle Atlantic continental shelf (Shuster 1979); based on electrophoretic evidence (Selander et al. 1970), there is gene flow between widely separated populations.

Hydraulic surf clam dredges are efficient samplers of large benthic infauna (Meyer et al. 1981), but an evaluation of this dredge as a means of capturing *L. polyphemus* is lacking. Given its sluggish habits, it is unlikely that gear avoidance by horseshoe crabs significantly affects our results; indeed, much more active lady crabs, *Ovalipes ocellatus*, are caught in large numbers (Meyer et al. 1981; Haskin, unpubl. data). However, in the absence of direct observations, it is perhaps best to consider our results as relative, rather than absolute abundances of horseshoe crabs off New Jersey. Because the temporal sequence of sampling varied yearly and because the effect of time on abundance was statistically significant, we do not encourage speculation on year-to-year variability based on these data.

The horseshoe crab is a dietary generalist; based on the limited number of animals dissected, molluscs, arthropods, and polychaetes are the major food items. Although Foraminifera were numerous, they are probably ingested inadvertently while digging out infauna. Opportunistic foraging was shown from the Stone Harbor group, which fed almost exclusively on *M. edulis*. Smith (1953) noted that crabs could locate discrete patches of soft-shell clam, *Mya arenaria*, but the behavioral basis for patch selection is unknown.

Horseshoe crab predation may be an important source of juvenile surf clam mortality. In aquaria, crabs ingested only the meats of 4 cm *S. solidissima*; this implies that this species may be more important as food than is apparent from visual stomach content analysis, which relies heavily on shell remains. Young *S. solidissima* may have been underestimated because many small (0.5-2.0 mm) shells were categorized only as "unidentified bivalves." Further studies of the food habits of horseshoe crabs, and of the abundance and diets of other predators, are necessary to evaluate the importance of predation in the survivorship of juvenile surf clams in New Jersey.

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DIEL VARIATIONS IN THE FEEDING HABITS OF PACIFIC SALMON CAUGHT IN GILL NETS DURING A 24-HOUR PERIOD IN THE GULF OF ALASKA

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ABSTRACT

Changes in prey composition and stomach fullness indicate diel variations in feeding behavior of sockeye, pink, and coho salmon caught in surface gill nets set for 2 hours each over a 24-hour period at a station in the Gulf of Alaska. All of these species of salmon switched from feeding primarily on squids, fishes, and amphipods during the day to euphausiids at night. Apparently dense concentrations of euphausiids can be exploited by salmon in surface waters at very low light intensities, even during an overcast night. Day-night changes were less obvious in the food of chum salmon, which fed largely on salps. Total catches of salmon and catches in the near-surface portion of the gill nets were highest between sunset and sunrise, suggesting that diel vertical movements contribute to the higher night than day catches of surface gill nets.

Although many studies have been published on the feeding habits of salmonids in oceanic waters of the North Pacific Ocean (Andrievskaya 1957; Allen and Aron 1958; LeBrasseur 1966; Ito 1964; Manzer 1968; Takeuchi 1972), most studies of daily feeding patterns have been conducted on juvenile salmon in fresh water or in coastal waters. These have generally shown that juvenile pink, sockeye, and chum salmon are diurnal or crepuscular (dawn and dusk) feeders (see Godin 1981 for review). The few studies conducted on diel feeding variations of adult or maturing Pacific salmon in oceanic waters of the northwestern Pacific Ocean have not revealed a consistent pattern (Machidori 1968; Shimazaki and Mishima 1969; Ueno et al. 1969).

To further elucidate the diel feeding patterns of these fishes, we collected and examined stomach contents of four species of Pacific salmon caught in the Gulf of Alaska during one 24-h period.

METHODS

Two gill nets, each 800 m long and 6 m deep, with 300 m of 115 mm, 250 m of 121 mm, and 250 m of 130 mm (stretch) mesh, were alternately fished for about 2-h periods over a 24-h period in the Gulf of Alaska from the *Oshoro Maru*, training ship of the Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido. The first net was set at 1200 h local time (GMT - 9 h) on 13 July; the last set was hauled at 1206 h on 14 July 1981 (Table 1). The time that the gill nets were fishing varied in the first 11 sets from 140 to 152 min (from start of set to start of

TABLE 1.—Summary of gill net sets and catches for salmon, 13-14 July 1981.

Set no.	Start of set and haul (h)	Number of salmon					
		Sock-eye	Chum	Pink	Coho	Steel-head	Total
1	1200 1422	8	4	1	0	0	13
2	1400 1629	2	0	1	5	0	8
3	1600 1821	2	8	4	7	0	21
4	1800 2020	7	1	5	2	0	15
5	1957 2227	15	1	5	3	1	25
6	2158 0025	9	5	11	11	1	37
7	2359 0224	11	7	8	7	0	33
8	0159 0430	17	8	7	8	0	40
9	0358 0627	6	2	11	5	2	26
10	0600 0832	11	3	2	1	2	19
11	0758 1026	7	1	6	1	0	15
12	0957 1206	12	4	7	1	0	24
	Total	107	44	68	51	6	276

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hauling) and 129 min in the last set. Five to eight minutes were required to set the nets, 12-20 min to retrieve them.

The study area was between lat. 54°51.5′ and 54°57.9′N, long. 144°55.1′ and 145°11.3′W. On consecutive sets the gill nets were set 1.5-30 km apart to reduce the possibility of one net influencing the catch of another. Gill nets were set along a ship course of 040°, except for the first two nets which were set along 230°. In general, nets drifted 0.4-6.5 km northeastward during the sets.

The vertical location in the gill net (upper, middle, and lower 2 m) and species of each captured salmon were noted as the gill net was hauled aboard. Fish were removed from the gill nets, measured (fork length), and weighed with a beam balance. Stomachs were removed, weighed to the nearest gram with a beam balance, placed in a tray, and cut open with scissors. The fullness of cardiac and pyloric portions of the stomach was estimated visually as a) empty, b) trace amounts (few individual organisms with cumulative weights of a gram or less), c) <⅓ full, d) ⅓-⅔ full, and e) full (rugae fully distended, stomach lining thin and translucent). The degree of digestion was estimated as a) fresh (prey intact, no obvious digestion; fishes and squids with intact skin, euphausiids translucent), b) partially digested (fishes and squids identifiable, their skin, but not flesh, largely digested; euphausiids opaque, appendages often absent), and c) digested (fishes consisting of pieces of white flesh and vertebrae, crustaceans in pieces, euphausiids sometimes identifiable from fragments, especially their eyes).

The percentage composition by volume of prey taxa (euphausiids, amphipods, squids, fishes, salps, pteropods, copepods) was visually estimated for the cardiac and pyloric portions of each stomach. Stratification of food taxa in the cardiac portion was noted. Stomachs with diverse prey taxa were flushed into a petri dish to facilitate identification and estimation of prey compositions. Samples of prey organisms were preserved in Formalin[4] for verification and identification to lower taxa. Stomachs with more than trace amounts of food were then rinsed with water to remove adhering food items, blotted, and reweighed to the nearest gram.

The data were all obtained during the 2-h periods after setting one gill net and hauling the other.

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

RESULTS

Catches of Salmon

A total of 107 sockeye, 68 pink, 51 coho, and 44 chum salmon and 6 steelhead trout were caught in the 12 sets (Table 1). In general, the catches of each species were highest between sunset (2113 h) and sunrise (0420 h). This trend is clearly shown in Table 1. Catches were several times larger during night sets (1957-0627 h, sets 5-9) than sets that fished during daylight periods.

To illustrate diel trends in the vertical distribution of the salmon captured in the gill net, catches of a species were combined (because of the low numbers of individual species caught per set in each vertical section of the net) for afternoon (sets 1-5), night (sets 6-8), and morning (sets 9-12). Figure 1 shows that the average percentage of all species of salmon caught in the upper 2 m of the gill net was highest at night. Moreover, as the lower part of Figure 1 illustrates, peak catches of all species combined occurred at night.

Length-frequency distributions of the four species of salmon from the catches at all sets combined are shown in Figure 2. Fish of several ocean

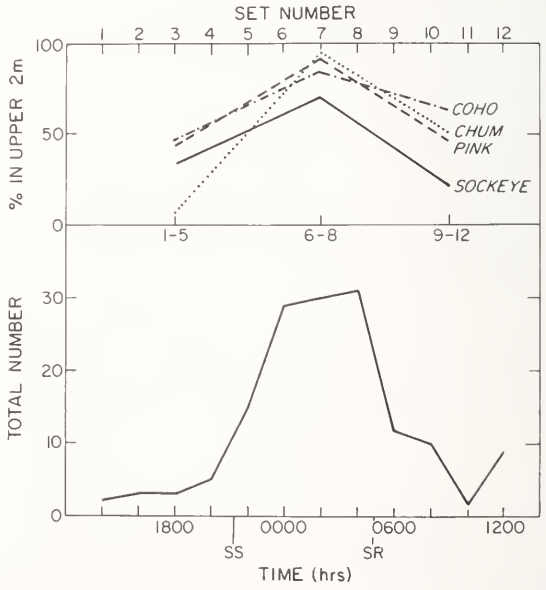

FIGURE 1.— Average percent of the total catch of the four species of salmon caught in the upper 2 m of the gill net during afternoon (sets 1-5), nighttime (sets 6-8), and morning hours (sets 9-12) (upper panel), and the total number of all species of salmon caught in the upper 2 m of the gill nets per set during the 24-h period (lower panel).

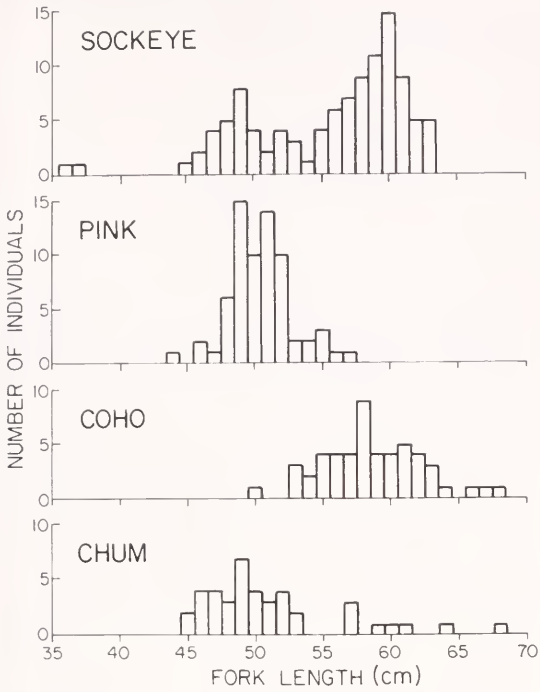

FIGURE 2.—Length-frequency histograms for the four species of salmon caught in the 24-h study.

ages are represented for sockeye and chum salmon. All pink and coho salmon were probably beginning their second year of ocean life. Comparisons of length-frequencies between day (sets 1-4 and 10-12) and twilight and night (sets 5-9) were not significantly different for sockeye, pink, and chum salmon, but were significant for coho salmon (Kolmogorov-Smirnov test, $P < 0.05$). Coho salmon were 2.4 cm larger in the twilight-night sets.

Feeding Habits

Stomach fullness of the four species of salmon, calculated as a percentage of body weight, were usually variable, ranging from 0% (empty) to a maximum of 4% for sockeye, 3.0% for chum, 3.3% for coho, and 2.3% for pink salmon (Fig. 3). Some individuals of all species had empty stomachs during most sets, regardless of time of day. Although ranked differences of the stomach weight:fish weight ratio were not significantly different between day (sets 1-4 and 10-12) and night-twilight (sets 5-9) for each of the four species of salmon (Mann-Whitney U-test, $P > 0.05$), the highest percentages of stomach weight to body weight for sockeye (>3%) and coho and pink salmon (>2%) were obtained from nighttime sets (Fig. 3). Moreover, our visual estimates of stomachs also indicated that full, distended stomachs of sockeye, coho, and pink salmon occurred only at night. There were no suggestions of diel periodicity of stomach fullness for chum salmon, however.

The frequency of occurrence and percent composition of the most common prey taxa (euphausiids, amphipods, squids, fishes) in the cardiac portions of salmon stomachs containing more than trace amounts of food are summarized in Table 2. All species of salmon consumed all of the four major categories of food. The most frequently occurring major taxa was euphausiids in sockeye and coho salmon, amphipods in pink salmon, and "other taxa" (mainly salps, but often unidentified material and sometimes pteropods and polychaetes) in chum salmon stomachs. Amphipods were the second most frequent taxa in

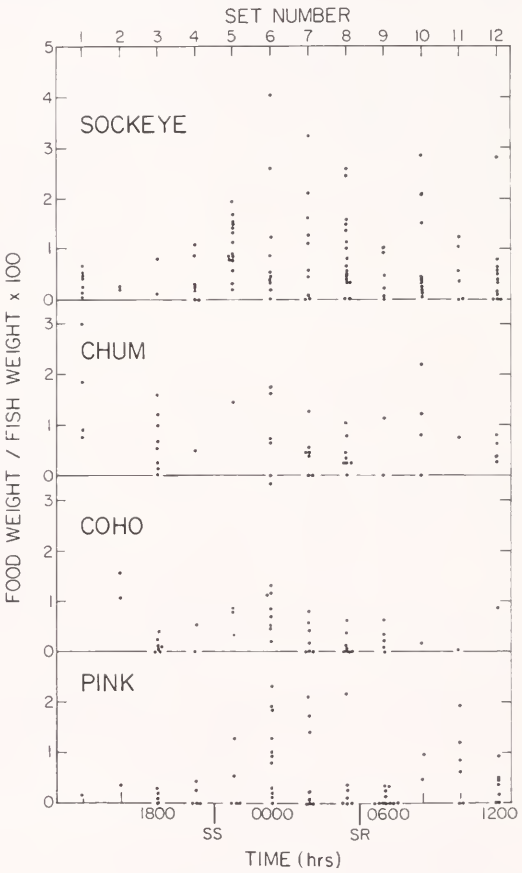

FIGURE 3.—Stomach fullness, expressed as a ratio of food weight to fish weight, for the four species of salmon caught in each of the 12 gill net sets during the 24-h period.

TABLE 2.—Frequency of occurrence and mean percent composition of major prey taxa in the gastric portions of salmon stomachs containing more than trace amounts of food.

		% occurrence					% volume				
	No. of stomachs	Euphausiids	Amphipods	Squids	Fishes	Other	Euphausiids	Amphipods	Squids	Fishes	Other
Sockeye	92	73	40	17	18	17	53	18	9	14	5
Pink	35	49	63	17	17	11	37	35	9	14	4
Chum	27	41	37	4	7	78	29	10	2	4	56
Coho	30	63	33	43	3	0	54	3	39	4	0

sockeye, euphausiids in pink and chum salmon, and squids in coho salmon stomachs.

The same taxa that ranked first and second on a frequency of occurrence basis usually ranked first and second on the basis of mean percent volume. Euphausiids (mainly *Euphausia pacifica* and *Thysanoessa longipes*) were most important for sockeye, pink, and coho salmon; "other taxa" were most important for chum salmon. Amphipods (mainly *Parathemisto pacifica* and *Hyperia medusarum*) ranked second in sockeye and pink salmon. Gonatid squids ranked second in coho stomachs and euphausiids ranked second in chum salmon stomachs. Thus sockeye fed primarily on euphausiids and secondarily on amphipods and myctophid fishes. Pink salmon fed mostly on euphausiids and amphipods. Coho fed mainly on euphausiids and squids, and chum on salps and euphausiids (see Table 2). Squids comprised only 2% of the volume of the stomach contents of chum salmon, and fishes comprised only 4% of the volume for chum and coho salmon. Copepods were not important (<1% of volume) for any species of salmon captured during the study.

Dietary overlap, based on the sum of minimum percentage volumes (percent similarity index, PSI, Sanders 1960) of the four main prey taxa, was 78% between sockeye and pink, 69% between sockeye and coho, and 53% between pink and coho. Because chum salmon had the most unique diet of the four species consuming mainly salps and gelatinous zooplankton, they had overlap values of only 45% with sockeye and pink and 38% with coho.

Although all species of salmon fed on a variety of taxa, individual fish usually contained only a few prey taxa. Only two major prey taxa were found in 85%, 89%, 93%, and 89% of the cardiac portions of sockeye, pink, coho, and chum salmon stomachs, respectively, containing more than trace amounts of food. Most sockeye and pink salmon had only one taxon of food in their stomachs. When salmon had only one food type in their stomachs, it was euphausiids in 65%, 52%, 85%, and 28% of the individual sockeye, pink, coho, and chum salmon, respectively. Euphausiids were obviously the most important prey for sockeye, pink, and coho salmon during this study. They were often the exclusive prey.

Sometimes the contents of the cardiac portion of sockeye and pink salmon stomachs were clearly divided with one type of prey in the anterior and one in posterior portion of the stomach. Generally this "stratification" involved euphausiids and amphipods, or euphausiids and squid. Usually, however, the cardiac and pyloric portions of the stomach had similar percentage compositions of major taxa (excluding empty stomachs and stomachs with trace amounts). Cardiac and pyloric contents were similar for 70% of the sockeye, 72% of the pink, and 60% of the coho and chum salmon. When sockeye and coho had the same prey composition in cardiac and pyloric stomachs, both portions usually contained only euphausiids. When pink salmon had the same prey composition, amphipods or euphausiids were found.

The relative composition of major prey taxa in the stomachs of each species caught in the 12 gill net sets is illustrated in Figure 4 and is discussed below. Open circles in Figure 4 indicate when fresh prey were common, except for amphipods which usually showed little evidence of being digested.

Sockeye Salmon

Prey composition of sockeye salmon had a distinctive diel pattern. Sockeye caught at night (2158-0430 h) contained a high percentage of euphausiids compared with the afternoon and morning sets (Fig. 4). In these night sets, euphausiids averaged over 80% of the volume of the stomach contents, and about 90% of the sockeye contained only euphausiids. Fish caught during and after sunset (1957-0224 h) also contained large numbers of freshly ingested euphausiids. Some fish in set 5 (1957-2227 h) had a clear division between euphausiids in the fore portion and amphipods in the posterior portion of the cardiac

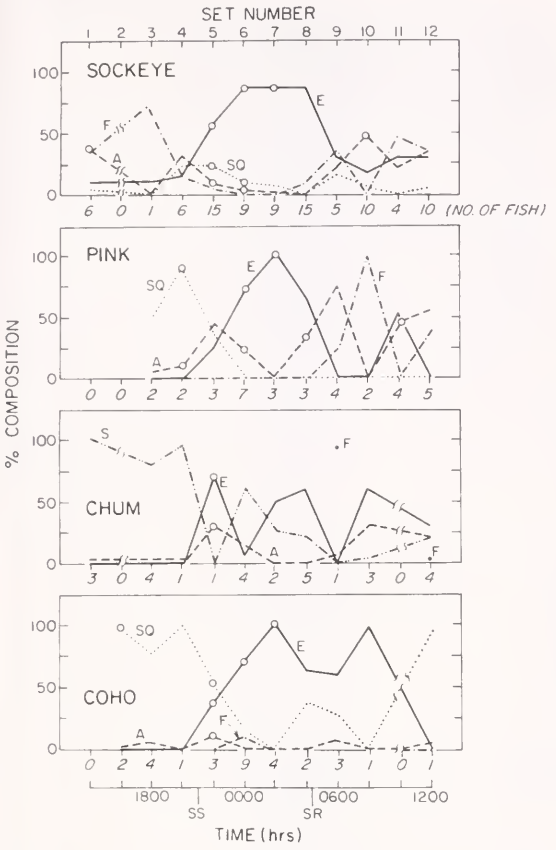

FIGURE 4.—Diel variations in the percent composition of major prey taxa in the stomachs of the four species of salmon containing more than trace amounts of food. E = euphausiids, A = amphipods, F = fishes, SQ = squids, S = salps. Open symbols show when fresh prey was common. The number under each figure indicate the number of fish with more than trace amounts of food in their stomachs. SS = sunset; SR = sunrise.

stomach, indicating a switch from amphipods to euphausiids during dusk. Euphausiids comprised <30% of the food in sets before sunset and after sunrise, and no fresh euphausiids were noted during these daytime periods. Amphipods and fishes formed the highest percentage of the food during daytime. Squids were also eaten by sockeye salmon and were most important during late afternoon and sunset (1800-2227 h) and during sunrise (0350-0627 h). Fresh squids were noted in stomachs of fish caught in sets that fished from 1957 to 0025 h.

Pink Salmon

As with sockeye salmon, euphausiids attained peak importance as prey for pink salmon after sunset (2158-0430 h), when they comprised over 65% of the food and were often in fresh condition. All three fish with over trace amounts of food in the set that fished from 2359 to 0224 h contained 100% euphausiids. Squids and amphipods are most important in the afternoon (1600-2020 h), and fresh squids were found in stomachs of pink salmon caught from 1800 to 2020 h, just before sunset. Fishes and amphipods were the most important prey during the morning daylight period.

Chum Salmon

A diel trend for this species, which fed on a variety of prey taxa, was less obvious than for other species of salmon (Fig. 4). Salps composed over 75% of the stomach contents during the afternoon (1200-2020 h). Euphausiids were the most common prey taxa from sunset to the last set at midday, with the exception of a single chum salmon caught at 2158-0025 h whose stomach contained many salps and a salmon caught at 0358-0627 h whose stomach contained 95% fish. Most euphausiids in the stomachs of fish caught about the time of sunset (1957-2227 h) appeared to be recently ingested. Squids, which were only a minor part of the stomach contents, are not indicated in Figure 4.

Coho Salmon

Coho salmon fed mainly on euphausiids during the night and on squids during the day. Euphausiids were not observed in stomachs of coho salmon during the afternoon but increased in importance from 0 to 100% of the stomach volumes between 1800 and 0240 h (Fig. 4). Most of the euphausiids during this period were in fresh condition. Euphausiids also comprised most (>60%) of the stomach contents during the morning hours (0159-0832 h) but were never fresh. Squids were the most important prey of coho salmon caught during the afternoon-daylight period and in the last set in late morning. Amphipods and fishes were of minor importance.

DISCUSSION

The larger catches of salmon in surface gill nets during twilight-night periods than in daytime periods have three possible explanations: Avoidance of nets during the daytime when visual acuity of salmon is highest, increased swimming

activity in surface water at night compared with daytime, and diel vertical ascent of salmon into near-surface waters at night. The higher catches in the upper 2 m of the gill net at night than day lend support to the last possibility, but not to the exclusion of the other possibilities.

Most other authors favor vertical migration as an explanation for diel peaks in gill net catches (Taguchi 1963; Manzer 1964; Mishima et al. 1966). Birman (1964) noted visual avoidance of "sweep nets" by day, but concluded that salmon migrate into upper waters primarily as a response to vertical movements of their zooplanktonic prey which they feed on during periods of low light intensity, chiefly before dawn.

Swimming activity could also influence catchability, but neither Ichihara et al. (1975) nor Ichihara and Nakamura (1982) found large differences in day-night swimming speeds of chum salmon tagged with ultrasonic transmitters.

The most interesting finding of our study is the distinct diel change in composition of major prey. Stomach contents of sockeye, pink, and coho salmon were comprised largely of euphausiids after sunset and during the night (Fig. 4). The largest number of full stomachs, usually containing only fresh euphausiids, were also found during the nighttime. These three species of salmon preyed intensively on euphausiids at night, often to the exclusion of other types of prey.

This change to feeding on euphausiids was first observed in the salmon caught during the time that the 24-kHz sonic scattering layer ascended into surface waters (Fig. 5). We assume that euphausiids were an important component of this scattering layer (see Suzuki and Ito 1967).

A 1.8 m Isaacs-Kidd midwater trawl collection (three mesh sizes: 70, 11, and 4 mm stretch) in the upper 10 m at night at the 24-h gill net station caught mainly salps and medusae, but euphausiids were abundant (19g/1,000 m^3). Euphausiids were also abundant in a 1.3 m ring net (1.0 mm mesh) towed at the surface after sunset at this station. The most common euphausiids caught were *Euphausia pacifica* and *Thysanoessa longipes*, the same species common in salmon stomachs. *Euphausia pacifica* were found to undertake diel vertical migrations at the Canadian Weather Station located at lat. 50°N, long. 145°W (Marlowe and Miller 1975). Frost and McCrone (1974) also found evidence for diel vertical migration of *E. pacifica* at this location but not for *T. longipes*. The intense predation on euphausiids at night is therefore thought to be related to their dense concentration and increased vulnerability in surface waters after dark.

Most of the studies of the diel periodicity or chronology of feeding in salmon have been juveniles in fresh or coastal waters (Godin 1981). In general, these indicate diurnal or crepuscular feeding patterns for juveniles of pink salmon (Ali 1959; LeBrasseur and Barner 1964; Bailey et al. 1975; Parker and Vanstone 1966; Parker 1969; Godin 1981), chum salmon (Bailey et al. 1975; M. C. Healey as cited in Godin 1981), sockeye (Narver 1970; McDonald 1973; Doble and Eggers 1978), and coho salmon (Mundie 1971). Bailey et al. (1975) concluded that pink and chum salmon fry did not feed during cloudy moonless nights. Nighttime feeding by sockeye apparently occurs during moonlight but not on cloudy or moonless nights in Babine Lake (Narver 1970). Experiments conducted by Brett and Groot (1963) and Ali (1959) indicated that juvenile pink salmon changed their mode of capturing prey below 10^0 mc (meter candle), an intensity where the change from phototopic to scotopic vision apparently occurs, and their feeding activity decreased between intensities of 10^0 to 10^{-4} mc and most ceased between 10^{-3} and 10^{-5} mc. Experiments by Bailey et al. (1975) showed almost no feeding by pink salmon fry at light intensities below 10^1 mc.

In our study, salmon fed intensively on euphausiids at night under an obscured, overcast sky. From the general data given by Brown (1952) and Blaxter (1970) we estimated that the light intensities on this night were between 10^{-3} and about 10^{-5} mc. But, despite these low light intensities, with attendant reduction in contrast of prey and sighting range to prey (Eggers 1977; Anthony 1981), salmon were capable of actively feeding on small, euphausiid-sized prey. At night, larger prey such as squids and fishes are probably encountered less frequently than euphausiids and evade capture more easily because of reduced sighting and tracking ranges of salmon. Euphausiids may not be as capable of active predator evasion and, when abundant in near-surface aggregations at night, are encountered frequently and actively selected. Bioluminescense produced by euphausiids may facilitate detection and capture by salmon. Thus, escape responses and sighting ranges at different light intensities may influence the size and type of prey selected at different times of a diel period.

Machidori (1968) reported that the indices of stomach:body weight of sockeye and chum salmon caught in gill nets that fished different depths

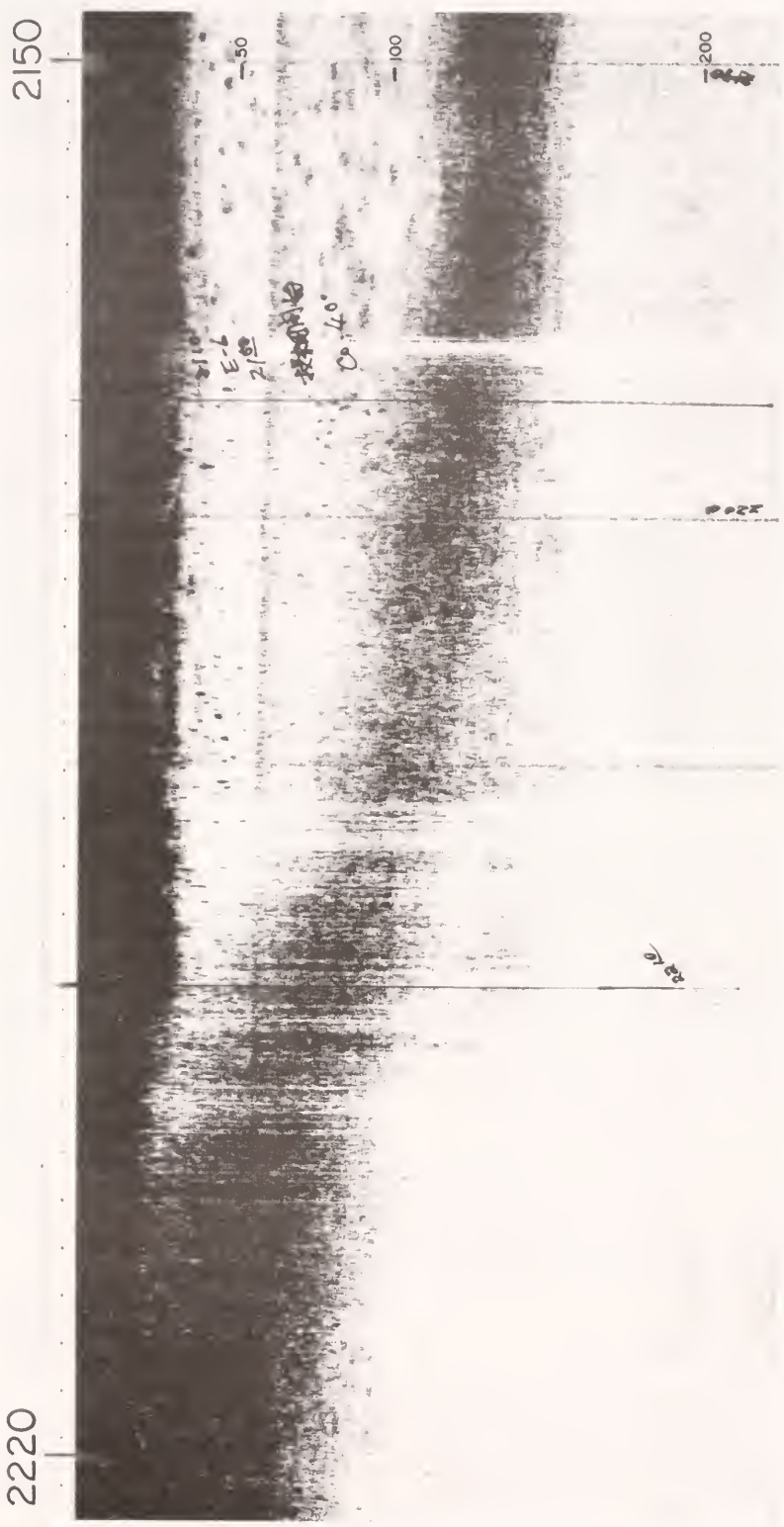

FIGURE 5.—24-kHz echogram from 2150 to 2220 h on 13 July 1981 showing the ascent of a sonic scattering layer into near-surface waters

between 0 and 50 m in the northwestern Pacific were usually highest in near-surface depths by day and below 10 m at night. Euphausiids were an important food taxa only in salmon caught below 10 m during the day. Since average stomach fullness indices were higher during the day than the night, Machidori concluded that light was necessary for salmon to feed. Takagi (1971) reported that surface longlines and gill nets caught salmon during morning and evening, but during the night salmon were caught in gill nets but not by longlines. These observations indicate reduced feeding activity of salmon at night.

Shimazaki and Mishima (1969) concluded from diel trends in the feeding of maturing pink and chum salmon at two locations in the Sea of Okhotsk that feeding activity was high in the evening before and after sunset and low in daytime. They found peak stomach fullness values after sunset. In three of four instances these peak values were the first values after sunset, and may have been the result of crepuscular feeding. In one instance involving pink salmon, however, stomach fullness increased from 1917-2040 h to a peak at 2119-2245 h, indicating active feeding at night. Amphipods, squids, and fishes were the dominant food on a wet weight basis.

Additionally, Ueno et al. (1969) found that pink and chum salmon had full stomachs during the late afternoon as well as after dark in waters off Kamchatka. Suzuki (1970) compared the volume of food in stomachs of chum salmon caught in gill nets off the Kamchatka Peninsula during night (2100-2330 h) and morning daylight hours (0330-0610 h) and concluded that no major differences existed. He found that myctophid fishes always comprised a larger percentage of the stomach contents during the morning and pteropods usually comprised a larger percentage at night.

Thus the above studies plus our own clearly document that salmon are capable of feeding during both day and night periods in oceanic waters. Their feeding behavior is flexible and variable, permitting opportunistic exploitation of a profitable food resource regardless of when it is encountered.

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ARCTIC CHAR PREDATION ON SOCKEYE SALMON SMOLTS AT LITTLE TOGIAK RIVER, ALASKA[1]

GREGORY T. RUGGERONE AND DONALD E. ROGERS[2]

ABSTRACT

Observations of Arctic char feeding on migrating sockeye salmon smolts at Little Togiak River, Alaska, indicate a Type II functional response where the number of smolts consumed increased with smolt abundance. The number of smolts migrating was usually low (<20,000 smolts/24 hours) and the corresponding consumption of smolts averaged 0.8 smolts/char per 24 hours. When large smolt migrations occurred (>80,000 smolts/24 hours), char consumption of smolts generally increased to 5.6 smolts/char per 24 hours. In addition to smolt abundance, smaller smolts and longer char were correlated with an increase in the number of smolts consumed. Estimates of percent smolt mortality, based on two hypothetical char numerical responses to varying smolt abundances, indicate that smolts were migrating at densities most susceptible to predation.

A comparison of length of smolts consumed by char with those in the migration shows that char consumed larger than average smolts when their stomachs were not full and smaller than average smolts when char approached stomach fullness. This may be explained by the migration of larger smolts during the feeding period of char and the possibility of char feeding less effectively when approaching fullness. Although major hatchery releases often exceed 100,000 smolts per day, these data suggest that hatchery-released smolts may be less susceptible to predation in small rivers when released during the night in large numbers (>20,000 smolts/24 hours).

The relationship between predation on juvenile salmon and relevant biological and environmental factors is important to the understanding of salmon population dynamics. Development of these relationships may be useful for establishment of "optimal" escapement levels and for maximum production from salmon enhancement projects. A few investigations have related predation rates to juvenile salmon abundance and have reported up to 85% juvenile mortality (Neave 1953; Hunter 1959; Parker 1968; Peterman and Gatto 1978). Other investigations have examined the effect of biological or environmental variables such as juvenile salmon size (Parker 1971), predator size (Ricker 1941; Hunter 1959; Rogers et al. 1972), infection by parasites (Burke 1978), river velocity and turbidity (Ginetz and Larkin 1976), thermal stress (Sylvester 1972; Coutant 1973), or several variables independent of juvenile salmon density (Fresh et al. 1980). No investigation has analyzed predation while concurrently assessing the partial effect of prey density along with the partial effect of biological and environmental factors.

This investigation represents a 5-yr study of predation by Arctic char, *Salvelinus alpinus*, on emigrating sockeye salmon, *Oncorhynchus nerka*, smolts at Little Togiak River, Alaska (Fig. 1). Predator-prey interaction appears to be especially refined in this river. With the onset of the smolt emigration each spring, char migrate to the interconnecting rivers in the lake system where migrating smolts are most vulnerable (McBride 1979). After the smolt migration ends, char return to their spawning streams in the fall. The objectives of this investigation, which were tested during this brief period of predator-prey interaction, were 1) to empirically model the daily functional response of char (i.e., the relationship between smolt abundance and number of smolts consumed/char per 24-h period (Fig. 2)) while concurrently measuring the effect of biological and environmental variables; 2) to estimate percent smolt mortality in relation to smolt abundance; and 3) to test for disproportional consumption of large or small smolts by char that differ in stomach fullness and fork length.

Numerous biological and environmental variables are likely to influence char predation on salmon smolts. The variables concurrently tested in the functional response model were 1) the number of migrating smolts during the 24-h period prior to sampling the char; 2) the number of migrating smolts during the 24-48 h period prior to sampling; 3) smolt weight; 4) char length; 5)

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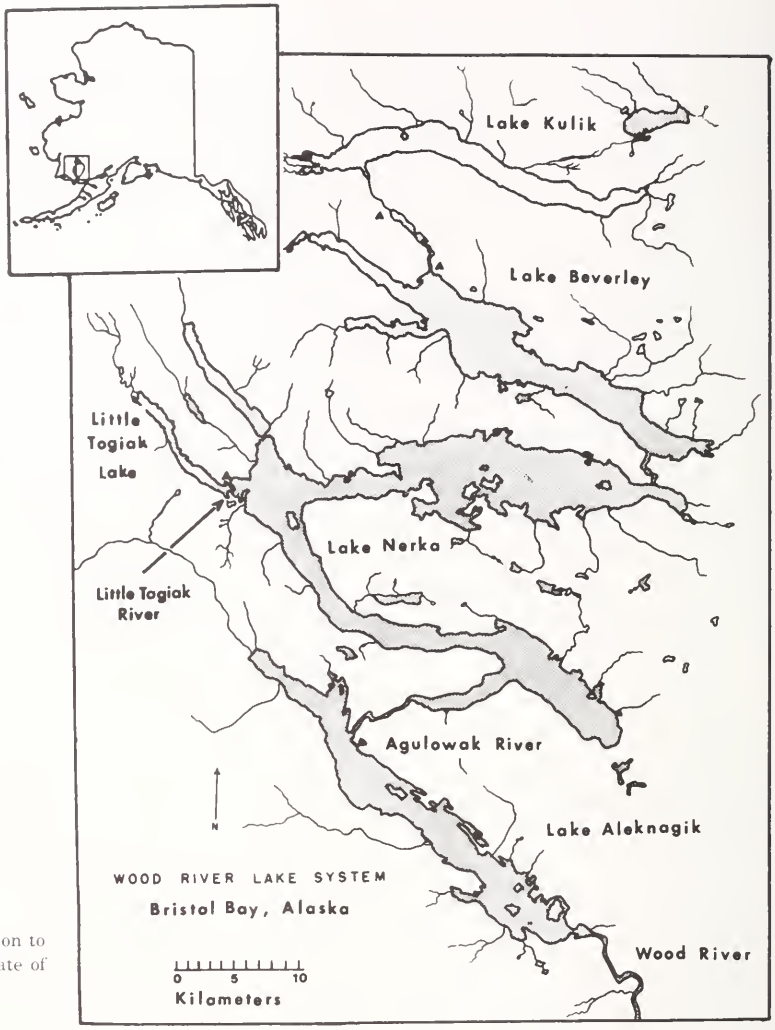

FIGURE 1.—Little Togiak River in relation to the Wood River lake system and the State of Alaska.

number of smolts migrating during the daylight; 6) percent of migration during the daylight; 7) presence of adult sockeye in the river; 8) days after ice-out; 9) river temperature; 10) river depth; 11) light intensity at dusk; and 12) incident solar radiation.

METHODS

Description of Study Site

Little Togiak River is a small nonturbid river located in the Wood River lakes system, Alaska (Fig. 1). River length is about 200 m as it flows from the smaller Little Togiak Lake to the larger Lake Nerka. River width is about 20 m and average depth ranges from about 2 m during spring high water to <1 m during midsummer.

Collection of Char Samples

Arctic char were collected from Little Togiak River from 1976 to 1980. Each year the sampling season began soon after ice breakup (about 7 June) and terminated at the end of the smolt migration near the end of July. About 10 char were collected daily during the morning and/or the evening (shortly before and after the peak smolt migration), and their stomach contents were analyzed within 1 h after capture. Information on the size of smolts consumed and on the population size of char at Little Togiak River was collected only in 1980.

Char were collected by fishing with unbaited

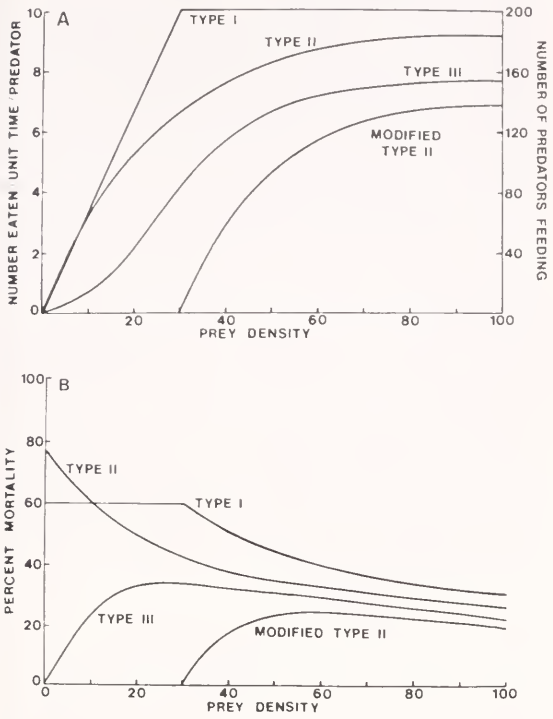

FIGURE 2.—Shapes of different types of hypothetical functional (left ordinate) and numerical responses (right ordinate) (A) and percent mortality curves (B) (redrawn from Holling 1959; Peterman and Gatto 1978).

lures from 1976 to 1979. In 1980, the primary method of char capture was a variable mesh size (5.1, 6.4, 7.6, and 10.2 cm stretch measure), monofilament gill net set across the river and allowed to drift downstream for 15 min. Nonparametic statistical analysis of 99 char caught by hook and line or gill net on the same day indicated no significant difference in char consumption of smolts estimated by each method (Mann-Whitney U-test: $0.10 < P < 0.20$). The collected char were anesthetized with tricaine methane sulfonate (MS-222), then their stomach contents were flushed out by a stomach pump. Examination of stomach contents from sacrificed char showed that about 90% of the smolts were removed by the pump. Before returning the char to the river, we measured the fork length and placed a numbered Dennison flag-type tag just below the dorsal fin. Stomach fullness was estimated visually and categorized as either full or less full.

Consumed Smolt Analysis

Smolts consumed by char were counted and measured after standardizing their length in 10% Formalin[3] for at least 24 h (Burgner 1962). The consumed smolts were measured by one of three methods and converted to fork length using one of the following regression equations (Ruggerone 1981):

1) Fork length (mm) = 0.44 + 1.09 (standard length); $r^2 = 0.99$;
2) Fork length (mm) = 3.70 + 1.37 (pectoral fin to hypural bone plate); $r^2 = 0.98$.

The preferred method of measurement was fork length; the next preferred method was standard length. When neither of these methods was adequate, the length from the pectoral fin insertion to the hypural bone plate was measured. Preserved fork length measurements were multiplied by a factor of 1.042 to convert back to "live" fork lengths (Rogers 1964).

Collection and Enumeration of Migrating Smolts

Migrating smolts were collected and enumerated with a winged-fyke net placed in an area of intermediate, but substantial water flow. Smolts trapped in the "live box" were counted and set free every 4 h during the day (0800-2200 h) and continuously during the major migration period (2200-0200 h). Daily smolt abundance was estimated by multiplying the fyke net counts by a river width factor. Previous experimentation with two fyke nets indicated an even distribution of smolts across the river. At least one sample containing 30 or more smolts was collected each night for length measurements, and when a substantial number of smolts migrated during the day, an additional sample was collected. Samples to determine a length-weight relationship were collected about every 10 d. Fork lengths were measured to the nearest mm and weights to the nearest 0.01 g.

Environmental Data Collection

The water temperature of Little Togiak River was measured to the nearest 0.1°C several times each day. To account for smolt density in the water column, we measured the water level of Lake Nerka as an approximation of the relative water depth in Little Togiak River. The water level was

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

measured continuously with a lake level recorder and calibrated every 2 wk with benchmark measurements in Lake Nerka. To measure the effect of light on the feeding success of char, we measured incident solar radiation continuously with a pyrheliometer. As a qualitative measure of light intensity after sunset, we used a scale from 0 to 4 where 0 represented clear skies with relatively high light intensity and 4 represented low overcast skies with relatively low light intensity.

Data Analysis Procedures

Functional Response of Char

To determine the functional response of char and the effects of other variables on the number of consumed smolts, we grouped the data into 24-h periods with 1200 h as the first hour of the day. The number of smolts consumed per 24 h by an individual char was calculated by the following equation:

$$N = S\left(\frac{24}{D}\right),$$

where N = number of smolts consumed/char per 24 h
S = number of smolts observed in a char stomach
D = digestion time.

Average digestion time (h) was determined from data collected by Meacham and Clark (1979) and calculated by the following curvilinear equation (Fänge and Grove 1979):

$$\ln D = 4.892 - 0.143\,(T),$$

where D = digestion time
T = temperature (°C).

The functional response model based on multiple regression analysis was developed with the SPSS nonlinear program utilizing Marquardt's method of least squares estimation (Marquardt 1963). Residual and partial residual analysis were used to determine which independent variables should be added and the shape of their partial effect curve (Larsen and McCleary 1972; Draper and Smith 1981). This method allows for analysis of each new variable while including the effect of previous variables.

Percent Smolt Mortality

The average number of smolts consumed per char, as described by the functional response, may not represent the entire char population. Char may migrate to the river to feed, then return to the nearby lake environment for several days. Evidence for this behavior stems from gill net catches of char along the nearby lake shore and several underwater observations of relatively few char in the river during midday. Because the numerical response of char is not known, 2% mortality curves were developed from two hypothetical responses. The first percent-mortality curve was based on the assumption that the entire char population of 1,100 fish (Ruggerone 1981) fed each day (Type I numerical response; Fig. 2A). The second curve was based on the assumption that char immigrate to the feeding area in response to smolt abundance, thus a Type II numerical response was assumed (Fig. 2A).

Char Consumption of Smolts by Length

A two-factor analysis of variance with replication (Zar 1974) was used to test for random consumption of smolts by char. We divided the char data into three time periods containing two levels of char stomach fullness (full or less full) and three sublevels of char length (295-445 mm; 446-470 mm; 471-502 mm). To concurrently compare the length of smolts consumed by char with those smolt lengths available in the migration, we calculated the difference between average length of smolts consumed and average length of smolts available. This difference was utilized in each level of analysis.

RESULTS

Char Functional Response

Nonlinear regression analysis indicated that 4 of the 12 variables tested affect the number of smolts consumed/char per 24 h. The most important of these variables was the number of smolts migrating during the previous day's migration (approximate partial F, $P < 0.01$). The next important variable was the average weight of migrating smolts ($P < 0.01$), then the number of smolts migrating during the day of capture ($P < 0.01$), and finally char length ($P \leq 0.08$). The amount of variability explained by all four variables was 59% and the standard deviation was ± 0.8 smolts

consumed/char per 24 h. Other variables such as the number of smolts migrating during the daylight, the percent of smolts migrating during the daylight, the presence of adult sockeye, days after ice-out, river temperature, incident solar radiation, light intensity during the evening as a function of cloud cover, and river depth as a function of lake level did not add any new information.

The model describing char consumption of smolts has the following form:

$$N = a + b(1 - e^{-cP}) + de^{W} + f(1 - e^{-gC}) + hL^{3.02}$$

where a, b, c, d, f, g, h = empirical constants
N = number of smolts consumed/char per 24 h
P = number of smolts during previous migration
W = smolt weight
C = number of smolts during day of capture migration
L = char length.

A graphical interpretation of the empirically derived model is shown in Figure 3. Confidence intervals about each curve are difficult to interpret because they do not consider the concurrent value of other parameters (Draper and Smith 1981) and are not shown. Instead, a plot of smolts consumed by char versus the number of smolts migrating in the previous day's migration demonstrates the initial variability and the basis for the model (Fig. 4). The average predicted consumption rate was 0.8 smolts/char per 24 h and the maximum was 5.6 smolts/char per 24 h. These predictions were similar to the observed average and maximum consumption rates of 0.8 and 6.0 smolts/char per 24 h.

The functional response of char was best described as a Type II response and was separated into two curves: consumption of smolts versus smolt abundance during the day of char capture and consumption of smolts versus smolt abundance during the previous day (Fig. 3A). Two curves were needed because most char digestion times were longer than 24 h. Thus, the predicted number of smolts consumed/char per 24 h was an average based on 2 successive days of feeding. The maximum partial effect of smolt abundance on the char consumption rate was about 3.7 smolts/char per 24 h when other variables were held at their mean values.

Smaller smolts and larger char were associated with increased consumption rates by char. Consumption of smolts increased exponentially with

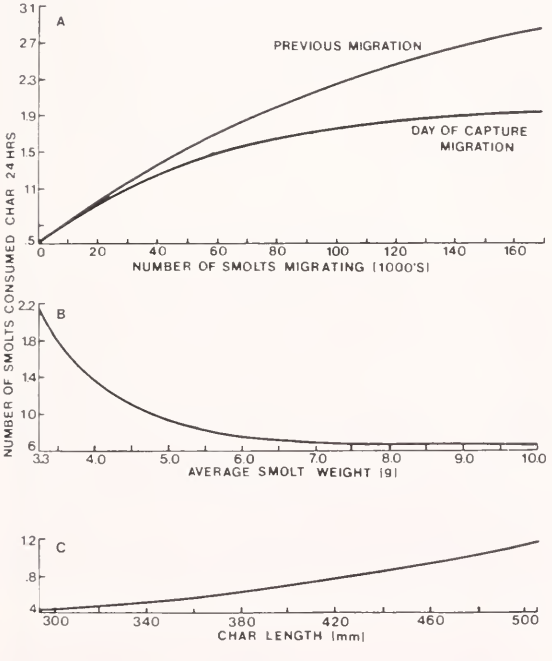

FIGURE 3.—The partial effect of the previous day's migration, the day of capture migration (A), average smolt weight (B), and Arctic char fork length (C) on the number of smolts consumed/char per 24 h. Smolt consumption was calculated by setting the alternate variables to their mean value.

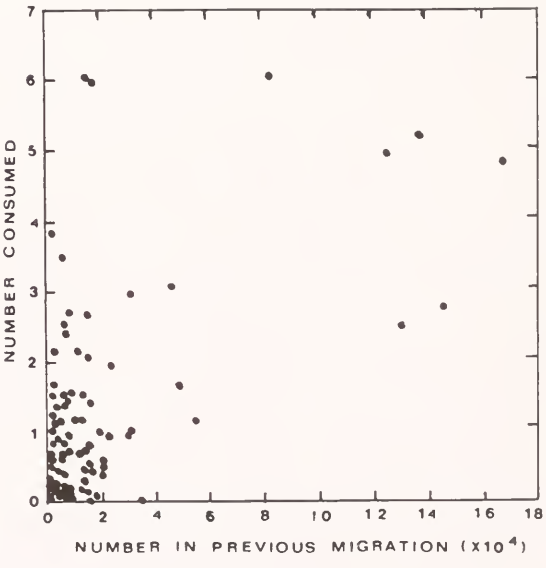

FIGURE 4.—Smolt consumption/Arctic char per 24 h in comparison with smolt abundance during the previous day's migration.

lighter smolts and increased curvilinearly with longer char (Fig. 3B, C). The maximum increase in char consumption of smolts due to changes in smolt weight and char length was about 1.4 and 0.8 smolts/char per 24 h, respectively.

The predicting power of this model is weak at high consumption rates by char. This problem arises from increasing residual variability as the predicted value increases. Increasing residual variability is usually corrected by using a weighting factor; however, when applied, the only data points carrying weight were those near the origin and any relationship between the variables was lost. Linear models were attempted, but did not approach the fit of the nonlinear model. Thus, at high rates of consumption by char, the model is best used for descriptive purposes.

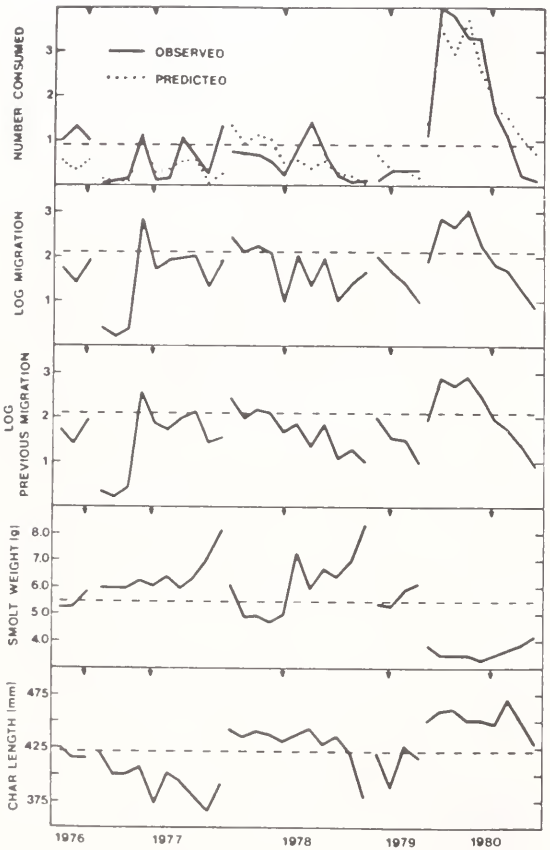

FIGURE 5.—Comparison of observed and predicted smolt consumption/Arctic char per 24 h with smolt abundance, average smolt weight, and char length during each sampling year. Data grouped into 3- to 5-d sampling periods. Dash line indicates mean value for all years. Log smolt abundance calculated from hundreds of smolts migrating. Arrows indicate entry of adult sockeye salmon in to Little Togiak River.

Comparison of consumption rates by char between years demonstrates the large variability that may be explained by smolt abundance, smolt weight, and char length (Fig. 5). During 1980 there were more than three times the number of migrating smolts, the weight of smolts was 30-50% less, and length of char was 24-68 mm greater than in any of the previous years. The combined effects of these variables resulted in a relatively large number of consumed smolts per char, which was also predicted by the model.

Percent Smolt Mortality

Two different percent smolt mortality curve types were produced from the two hypothetical numerical responses (number feeding) and the estimated consumption rates of char. A Type II curve (Fig. 2B) exhibiting an inverse relationship between percent smolt mortality and smolt abundance was produced from the assumption that all 1,100 char fed each day (Fig. 6A). Smolt mortality ranged from 0 to 100% when the number of migrating smolts was $<$ 6,750 smolts/24 h and $<$15% when the number of migrating smolts exceeded 20,000 smolts/24 h. A Type III percent mortality curve was produced from the assumption that the number of char feeding varied with smolt abundance (Fig. 6B). Although variability exists, percent mortality increased at low smolt abundances ($<$20,000 smolts/24 h), then decreased after char became overwhelmed and/or satiated[4] by smolts.

Char Consumption of Smolts by Length

The comparison of mean lengths of smolt consumed by char with mean length in the migration indicates that less full char consumed larger than average smolts ($\bar{d}$ = 1.7-2.9 mm, α = 0.05; Fig. 7). Char with full stomachs consumed smolts that were not different than the average length in the migration ($\bar{d}$ = $-$0.1-0.6 mm, α = 0.05). The length of char did not have a significant effect on the length of smolt consumed.

The comparison of length of smolts consumed in each stomach fullness category with the length

[4]During days of large smolt migrations, the number of smolts observed in individual char ranged from 0 to 45 smolts (not corrected by digestion period). Because of this variability in consumption, it is difficult to determine whether the char were overwhelmed by smolt abundance or satiated. This observed variability in consumption may be due to individual char migrating from the local lake area to the river at different times, thereby causing variable feeding durations.

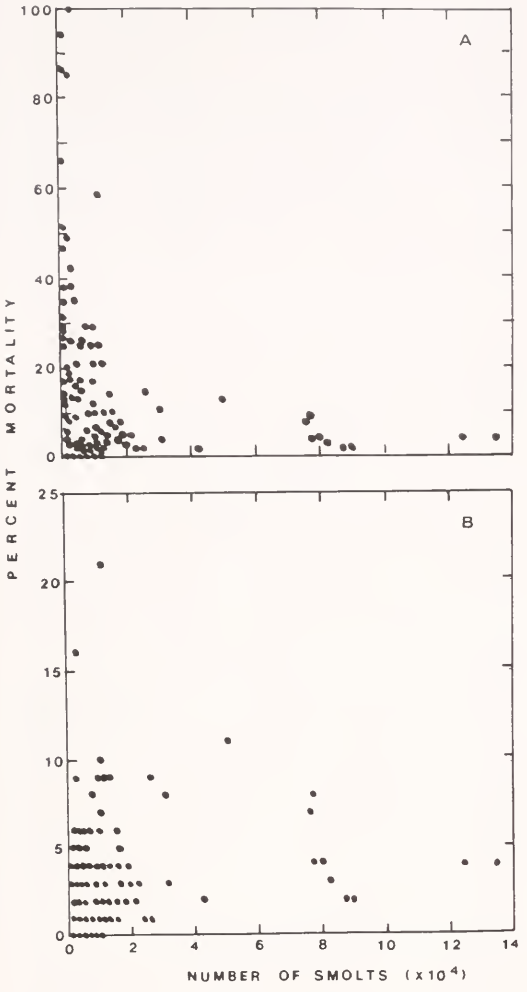

FIGURE 6.—Percent mortality at various levels of smolt abundance. (A) Entire population of 1,100 Arctic char fed each day; (B) number of feeding char equaled $1{,}100\,(1 - e^{-0.00004M})$, where M = number of migrating smolts.

distribution of smolts in the migration indicates the vulnerability of the smallest and largest smolts (Fig. 7). The large peaks represent age I smolts and the smaller peaks to the right are age II smolts. In each of the three time periods, the distribution of smolts from full char was consistently broader than the distribution of smolts in the migration, indicating that smolts average in length have a greater probability of escaping predation. The length distribution of smolts consumed by less full char was also broader than the distribution of smolts in the migration, but was skewed to the right. Thus, a greater proportion of age II smolts was consumed by less full char and to a lesser extent by full char than proportionately available in the migration.

When smolts consumed by full and less full char were combined, the average consumed smolt length was significantly larger than the average length from the migration ($\bar{d}$ = 0.1-1.1 mm, α = 0.05); however, the length distribution of the consumed smolts was similar to the smolt length distribution from the full char. This was due to the large proportion of smolts consumed by full char.

DISCUSSION

Char Functional Response

The functional response of char at Little Togiak River was similar to those reported for other salmon predators in one aspect (Ricker 1941; Cameron 1958; Hunter 1959; MacDonald *in* Foerster 1968). Because smolt abundance was usually low, char normally operated at the low end

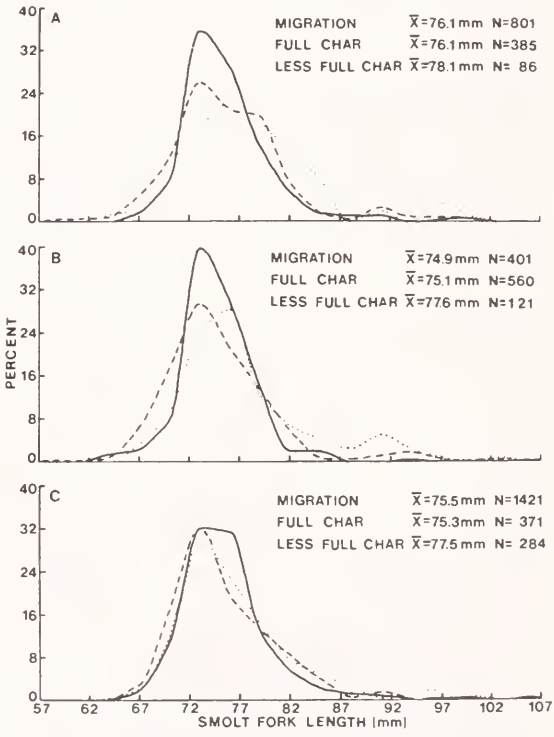

FIGURE 7.—Length distribution of smolts in the migration and in Arctic char stomachs according to stomach fullness. Solid line refers to smolts in the migration, dash line refers to smolts from full char, and dotted line refers to smolts from less full char. Sampling period from 9 to 16 June (A), 16 to 20 June (B), and 20 June to 17 July (C).

of their functional response where smolts could potentially be more vulnerable. Contrary to results of Ricker (1941) and Cameron (1958), consumption rates by char were proportional to smolt abundance and smolts did not find refuge at low migration numbers. On occasion (primarily in 1980) smolt abundance was great and consumption rates of char were disproportionately low, a response observed by Neave (1953). Thus, char at Little Togiak River exhibited a Type II functional response where vulnerability of smolts to predation may be greater at lower migration densities. This increased vulnerability ultimately depends on the numerical response of char to smolt abundance.

The inclusion of smolt weight and char length in the functional response multiple regression model further described important variables that influence char predation, as well as reducing within- and between-year variability. The exponential increase in consumption rates by char during migrations of smaller smolts is probably due to more smolts needed to decrease feeding activity and a greater ease in capturing small smolts. Because juvenile salmon growth is density dependent (i.e., smaller smolts at greater densities; Rogers 1968), increased consumption during migrations of smaller smolts may act to cancel the proportionately lower consumption rates of char at greater smolt abundances. Thus, it is important to test concurrently the effect of smolt weight and smolt density when describing the functional response of char.

The relationship of char length to consumption of smolts by char was best described by the allometric conversion (Moriarty 1977) of char length to char weight. According to regression analysis, the significance of char weight (as converted from char length) is questionable; however, char length was included in the model because it seems reasonable that a larger predator would require more food and may be able to capture mobile prey easier than a smaller predator. Rogers et al. (1972) reported larger char consumed more smolts than smaller char.

The average number of smolts consumed per char, as predicted by the model, was 0.8 smolts/24 h, and the maximum was 5.6 smolts/24 h. These values were corrected for smolt weight and char length. The low average of consumed smolts reflects the low number of smolts that generally migrate. The predicted maximum of 5.6 smolts/char corresponds quite well with the observed maximum of 6.0 smolts/char per 24 h. These estimates are lower than the average and maximum consumption rates by char at the Agulowak River (3.4, 8.4 smolts/char per 24 h, respectively) calculated from weekly estimates (Meacham and Clark 1979). This difference between the two rivers may be explained, in part, by the larger char size (Moriarty 1977) and the probable extension of the daily migration period at the Agulowak River, which is a large river that intercepts smolts from several lakes in the Wood River system.

Percent Smolt Mortality

The shape of a percent-mortality curve can provide valuable information on the stability characteristics of a salmon population (Peterman 1977) and provide information to a hatchery manager planning to release smolts. For example, percent smolt mortality could vary as in a Type III or modified Type II curve where smolt mortality increases up to a certain threshold density of smolts before decreasing. In this example, a hatchery manager should release smolts at densities greater than the threshold density.

Results from this investigation indicate the char numerical response (number feeding) may influence the type of percent-mortality curve. If the char numerical response is constant, then percent mortality will decrease as more smolts migrate. However, if the numerical response of char varies with smolt abundance, as we suspect, then percent mortality may increase with more smolts up to a threshold density. Beyond this threshold density, percent mortality decreases. The importance of the percent-mortality curve is to indicate the smolt density at which mortality is minimized. Smolts at Little Togiak River experience less risk of predation at daily migration abundances of about 20,000 smolts or greater. However, migration densities of this magnitude were rare.

Char Consumption of Smolts by Length

Char with less full stomachs contained smolts that were, on average, significantly larger than those in full char and those in the migration. A plausible explanation for the greater average smolt length in less full char than full char involves the effect of hunger on feeding behavior. Char containing only a few smolts may be hungry and aggressive (Ware 1972), which may induce a high success rate when feeding on the larger, more mobile smolts. When char approached stomach fullness, their hunger and aggressiveness may

have been lower, thereby reducing their success rate when attacking the larger smolts in the migration.

The larger smolts in less full char as compared with average smolt length in the migration may be due to the relationship between light intensity, migrating smolt size, and decreased feeding activity by char during the darkest portion of the night. Smolts migrating at night were significantly shorter than those migrating during the day (Ruggerone 1981; Burgner 1962; Aspinwall 1963). Feeding activity of char was observed to decrease substantially during the darkest 1-2 h of the night (often char would leap from the water while feeding). Also, hook and line fishing with lures was notably less effective during darkness. Therefore, the difference in average length of smolts consumed by less full char and those in the migration resulted from a decrease in smolt consumption when smolts in the migration were smaller. These results indicate that predation may be reduced by releasing hatchery salmon during the night.

The difference between smolt length in all char and length in the migration was relatively small. In part, this was due to the large proportion of smolts observed in full char, which was related to high smolt abundance. Because fewer char will reach stomach fullness during years of fewer smolts, the difference between length of smolts consumed and length in the migration is likely to be greater.

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FEEDING ECOLOGY OF WALLEYE, *STIZOSTEDION VITREUM VITREUM*, IN THE MID-COLUMBIA RIVER, WITH EMPHASIS ON THE INTERACTIONS BETWEEN WALLEYE AND JUVENILE ANADROMOUS FISHES[1]

The walleye, *Stizostedion vitreum vitreum*, is widely distributed in the United States and Canada and has been studied throughout most of its native range (Colby et al. 1979). The walleye is exotic to the Pacific Northwest and its biology here has not been fully investigated. The exact circumstances of walleye introduction into the Columbia River system are not documented; however, this piscivorous, cool-water fish is found throughout the mid-Columbia River (Fig. 1) and downstream of Bonneville Dam (Durbin[2]). As populations of walleye in the Columbia River have increased and their range extended, interest in them has focused on the potential sport fishery for walleye and on the impact of walleye on native salmonid populations (Carlander et al. 1978; Brege 1981).

[1]Technical Paper No. 6722, Oregon Agricultural Experiment Station, Oregon State University, Corvallis, Oreg.

[2]Durbin, K. 1977. News column. Oregon Department of Fish and Wildlife, Portland, Oreg.

FIGURE 1.—Map of the lower and mid-Columbia River showing the locations of the major dams and the John Day pool study area where walleye were collected during 1980 and 1981.

Construction of dams has transformed the Columbia River into a series of low velocity impoundments with physical characteristics (Table 1) that are well suited for walleye (Colby et al. 1979). Thus, the Columbia River fits the model for ideal walleye habitat proposed by Kitchell et al. (1977). This transformation has increased the time required for emigration of juvenile salmonids and increased their mortality partly due to increased predation (Raymond 1979).

The purpose of this study was to describe the spring and summer feeding ecology of walleye in the John Day pool of the Columbia River. Emphasis was placed on walleye interaction with juvenile salmonids and young-of-the-year American shad, *Alosa sapidissima*, an anadromous fish that is morphologically and behaviorally similar to outmigrant salmonids and is abundant in the Columbia River in the late summer. We concentrated on seasonal variation in walleye diets, diel feeding periodicity, and food selection as influenced by walleye size. Preliminary findings regarding the spring diets of these walleye were reported by Maule (1982).

TABLE 1.—Summary of limnological data for the John Day pool of the Columbia River, from Hjort et al. (1981). All data collected in August 1979, except for surface temperatures, which were taken in 1981.

Characteristic	Range for John Day pool	Range for study area
Water velocity (m/s)	0.1 - 1.4	0.5 - 1.4
Secchi depth (m)	1.0 - 2.2	1.5 - 1.7
Dissolved O_2 (ppm) surface-bottom	16.0 - 8.0	14.0 - 10.0
Average surface temperature Apr.-July-Sept. (maximum)	7.0°-24.5°-20.5(24.8°)°C	
Temperature profile surface-bottom	22.0° - 20.8°C	21.0° - 21.0°C
Pool width (km)	0.8 - 4.2	0.8 - 1.8
Midpool depth (m)	11 - 48	11 - 20
Pool length (km)	≈120	23

Methods

We collected walleye for this study in the first 23 km of the John Day pool immediately downstream from McNary Dam on the Columbia River (Fig. 1) from 2 April to 30 September 1980 and from 30 March to 30 September 1981. During each month we attempted to collect a minimum of 10 walleye during each of four generalized times of day: dawn, midday, dusk, and night. In 1980 we captured

walleye with either a 38.1 × 1.8 m sinking gill net with multifilament, variable, stretched mesh of 3.81, 5.08, 6.35, 7.52, and 10.16 cm, or a 76.2 × 3.7 m monofilament, floating gill net with 15.25 cm stretched mesh. All gill net sets were set at a maximum of 2.5-h duration in order to minimize regurgitation or digestion of stomach contents of the walleye. In 1981 we used gill nets and a 6.15 m electroshock boat with a 3,500-W generator and front mounted electrodes utilizing pulsed direct current at 1-4 A. Potential prey fish were periodically sampled with a 30.48 × 2.44 m beach seine of 6.35 mm stretched mesh. When we caught potential prey by means of gill nets, seines, or electroshock gear, we recorded numbers and fork lengths by species. Gear selectivity prohibited reliable estimates of numerical abundance of species, however, we used catch per unit of effort (CPUE) to estimate change in intraspecific abundance through time.

For each walleye captured, we recorded fork length (FL, mm), weight (g), sex, and stage of maturity, took scale samples, and preserved the stomach in 10% buffered Formalin[3]. Subsequently, each stomach was examined and each prey item was identified to the lowest possible taxon and its volume was recorded. A reference bone collection of potential prey species aided in the identification of partially digested prey. The most useful bones were pharyngeal teeth, opercles, preopercles, and jaw bones. Characteristics of the internal morphology, e.g., the black peritonium of bridgelip suckers, *Catostomus columbianus*, or the number of pyloric ceca in salmonids (Scott and Crossman 1973), were also useful in identifying prey items.

We separated stomach content data into subpopulations based on season and year of capture, and tested for statistically significant differences in numbers and volumes of individual prey items. We computed statistical significance using a nonparametric, multivariate test, $L_{N,t}$, which has approximately a chi-squared distribution with $p(v-1)$ degrees of freedom, where p is the number of conditions (prey taxa) and v is the number of populations (Koch 1969). To identify changes in the importance of food items we examined changes in the Index of Relative Importance (IRI), which is equal to the sum of the percent by volume and the percent by number, multiplied by the percent frequency of occurrence (Pinkas et al. 1971).

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

Results

Seasonal Diet

The walleye size ranges were similar for both years, about 200-750 mm FL (Fig. 2). In both years fish accounted for over 99% of the total prey volume (Tables 2, 3). Based on IRI (Table 4), prickly sculpin, *Cottus asper*, was the most important species found in walleye stomachs. Excluding un-

TABLE 2.—Percent by volume, percent by number, and percent frequency of occurrence of foods found in the stomachs of walleye collected in the John Day pool of the Columbia River April-September 1980. Sample size equals 189 walleye, with 38.1% empty stomachs. (Raw data are in parentheses.)

Prey taxon	% volume (ml)[1]	% number[1]	% occurrence
Salmonidae (juvenile)	5.5 (89)	8.7 (22)	12.8 (15)
Oncorhynchus tshawytscha	1.7 (27)	2.7 (7)	8.5 (10)
Unidentifiable Salmonidae	3.8 (62)	6.0 (15)	4.3 (5)
Castostomidae	39.4 (638)	6.0 (15)	12.0 (14)
Catostomus columbianus	7.3 (118)	2.0 (5)	4.3 (5)
C. macrocheilus	12.8 (200)	1.2 (3)	2.6 (3)
Unidentifiable Catostomidae	19.3 (320)	2.8 (7)	5.1 (6)
Cyprinidae	15.2 (247)	5.6 (14)	12.0 (14)
Acrocheilus alutaceus	2.2 (36)	3.2 (8)	6.8 (8)
Mylocheilus caurinus	11.8 (192)	1.2 (3)	2.6 (3)
Ptychocheilus oregonensis	0.4 (6)	0.4 (1)	0.9 (1)
Unidentifiable Cyprinidae	0.8 (13)	0.8 (2)	1.7 (2)
Miscellaneous fishes	40.0 (646)	75.4 (190)	85.6 (101)
Cottus asper	33.7 (544)	30.6 (77)	32.5 (38)
Lampetra spp	0.1 (2)	0.4 (1)	0.1 (1)
Alosa sapidissma (juvenile)	1.9 (30)	9.9 (25)	7.7 (9)
Unidentifiable	4.3 (70)	34.5 (87)	45.3 (53)
Invertebrates	0.04 (0.7)	4.4 (11)	7.7 (9)
Ephemeridae	0.03 (0.56)	2.4 (6)	5.1 (6)
Chironomidae	<0.01 (0.04)	1.2 (3)	0.9 (1)
Talitridae	<0.01 (0.05)	0.4 (1)	0.9 (1)
Gammaridae	<0.01 (0.05)	0.4 (1)	0.9 (1)

[1]Volumes and numbers of individual prey taxa were significantly different from those of 1981 ($P < 0.005$).

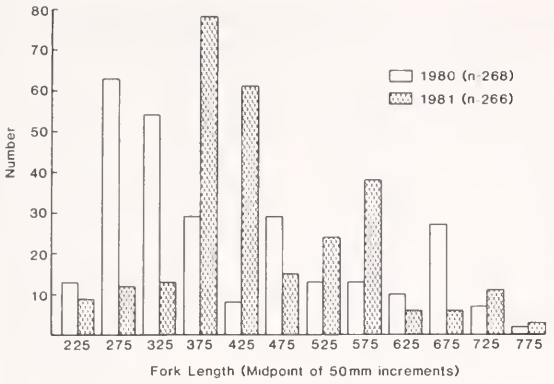

FIGURE 2.—Length-frequency distribution of walleye collected from the John Day pool of the Columbia River, April through September 1980 and 1981.

identifiable fish remains, the next most important foods were catostomids (largescale suckers, *Catostomus macrocheilus*, and bridgelip suckers) and cyprinids (primarily chiselmouth, *Acrocheilus alutaceus*, and peamouth, *Mylocheilus caurinus*). These species are generally associated with the benthos (Scott and Crossman 1973; Wydoski and Whitney 1979). In 1980, juvenile salmonids, primarily chinook salmon, *Oncorhynchus tshawytscha*, and juvenile American shad were equal to cyprinids in importance; however, in 1981, the importance of salmonids and shad was greatly reduced (Table 4).

All statistical tests were conducted with foods at the lowest taxon, and the data for individual species are presented in Tables 2, 3, and 4; however, in the interest of concise reporting we discuss results based on the following groups: catostomids, cyprinids, salmonids, cottids, shad, and invertebrates. Numbers and volumes of individual prey were significantly different between 1980 and 1981 ($P < 0.005$); to further investigate these differences, we tested for seasonal variation within and between years. We found no significant difference in numbers or volumes of prey between spring (April-June) 1980 and spring 1981 ($P > 0.25$); however, there were significant differences in diets (numbers and volumes) between summer (July-September) 1980 and summer 1981 ($P < 0.05$) and between the spring and summer of each year ($P < 0.01$).

We examined seasonal changes in IRI to detect which prey could account for significant differences in walleye diet (Table 4). From 1980 to 1981 there is a reduction in the importance of salmonids, cottids, and shad, and an increase in importance of catostomids, cyprinids, and invertebrates. Seasonal changes are not consistent; however, there are reductions in importance of cottids, increases in importance of cyprinids, and no changes in importance of invertebrates from spring to summer each year. Our CPUE data (Table 5) reflect annual and seasonal changes in the abundance of juvenile shad, juvenile

TABLE 3.—Percent by volume, percent by number, and percent frequency of occurrence of foods found in the stomachs of walleye collected in the John Day pool of the Columbia River, April-September 1981. Sample size equals 236 walleye, with 39.0% empty stomachs. (Raw data are in parentheses.)

Prey taxon	% volume (ml)[1]	% number[1]	% occurrence
Salmonidae (juvenile)	3.6 (62)	4.4 (14)	7.0 (10)
Oncorhynchus tshawytscha	2.8 (48)	3.2 (10)	1.4 (2)
Unidentifiable Salmonidae	0.8 (14)	1.2 (4)	5.6 (8)
Castostomidae	32.5 (563)	11.4 (36)	18.1 (26)
Catostomus columbianus	11.6 (201)	2.5 (8)	4.2 (6)
C. macrocheilus	1.2 (21)	0.6 (2)	1.4 (2)
Unidentifiable Catostomidae	19.7 (321)	8.3 (26)	12.5 (18)
Cyprinidae	34.1 (590)	13.0 (41)	25.7 (37)
Acrocheilus alutaceus	28.3 (490)	5.7 (18)	11.1 (16)
Mylocheilus caurinus	1.8 (32)	2.5 (8)	5.6 (8)
Ptychocheilus oregonensis	1.7 (30)	1.6 (5)	2.8 (4)
Cyprinus carpio	0.3 (6)	0.3 (1)	0.7 (1)
Carassius auratus	0.5 (8)	0.6 (2)	1.4 (2)
Unidentifiable Cyprinidae	1.5 (24)	2.3 (7)	4.1 (6)
Miscellaneous fishes	29.3 (508)	58.2 (184)	77.8 (112)
Cottus asper	22.5 (390)	25.6 (81)	36.8 (53)
Alosa sapidissma (juvenile)	0.1 (1)	0.3 (1)	0.7 (1)
Ictaluridae	0.2 (4)	0.3 (1)	0.7 (1)
Unidentifiable	6.5 (113)	32.0 (101)	39.6 (57)
Invertebrates	0.5 (8.23)	13.0 (41)	11.1 (16)
Ephemeridae	0.3 (5.98)	12.0 (38)	10.4 (15)
Chironomidae	0.01 (0.20)	0.3 (1)	0.7 (1)
Gammaridae	<0.01 (0.05)	0.3 (1)	0.7 (1)
Astacidae	0.1 (2.00)	0.3 (1)	0.7 (1)

[1]Volumes and numbers of individual prey taxa were significantly different from those of 1980 ($P < 0.005$).

TABLE 4.—Index of Relative Importance (IRI) (Pinkas et al. 1971) of foods found in spring (April through June) and summer (July through September)

Prey taxon	1980 Combined[1]	Spring	Summer
Salmonidae	182 (1.7)	293 (2.5)	148 (1.2)
Oncorhynchus tshawytscha	37 (0.9)	99 (1.7)	104 (2.4)
Unidentifiable Salmonidae	42 (1.0)	51 (0.9)	4 (0.1)
Catostomidae	545 (5.0)	548 (4.6)	749 (6.1)
Catostomus columbianus	40 (0.9)	12 (0.2)	121 (2.7)
C. macrocheilus	36 (0.8)	12 (0.2)	66 (1.5)
Unidentifiable Catostomidae	113 (2.6)	226 (3.9)	37 (0.8)
Cyprinidae	250 (2.3)	98 (0.8)	491 (4.0)
Acrocheilus alutaceus	37 (0.8)	2 (<0.1)	162 (3.7)
Mylocheilus caurinus	34 (0.8)	62 (1.1)	16 (0.4)
Ptychocheilus oregonensis	1 (<0.1)		4 (0.1)
Other Cyprinidae	3 (0.1)		6 (0.1)
Miscellaneous fishes	9,879 (90.7)	10,859 (91.5)	10,795 (88.3)
Cottus asper	2,090 (48.6)	3,621 (62.8)	1,335 (30.7)
Alosa sapidissma	91 (2.1)		480 (11.1)
Other (unidentifiable fish; *Lampetra* spp., Ictaluridae)	1,784 (41.3)	1,677 (29.0)	2,012 (46.4)
Invertebrates	34 (0.3)	74 (0.6)	40 (0.3)

[1]IRI's are not additive across columns.

TABLE 5.—Catch-per-unit-effort (CPUE) for various juvenile (Juv.) and adult fishes caught in the John Day pool of the Columbia River, April-September 1980-81.

Seines

Dates	Effort Sets	CPUE Juv chinook	Juv shad	Juv peamouth
Apr.-Jun. 1980	45	16.65	0	0
Apr.-Jun. 1981	37	10.70	0	0
Jul.-Sept. 1980	35	2.65	92.76	6.88
Jul.-Sept. 1981	39	1.36	42.87	5.77

Gill nets

Dates	Hours	Chiselmouth	Largescale sucker	Bridgelip sucker
Apr.-Jun. 1980	122	0.23	0.86	0.40
Apr.-Jun. 1981	212	0.32	0.90	0.67
Jul.-Sept. 1980	330	0.37	0.54	0.74
Jul.-Sep. 1981	154	0.31	0.84	0.61

peamouth, and juvenile chinook salmon. However, Sims et al. (1982) reported no significant seasonal differences in the estimated numbers of juvenile salmonids emigrating past the John Day Dam (53,000 and 44,000 daily from 21 April to 30 June and from 1 July to 28 September 1981, respectively), 90 km downstream of our study area. Similar estimates are not available for 1980, but the smolt emigration past the John Day Dam was estimated at 8.3 million (Sims et al. 1981) and 7.7 million (Sims et al. 1982) in 1980 and 1981, respectively. Unfortunately cottids, the most important food, were rare in our CPUE data for 1980, and in 1981, the electroshock CPUE was <0.1, a level too low to detect changes.

Seasonal shifts in walleye diets are often the result of high spring-time availability of aquatic insects and/or increased availability of prey fish in the summer (Eschmeyer 1950; Parsons 1971). In this study, invertebrates represented 4-13% of the numbers of prey items (Tables 2, 3), however they contributed little to the total caloric intake of the walleye because of their almost negligible volume and poor assimilation by walleye (Kelso 1972). Moreover, invertebrates did not exhibit significant seasonal variation in walleye dietary importance (Table 4).

Diel Periodicity

The mean index of fullness, measured as the volume of stomach contents (ml) divided by walleye body weight (kg), for all walleye sampled is plotted against time of capture (2-h intervals) in Figure 3. The shape of this curve suggests the

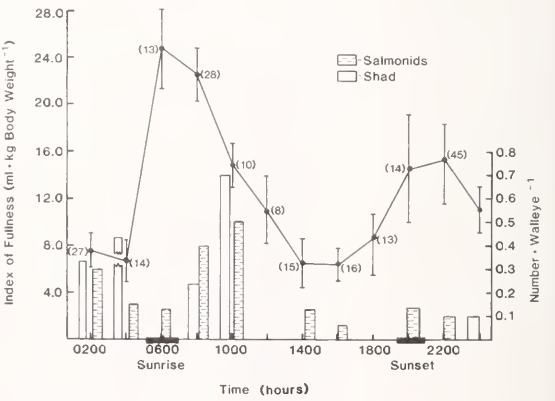

FIGURE 3.—Index of fullness and numbers of juvenile salmonids and shad consumed per walleye captured during 2-h intervals. Data collected from the John Day pool of the Columbia River, April to September 1980 and 1981. (Sample size in parentheses.)

stomachs of walleye collected in the John Day pool of the Columbia River in the 1980 and 1981. Numbers in parentheses are percent IRI.

Prey taxon	1981		
	Combined[1]	Spring	Summer
Salmonidae	56 (0.6)	53 (0.5)	58 (0.6)
Oncorhynchus tshawytscha	8 (0.2)	4 (0.1)	
Unidentifiable Salmonidae	11 (0.3)	26 (0.5)	58 (1.5)
Catostomidae	795 (8.8)	88 (0.9)	816 (8.3)
Catostomus columbianus	59 (1.4)	65 (1.1)	69 (1.7)
C. macrocheilus	3 (0.1)	1 (<0.1)	8 (0.2)
Unidentifiable Catostomidae	350 (8.4)	418 (7.3)	293 (7.3)
Cyprinidae	1,211 (13.4)	649 (6.3)	2,776 (28.4)
Acrocheilus alutaceus	377 (9.0)	462 (8.1)	298 (7.5)
Mylocheilus caurinus	24 (0.6)	1 (<0.1)	162 (4.1)
Ptychocheilus oregonensis	9 (0.2)	2 (<0.1)	41 (1.0)
Other Cyprinidae	34 (0.8)	1 (<0.1)	234 (5.9)
Miscellaneous fishes	6,808 (75.5)	9,480 (91.3)	6,028 (61.6)
Cottus asper	1,770 (42.2)	2,376 (41.7)	1,314 (32.9)
Alosa sapidissma	<1 (<0.1)		2 (<0.1)
Other (unidentifiable fish; *Lampetra* spp., Ictalurdae)	1,544 (36.8)	2,336 (41.0)	1,511 (37.9)
Invertebrates	150 (1.7)	113 (1.1)	106 (1.1)

same bimodal feeding periodicity as reported for other walleye populations during times of high prey densities (Swenson 1977). We found no annual or seasonal variation in this periodicity. Numbers of juvenile salmonids and shad consumed per walleye at various times of the day peak from late night to midmorning, drop to a low level at midday, and remain low through the evening peak in walleye feeding.

Size of Prey Consumed

Parsons (1971) showed a positive relationship between walleye length and length of prey consumed in Lake Erie. Walleye in the mid-Columbia River exhibit the same relationship, and size of prey is correlated to different prey taxa. The change in the percent of the IRI of various prey groups, as a function of walleye fork length, is

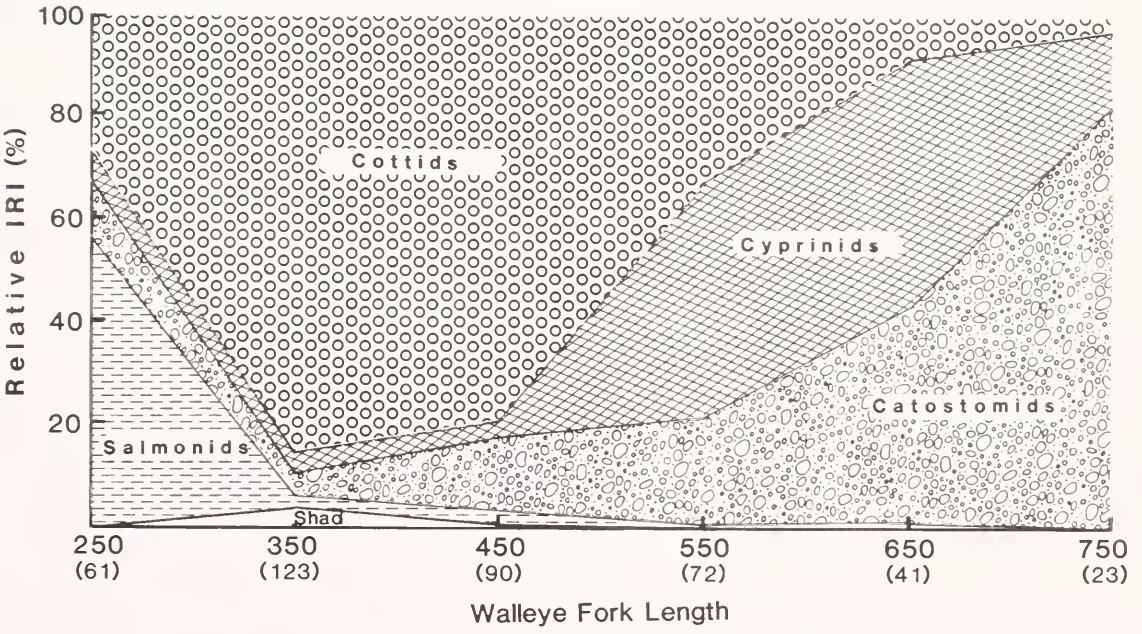

FIGURE 4.—Change in percent of total Index of Relative Importance (IRI) (Pinkas et al. 1971) of prey components as a function of walleye fork length (100 mm increments). Walleye collected in the John Day pool of the Columbia River, April through September 1980 and 1981. (Sample size in parentheses.)

charted in Figure 4. Small walleye (200-400 mm FL) primarily consume salmonids, cottids, and shad, while midrange walleye (400-600 mm FL) rely more heavily on cyprinids, cottids, and catostomids. For large walleye (>600 mm FL), suckers are the most important prey and the importance of cyprinids and cottids is reduced. Figure 5 contains the length frequencies of walleye prey collected in 1981 and shows peaks which correspond to the size of walleye most likely to consume that prey, i.e., cottids, juvenile shad, and juvenile salmonids are small (25-125 mm FL); cyprinids, excluding juvenile peamouth, are midrange in length (125-300 mm FL); and catostomids are present in a large range of sizes (150-450 mm FL) with peaks >300 mm FL.

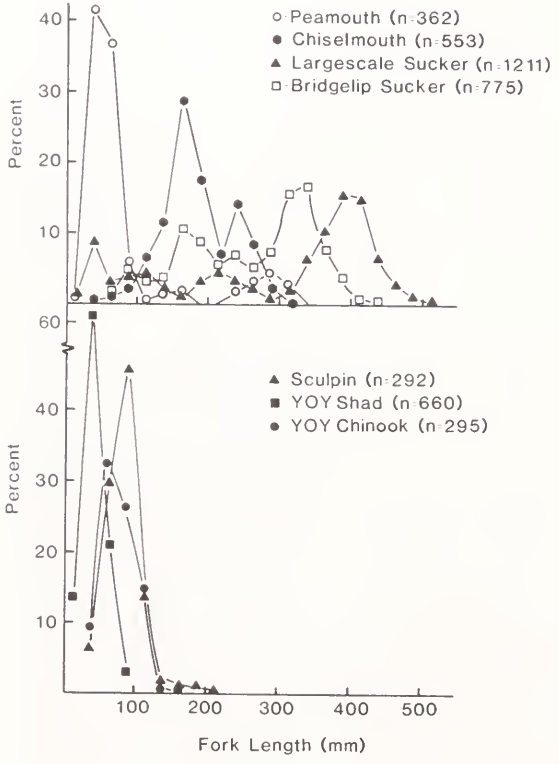

FIGURE 5.—Length frequencies of potential walleye prey collected in the John Day pool of the Columbia River, April through September 1981. (Sample size in parentheses.)

Discussion

Walleye have been described as opportunistic (Eschmeyer 1950; Ryder and Kerr 1978), crepuscular, or nocturnal feeders which primarily search the bottom for prey (Ali et al. 1977; Ryder 1977) and, in areas of abundant prey, select prey based on size preference (Parsons 1971; Wagner 1972). Walleye of the mid-Columbia River fit this general description; however, the species composition of their diet is different from that reported elsewhere. This difference is undoubtedly due to differing arrays and abundances of potential prey. Our data suggest no significant change in annual or seasonal variation in abundances of adult catostomids and cyprinids (chiselmouth) (Table 5); therefore, we believe that the variations in walleye diets (Tables 2, 3, 4) are the result of changes in availability of juvenile prey fish (Table 5).

Our data do not clearly explain the dietary role of juvenile anadromous fish that normally have seasonal abundances in excess of 10 million fish (Sims et al. 1981, 1982). We hypothesize that different behavioral responses of walleye, juvenile salmonids and shad, and alternate prey result in the walleye's apparent low dietary utilization of juvenile anadromous fish. The walleye's subretinal tapetum lucidum greatly enhances its visual acuity at twilight, when many potential prey have reduced visual acuity and are inactive (Ali et al. 1977; Ryder 1977). Yellow perch, *Perca flavescens*, are walleye's primary prey over most of their coextensive habitats (Colby et al. 1979), and the yellow perch's behavior in dim light is described as settling to the bottom and becoming inactive (Ryder 1977). Ali et al. (1977) suggested that were it not for their complimentary behavior at dawn and dusk, walleye and yellow perch interaction would not be as significant as it appears to be. In dimming light, emigrating juvenile Pacific salmon rise to the surface, increase swimming activity, and move downstream (Hoar 1958; Ali 1959). Similar behavior has been reported for juvenile shad (Loesch et al. 1982). Emery (1973) studied the diel movements of 21 species of Catostomidae, Clupeidae, Cottidae, Cyprinidae, and Percidae, and all but two species of Clupeidae were on or near the bottom at twilight and during the night. Emery (1973) further reported that these fish could be more closely approached by a diver at night than during the day. Therefore it appears that juvenile salmonids and shad are buffered from walleye predation by an abundance of alternate prey (Tables 2, 3, 5) of a wide size range (Figs. 4, 5) and by a separation in space and time during one of the walleye's peak feeding periods (Fig. 3).

We caught no walleye <200 mm FL (Fig. 2), even though our gear captured numerous specimens of other species <100 mm FL (Fig. 5). We

believe that inclusion of this smaller size group of walleye would not seriously alter our results or conclusions as they relate to predation on juvenile salmonids. They might, however, increase the importance of shad in walleye diets. Walleye <200 mm FL will primarily be juvenile walleye and will not reach 150 mm TL until mid-September (Brege 1981; Maule 1983). The length frequencies of juvenile chinook salmon which we sampled peaked at about 100 mm FL and, generally, chinook salmon complete their emigration by early fall (Raymond 1979; Sims et al. 1981). Juvenile shad, however, are generally smaller than juvenile salmonids (Fig. 5) and emigrate in late fall (Stainbrook 1983). Whereas juvenile salmonids may be buffered from the juvenile walleye predation by a size and time separation, juvenile shad may become a more important juvenile walleye food in late summer through fall.

This hypothesis is based on the current fish abundances within the John Day pool of the Columbia River. Should these abundances change, i.e., an increase in walleye abundance or a decrease in alternate prey, then we would expect a change in the walleye-juvenile anadromous fish interactions. The impact of walleye on the anadromous fish populations cannot be addressed without adequate estimates of walleye and prey fish abundances.

Acknowledgments

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BATHYMETRIC DISTRIBUTION, SPAWNING PERIODICITY, SEX RATIOS, AND SIZE COMPOSITIONS OF THE MANTIS SHRIMP, *SQUILLA EMPUSA*, IN THE NORTHWESTERN GULF OF MEXICO[1]

The mantis shrimp, *Squilla empusa*, ranges in the western Atlantic Ocean from Maine through the Gulf of Mexico (Gulf) to Surinam (Manning 1969). This stomatopod occurs in high-salinity waters (Gunter 1950; Franks et al. 1972) and is one of the more common macrocrustaceans in the northern Gulf (Hildebrand 1954). *Squilla* sp. may be important predators of other crustaceans, polychaetes, and fish (Camp 1973; Caldwell and Dingle 1976), but they also serve as food for many fishes including *Rachycentron canadum*, *Lutjanus campechanus, Sciaenops ocellatus, Micropogonias undulatus*, and *Rhomboplites aurorubens* (Knapp 1951; Moseley 1966; Overstreet and Heard 1978a, b; Grimes 1979).

Despite its importance, little detail is known of the life history of *Squilla empusa*. The pelagic larval stages have been described (Morgan and Provenzano 1979; Morgan 1980), and much information has been published recently on the worldwide zoogeography and distributional interrelationships, evolutionary ecology, and life history patterns of stomatopods, primarily coral-dwelling taxa (Reaka 1979, 1980; Reaka and Manning 1980). However, the latter information does not deal with *S. empusa*, and it may not be valid to extrapolate to this species. Reaka (1979: table 5) reported that the coral-dwelling taxa were long-lived and gave estimates of 26-34 yr to reach median size (using mean growth increments and mean molting frequencies), 12-14 yr (using mean growth and maximum molting), or 4-8 yr (using maximum growth and molting). Although we could not determine age of *S. empusa* readily from length-frequency analysis, a much shorter maximum life span (1-3 yr) is part of what appears to be a common pattern of population dynamics in the white and/or brown shrimp communities where *S. empusa* occur (Chittenden and McEachran 1976; Chittenden 1977).

This paper describes bathymetric distribution, size at maturation, spawning periodicity, sex ratios, size compositions, and morphometric relationships for *S. empusa* collected in the northwestern Gulf during routine trawling operations.

[1]Technical article TA 18359 from the Texas Agricultural Experiment Station, Texas A&M University, College Station, TX 77843.

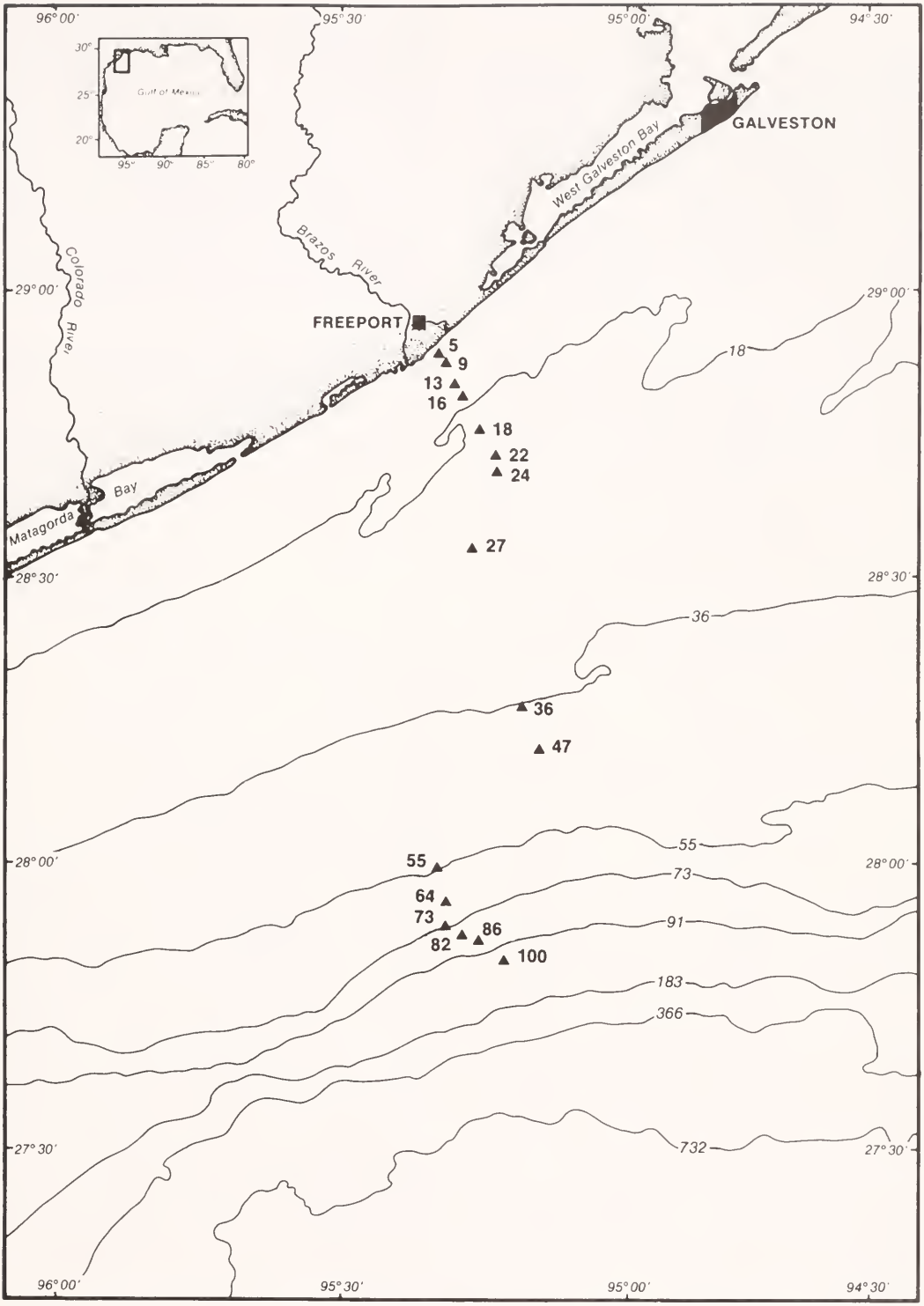

FIGURE 1.—Location of sampling areas. Station depths and bathymetric contours are indicated in meters.

Methods

Squilla empusa were collected fortnightly along a transect in the Gulf off Freeport, Tex. (Fig. 1) aboard a chartered shrimp trawler using twin 10.4 m (34-ft) trawls with a 4.4 cm stretched mesh cod end and tickler chain. Except for August and September 1979, a day and a night cruise were made each month in the period July 1979-October 1980 (Table 1). Data for *Squilla* were obtained from the first of two 10-min tows (bottom time) made at depths of 5, 9, 13, 18, 24, 27, 36, 47, 55, 64, 73, 82, 86, and 100 m, from 4 tows at 16 m, and from 12 tows at 22 m.

All *S. empusa* were culled from the catch, preserved in 10% Formalin[2], washed in fresh water, then stored in 70% ethanol. Specimens from the period July 1979-June 1980 were later processed to determine sex, total length (TL), and total wet weight (TW). Carapace length (CL), abdominal length (AL), abdominal width (AWD), and abdominal wet weight (AW) were measured on all specimens collected during seven cruises. Measurements follow Manning (1969), except that abdominal length was measured along the dorsal midline from the anteriormost portion of the first abdominal somite to the apices of the submedian teeth of the telson. Females collected during the period July 1979-October 1980 were assigned gonad maturity stages described in Table 2. Typical maximum size was approximated as a length l_L correlated with the Beverton-Holt yield model parameter t_L (Gulland 1969) following Alverson and Carney's (1975) definition that only 0.5-1% of the catch exceeds age t_L. All length measurements presented herein are total length unless stated otherwise.

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

TABLE 1.—Total length composition statistics (mm) by cruise for *Squilla empusa* from the Gulf of Mexico off Freeport, Tex., July 1979-October 1980. Night and day cruises are indicated by N and D.

Collection	n	Length (mm) Range	Mean	s	99% confidence limits of observations
5-9 July 79 N	695	26-132	85.7	17.1	41.7-129.7
19-22 July 79 D	6	77-108	88.2	14.0	31.8-144.6
22-25 Aug 79 D	2	76-91	83.5	10.6	—
22-25 Sept 79 D	491	37-124	71.7	14.3	34.9-108.5
2-6 Oct 79 N	1,049	40-113	75.2	12.4	43.3-107.1
16-19 Oct 79 D	458	47-109	75.0	11.1	46.4-103.6
3-6 Nov 79 N	614	38-112	76.2	12.1	45.0-107.4
15-18 Nov 79 D	72	51-96	71.0	9.5	46.5-95.5
1-4 Dec 79 N	137	53-102	75.4	11.9	44.7-106.1
14-19 Dec 79 D	96	32-115	83.8	14.7	45.9-121.7
3-6 Jan 80 N	857	29-123	77.0	15.5	37.1-116.9
16-20 Jan 80 D	71	49-116	82.9	14.5	45.5-120.3
4-11 Feb 80 N	948	33-116	78.6	15.1	39.7-117.5
15-20 Feb 80 D	236	35-109	77.6	13.4	43.1-112.1
5-8 Mar 80 N	680	34-113	79.2	11.8	48.8-109.6
19-23 Mar 80 D	447	40-110	75.5	12.5	43.3-107.7
1-5 Apr 80 N	197	37-106	77.1	12.7	44.4-109.8
16-20 Apr 80 D	313	33-110	76.0	13.6	41.0-111.0
5-10 May 80 N	914	37-117	74.1	14.7	36.2-112.0
19-22 May 80 D	215	46-113	72.9	13.4	38.4-107.4
2-6 June 80 N	872	42-126	82.1	10.9	54.0-110.2
19-24 June 80 D	56	65-115	85.3	10.5	58.3-112.3
7-11 July 80 N	335	63-114	89.0	8.5	67.1-110.9
21-24 July 80 D	1	61	61.0	—	—
5-15 Aug. 80 N	478	32-122	75.5	15.6	35.3-115.7
26-29 Aug 80 D	0	—	—	—	—
7-11 Sept 80 N	74	54-115	84.2	11.9	53.5-114.9
22-25 Sept. 80 D	45	26-114	73.9	19.4	23.9-123.9
6-9 Oct 80 N	60	46-117	83.2	12.3	51.5-114.9
20-31 Oct 80 D	77	28-118	82.2	20.1	30.4-134.0

TABLE 2.—Descriptions of gonad maturity stages assigned to female *Squilla empusa*.

Stage		Description
1	Immature, Spent, or Resting	Ovaries narrow transparent tubes. We could not distinguish visually between immature, spent, or resting individuals, nor assign age based on length frequency analysis.
2	Early Developing	Ovaries with slight yellow coloration occupy 0-25% of abdominal cavity.
3	Late Developing	Ovaries with orange coloration occupy 25-50% of abdominal cavity; little or no expansion of ovaries within each segment.
4	Gravid	Ovaries deep orange in color occupy 50-100% of abdominal cavity; ovaries in each segment definitely expanded

Results

Bathymetric Distribution and Diel Periodicity

Squilla empusa were collected from 5 to 86 m depths. Maximum abundance (male: 14.4-16.2 individuals/tow; female: 17.5-19.6 individuals/tow) occurred at 9-16 m (Fig. 2). Abundance was much lower at 5 m (male: 4.6 individuals/tow; female: 5.9 individuals/tow) and approximated that at 27 m. Abundance was even lower but uniform (< 2.0 individuals/tow) from 36 to 55 m; only one specimen each was collected at 64 and 86 m.

Size compositions of *S. empusa* varied with depth, although trends were similar for each sex. Individuals from the entire observed size range (26-132 mm) occurred in depths of 5-27 m (Fig. 3); size compositions of each sex were similar throughout these waters. Deeper waters were occupied primarily by individuals in each sex greater than the average size of 77 mm. Few individuals < 80 mm (< 1%) occurred deeper than 27 m, and no individuals < 80 mm occurred deeper than 55 m.

Catches of *S. empusa* were greatest at night. Mean catch/tow during the 1-yr period October 1979-September 1980, when both day and night

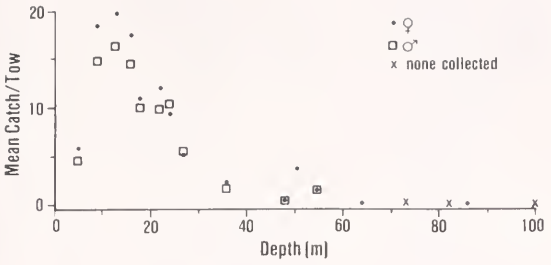

FIGURE 2.—Mean catch/tow (numbers) of *Squilla empusa* by depth for each sex.

cruises were made each month, was 6.79 during the day but 23.93 at night. The difference is significant at $\alpha = 0.01$ using a one-way analysis of variance ($F = 15.13$; 22 df), even though this simple model maximizes the error mean square in comparison to more complex models.

Size at Maturity and Spawning Periodicity

Squilla empusa begin to mature at 70 mm. No individuals < 70 mm were in Early-Developing, Late-Developing, or Gravid stages (Fig. 4). Only a small fraction of all Gravid females (15%) were 70-80 mm, but half were gravid by 90 mm. There was little difference in size between individuals in the Early-Developing, Late-Developing, or Gravid stages, respective means being 88, 90, and 91 mm.

Spawning apparently occurs over an 8-mo period that begins in January and ends in July-August. Few or no Early-Developing, Late-Developing, or Gravid individuals were captured from September through December either year (Fig. 5). Individuals in these stages were abundant in January and remained so through July-August. Immature and Spent or Resting individuals greatly predominated during the period September-December each year.

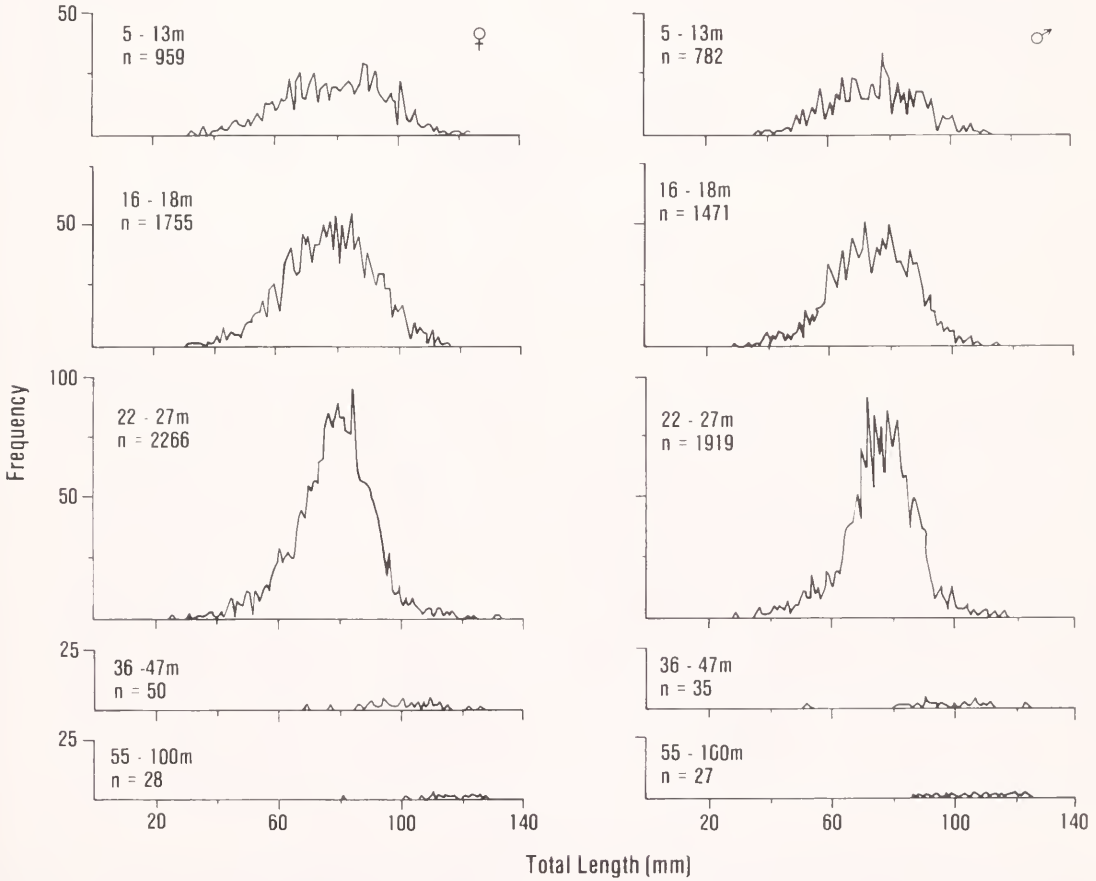

FIGURE 3.—Length frequencies of *Squilla empusa* by depth for each sex.

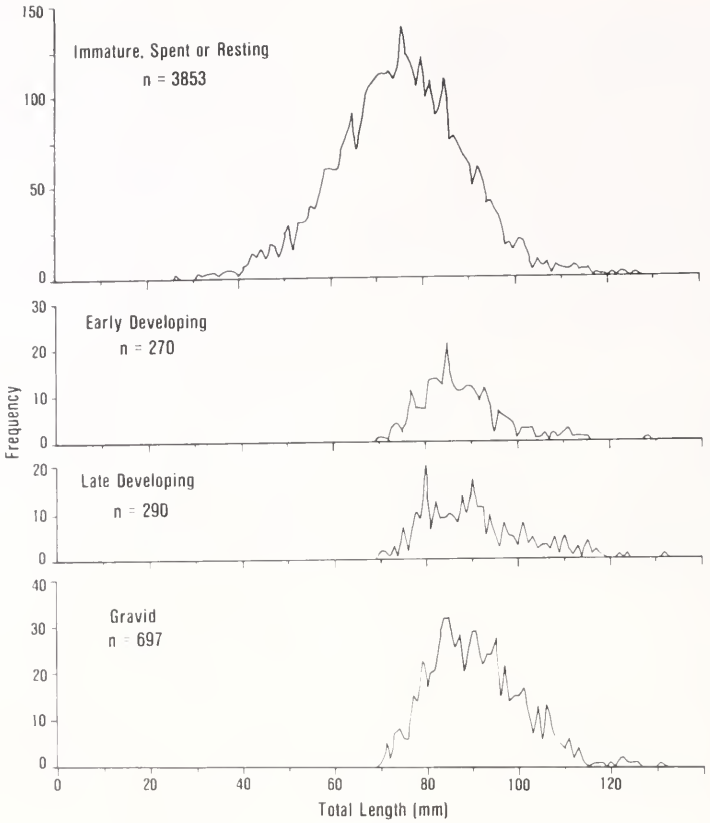

FIGURE 4.—Size of female *Squilla empusa* by maturity stage. Maturity stages are described in Table 2.

Sex Ratios

Females made up 54% of the overall catch of *S. empusa* and were significantly more abundant than males ($\chi^2 = 71.53, P < 0.05$). Except in August 1979 when only two individuals were caught, females predominated and made up 52-63% of the 500-1,000 *S. empusa* usually caught each month. Sex ratios did not differ significantly between depths ($\chi^2 = 1.82, 4$ df, $P > 0.05$). Sex ratios generally were equal from 30 to 80 mm, but females increasingly predominated at larger sizes (Fig. 6). Sex ratios did not differ significantly from a 1:1 ratio until *S. empusa* exceeded 80 mm (Table 3).

TABLE 3.—Observed sex ratios and chi-square statistics for *Squilla empusa* divided into 10 mm length groups, July 1979-June 1980. Asterisks indicate significant χ^2 at $\alpha = 0.05$.

Length range (mm)	No. individuals		χ^2
	Male	Female	
21-30	3	1	1.00
31-40	28	29	0.02
41-50	117	138	1.73
51-60	381	382	0.00
61-70	835	837	0.00
71-80	1,353	1,357	0.01
81-90	1,069	1,339	30.27*
91-100	387	699	89.64*
101-110	94	241	32.25*
111-120	19	69	28.41*
121-130	4	16	7.20*
131-140	—	2	2.00
Total	4,290	5,110	—

Maximum Size and Intrayear Variations in Size

Typical maximum size reached by *S. empusa* in the northwestern Gulf is 110-115 mm. The largest of 9,400 specimens we captured was only 132 mm, 99% were <110 mm, and 99.5% were <114 mm (Fig. 7).

Size compositions showed little change throughout the sampling period. Except for the

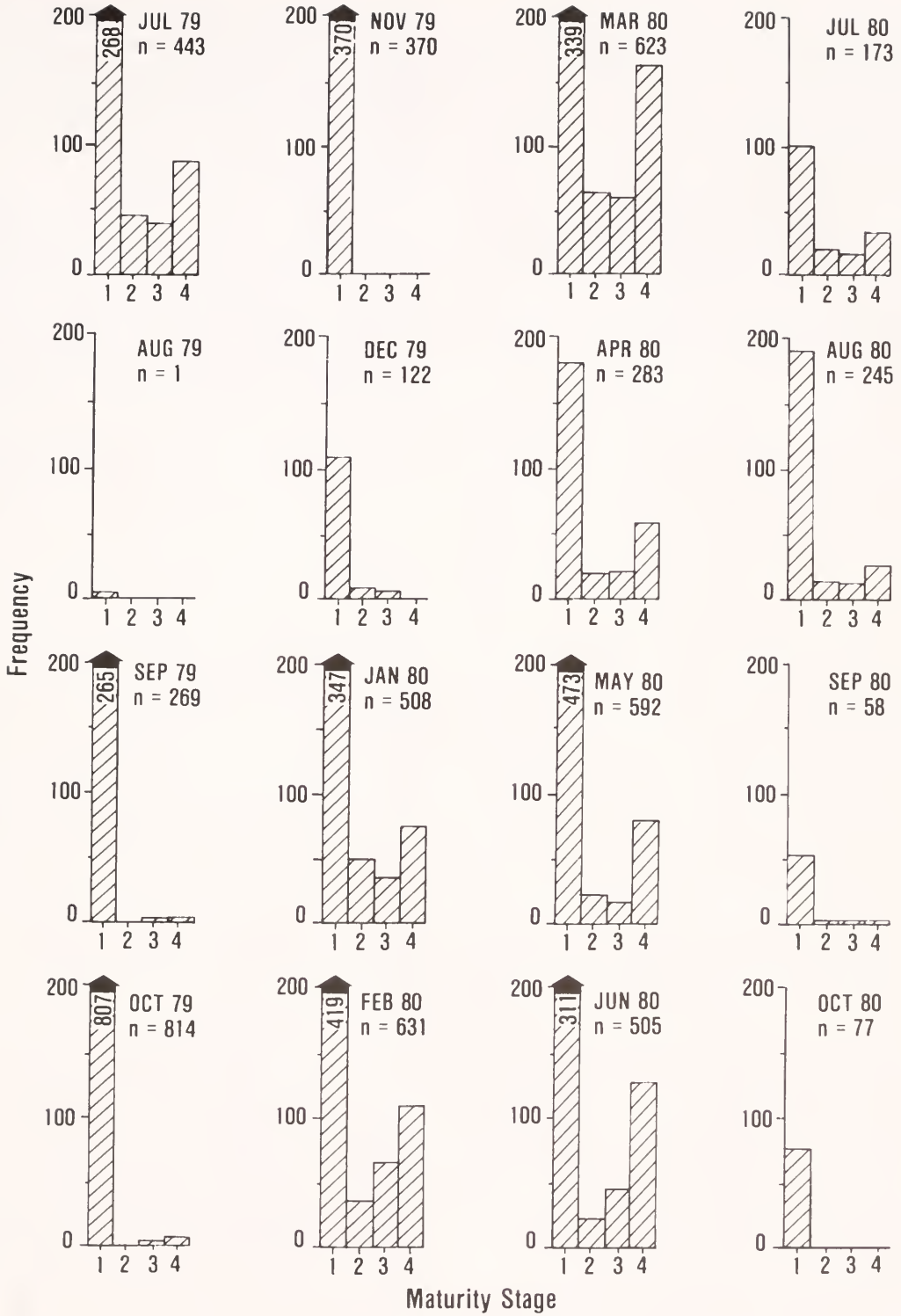

FIGURE 5.—Monthly numbers of female *Squilla empusa* by maturity stage for the period July 1973-October 1980. Stages (see Table 2) are 1) Immature, Spent or Resting, 2) Early Developing, 3) Late Developing, 4) Gravid.

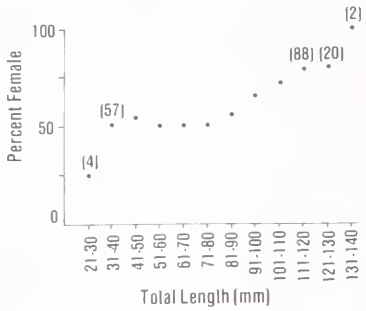

FIGURE 6.—Percentage of female *Squilla empusa* by size. Sample sizes are 255-2,710 size class, except where indicated.

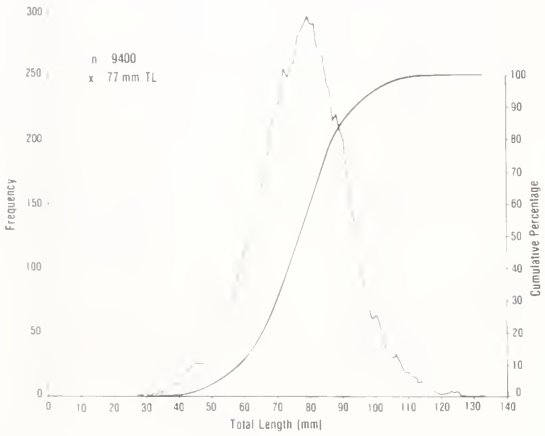

FIGURE 7.—Length frequency (moving averages of three) and cumulative percentage of all *Squilla empusa* collected off Freeport, Tex., July 1979-June 1980.

21-24 July 1980 day cruise when only one specimen was captured, mean sizes on each cruise ranged between only 71 and 89 mm (Table 1). In addition, 99% confidence limits for observations also showed little variation during this period.

Length-Weight-Width-Relationships

Length-length, length-weight, and length-width relationships are presented in Table 4. Length-weight regression coefficients were significantly different between the sexes ($F = 5.03$; 1, 9,381 df; $P < 0.05$). However, the minor difference ($b = 2.94$ vs. 2.96) may have little biological meaning, thus pooled regression statistics are also presented to simplify stock assessment. Calculated length-weight regression coefficients significantly exceeded $\beta = 3.0$ at $\alpha = 0.05$ (data pooled, $t = -12.23$; males, $t = -5.89$; females, $t = -10.42$).

Discussion

Bathymetric Distribution and Diel Periodicity

Squilla empusa occur on a mud or sandy-mud bottom (Franks et al. 1972) as do several of its congeners (Reaka and Manning 1980). This species ranges on such bottoms across most of the continental shelf in the northern Gulf. We captured *S. empusa* to depths of 86 m in agreement with Hildebrand (1954) and Franks et al. (1972), who captured specimens to 82 and 91 m, respectively. Our findings that *S. empusa* were common

TABLE 4.—Length-length, length-weight, and length-width regressions for *Squilla empusa*, sexes pooled unless indicated, with supporting statistics. Measurements are in grams and millimeters. Size range for each equation is 26-132 mm TL. All regressions are significant at $\alpha = 0.001$. Corrected total sum of squares is for y unless x is designated; r is from Ricker's (1973) GM functional regression. See below for definition of symbols.

	Equation	n	$100\,r^2$ (%)	Residual Mean square	Corrected total sum of squares	r	$\bar{x}$
[1]CL	0.82 + 0.20 TL	1,021	93.4	0.4345	6,728.42	0.21	76.74
TL	1.21 + 4.70 CL	1,021	93.4	10.2521	158,764.13	4.86	16.09
AL	−0.36 + 0.62 TL	1,023	97.6	1.4486	62,048.05	0.63	76.70
TL	2.40 + 1.58 AL	1,023	97.6	3.7213	159,395.26	1.60	46.92
AW	0.01 + 0.63 TW	1,026	99.1	0.0423	4,963.75	0.63	7.13
TW	0.08 + 1.58 AW	1,026	99.1	0.1067	12,505.14	1.59	4.46
AWD	0.11 + 0.38 AL	1,028	94.6	0.5012	9,555.32	0.39	46.87
AL	2.81 + 2.49 AWD	1,028	94.6	3.2828	62,590.81	2.56	17.70
AWD	0.41 + 0.24 TL	1,023	93.9	0.5669	9,486.92	0.25	76.70
TL	6.33 + 3.97 AWD	1,023	93.9	9.5249	159,395.26	4.10	17.72
All Data							
$\log_{10}$ TW	−4.7725 + 2.9430 $\log_{10}$ TL	9,383	97.7	0.0014	581.99; 65.65(x)	2.9774	1.88(TL) 0.76(TW)
Males							
$\log_{10}$ TW	−4.7974 + 2.9574 $\log_{10}$ TL	4,280	97.7	0.0014	247.66; 27.61(x)	2.9950	1.87(TL) 0.74(TW)
Females							
$\log_{10}$ TW	−4.7615 + 2.9362 $\log_{10}$ TL	5,103	97.8	0.0014	330.23; 37.47(x)	2.9686	1.89(TL) 0.78(TW)

[1]CL = Carapace length; TL = total length; AL = abdominal length; AW = abdominal wet weight; TW = total wet weight; AWD = abdominal width.

inshore of 24 m and most abundant at 9-16 m agree with Camp's (1973) data off west central Florida, but contrast with the data of Hildebrand (1954), who found greatest abundance at 35-42 m off Louisiana. *Squilla empusa* apparently reach peak abundance in much deeper water in the north central Gulf than off Texas, which may simply reflect the phenomenon that the inshore white shrimp community penetrates into deeper water there than it does in the northwestern area (Chittenden and McEachran 1976).

We captured greater numbers of *S. empusa* at night as did Hoese et al. (1968), who suggested that *S. empusa* retreat to burrows during the day and consequently are more likely to avoid trawls.

Spawning Periodicity

The prolonged spawning period of January to July-August that we found agrees, in part, with Franks et al. (1972), who collected stomatopod larvae in the plankton from April through September off Mississippi, and with Swingle (1971), whose limited data from Mobile Bay, Alabama, suggested winter and spring spawning. In addition, *S. empusa* 10-25 mm long occurred May-December in the stomachs of *Centropristis philadelphica* collected in conjunction with our study (Pavela and Ross[3]); *S. empusa* were most abundant in these stomachs in September and October. About 4-5 mo elapsed between our first collection of gravid *S. empusa* and their first appearance in *C. philadelphica* stomachs. These data suggest *S. empusa* spawn over an extended period of time and spend an extended time in the egg mass, propelagic, or pelagic stages of development, as occur in other closely related stomatopod species (Reaka 1979; Senta 1967 and Pyne 1972 cited in Morgan 1980).

Sex Ratios and Maximum Size

The change in sex ratio we observed at 80 mm, which is about the size at which females mature, may reflect different mortality rates between the sexes after maturity or growth cessation in larger males. Our data do not permit a choice between these possibilities.

The maximum size of 132 mm that we observed is similar to other maximum sizes for this species reported from the northern Gulf (Hoese et al. 1968, 120 mm SL; Christmas and Langley 1973, 145 mm). Much larger specimens have been reported from the Atlantic coast north of Cape Hatteras, N.C. (Bigelow 1941, 180 mm, type of length not given). These geographic differences in maximum sizes of *S. empusa* appear similar to differences in size that are found in many fishes (White and Chittenden 1977; Shlossman and Chittenden 1981; Geoghegan and Chittenden 1982; Murphy and Chittenden[4]). Therefore, our findings may reflect the zoogeographic change in population dynamics that these authors suggest occurs in the area of Cape Hatteras. Fishes, and possibly other taxa, as our data on *S. empusa* suggest, show smaller sizes, shorter life spans, higher mortality rates, younger age at maturity, more rapid turnover of biomass, and greater ability to avoid growth overfishing (see Gulland 1980) in the warm-temperate Carolinean Province waters of the Gulf of Mexico and South Atlantic Bight than do their conspecifics and congeners in the cold-temperate waters north of Cape Hatteras.

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DISTRIBUTION, LENGTH-WEIGHT RELATIONSHIP, AND LENGTH-FREQUENCY DATA OF SOUTHERN KINGFISH, *MENTICIRRHUS AMERICANUS*, IN MISSISSIPPI[1]

Populations of southern kingfish, *Menticirrhus americanus* (Linnaeus), are found in coastal waters from Long Island, N.Y., to Argentina (Stevens 1962; Miller 1965; Richards and Castagna 1970; Irwin 1970; Johnson 1978). Distribution appears to be continuous, but they are of greatest importance to commercial and sport fisheries along the South Atlantic and Gulf states. In 1978, 87,610 kg of southern kingfish valued at $36,085 were landed commercially in Mississippi (U.S. Department of Commerce 1977-78). Southern kingfish are caught incidentally by commercial fishermen using otter trawls in Mississippi coastal areas when fishing for shrimp or finfish such as croakers, red drum, and flounders. Southern kingfish ranked ninth in 1978 in economic value among commercial finfish species in Mississippi (third among trawl caught edible finfish) and is valued along the Gulf coast by sport fishermen who consider it an excellent food fish.

The majority of data available on southern kingfish is from studies conducted on the Atlantic coast (Welsh and Breder 1924; Hildebrand and Schroeder 1928; Irwin 1970). Little research has been conducted on southern kingfish in Mississippi, although information obtained on this species has been part of a large assessment program on finfishes along the Gulf coast (Christmas and Waller 1973; Loman 1978). Loman (1978) presented the only published works on length frequencies and length-weight relationships for southern kingfish in Mississippi.

The present study was conducted to investigate the distribution of southern kingfish in Mississippi coastal waters in relation to geographic range, season, temperature, and salinity. Length-weight relationship and length-frequency data are also presented.

Study Area

The study area consisted of the Mississippi coastal waters offshore to a depth of 91.4 m and included four estuarine systems: Biloxi Bay, Bay St. Louis, Pascagoula estuaries, and the smaller Pearl River system (Figs. 1, 2). Salinities and

[1]This paper is adapted from the author's unpublished Masters Thesis submitted to the University of Mississippi.

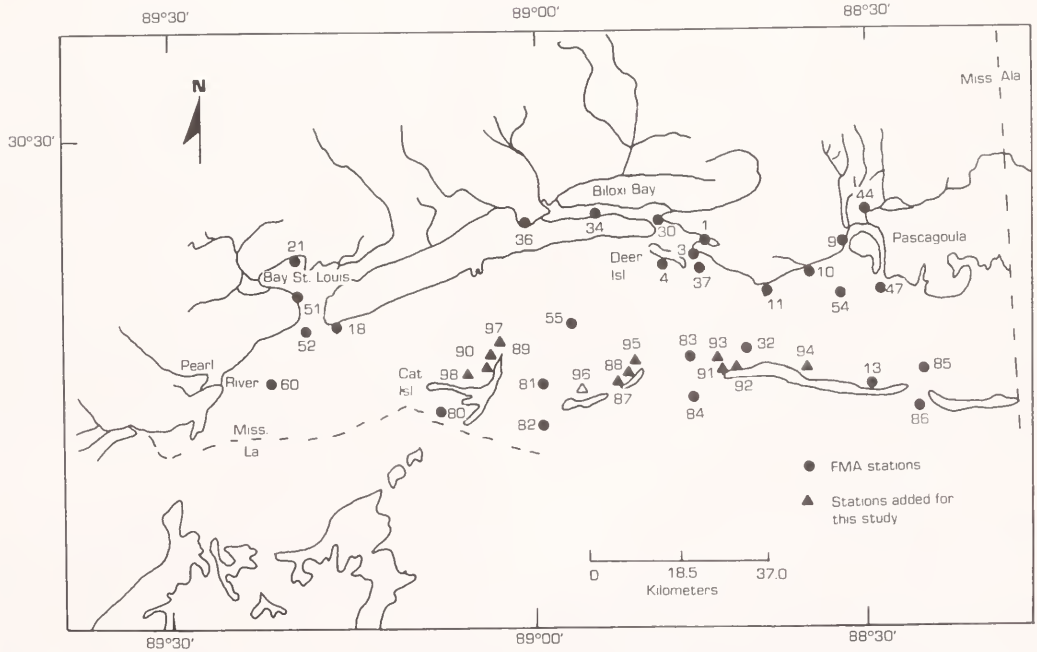

FIGURE 1.—Locations of stations for southern kingfish in estuaries, barrier islands, and offshore areas of the Mississippi Gulf coast sampled monthly.

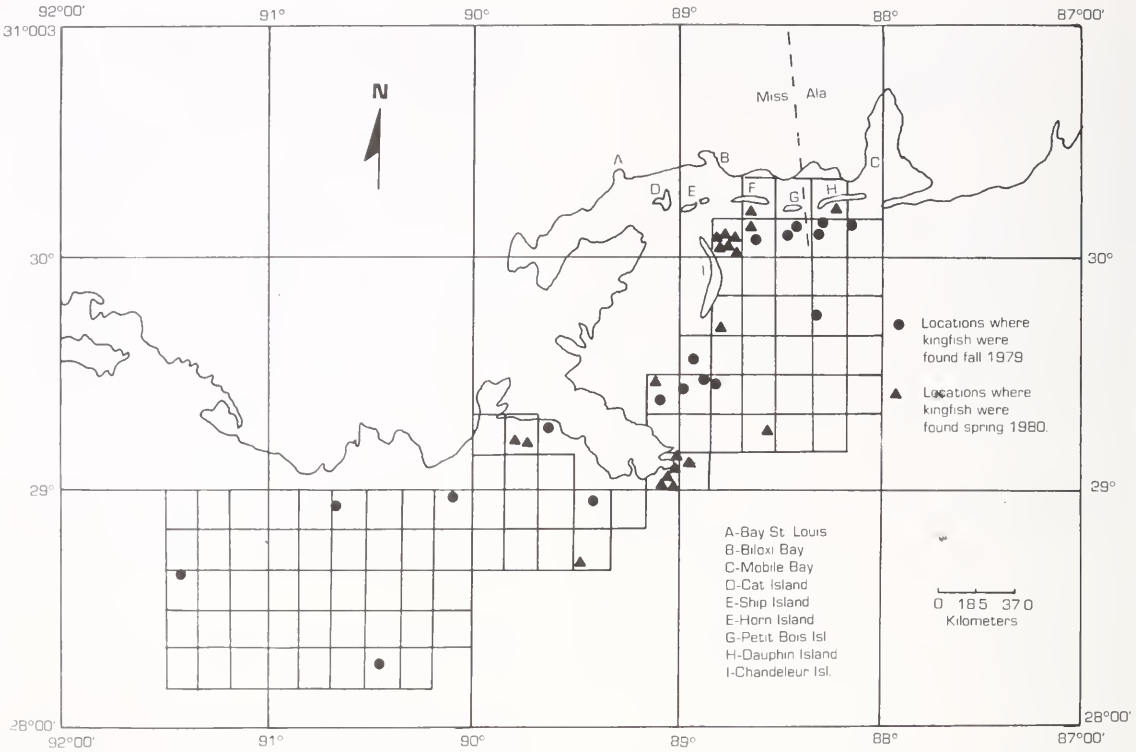

FIGURE 2.—Area of the Gulf of Mexico sampled for southern kingfish during the fall offshore cruise (25 October 1979 through 14 November 1979) and during the spring offshore cruise (10-18 April 1980). Grids represent station sites established by the National Marine Fisheries Service.

temperatures of the waters in these regions are influenced greatly by input from rivers and freshwater runoff. The estuaries drain into the Mississippi Sound which is bordered on the south by barrier islands. A complete description of the Mississippi Sound is given by Eleuterius (1978).

Areas sampled varied geomorphologically with location. Bottom types ranged from mud and silt in the rivers and upper estuaries to sandy tidal zones on the north side of the barrier islands. Overall depths varied from 0.3 m at seine stations to 91.4 m at offshore trawl stations. Sample areas in the estuaries ranged from 0.3 m to 12.2 m with relatively small tidal variations (0.1-0.6 m).

Materials and Methods

Monthly collections of southern kingfish were made from October 1979 through September 1980 (Fig. 1, Table 1), with the exception of stations 93 through 98 which were sampled monthly from February 1980 through September 1980. Twenty-eight of the stations were sampled in conjunction with the Fisheries Monitoring and Assessment Program at the Gulf Coast Research Laboratory, Ocean Springs, Miss. (Christmas 1978).

The type of gear used was dictated by the bottom topography and geographic location. At five stations along the barrier islands and in the estuaries, a 15.2 m bag seine with 6.4 mm bar mesh was used to collect juveniles. Larval and postlarval fish were collected by towing a Renfro beam plankton net (BPL) with 50 holes/cm² and a 1.8 m diameter mouth, in a 45.7 m semicircle at five stations. During the 10-min tows, young-of-the-year and adult southern kingfish were sampled with a 4.9 m standard otter trawl with 19.9 mm

TABLE 1.—Bottom salinities at monthly stations where southern kingfish were collected.

	Number of observations	Maximum salinity (‰)	Minimum salinity (‰)	Average salinity (‰)
Rivers	10	34.5	9.0	26.1
Estuaries	27	27.5	2.0	17.1
Mississippi Sound	37	33.0	14.5	24.7
Barrier Islands	29	29.0	5.0	22.2
Offshore	35	33.5	6.0	26.7

mesh, 6.4 mm tail mesh, and 0.9 m doors at 18 stations in the Mississippi Sound and with a 12.2 m standard otter trawl with 19.1 mm mesh, 6.4 mm tail mesh, and 1.3 m doors at 6 stations in the passes and outside the barrier islands. One sample was taken at each station per month, except at Fort Point (station 30) where two samples were taken: one with the 15.2 m seine and one with the BPL.

In the fall of 1979 and the spring of 1980, collections were made during National Marine Fisheries Service groundfish cruises (U.S. Department of Commerce 1979, 1980). Samples were taken by the RV *Oregon II* in depths of 9.1-91.4 m (5-50 fathom lines) from Mobile Bay, Ala., to Ship Shoal, La., extending to the east and west beyond Mississippi coastal waters (Fig. 2). Three successive 10-min tows were made at each station with a 12.2 m standard otter trawl with 19.1 mm mesh, a 1.22 m vertical opening, and 2.44 m doors, and samples were randomly taken. Specimens were frozen on board the ship, except ripe females which were preserved in 10% Formalin[2] for future use in fecundity estimates.

In the laboratory, each fish was weighed to the nearest 0.1 g and standard length measured to the nearest 1 mm. If the sample exceeded 50, a subsample of 50 was weighed and measured individually. The remainder of the catch exceeding 50 was counted and gross weight taken.

Salinity was determined with a refractometer (accuracy of 1‰) at stations sampled monthly, and on the groundfish cruises by titration at the National Marine Fisheries Service Laboratory (U.S. Department of Commerce 1979, 1980). Temperature was taken with a YSI Model 54 oxygen meter at monthly stations and with a centigrade thermometer on the groundfish cruises. Where a trawl was used, bottom water samples were collected with a Niskin or a Kemmerer bottle depending on the location and vessel used.

The length-weight relationship was calculated for southern kingfish by following the procedure of Rounsefell and Everhart (1953).

Results

Geographic Range

The distribution of southern kingfish in Mississippi extends from as far north as Bayou Bernard (station 36) to offshore beyond the barrier islands (Fig. 1). Fish were captured at all monthly sample sites at some time during the year except at seven stations where water depth ranged from 0.3 to 19.5 m.

During the fall groundfish cruise, southern kingfish were captured from 4.8 km south of the barrier islands to below the Mississippi River Delta and from long. 88°10′-91°25′W (Fig. 2). During the spring cruise the geographic range was about the same; however, populations were denser near the Chandeleur Islands and at the southern tip of the Mississippi River Delta. Catches of shrimp, a primary food of southern kingfish, were high in these areas, indicating the fish could have concentrated because of an abundant food supply.

Size of the southern kingfish captured varied with the geographic location. Specimens 50-150 mm SL frequented estuaries and inshore waters, while adults exceeding 150 mm SL were found on the Gulf of Mexico side of the barrier islands and offshore in waters as deep as 69.5 m. Distribution and size of the fish captured were also related to gear selectivity—trawls were used to capture adults in the passes and offshore, whereas smaller mesh gear types were more effective for obtaining juveniles and young-of-the-year in estuaries and inshore waters. Trawls accounted for 42% of the total catch at monthly sample sites.

Seasonal Distribution

A total of 1,554 southern kingfish was captured from October 1979 through September 1980. The numbers of fish gradually increased from December with a peak in February; from March through September there was no apparent numerical pattern (Fig. 3). On the other hand, the monthly catch by weight peaked in April with a lesser peak in January. Weight gradually declined during the remainder of the year.

Although overall catches for January and February were high, stations in the passes between the barrier islands and offshore accounted for the majority of southern kingfish in these months. Few southern kingfish were found in the estuaries during winter, and no kingfish were landed at any of the offshore stations during May, June, and July.

During the fall offshore groundfish cruise, 121 southern kingfish (100-280 mm SL) were captured. The spring cruise was more productive with 307 fish (70-270 mm SL) taken. No previous data on

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

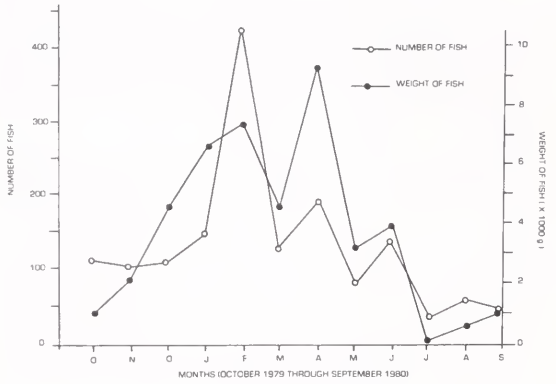

FIGURE 3.—Summary by number and by weight of the catch data for southern kingfish at stations sampled monthly from October 1979 through September 1980.

the distribution of this species in these offshore areas of Mississippi are available for comparison.

Salinity Range

Southern kingfish were captured in waters ranging in salinity from 2.0 to 36.6‰, with the majority found above 20.0‰ (Table 1). The mean salinity for the Mississippi coastal waters where southern kingfish occurred at regularly sampled stations was 23.4‰. During the fall groundfish cruise, bottom salinities where southern kingfish were taken ranged from 31.4‰ west of the Mississippi River Delta to 36.6‰ south of Horn Island, with an average bottom salinity of 34.5‰. No bottom salinities were available during the spring offshore cruise because of equipment problems.

Temperature Range

Young-of-the-year and adult southern kingfish were captured in waters with bottom temperatures ranging from 8.0°C in December to 37.3°C in August. The largest catches were taken in waters ranging from 20.0° to 30.0°C. Larval and postlarval fish (0.5-20.0 mm SL) were found from May through November in the shallow inshore waters and northern tidal zones of the barrier islands at temperatures ranging from 12.0° to 37.3°C.

The bottom water temperatures where southern kingfish were taken for the fall groundfish cruise ranged from 22.4° to 25.5°C (average of 23.2°C) and for the spring cruise ranged from 22.4° to 25.5°C (average of 22.3°C). In general, bottom temperatures on offshore cruises decreased with increasing depths.

Length-Weight Relationship

The length-weight relationship was calculated for the 1982 southern kingfish (ranging from 0.5 to 291.0 mm SL) by the following regression equation:

$$\text{Log } W = -4.48683 + 2.92908 \text{ Log } L$$

where W = weight in grams and L = standard length in millimeters (Fig. 4). The coefficient of determination R^2 was 0.9779.

Length-Frequency Data

At stations sampled monthly, southern kingfish juveniles (<50 mm SL) were most common from May through October; fish in the 100-150 mm SL range were fairly constant all year with a peak in March; and fish in the 150-250 mm SL range were rare during all months except April (Fig. 5). August was the only month where fish 10 mm SL or less were captured. The majority of the fish captured during the two offshore cruises were >100 mm SL with an average of 174 mm SL (Fig. 6).

The mean sizes of southern kingfish taken at the monthly stations were generally much smaller than those from the offshore groundfish cruises because young-of-the-year utilize the estuaries and inshore waters as nursery grounds. Gear selectivity must also be taken into account because the larger trawls used offshore are inefficient for capturing juveniles.

Discussion

Young-of-the-year frequented estuaries and inshore waters, while adult southern kingfish were found to be more abundant offshore in deeper waters. This was also reported by Pearson (1941) for the Chesapeake Bay area and by Geagan (1962) for the coastal waters of Louisiana. Irwin (1970) found the most common habitat for juveniles <50 mm SL to be open surf on sandy beaches, whereas in this study they occurred most often in sandy tidal zones of the barrier islands and estuaries.

High offshore catches and very low inshore catches from December through April support reports by Gunter (1938, 1945) and Christmas and Waller (1973) that adult southern kingfish migrate offshore during winter months and are summer residents of the estuaries. Similar reports were made by McIlwain (1978) for recreational

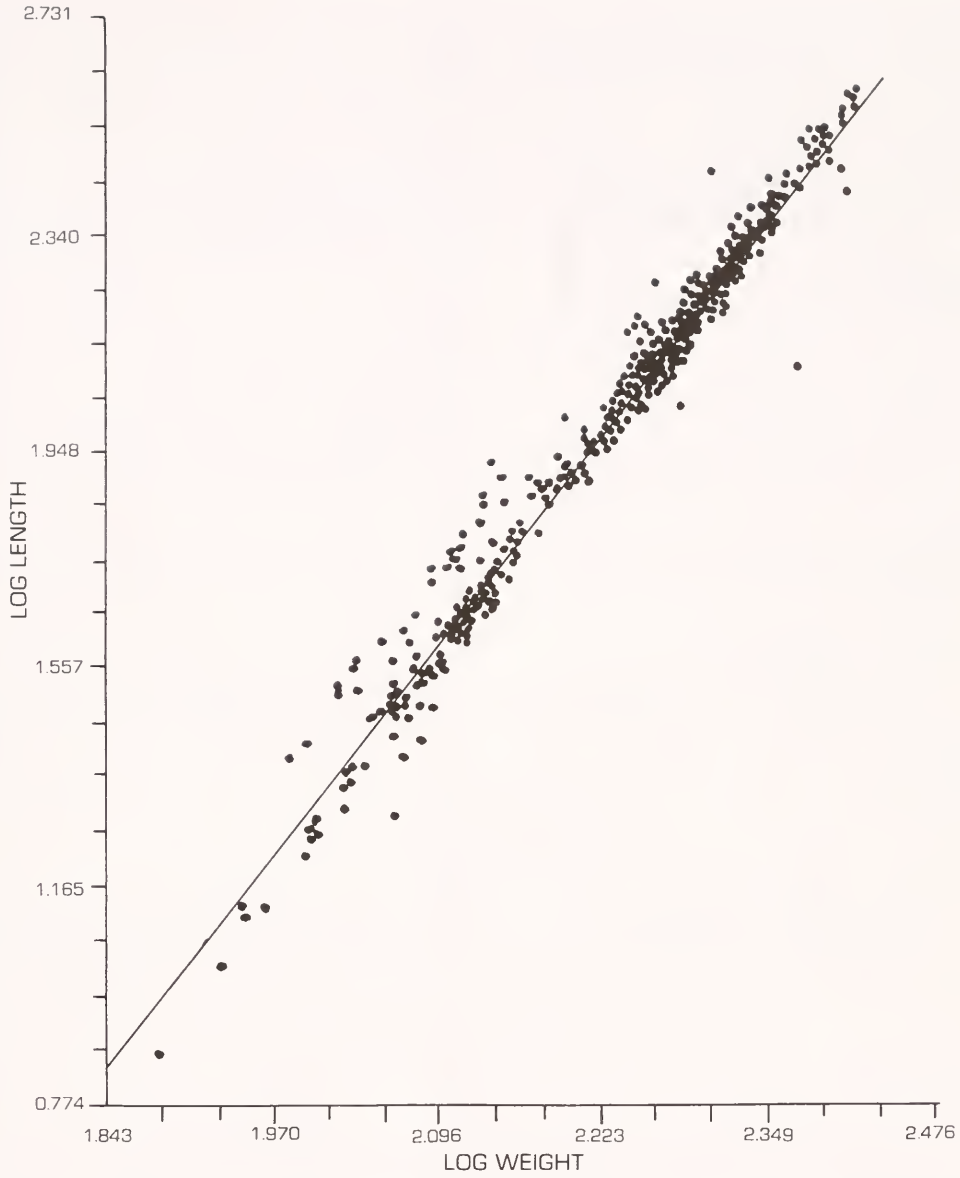

FIGURE 4.—Length-weight regression for all southern kingfish caught from October 1979 through September 1980.

catches from Biloxi Bay, Miss., and by Miller (1965) while trawling off Port Aransas, Tex.

The salinity range of 2.0-36.6‰ is slightly broader than the range of 5.0-35.5‰ reported by Christmas and Waller (1973). Loman (1978) reported that the highest catches of southern kingfish in Mississippi were between 15.0 and 30.0‰ and that mean length increased as salinity increased. The latter was also true in this study since larger fish were captured offshore where salinities were higher, and only postlarval and young-of-the-year fish were found in salinities below 15.0‰.

I concur with most authors that this species is eurythermal (Gunter 1945; Franks 1970; Christmas and Waller 1973; Loman 1978). While Loman (1978) reported southern kingfish in Mississippi coastal waters with temperatures as low as 7.0°C, the highest previously recorded temperature was 31.0°C reported by Springer and Woodburn (1960)

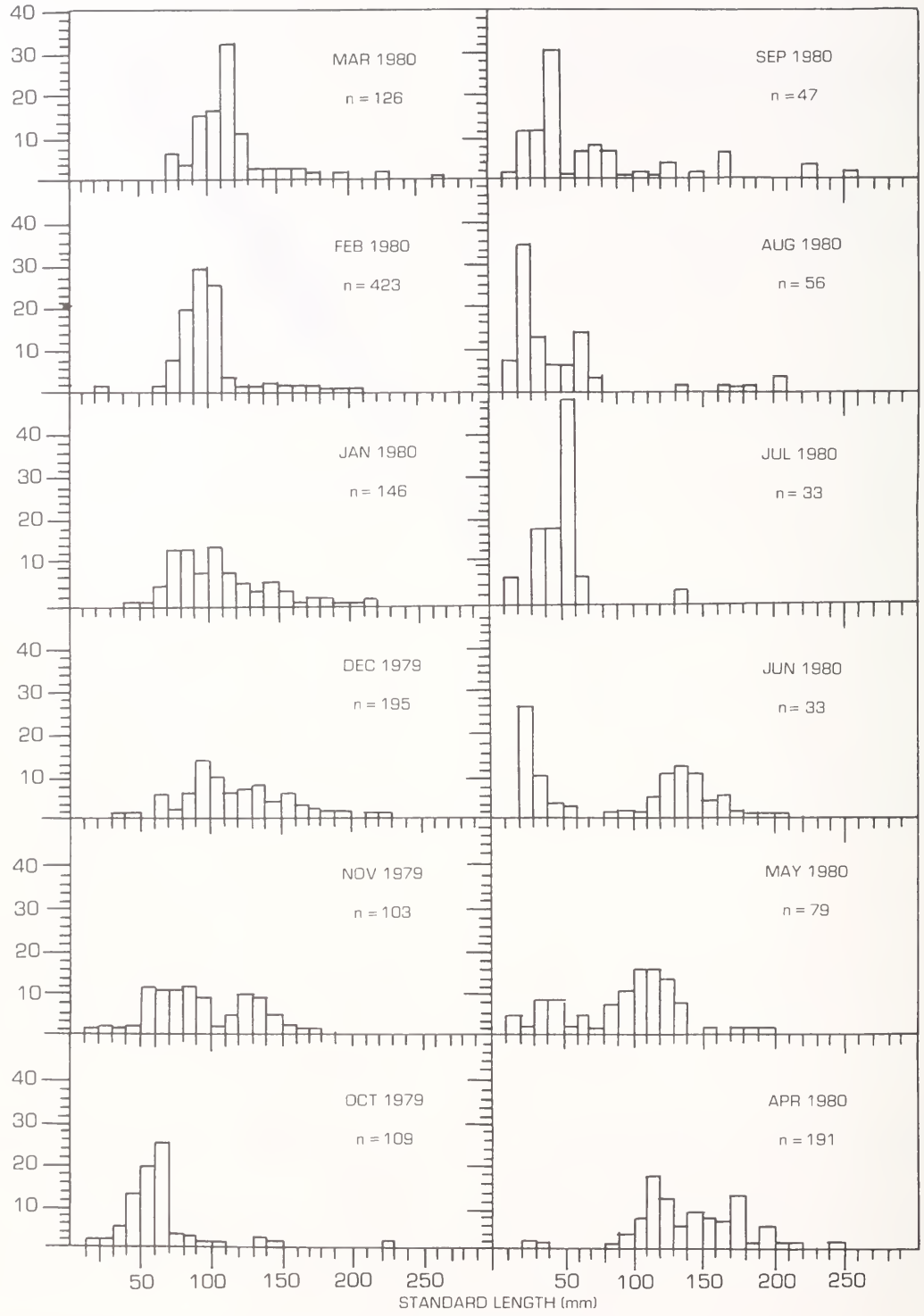

FIGURE 5.—Standard length frequencies of southern kingfish captured at regular monthly stations from October 1979 through September 1980. Total number of fish per month is represented by "n".

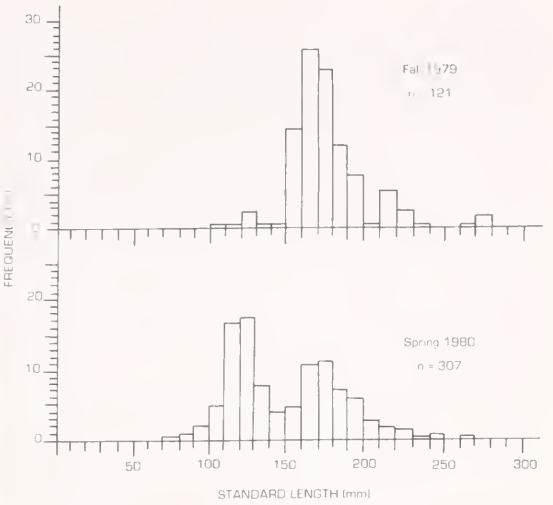

FIGURE 6.—Standard length frequencies of southern kingfish caught during the fall and spring offshore cruises in the Gulf of Mexico. Total number of fish per cruise is represented by "n".

in the Tampa Bay area. Loman (1978) reported a much narrower temperature range of 24.0-30.0°C for larval and postlarval fish (4.0-20.0 mm SL).

The length-frequency distribution recorded during 1979-80 is comparable to the published reports for 1973-76 (Loman 1978). Growth of southern kingfish is fairly consistent among individuals with the most rapid growth during the first year, as also reported by Hildebrand and Cable (1934) and Bearden (1963) for southern kingfish on the Atlantic coast. Young-of-the-year averaged about 100 mm SL by November. Bearden (1963) also reported southern kingfish in South Carolina to reach about 100 mm SL by November of the first year, whereas Hildebrand and Cable (1934) reported a slightly higher average of 135 mm TL by November of the first year in Beaufort, N.C.

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SCANNING ELECTRON MICROSCOPE EVIDENCE FOR YEARLY GROWTH ZONES IN GIANT BLUEFIN TUNA, *THUNNUS THYNNUS*, OTOLITHS FROM DAILY INCREMENTS

Atlantic bluefin tuna, *Thunnus thynnus*, are found throughout the Atlantic Ocean, the Mediterranean Sea, and the Gulf of Mexico (Gibbs and Collette 1967). Bluefin tuna are both commercially and recreationally important. Thus, it is important that the population dynamics of this species be understood in order that international policies can be developed.

Age determination and subsequent growth estimation are critical for tuna management. However, confusion and controversy surround age estimation in tunas. The earliest record of age and growth of tunas (probably bluefin) was by Greek fishermen nearly 2,000 yr ago as documented in Aristotle's "Historia Anumalium" (Bell 1964). In recent times, the aging of tunas has become much more important and has been critiqued by Hayashi (1958), Bell (1964), and Shomura (1966). These reviews point to the problems and difficulties in aging tuna. These problems and difficulties appear to be more evident in aging bluefin tuna.

Bluefin tuna are usually aged by counting growth increments on their hard parts. Vertebrae have provided acceptable ages (Rodríguez-Roda 1964; Butler 1971; Nichy and Berry 1976; Berry et al. 1976), but the aging of large or "giant" (>250 kg) bluefin tuna is suspect because the outer increments appear very close together. Otoliths have also been used to study age and growth of bluefin tuna (Butler et al. 1977). Berry et al. (1976) compared otolith age estimates with vertebra estimates and discovered a discrepancy. They found corresponding marks on both vertebrae and otoliths for the first 10 yr, but not thereafter, when otoliths had more incremental zones. They hypothesized that more than one incremental zone was deposited yearly in otoliths after the first 10 yr.

Daily increments in yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*, otoliths were studied by Wild and Foreman (1980) and Uchiyama and Struhsaker (1981). Taubert and Tranquilli (1982) used daily increments to verify annuli in the otoliths of large mouth bass, *Micropterus salmoides salmoides*, and it is proposed that an analogous investigation would provide corroborative evidence for the annual nature of outer major increments in giant bluefin tuna otoliths.

Methods and Materials

Sagittal otoliths were collected in November 1978, from giant bluefin tuna which were reared in the sea ranching program of St. Margaret's Bay, Nova Scotia, Canada. Fish were weighed and measured (TL) and the otoliths were collected as described by Caddy et al. (1976). All otoliths were washed in water and stored dry.

Whole otoliths from four fish were placed in epoxy resin and sectioned on a Buehler Isomet[1] saw. Sections 200 μm thick were acquired from the region judged to contain the core. A diagrammatic view of a cross section of a bluefin tuna otolith is

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

shown in Figure 1. Ten to 15 sections were sawed from each otolith. The number of sections viewed was dependent upon the clarity of the increments.

Each otolith section was fastened to an aluminum scanning electron microscope (SEM) stub with 5-min epoxy. The otolith section was highly polished with 0.3 μm alumina paste and etched with 6% EDTA (ethylenediaminetetraacetatic acid, adjusted to pH 8 with NaOH) for 1 to 20 min. The otolith sections were washed in water, dried, coated with gold, and viewed on a SEM at various magnifications. Observations and counts were made while the otolith section was in the SEM.

It was discovered that different areas of the rostral lobe of the otoliths were made clear by different etching times. Sequential etching made it possible to view microincrements in the outer 10 major increments. Individual sections were etched for different periods of time, with 15- to 20-min etching times showing the inner increments more clearly. The 10 outermost major increments were clearly visible in all sections and could be followed from section to section regardless of etching time. Each major increment was chosen to be from the center of one ridge to the center of the successive ridge; sequential etching revealed the microincrements between the ridges. It was not possible to count the microincrements from the edge of the otolith inward past the 10th major increment on any individual section. Consequently, sequential cross sections from each otolith were etched for different periods of time, in steps of 1 min, in order to follow the progression of the microincrements.

In the present study, a microincrement was defined as an unbroken incremental zone with discontinuous zones as boundaries (Radtke and Dean 1982) and was considered to be a daily increment.

Results and Discussion

SEM techniques made it possible to view microincrements in bluefin tuna otoliths from four individual fish. The most visually distinct increments were found on the rostral lobe of the otolith cross section (Fig. 1). Thus this area was used predominantly for SEM observations. The major increments of the otolith can readily be seen in Figure 2. Higher magnification (10,000 $\times$) revealed that the major increments were constructed of smaller increments which in turn were composed of microincrements (Figs. 3, 4).

Differential etching caused the problem that not all the increments could be viewed at the same time. This was overcome through the use of suc-

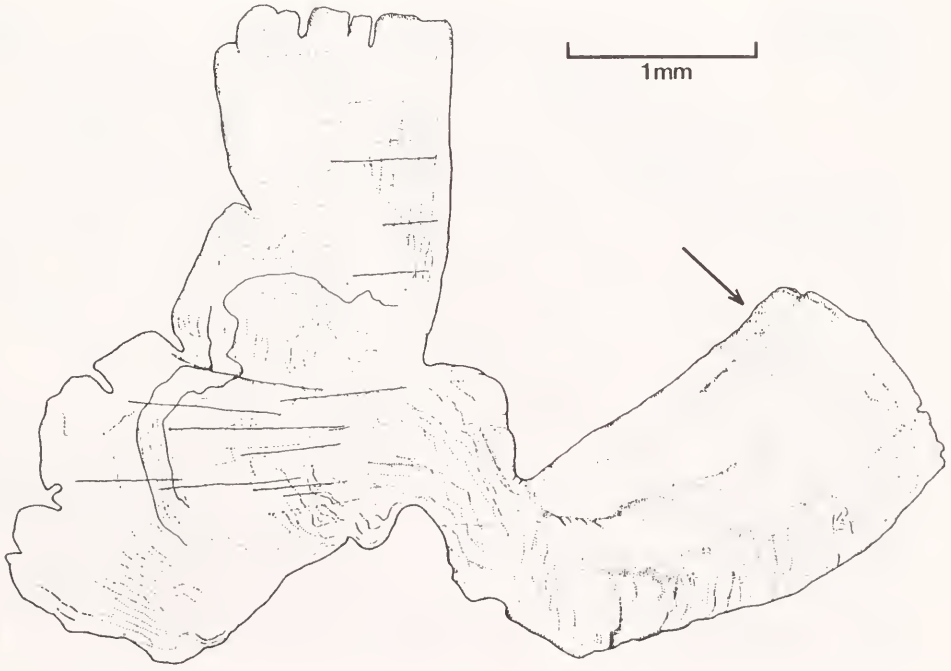

FIGURE 1.—Cross section of a bluefin tuna otolith showing the area (arrow) studied for microincrements. This area is on the rostral lobe of the otolith.

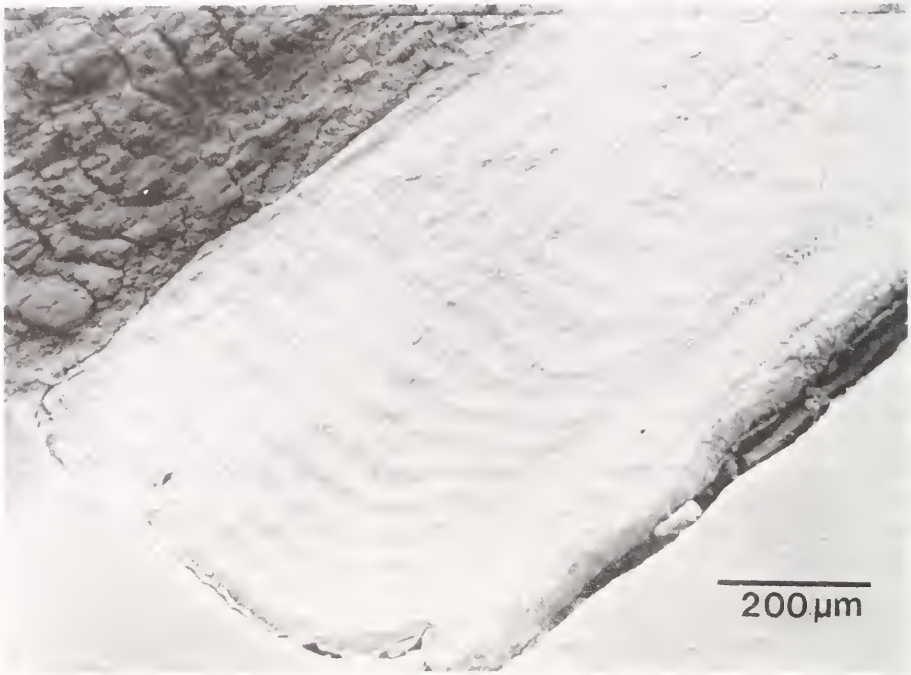

FIGURE 2.— Bluefin tuna otolith etched with EDTA which shows distinctive major increments. A short etching time gave good resolution to the outermost increments.

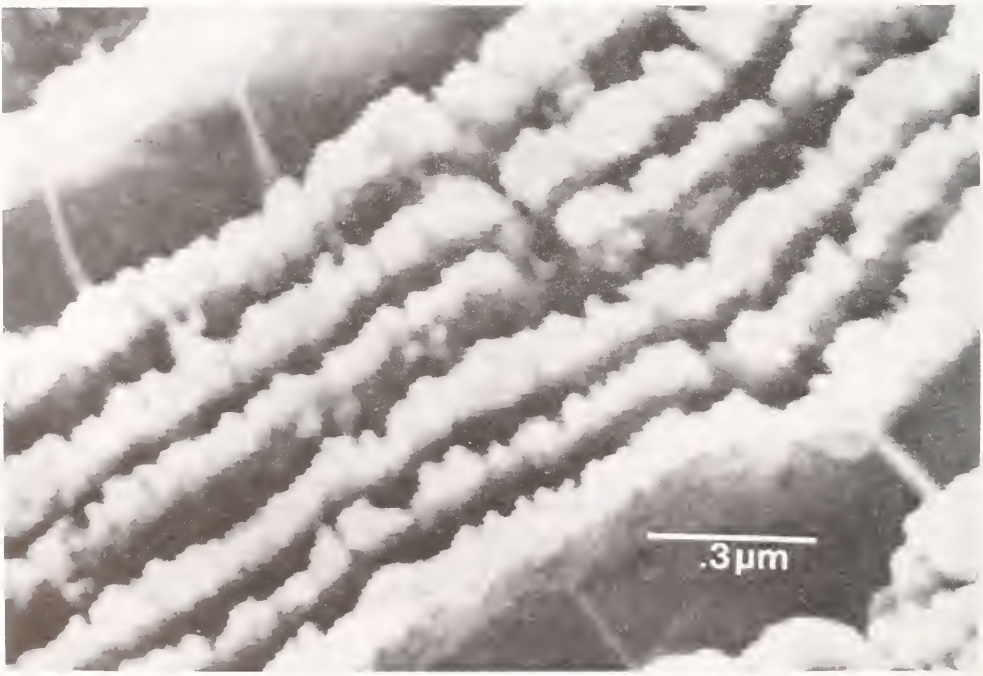

FIGURE 3.—Protein ridges of microincrements from a bluefin tuna. Strands of protein can be seen to interconnect the ridges.

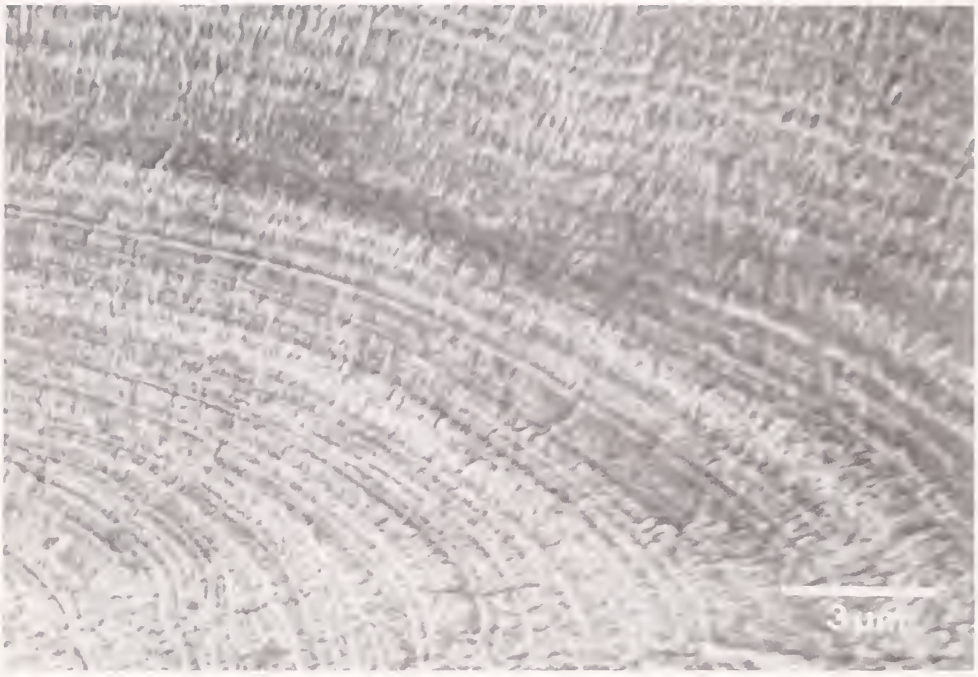

FIGURE 4.—Microincrements detected on the slope of a major protein ridge from a bluefin tuna. Differences in widths cause the yearly increments.

cessive cross sections which were etched for different time periods. This sequential etching made it possible to follow microincrements within the major increments. A difference in etching can be seen in Figures 2 and 5. Although major increments were clear in most etching times, the microincrements were not. Through the utilization of these techniques it was possible to obtain microincremental numbers for major increments (Table 1).

The microincrement counts in each major increment varied from 273 to 385 with the lowest count being found on the edge of the otolith. The summations of the microincrement counts for each fish were remarkably close and not significantly different ($P > 0.05$). Also, means of microincrements for each fish were not significantly different ($P > 0.05$) from the expected of 365 per year. These data increase the credibility of the microincrements being daily and present a plausible verification of the major increments as being annual.

Each microincrement is composed of a protein matrix with calcium carbonate crystals, in the aragonite crystal configuration, deposited within the matrix. Etching with EDTA dissolves the aragonite crystals leaving areas with a higher protein content to form discernible increments (Figs. 3, 4). Extended etching (times varied depending on the area of the otolith) can cause the protein ridges to collapse and prevent counting of the microincrements. Thus, etching times were critical to the acquisition of viewable increments.

TABLE 1.—Numbers of microincrements found in the major increments on the outer edge of the rostral lobe of the sagittae of four bluefin tuna, *Thunnus thynnus*.

Fish	1	2	3	4
Weight (kg)	496	381	405	470
Fork length (cm)	275	216	251	268
Sex	M	F	F	F
Estimated age[1]	25	19	19	24
Major increment	Counts	Counts	Counts	Counts
1	278	273	300	289
2	368	375	337	321
3	355	310	366	374
4	339	370	339	342
5	385	344	376	323
6	366	376	370	372
7	313	355	347	349
8	369	356	358	373
9	341	369	315	348
10	328	348	365	329
Total	3,442	3,476	3,473	3,420
Mean ± SD	344±32	348±33	347±25	342±27

[1]From counts of major increments by light microscopy.

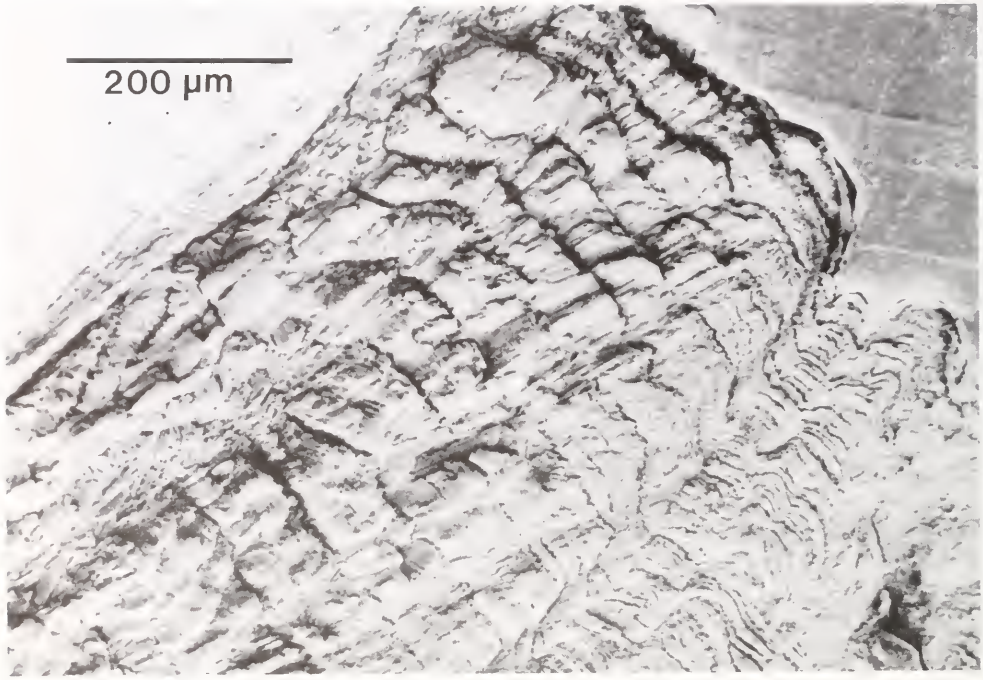

FIGURE 5.—Neighboring area of a bluefin tuna otolith shown in Figure 2 which demonstrates the uneven effects of etching.

The width of each microincrement varied in accordance with its position within a major increment. Microincrement width was probably a function of the time of the year when deposited. The widest microincrements were displayed between the ridges. Furthermore, the microincrements formed at the edge of the sagittae were wide and deposited during a time when the fish were fed large amounts of mackerel as part of the sea ranching operations. Observations on microincrement width suggest that wide microincrements were deposited during summer feeding and growth, while finer microincrements were deposited during the winter. It was these differences in width that accounted for the formation of yearly increments.

Most fish species investigated for daily age estimates have been found to possess daily increments in their otoliths (Pannella 1971; Brothers et al. 1976; Struhsaker and Uchiyama 1976; Taubert and Coble 1977; Methot and Kramer 1979; Steffensen 1980; Wild and Foreman 1980; Townsend and Graham 1981; Uchiyama and Struhsaker 1981; Radtke and Dean 1982). Thus, it is conceivable that the microincrements displayed in bluefin tuna otoliths are also daily. In tunas, Wild and Foreman (1980) studied daily increments in yellowfin and skipjack tuna, and Uchiyama and Struhsaker (1981) also investigated daily increments in yellowfin and skipjack tuna. Yellowfin tuna are found to deposit daily increments in both studies, whereas Wild and Foreman (1980) suggested that skipjack tunas have 25% fewer increments than would be expected if the increments occurred daily, while Uchiyama and Struhsaker (1981) advocated that daily increments did occur in skipjack tuna. In light of the present data, Wild and Foreman (1980) may have not detected increments formed during winter or colder periods. For giant bluefin tuna it is suggested that the microincrements are formed daily. If bluefin tuna did not deposit microincrements on a daily schedule, it would be expected that fewer daily increments would be detected in each major increment. Since this is not the case, it corroborates the idea that daily increments are formed in bluefin tuna otoliths and groups of daily increments form annual increments.

Otoliths may be the most useful hard structure for aging fish. Vertebrae and other hard structures are much more susceptible to resorption during times of physiological stress, while otoliths are

capable of permanently storing important ecological information since they are not susceptible to resorption (Mugiya and Watabe 1977). Otoliths have been shown to be the more accurate method of age determination in several fish species (Six and Horton 1977; Kimura et al. 1979). Otoliths are probably the most accurate means of age resolution in bluefin tuna.

In conclusion, the observation that microincrements in the sagittae of giant bluefin tuna about 365 in number for each outer major increment verifies the annual nature of these structures and strongly suggests that the microincrements are daily. Although it is not feasible to view large numbers of tuna otoliths by SEM techniques, the application of such techniques can provide answers to important biological questions.

Acknowledgments

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YEARLY CHANGES IN ABUNDANCE OF HARBOR SEALS, *PHOCA VITULINA*, AT A WINTER HAUL-OUT SITE IN MASSACHUSETTS

Information on the abundance of the harbor seal, *Phoca vitulina concolor*, population in New England consists of outdated estimates in the literature (King 1964; Maxwell 1967; Hewer 1974; Bonner 1976). A more recent series of unpublished reports (Richardson[1]; Knapp and Winn[2]; Kraus[3]; Gilbert and Stein[4]) suggests a harbor seal population which is increasing in numbers from its present breeding range north of Massachusetts southward into southern New England. A primary research need identified by Prescott et al.[5] was confirmation of this suspected increase in the harbor seal population throughout New England. This study summarizes available data on annual fluctuations in seal numbers since 1972 at one site in southeastern Massachusetts.

The study was conducted at Stage Point, Manomet, Mass. (lat. 41°55'N, long. 70°32'W). Harbor seals occur seasonally at Stage Point from late October through May (Schneider and Payne 1983). A rapid decrease in numbers occurs at this site in May (Schneider and Payne 1983), prior to the pupping season which occurs mid-May to mid-June in Maine (Richardson footnote 1; Wilson[6]). A few seals are reported throughout the summer but most move northward out of the study area by June.

The study site consists of a shoreline with a sandy cliff to 25 m. Sand, rock, and cobble extend from the base of the cliff into the water. Seals haul out exclusively on the larger rocks in the immediate subtidal zone from about 1-2 h before to 1-2 h after low tide (Schneider and Payne 1983). A similar haul-out pattern has been described at other rock-ledge sites in New England (Richardson footnote 1; Wilson footnote 6). Because of the synchronized haul out observed at Stage Point, the number of seals seen on the rocks is considered representative of the number of seals in the immediate vicinity (Schneider and Payne 1983) and, therefore, a useful index for monitoring changes in the abundance of harbor seals at this location.

Methods

Counts at Stage Point were made by direct observation within 2 h of low tide from the cliffs above the haul-out site. Schneider and Payne (1983) found that during 1979-80 the average number of seals observed at Stage Point peaked in January; therefore, the average number of seals ($\pm$SE) seen per daily count in January of each year was used in analyses among years. We transformed the January averages into logarithmic values, and the coefficient of correlation (r) from the linear regression was used to describe the relationship between the average number of seals seen per daily count in January 1972 and 1983.

In addition, air temperature, wave intensity, and human disturbance influence the total number of seals seen per daily count at Stage Point

[1]Richardson, D. T. 1973. Distribution and abundance of harbor and gray seals in Acadia National Park. Final report to National Park Service and Maine Department of Sea and Shore Fisheries, State of Maine Contract No. MM4AC009, 59 p.

[2]Knapp, C. L., and H. E. Winn. 1978. Harbor seals, New Hampshire to Long Island. Unpubl. rep., University of Rhode Island, Graduate School of Oceanography, Kingston, RI 02881, 36 p.

[3]Kraus, S. 1980. The population of harbor seals (*Phoca vitulina*) in southern New England. Unpubl. rep. of harbor seal workshop, 5 March 1980, Boston, Mass. New England Aquarium, Boston, MA 02109, 9 p.

[4]Gilbert, J. R., and J. L. Stein. 1981. Harbor seal populations and marine mammal fisheries interactions. University of Maine, Department of Forestry and Wildlife Resources, Orono, Maine. Annual Report to NEFC/NMFS/NOAA, Contract No. NA-80-FA-C-00029, 55 p.

[5]Prescott, J. H., S. D. Kraus, and J. R. Gilbert. 1980. East Coast/Gulf Coast cetacean and pinniped workshop. Final Report for Marine Mammal Commission, contract 79/02. Available National Technical Information Service, Springfield, VA 22151 as PB80-160104, 142 p.

[6]Wilson, S. C. 1978. Social organization and behavior of harbor seals *Phoca vitulina concolor* in Maine. Final Report to Marine Mammal Commission, Contract No. GPO PB 280-3188. Available National Technical Information Service, Springfield, VA 22151 as PB 280 188, 103 p.

(Schneider and Payne 1983). Prior to the winter of 1979-80, a record of environmental conditions at the time of the count was not maintained. Since it is not known to what extent weather or human disturbance near the haul-out site had on zero or near-zero counts previous to 1979-80, all daily counts in January with less than five seals were considered unreliable and excluded from the analyses. There were no available data for January 1973 or January 1977.

Results and Discussion

The average number of seals observed per daily count in January (Table 1) ranged from 9.3 seals (1974) to 88.25 seals (1980) with considerable variability among years. However, the observed number of seals was not randomly distributed among years; the January averages increased significantly ($P < 0.05$, $r = 0.63$, df = 9) between 1972 and 1983 (Fig. 1).

The average annual rate of increase since 1972 at Stage Point (based on expected values from the semilogarithmic regression, Table 1) was 11.9%/yr. The expected average number of seals per daily count in January at Stage Point (Table 1) doubled between 1973 and 1980.

The observed increase in the average number of seals at Stage Point has followed the termination in 1962 of a Massachusetts bounty on harbor seals and passage in 1972 of the Marine Mammal Protection Act. Rapid expansion of seal populations after the passage of protective legislation has been observed in the past (Hewer 1974; Bonner 1975; Everitt and Beach 1982) and has likely facilitated the increase since 1972 of the number of seals seen at Stage Point.

TABLE 1.—January averages of seals observed per daily count, 1972-83, at Stage Point, Manomet, Mass. n.d. = no data.

Year	No. daily counts	$\bar{x}$ no. (±SE) seals/daily count	Expected $\bar{x}$ no. seals/daily count[1]
1972	2	12.5 (6.52)	12.86
1973	n.d.		14.39
1974	3	9.3 (1.85)	16.11
1975	15	18.8 (2.32)	18.02
1976	2	34.0 (4.00)	20.17
1977	n.d.		22.58
1978	9	20.0 (3.07)	25.28
1979	9	35.56(7.00)	28.29
1980	28	88.25(6.06)	31.66
1981	18	21.67(6.92)	35.43
1982	18	21.88(2.94)	39.66
1983	19	48.00(5.63)	44.39

[1]From the linear regression: $y = 11.4898\ e^{(0.11263)x}$, $r = 0.628$, $P < 0.05$ (Fig. 1).

An increase in seal populations (after protection) due to unrestricted dispersion of juvenile seals has also been noted elsewhere (Bonner and Witthames 1974; Reijnders 1983). Bonner and Witthames (1974) suggested that the population of common seals, *P. v. vitulina*, located at the Wash in England, acted as a reservoir from which other reduced populations were replenished. Existence of a seal population in the Dutch Wadden Sea depends on unrestricted dispersal of juvenile seals from adjacent rookeries (Reijnders 1983). Since no rookeries occur south of Maine, it is apparent that the population increase seen at Stage Point (and throughout southern New England) has occurred through the southward dispersion of seals from Maine rookeries, after protection was established in Massachusetts.

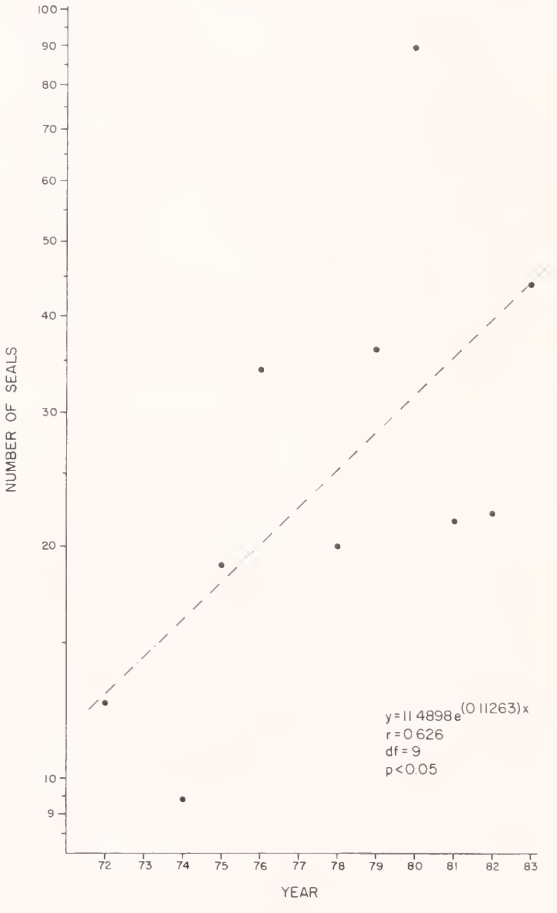

FIGURE 1.—Semilogarithmic plot of the average number of seals observed per daily count in January at Stage Point, Manomet, Mass., 1972-83.

Several investigators have reported an increase in seal numbers elsewhere in New England over the past decade. Gilbert and Stein (footnote 4) reported a total of 10,483 seals counted in June 1981 between Isles of Shoals on the Maine-New Hampshire border and the Canadian border. This nearly doubled the 1973 census of 5,786 seals reported for the same area by Richardson (footnote 1). Our data at Stage Point confirm this increase in southern New England.

The possibility does exist that the increase observed at Stage Point is merely the result of more thorough survey coverage in recent years; however, coastal bird observations were made regularly at Stage Point before 1973-74 by staff at the Manomet Bird Observatory. Any large number of seals would have been noticed during such counts.

The present harbor seal distribution, abundance, and breeding status in Massachusetts have changed considerably from the past. Allen (1869) reported "hundreds" of seals during the summer in Boston Harbor. As late as the 1930's and 1940's, harbor seals were permanent residents on Cape Cod (Prescott 1981) and pupping occurred throughout Massachusetts. Katona et al. (1983) suggested that the retention of the bounty until 1962 led to the extirpation of breeding activity in Massachusetts. The continued protection of an increasing harbor seal population throughout New England may result in expansion of the present breeding range southward into areas formerly used for pupping.

Acknowledgments

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POSTOVULATORY FOLLICLE HISTOLOGY OF THE PACIFIC SARDINE, *SARDINOPS SAGAX*, FROM PERU[1]

The use of the postovulatory follicle as a means of estimating incidence of spawning in multiple spawning fishes was originally developed by Hunter and Goldberg (1980) for the northern anchovy, *Engraulis mordax*, from southern California. This technique has proven to be quite useful for biomass assessment using the "Egg Production Method" (Parker 1980).

As a result of this work, the postovulatory follicle has assumed new importance. In the work of Hunter and Goldberg (1980), *E. mordax* were spawned artificially in the laboratory (Leong 1971). Fish were sacrificed at different time intervals, and histological conditions of the postovulatory follicles were noted. As an alternative to this method, in the current report we have aged postovulatory follicles of the Pacific sardine, *Sardinops sagax*, from Peru by establishing the time of spawning (egg collections) and by making periodic collections of *S. sagax*.

Methods

Samples of *Sardinops sagax* were collected during September-October 1982 near Chimbote, Peru (lat 09°05′, long. 78°35′). Ovaries were preserved immediately on collection in 10% neutral, buffered Formalin[2]. Later, samples from a total of 270 ovaries were dehydrated in ethyl alcohol and embedded in Paraplast. Histological sections were cut at 6μ. Slides were stained with Heidenhain's iron hematoxylin or Harris' hematoxylin followed by eosin counterstain.

Sardine egg samples from Peru indicated 0100 h to be the midpoint of the daily spawning interval (Smith[3]). Therefore, by knowing the hour of collection and assuming that spawning occurred around 0100 h, we calculated the approximate age of postovulatory follicles.

Results and Discussion

The sardine is a multiple spawning fish (Clark 1934), and during the spawning season we typically observe a mature yolk-filled mode of eggs representing the next spawning session and a vitellogenic mode for a subsequent spawning.

Postovulatory follicle, Day 0 (0-6 h after spawning)

The new *S. sagax* postovulatory follicles (Fig. 1A, B) were striking in their strong resemblance to the age 0-day postovulatory follicles of *E. mordax* (elapsed time from spawning <24 h) (Hunter and Goldberg 1980). The newly formed follicles of *S. sagax* contained many involutions or corrugations and were composed of columnar epithelium resting on a connective tissue theca. Nuclei had a basal location. The lumina occasionally contained eosinophilic granules of unknown origin (Hunter and Goldberg 1980) similar to those reported in the newly formed postovulatory follicles of *E. mordax*.

Postovulatory follicle, Day 1 (7-30 h after spawning)

These structures showed the beginning (Fig. 1C) of a breakdown in organization in comparison to day-0 postovulatory follicles. This included a size decrease to about one-half and marked degeneration of the columnar epithelial cell lining. Many epithelial cells had irregular shapes, vacuoles, and pycnotic nuclei. The convoluted structure was not as distinct as in day-0 postovulatory follicles. The linear arrangement of columnar epithelial cells was still evident. This is important, and constitutes the chief character that should be used for distinguishing day-1 from day-2 postovulatory follicles in *S. sagax*. This linear arrangement was absent in day-2 *S. sagax* postovulatory follicles.

Postovulatory follicle, Day 2 (31-53 h after spawning)

Degeneration of the *S. sagax* postovulatory follicle was clearly more advanced (Fig. 1D) at this stage. Distinguishing them from old atretic follicles is now a critical problem. Lumina were typically occluded and contained irregularly shaped cells with pycnotic nuclei, representing the final stages in the degeneration of the columnar epithelial cells that were previously so evident (Figs. 1A, B) in day-0 *S. sagax* postovulatory follicles. Vacuoles may be present. While the greatly convoluted structure that characterized earlier postovulatory follicles is no longer pronounced, there

[1]Publication No. 11 of PROCOPA.

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

[3]P.E. Smith, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. March 1983.

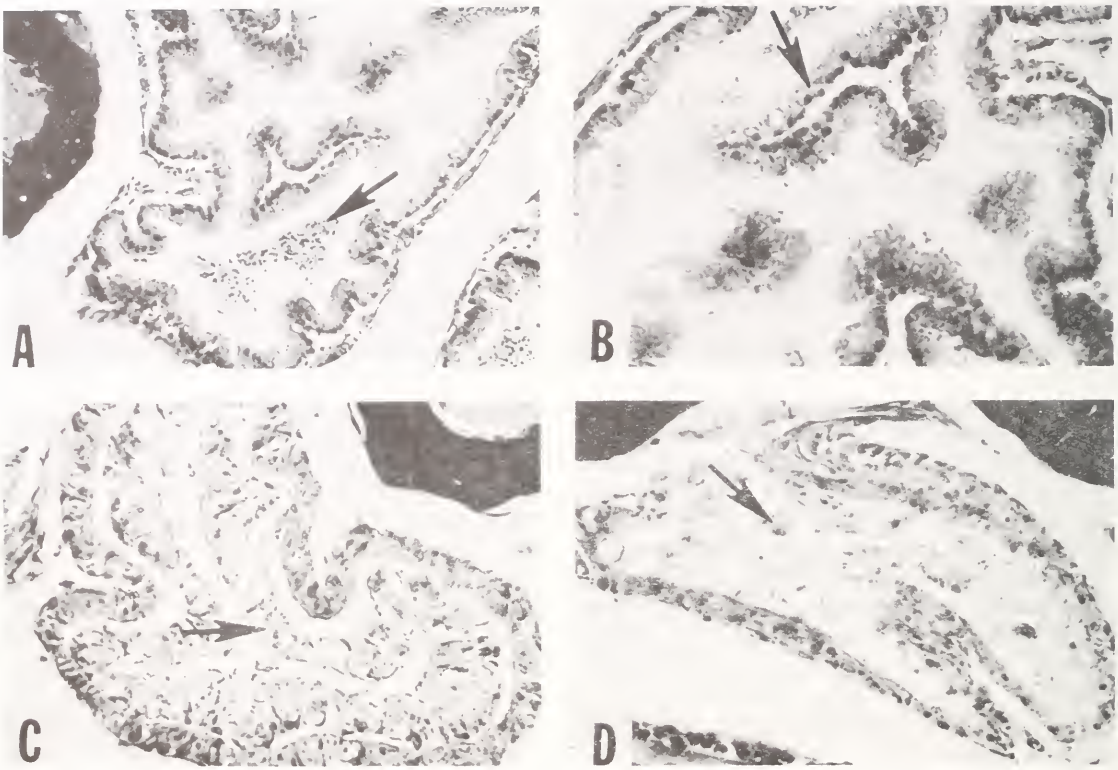

FIGURE 1.—Photomicrographs of *Sardinops sagax* postovulatory follicles. (A) Day 0, showing highly convoluted morphology. Note cluster of eosinophilic granules (arrow) in lumen (250×). (B) Day 0, showing columnar epithelial cell lining (arrow) (400×). (C) Day 1, columnar epithelial cell lining (arrow) undergoing degeneration. Underlying layer is connective tissue theca (400×). (D) Day 2, lumen contains scattered degenerated columnar epithelial cells (arrow) (400×).

should be some suggestion of it. We therefore recommend careful observation of the convoluted structure of day-0 and day-1 structures before attempting to identify day-2 structures.

A useful criterion for distinguishing day-2 *S. sagax* postovulatory follicles from advanced atretic follicles would be the presence of yellow granules (irrespective of staining) that are found in advanced atretic structures (delta atresia) (Lambert 1970). These were occasionally noted in *S. sagax*. The presence of these yellow granules which appear in nucleated clusters conclusively indicates atretic structures.

We did not use the artificial spawning technique (Leong 1971) for aging postovulatory follicles in *S. sagax*. However, we feel that estimating their age from periodic collections of fish, after the spawning time is established from collections of egg samples (as done herein), will prove to be a useful alternative method. This is particularly true in situations where facilities are lacking for laboratory-induced spawning. Laboratory-induced spawning studies using *S. sagax* will be useful to provide estimates of the accuracy of our classification scheme.

While there are numerous accounts of the occurrence of postovulatory follicles in marine fishes, there are few reports describing their longevity and subsequent degeneration. They have been described previously as being short-lived structures by Yamamoto and Yoshioka (1964) and Hunter and Goldberg (1980). More studies are needed of a wide variety of fishes before our knowledge of their histology and function is completed. Of utmost value will be investigations on how to distinguish conclusively between old postovulatory follicles and old atretic follicles.

Acknowledgments

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A NOTE ON SPAWNING OF THE PACIFIC MARKET SQUID, *LOLIGO OPALESCENS* (BERRY, 1911), IN THE BARKLEY SOUND REGION, VANCOUVER ISLAND, CANADA

In California, *Loligo opalescens* (Berry, 1911), has large spawning schools and spawn masses (McGowan 1954; Fields 1965; Hobson 1965; Cousteau and Diole 1973; Hochberg and Fields 1980). Spawns and spawning effort of this squid in the Pacific Northwest are poorly known and, to our knowledge, large spawns or spawning events have not been quantitatively described.

Loligo opalescens spawns regularly in Barkley Sound near Bamfield, British Columbia, (lat. 48°50.0′N, long. 125°07.5′W) in spring. We examined and measured portions of a spawn using scuba during early June 1982. The largest single capsule mass aggregation in our 200 × 50 m survey area was measured. Adjacent areas of smaller solitary egg capsule masses were surveyed using transects to determine overall spawn dimensions and percent cover of individual capsule masses. Dimensions of 23 typical masses were determined. Four representative masses were collected; the number of capsules in each was counted; and from each, 10 capsules were randomly selected and the number of eggs in each capsule was determined. These eggs were examined microscopically to determine the developmental stage, which was compared with the embryological stages illustrated in Fields (1965) to estimate the time of deposition.

The spawn, including areas of continuous and solitary egg capsule masses, was larger than the area surveyed, as the spawn extended below our deepest possible survey depth. Within our survey area, the largest capsule mass aggregation covered about 69.3 m^2 and averaged 0.28 ± 0.09 m (n = 4) in thickness. The mean density of the individual masses was 1.3 ± 0.1/m^2, and the mean area covered by 23 masses was 0.28 ± 0.14 m^2/mass, with a range of 0.13-0.66 m^2. The mean number of egg capsules per solitary mass was 1,937 ± 912 (n = 4), with 149 ± 35 eggs/capsule (n = 40). Thus, the total number of eggs per isolated mass was 288,000 ± 125,000. For the large areas of isolated masses, the potential number of larvae produced per 100 m^2 ranged from 19 to 58 × 10^6, with a mean of 37 × 10^6. The number of potential larvae from the single large aggregation of 69.3 m^2 ranged from 27 to 204 × 10^6, with a mean of 72 × 10^6.

Based on embryological stages observed, deposition probably occurred during the night of 31 May-1 June 1982. Small squid schools were observed spawning near the survey area on that date. None of the embryos were old enough to be deposited before 31 May, and all were of the same embryological stage.

Female squids from Californian populations deposited about 21 capsules, each containing about 200 eggs, in one night (Fields 1965); fecundity data from our region are not available. Hochberg and Fields (1980) stated that *L. opalescens* females produce 180-300 eggs/capsule. Our data indicate a lower mean value of about 150 eggs/capsule. If each female deposited 20 capsules, the large measured aggregation would be the result of about 24,000 females.

In conclusion, northern *Loligo opalescens* populations form large spawning schools and deposit massive egg capsule masses similar to those observed in the Californian populations.

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ARITHMETIC VERSUS EXPONENTIAL CALCULATION OF MEAN BIOMASS

Mean biomass ($\overline{B}$) within a time interval (t) is used in the Ricker method of estimating yield per recruit and can be calculated either arithmetically as

$$\text{(i)} \qquad B_t = \frac{B_t + B_{t+1}}{2}$$

or exponentially as

$$\text{(ii)} \qquad B_t = \frac{B_t\,(e^{G_t - Z_t} - 1)}{G_t - Z_t}$$

(Ricker 1975). The choice of calculation method may influence the yield estimates and consequently the determination of optimal levels of exploitation.

Ricker (1975) and Paulik and Bayliff (1967) alluded to the importance of the difference in magnitude between instantaneous growth and total mortality rates ($G_t - Z_t$). They indicated that if the difference was small, arithmetic and exponential calculations approached one another. Ricker suggested using small intervals if the rates are rapidly changing. In this paper we 1) examine the difference in the two estimates of mean biomass as a function of the instantaneous rates of growth and mortality, and 2) reexamine the consequences of the choice of mean biomass estimates on estimates of equilibrium yield per recruit using data previously employed by Ricker (1975) and Paulik and Bayliff (1967), showing that under many conditions, exponential estimates of mean biomass are preferable.

The difference between arithmetic and exponential estimates of mean biomass increases rapidly as $G_t - Z_t$ increases in a positive direction, but diverges less rapidly when $G_t - Z_t$ increases in a negative direction. When B_t is arbitrarily taken in unity, the relationship is satisfactorily represented by a polynomial regression (Fig. 1).

With many fisheries it is only possible to estimate instantaneous fishing mortality (F_t) on an annual basis. Thus, a large interval must be used. The larger the interval, the more likely it is that $G_t - Z_t$ is of a magnitude that would cause significant differences in estimates of $\overline{B}_t$ calculated arithmetically and exponentially. Also, in heavily exploited fisheries there may be a large difference between growth and mortality rates within an interval especially at older ages.

We employed Ricker's (1975:242-243, table 10.3) example of bluegills from Muskellunge Lake to illustrate the difference between the two methods of computing mean biomass. This set was chosen because Ricker's data have been used previously as a historical data set and are readily available through his text. Mean biomass was computed arithmetically in the text example and also by Paulik and Bayliff (1967), who used the same data to introduce their computer program. We used the data in two separate runs to compute yield per

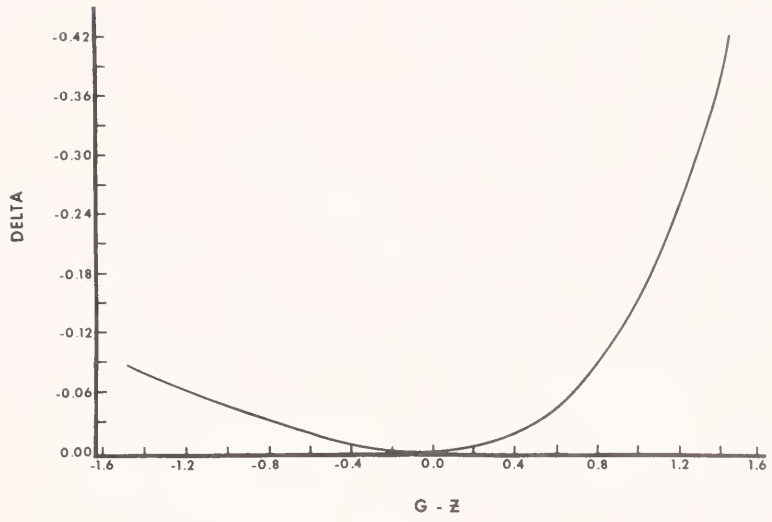

FIGURE 1.—Difference between arithmetic and exponential calculations of mean biomass when $dt = 1.0$ and $B_t = 1.0$, DELTA $= B_t(B_{t,\exp} - B_{t,\text{arith}}) = B_t^{\times}\{0.0061 + 0.0037(G_t - Z_t) - 0.1095((G_t - Z_t)^2) - 0.0491((G_t - Z_t)^3)\}$, $r = 0.998$.

recruit. In one, B_t was computed arithmetically, and in the other it was computed exponentially (Fig. 2). In both runs, the number of survivors was followed across the intervals and biomass was tracked within each interval. There were obvious significant differences. Evaluating various F-multiples and ages of entry, when B_t was calculated arithmetically, the maximum yield exceeded the maximum biomass of the stock (5,522.6

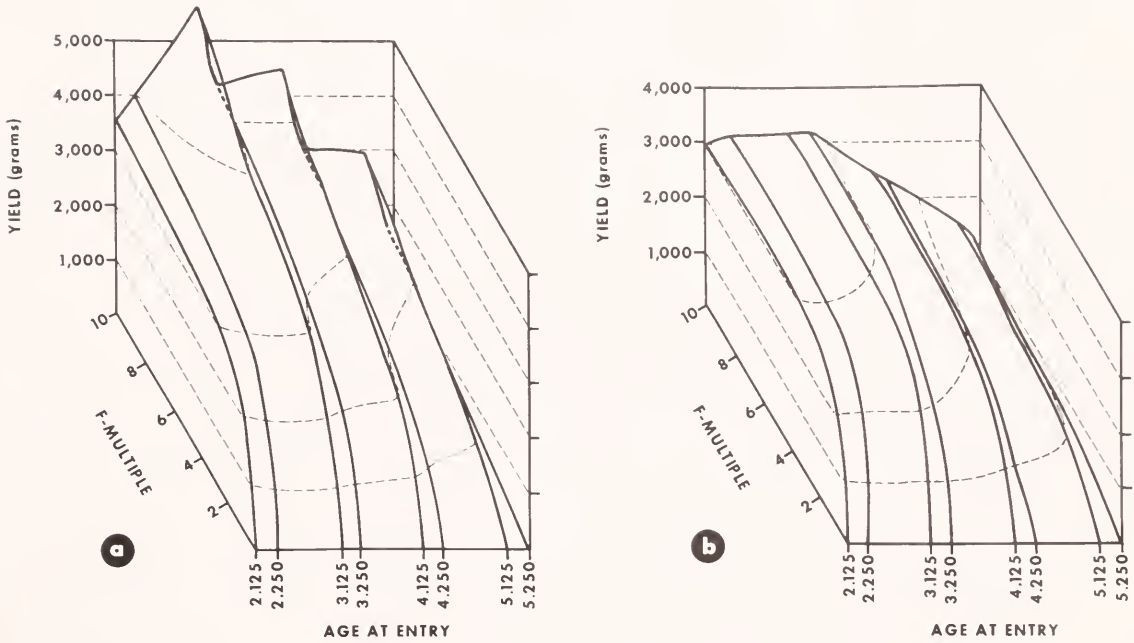

FIGURE 2.—Yield per recruit estimates for bluegills of Muskellunge Lake calculating mean biomass a) arithmetically and b) exponentially (data from Ricker 1975: table 10.3).

g vs. 3,439.2 g) when F-multipliers were large, which is impossible. Maximum biomass of the stock was estimated at F equals zero; the time intervals used were four one-eighth of a year intervals followed by one-half year intervals. Despite the small intervals, the difference between the yield per recruit estimates was large, indicating a need to minimize the $G_t - Z_t$ difference if B_t is calculated arithmetically, regardless of the size of the time intervals. Therefore, in similar circumstances and for the example data set, we recommend that B_t be calculated exponentially.

Acknowledgments

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Contents—continued

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Fishery Bulletin

Vol. 82, No. 3 July 1984

Notes

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Fishery Bulletin

CONTENTS

Vol. 82, No. 3 July 1984

Notes

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1984

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DENSITY-DEPENDENT SEARCHING TIME: IMPLICATIONS IN SURPLUS-PRODUCTION MODELS[1]

RICHARD E. CONDREY[2]

ABSTRACT

An initial theoretical consideration is presented to show how density-dependent searching time can be incorporated into surplus-production models of fisheries. A simple simulation is used to demonstrate the management implications associated with failure to account for this parameter in fisheries where handling time reduces the total time initially available for searching.

The failure to measure density-dependent searching time in assessing fishing effort can lead to erroneous conclusions concerning the collapse of a fishery. In this paper, I will develop my argument using two simple models: Graham's equilibrium yield model (Graham 1935; Ricker 1975) and Holling's (1959b) "disk" equation. I will conclude by drawing parallels between this simple theoretical treatment and patterns that have been observed in searching fisheries.

DEVELOPMENT OF THE MODEL

I begin with the normal definition of the instantaneous rate of fishing mortality, F, as

$$F = q \cdot f = C/N \tag{1}$$

where q is the instantaneous catchability coefficient and is the proportion of the stock (N) that is caught (C) by one unit of fishing effort (f); this fishing effort (f) is the total gear in use for a specific time (Ricker 1975). Following the example of Beddington (1979) and Fowler (1980), I depart from the normal treatment of f, by considering

$$f = f' \cdot t'_s \tag{2}$$

where f' is a physical measure of the total fishing gear in use and t'_s is the proportion of the total fishing time (t') which is available for and used in searching.

If searching time is a constant, independent of stock abundance N, then a linear relationship is normally expected between C/f' (or C/f) and N up to some theoretical limit, as in a Holling (1959a) Type I curve (Fig. 1A) or in the Palohemio and Dickie (1964) model.

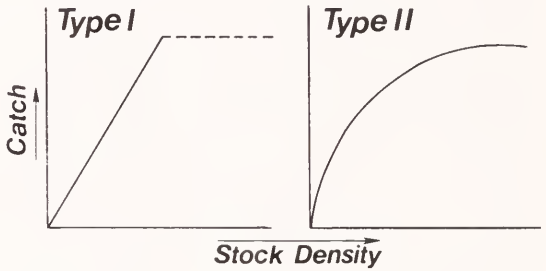

FIGURE 1.—Two types of functional responses of catch to stock density, after Holling (1959a).

If, however, fishermen must expend a substantial amount of time in harvesting the catch once it is sighted, this handling time (t'_h) will reduce the time initially available for searching (e.g., Gulland 1956, 1964; Rothschild and Suda 1977). Holling (1959b) describes one such dependence of t'_s on N as

$$t'_s = t' - t'_h\ (C/f'). \tag{3}$$

Equation (3) describes a curvilinear decline in C/f' with increasing stock abundance (Fig. 1B). Substituting Equation (3) into Equation (2) into Equation (1), we obtain

$$F = q \cdot f' \cdot (t' - t'_h \cdot C/f'), \tag{4}$$

which can be arranged to

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$$1 = \frac{q \cdot f' \cdot t'}{F} - \frac{q \cdot f' \cdot t'_h \, (C/f')}{C/N}$$

$$F = \frac{q \cdot f' \cdot t'}{1 + q \cdot t'_h \cdot N}.$$

Inserting this definition of F as a substitute in Graham's equilibrium yield model, then

$$Y_e = B_e \cdot F_e = k \cdot B_e \cdot (B_\infty - B_e)/B_\infty$$

$$= B_e \cdot q \cdot t' \cdot f'/(1 + q \cdot t'_h \cdot B_e) \quad (5)$$

where B_∞ is the maximum stock biomass, k is the instantaneous rate of increase of the stock as density approaches zero, B_e is the stock mass at an equilibrium position, Y_e is the equilibrium yield, and F_e is the fishing mortality rate which maintains the stock at B_e (Ricker 1975).

As expected a plot of Y_e against B_e or F_e will yield a symmetrical hyperbola, Figure 2A; a plot of q against B_e will denote that q is a constant regardless of the relative magnitude of t'_h to t'. This is not the case, however, if we ignore the effect that stock density has on searching time. For example, a plot of Y_e against $f' \cdot t'$ results in an asymmetrical hyperbola skewed to the right, Figure 2B. The distortion increases as the ratio t'_h/t' approaches 1 and is a result of the increased time the fleet must spend searching for fish as population biomass approaches zero, Figure 2C. Additionally, if searching time is assumed to be independent of stock abundance, q will be incorrectly measured as $q/(1 + q \cdot t'_h \cdot B_e)$ and will appear to be inversely related to population density, Figure 2D.

Note that when $t'_h > 0$, $f' \cdot t'$ will not peak at $B_e = 0$ (for the situation described in Equation (5)). Instead, it will peak at some intermediate level of B_e and will then decline, Figure 2E. Thus, even for the hypothetical equilibrium fishery, $f' \cdot t'$ would have to "voluntarily" decline from a maximum level as B_e approaches zero.

DISCUSSION

The assumptions inherent in Equation (5) limit its direct application as a qualitative model of existing fisheries. However, the general behavior described in Figure 2B, D has been noted in several recent papers (Fox 1974; Pope and Garrod 1975; Schaaf 1975b; MacCall 1976; Ultang 1976; Garrod 1977; Peterman 1980; Peterman and Steer 1981; Bannerot and Austin 1983). Two important examples occur with the Pacific sardine and Atlantic menhaden fisheries.

In their analysis of the available catch and effort data on the California based fishery on Pacific sardine, Fox (1974) and MacCall (1976) were forced to relax the usual restriction of a constant catchability coefficient which is independent of population size. Rather, they applied a density-dependent catchability coefficient of the form

$$q = \alpha N^\beta \quad (6)$$

where α and β are constants, assuming a constant catch per unit effort. The general patterns predicted by these analyses are similar to those in Figure 2B, D, with MacCall noting an inverse relationship between the apparent q and population abundance, and Fox noting a collapse of the fishery in plots of catch versus vessel-months, Figure 3. Both of these patterns may be the result of an inability to describe mathematically how the time available for searching increased as the population of sardines declined.

It is generally assumed that Atlantic menhaden have been overfished since the early sixties. Support for this conclusion was derived from the surplus-production work of Schaaf and Huntsman (1972), later updated by Schaaf (1975a). In both studies the available effort index (vessel-weeks) was modified in an attempt to correct for changes in fishing efficiency with time. Under the assumption of a constant q and lacking detailed information on vessel characteristics and catch, the authors adjusted effort by "multiplying the effort observed in each year by the relative change in q", using either 1965 (Schaaf and Huntsman) or 1971 (Schaaf 1975a) as a base year. The resulting pattern (Fig. 4A) strongly suggests that the fishery was operating on the descending arm of the catch-effort curve.

In another paper, Schaaf (1975b) observed an inverse relationship between his estimates of catchability coefficient and the population density, generating a pattern, like MacCall's (1976), similar to Figure 2D and at least partially explained by the lack of information on density-dependent searching time. However, Schaaf's apparent density-dependent estimate of q violates his early assumption of a constant q for use in standardizing the available effort data. The point is not trivial. Without this adjustment, the available effort data suggest that the Atlantic menhaden fishery is operating on the ascending arm of the catch-effort curve, Figure 4B.

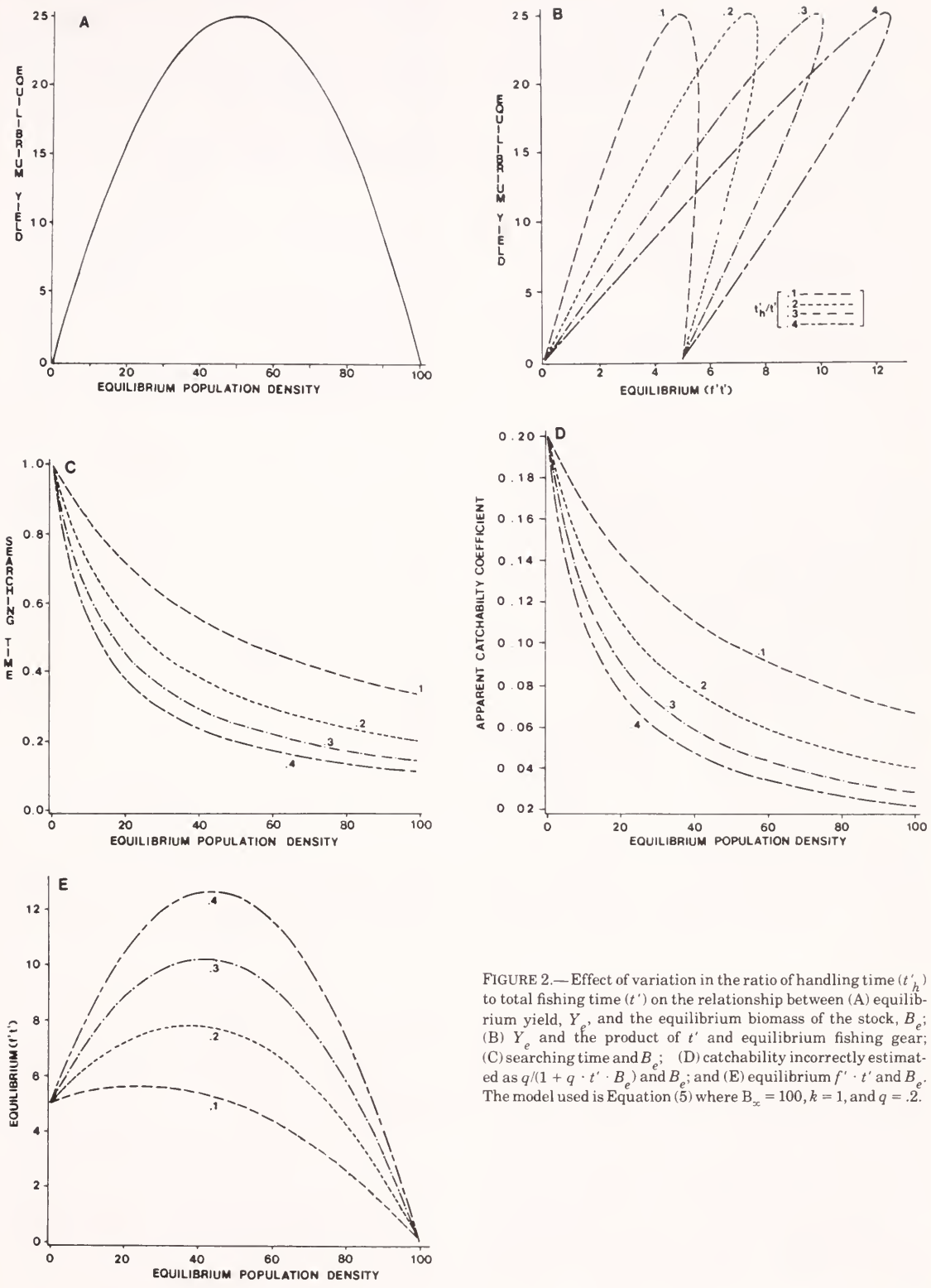

FIGURE 2.—Effect of variation in the ratio of handling time (t'_h) to total fishing time (t') on the relationship between (A) equilibrium yield, Y_e, and the equilibrium biomass of the stock, B_e; (B) Y_e and the product of t' and equilibrium fishing gear; (C) searching time and B_e; (D) catchability incorrectly estimated as $q/(1 + q \cdot t' \cdot B_e)$ and B_e; and (E) equilibrium $f' \cdot t'$ and B_e. The model used is Equation (5) where $B_\infty = 100$, $k = 1$, and $q = .2$.

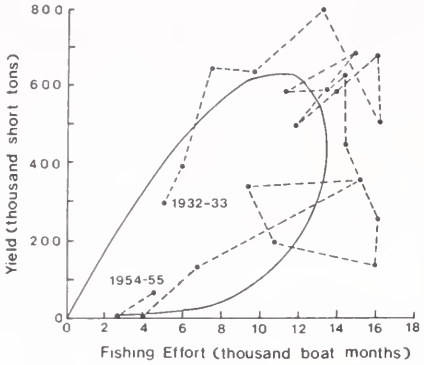

FIGURE 3.—Catch versus a nominal effort index for the California Pacific sardine fishery (after Fox 1974).

IMPLICATIONS

In this simple treatment, I have shown how some available estimates of fishing effort are inadequate to describe a fishery where searching time is stock-density dependent. More realistic models can be based upon an examination of detailed log-book data for inferences as to the relationships between searching time, stock abundance, prey and fleet distribution, and cooperation among the fleet. Hassel (1978) offers a comprehensive review of current approaches.

Even with better estimates of fishing effort a catastrophic collapse may be unavoidable because of parameters that cannot be measured or controlled (e.g., Clark and Manguel 1979). These estimates are important, however, in order to use surplus-production models for estimating the causes of such catastrophic collapses as that of the Pacific sardine fishery. Such estimates may also be necessary to suggest whether existing fisheries such as the Atlantic menhaden are actually being overfished.

ACKNOWLEDGMENTS

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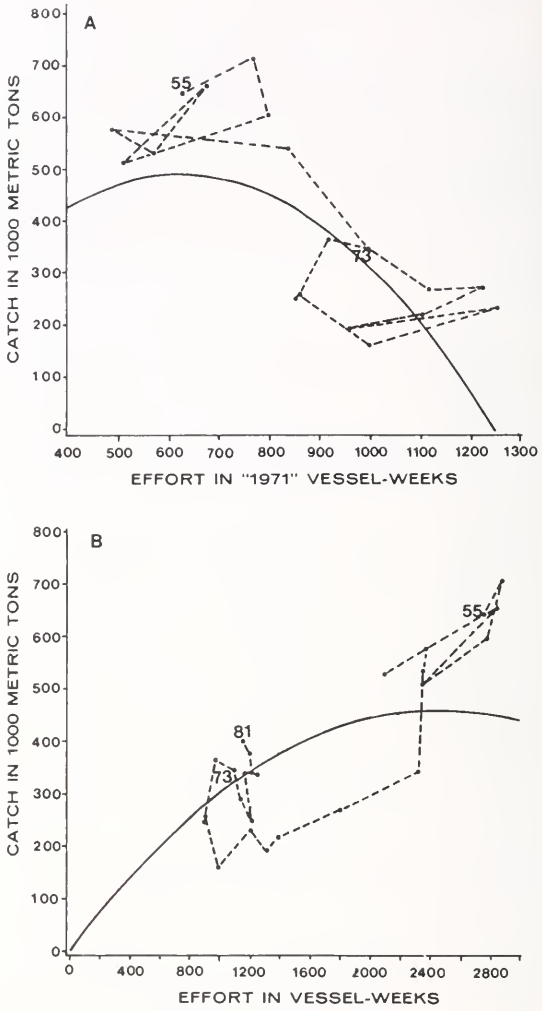

FIGURE 4.—Comparing the difference between fitting catch data for Atlantic menhaden when the effort is measured as (A) Schaaf's (1975a) 1971-vessel weeks and (B) vessel weeks. Curves were fit after the technique of Marchesseault et al. (1976).

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COMMUNITY AND TROPHIC ORGANIZATION OF NEKTON UTILIZING SHALLOW MARSH HABITATS, YORK RIVER, VIRGINIA[1]

STEPHEN M. SMITH,[2] JAMES G. HOFF,[2] STEVEN P. O'NEIL,[3] AND MICHAEL P. WEINSTEIN[3]

ABSTRACT

Nekton were collected by trawl and Wegener ring at each of two stations within tidal creeks and at adjacent shoal stations in the polyhaline and oligomesohaline zones of the York River estuary, Virginia. Species richness was significantly higher ($P < 0.05$) in Goalders Creek (oligomesohaline) compared with Blevins Creek (polyhaline) and may reflect the general absence of stenohaline marine "southern" taxa which seasonally occupy the tidal creeks of warm-temperate estuaries. In general, diversity was low in both creeks with dominance mainly shared by two species, *Leiostomus xanthurus* and *Anchoa mitchelli*. *Trinectes maculatus* also was abundant at the Goalders Creek shoal station, about 200 m outside of the creek mouth. A detailed analysis of the distribution of *L. xanthurus* indicated that after recruitment ceased, this species was largely resident in the creeks for several months, only emerging in the fall (October). Furthermore, emigration from Blevins Creek occurred earlier than at the upstream locality. Of the "transient" marine species encountered, *L. xanthurus* seemed to be the most tidal creek dependent. However, this may be due partly to the collection methodology employed.

Diet composition of six dominant species comprising >98% of the total number of individuals collected indicated that all were essentially trophic opportunists feeding on a wide variety of food items. Ontogenetic shifts in diet were also observed for the five most abundant species. Lack of dietary specialization and the consequently large degree of diet overlap in all species may reflect the nonlimiting nature of food abundance in the primary nurseries, however a seasonal change in relative fullness values may indicate periodic food scarcity.

The structural and functional role of shallow estuarine habitats has received increasing attention in the past few years. Although widely recognized as primary nurseries, two of these habitats, marshes and seagrass meadows, have only recently come under scrutiny in the lower Chesapeake Bay. Much of the impetus for these efforts was derived from priorities established by the Chesapeake Bay Program (Environmental Protection Agency 1979). As a result, areas covered with submerged aquatic vegetation (SAV) were investigated between 1977 and 1981. The role of SAV as primary nurseries, especially for blue crabs, *Callinectes sapidus*, was confirmed (Orth[4]). It was suggested (and, in some cases, demonstrated experimentally) that a principal function of vegetated habitats was that of predation refugium for the early life stages of many species (Heck and Thoman 1981; Lascara 1981; see also Nelson 1979 and Coen et al. 1981). Although seagrass meadows were contrasted with immediately adjacent unvegetated areas, their value compared with tidal salt marshes was not established.

To place the utilization of SAV and tidal creeks by the immature life stages of dominant species into better perspective, Weinstein and Brooks (1983) undertook a direct comparison of these areas along a contiguous marsh-seagrass ecosystem on the eastern shore of Virginia. Two results of their study were the observations that the dominant finfish in the area—spot, *Leiostomus xanthurus*—was nearly four times more abundant in the tidal creek throughout the study period, and that larger juvenile and adult blue crabs made nearly equal use of both habitats. A further outcome of this study was the obvious need for additional inventories of shallow waters of the lower Chesapeake Bay with regard to the relative value of different habitats to resident species.

For this reason we have extended our program to include a survey of habitat utilization by nekton occupying oligohaline and polyhaline tidal creeks

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of the York River estuary and have included a comparison of the tidal creeks with adjacent shoal areas (about 200 m outside of the tidal creek mouths). Along with data on community composition and structure, we have begun baseline studies of diet composition of dominant species. These aspects of community ecology of York River tidal marshes are reported herein.

STUDY AREA AND METHODS

The York River is one of six major tributaries which enter the Chesapeake Bay along its western shoreline. The narrow estuary covers about 208 km² and extends 46 km from Tue Marsh Light to West Point, Va. (Fig. 1). The upper portion of the York is characterized by broad, shallow flats and tidal creeks dominated by *Spartina* spp. along the shoreline. Upstream the river channel averages 8-9 m in depth, but broadens downstream and reaches a maximum depth of 18-23 m. The Guinea Marshes (Fig. 1) is a major *Spartina alterniflora*-dominated marsh system located near the estuary mouth. Much of the adjacent shallows in this region is carpeted with dense stands of eelgrass, *Zostera marina*, and widgeon grass, *Ruppia maritima*. Salinities are usually in the polyhaline range.

Two tidal creeks were selected for study. Goalders Creek (Fig. 1:location A) was located in the oligohaline-mesohaline zone just below the city of West Point. Blevins Creek (Fig. 1:location B), a part of the Guinea Marsh system, was situated in the polyhaline zone where salinities always exceeded 16‰. In each creek, one station was established as far upstream as possible, one near the creek mouth, and one about 200 m offshore. All collections were made monthly on consecutive days (March-October 1983), with sampling initiated as close to daytime high tides as possible. Miller and Dunn (1980) collected a greater proportion of fish with stomachs containing food at this time. Creek bottoms were of the mud-silt type and ranged from 1 to 1.5 m deep.

The primary collecting device utilized in this study was a 4.9 m otter trawl consisting of wings and body of 19 mm mesh and a liner of 6.3 mm mesh. This gear was towed for 2-min intervals at a speed of about 1.0 m/s at each station. In an earlier study at Guinea Marshes, Orth and Heck (1980) demonstrated that six hauls of the trawl were necessary in seagrass habitats to attain asymptotic returns on community information (as judged by several diversity indices). Because of the expectedly lower diversity in the tidal creeks (Weinstein and Brooks 1983), it was determined that four consecutive hauls at each tidal creek station would be sufficient to attain the same level of community information.

Ancillary collections were taken in the tidal creek with a modified Wegener ring (Wegener et al. 1973). The gear was used in depths <1 m, in the vicinity of the trawling stations. The side walls of the ring consisted of 1.5 mm woven netting, with the original design of the gear being changed to include a 305 mm "skirt" and chain attached to the

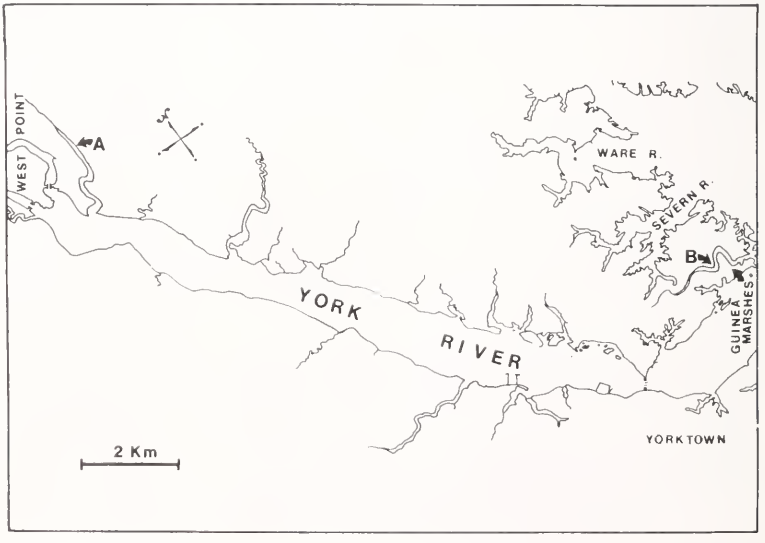

FIGURE 1.—Location of study areas in York River estuary, Va. Three permanent sampling stations were established—near the headwaters, at the mouth, and 200 m offshore of an oligomesohaline (A = Goalders Creek) and polyhaline (B = Blevins Creek) tidal creeks.

leadline hoop which helped fill contours along the bottom. Samples were obtained by tossing the ring from shore and then applying rotenone at a 30 ppb concentration within the confines of the net (Weinstein and Brooks 1983). Stricken fishes were then captured with dip net or swept off the bottom.

Fishes were sorted into 20 mm (or less) size classes and up to 20 randomly selected individuals from each class used for trophic analyses. Stomach fullness was recorded as a relative fullness index (RFI) value (Hyslop 1980). Stomach contents were subsequently analyzed using a modified Carr and Adams (1972) sieve fractionation technique. Total dry weights for each sieve fraction were then obtained and proportioned among the prey taxa identified from a five drop subsample taken before drying. On the assumption that particles of equal size have approximately the same weight, this method agglomerates food particles of roughly the same size.

The Carr and Adams technique provided rapid, accurate identification of food items for a large number of stomachs and has been used with success by several investigators (Sheridan 1979; Sheridan and Livingston 1979; Stoner 1980; Livingston 1982). A useful modification employed in this study was the application of a low pressure stream of compressed air delivered through a Pasteur pipette which greatly aided in removing food particles adhering to the finer screens of the sieves.

Numerical classification analysis used here is similar to the procedures employed by Weinstein (1979) and Weinstein and Brooks (1983). Briefly, marsh creek communities and trophic ecology of dominant species were compared by classification methods using "normal" and "inverse" classification (Clifford and Stephenson 1975). The former method groups sites (or predators) by their species (or prey taxon) attributes; while inverse classification (used only for community analysis purposes here) groups species according to their site of occurrence (i.e., the sites become the attributes of the species). Similarity between sites (or predators) was calculated as the complement of the Canberra metric index:

$$[1/n][\sum_{1}^{N}]|x_{1j} - x_{2j}|/(x_{1j} + x_{2j}) \qquad (1)$$

where n = number of attributes, and x_{1j} and x_{2j} are the values of the jth attribute for any pair of entities. The merits of the Canberra metric index have been discussed by Clifford and Stephenson (1975).

Separate matrices were constructed for each comparison from untransformed, pooled monthly data and clustered by the unweighted pair, group-average strategy (Clifford and Stephenson 1975). Species occurring at only one station (singletons) were eliminated prior to the community analyses. Combined trawl and Wegener ring data were used separately in these procedures. Dendrograms for site and species dissimilarity (community analyses) were constructed and cross-tabulated in a two-way coincidence table.

All nekton were preserved in 10% buffered Formalin[5]. Standard length (SL, carapace width for blue crabs) was recorded for all taxa. Up to 30 individuals/species were measured from each collection, subsampling for lengths was employed when sorted collections contained more than 30 individuals of a given species. Prior to each collection, temperature and salinity were recorded with an immersion thermometer and a temperature-compensated refractometer.

RESULTS

Abundance and Seasonality

Only two species—spot and the bay anchovy, *Anchoa mitchelli*—comprised >90% of the total number of individuals captured at Blevins Creek and adjacent shoals. Using this same criterion, upstream densities were more equitably distributed with four species in the creek and six on the shoal sharing dominance (Table 1). Blue crabs; white perch, *Morone americana*; and the hogchoker, *Trinectes maculatus*, were in this group in Goalders Creek, while in late summer and fall the Atlantic croaker, *Micropogonias undulatus*, and the weakfish, *Cynoscion regalis*, were also abundant at the shoal station (Table 1).

Species richness (S) was also greater in all months in the Goalders Creek system compared with the polyhaline Blevins Creek (Fig. 2) and was significantly greater for the entire study period (Wilcoxon sign-ranks test; $P < 0.05$). No apparent trend, however, was evident in the number of individuals captured at each locality (Fig. 2), except that peak catches of two dominant species, spot and bay anchovy, were greater in Blevins Creek and resulted in the large disparity in catches in

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

TABLE 1.—Pooled species abundance and percent composition for all trawl collections, York River estuary, Va. N = number of individuals.

Species	N	%
Goalders Creek upstream		
Leiostomus xanthurus	709	[1]70.69
Callinectes sapidus	83	[1]8.27
Anchoa mitchilli	69	[1]6.88
Morone americana	48	[1]4.79
Alosa aestivalis	35	3.49
Morone saxatilis	27	2.69
Ictalurus catus	25	2.49
Brevoortia tyrannus	3	0.30
Pomatomus saltatrix	1	0.10
Peprilus alepidotus	1	0.10
Anguilla rostrata	1	0.10
Trinectes maculatus	1	0.10
Total	1,003	100.00
Goalders Creek downstream		
Leiostomus xanthurus	1,646	[1]60.09
Trinectes maculatus	385	[1]14.05
Anchoa mitchilli	373	[1]13.62
Callinectes sapidus	144	[1]5.26
Ictalurus catus	75	2.74
Morone americana	57	2.08
Brevoortia tyrannus	17	0.62
Cynoscion regalis	16	0.58
Morone saxatilis	8	0.29
Paralichthys dentatus	3	0.11
Micropogonias undulatus	3	0.11
Alosa aestivalis	3	0.11
Opsanus tau	3	0.11
Pomatomus saltatrix	2	0.07
Peprilus alepidotus	1	0.04
Alosa sapidissima	1	0.04
Anguilla rostrata	1	0.04
Syngnathus fuscus	1	0.04
Total	2,739	100.00
Goalders Creek shoal		
Trinectes maculatus	1,439	[1]50.31
Leiostomus xanthurus	412	[1]14.40
Anchoa mitchilli	310	[1]10.84
Callinectes sapidus	308	[1]10.77
Micropogonias undulatus	91	[1]3.18
Cynoscion regalis	77	[1]2.69
Ictalurus catus	59	2.06
Morone americana	57	1.99
Anchoa hepsetus	33	1.15
Opsanus tau	28	0.98
Ophidion marginata	13	0.45
Paralichthys dentatus	12	0.42
Anguilla rostrata	8	0.28
Morone saxatilis	5	0.18
Menticirrhus saxatilis	3	0.11
Pomatomus saltatrix	2	0.07
Peprilus alepidotus	1	0.04
Brevoortia tyrannus	1	0.04
Gobiosoma bosci	1	0.04
Total	2,860	100.00
Blevins Creek upstream		
Leiostomus xanthurus	1,301	[1]46.51
Anchoa mitchilli	1,248	[1]44.62
Callinectes sapidus	162	5.79
Trinectes maculatus	35	1.25
Brevoortia tyrannus	23	0.82
Menidia menidia	17	0.61
Fundulus heteroclitus	5	0.18
Gobiosoma bosci	3	0.11
Cynoscion regalis	1	0.04
Morone americana	1	0.04
Microgobius thalassinus	1	0.03
Total	2,797	100.00
Blevins Creek downstream		
Leiostomus xanthurus	1,501	[1]73.69
Anchoa mitchilli	414	[1]20.32
Callinectes sapidus	103	5.05
Paralichthys dentatus	6	0.30
Menidia menidia	5	0.24
Gobiosoma bosci	2	0.10
Trinectes maculatus	2	0.10
Cobiesox strumosus	2	0.10
Peprilus triacantus	1	0.05
Microgobius thalassinus	1	0.05
Total	2,037	100.00
Blevins Creek shoal		
Leiostomus xanthurus	1,935	[1]80.03
Anchoa mitchilli	385	[1]15.92
Callinectes sapidus	49	2.03
Trinectes maculatus	10	0.42
Bairdiella chrysoura	10	0.42
Paralichthys dentatus	6	0.25
Opsanus tau	4	0.17
Micropogonias undulatus	3	0.12
Stenotomus chrysops	2	0.08
Anchoa hepsetus	2	0.08
Syngnathus fuscus	2	0.08
Gobiosoma bosci	2	0.08
Menidia menidia	2	0.08
Synodus foetens	2	0.08
Centropristis striata	1	0.04
Rachycentron canadum	1	0.04
Brevoortia tyrannus	1	0.04
Urophycis regia	1	0.04
Total	2,418	100.00

[1]Species comprising ~90% of the total number of individuals.

May and July. Except for the spike seen in Figure 2, resultant from a large influx of bay anchovy into Blevins Creek in July, combined catches of all other taxa were at a minimum for the summer months (June-August) coincident with peak summer temperatures.

Seasonal abundance of the more common species was typically associated with recruitment of young-of-year individuals into the tidal creeks and adjacent shoals. Young spot dominated in both creeks but were subsequently replaced by post-larval and juvenile bay anchovy (July), and thereafter at Goalders Creek by hogchoker (August), weakfish (August-September), and Atlantic croaker (October). In addition, white catfish, *Ictalurus catus*, and white perch were frequently captured in the Goalders Creek vicinity during early spring when salinities were at their lowest recorded levels. Because of the overall seasonal abundance, it was possible to examine spatial and temporal distributions of spot in greater detail (Fig. 3, Table 2). As expected, spot were more abundant outside of the creeks very early in recruitment; but by June had established a greater degree of residency within the creeks compared with the adjacent shoals. This pattern of large creek to shoal abundance ratios (Fig. 3) continued (with a single exception) until October when spot emerged from Blevins Creek. Note, however, that at the termination of the sampling program, this emigration had not taken place upstream. Similar

TABLE 2.—Relative abundance of *Leiostomus xanthurus* at tidal creek stations, York River estuary.

Location	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
Goalders Creek								
Upstream	0	1	401	85	51	58	68	45
Downstream	0	52	624	318	236	172	93	151
Blevins Creek								
Upstream	0	19	493	326	292	60	105	6
Downstream	0	18	586	337	102	150	221	87

patterns of earlier downstream emigration were observed during 1976-78 in the Cape Fear estuary, N.C. (Weinstein and Walters 1981; Weinstein pers. obs.), the cause of which remains unexplained. It is evident from Table 2 that spot may have been more restricted in their upsteam movement in Goalders Creek where salinities averaged about 2‰ lower at the upsteam station than at the creek mouth. The ratio of upstream to downstream station catch was twice as high at Blevins Creek, supporting this pattern. Other species which seem to prefer a specific portion of the tidal creek to shoal habitat gradient included hogchoker, weakfish, and Atlantic croaker which had creek-to-shoal ratios (over all months) of 0.13, 0.10, and 0.02, respectively. Moreover, these species were far more abundant at upstream sites (Table 1).

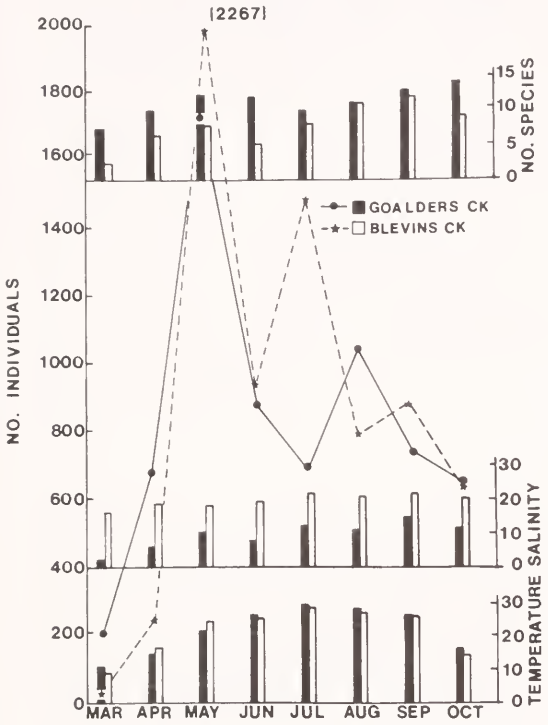

FIGURE 2.—Total numbers of individuals and species captured in monthly tidal creek collections. Temperatures and salinities are mean values recorded at each creek in each month.

Community Composition

A two-way coincidence table, using a similarity value of 0.200 to define clusters (Clifford and Stephenson 1975), was constructed in order to summarize species and site relationships for pooled monthly collections at each station (Table 3). Included in this analysis are samples collected with the Wegener ring, a gear which was expected to be more successful in collecting both cryptic species (e.g., Gobiidae) and shore-zone taxa (e.g., cyprinodonts [Cyprinodontidae] and silverside [Atherinidae]). It should be pointed out, however, that any comparisons between the Wegener ring and trawl samples are qualitative since no attempt was made to compare gear selectivity, efficiency, and area encompassed by a unit effort for each sampling device (Weinstein and Brooks 1983).

Species group IV (Table 3) was generally the most ubiquitously distributed assemblage over the range of environmental factors (particularly

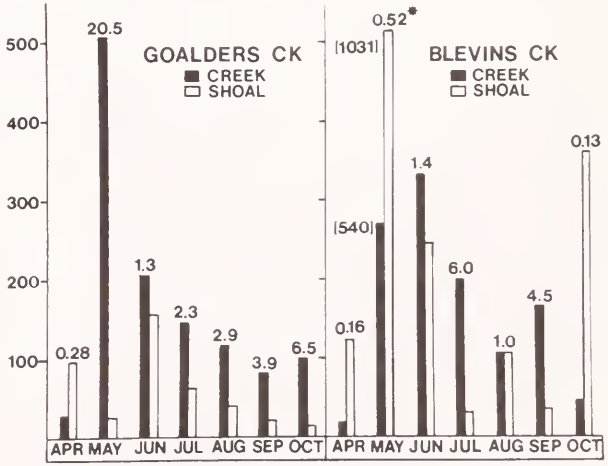

FIGURE 3.—Relative densities of *Leiostomus xanthurus* at tidal creek (values shown are monthly means for both creek stations) and shoal sampling localities. May values for Blevins Creek are drawn to half-scale. Values appearing above histograms are ratios of creek to shoal densities.

TABLE 3.—Two-way coincidence table comparing stations (Groups A-D) and species (groups I-VI) associations at York River estuary sites. Clustering by unweighted-pair group-average; similarity index = Camberra metric, all data $\log_{10}(x + 1)$ transformed, single station occurrences dropped. G = Goalders Creek, B = Blevins Creek, U = upstream, D = downstream, S = shoal stations, W = Wegener ring samples.

		A			B			C			D
Group	Species	GU	GD	GS	BU	BD	BS	GUW	BDW	BUW	GDW
I	*Paralichthys dentatus*		3	12		6	6				1
	Micropogonias undulatus		3	91			3				
	Opsanus tau		3	28			4				
	Anchoa hepsetus			33			2				
	Cynoscion regalis		16	77	1						
	Syngnathus fuscus			1			2	1			
II	*Pomatomus saltatrix*	1	2	2							
	Peprilus alepidotus	1	1	1							
	Anguilla rostrata	1	1	8							
	Morone saxatilis	27	8	5							
	Ictalurus catus	24	75	59							1
	Brevoortia tyrannus	3	17	1	23		1				7
III	*Alosa aestivalis*	35	3					1	1		5
	Fundulus heteroclitus				5			1	3	23	1
	Menidia beryllina							3	6		3
IV	*Morone americana*	48	57	57	1			2		1	10
	Leiostomus xanthurus	709	1,646	412	1,301	1,501	1,935	9	14	14	3
	Anchoa mitchilli	69	373	310	1,248	414	385	3		4	32
	Trinectes maculatus	1	385	1,439	35	2	10	1			
	Callinectes sapidus	83	144	308	162	103	49				
	Gobiosoma bosci			1	3	2	2	2	13	4	106
	Menidia menidia				17	5	2				24
V	*Fundulus majalis*									2	1
VI	*Microgobius thalassinus*				1	1					

salinity) examined. Nonetheless, within this group were several species which displayed area-specific distributions, in either relative numbers or presence/absence in a given creek system. Examples of the former include the hogchoker and bay anchovy and of the latter, white perch, which was far more prevalent upstream. The Goalders Creek nekton community was also dominated by members of groups I and II, whose members were rare or absent at downstream localities. Remaining species were generally not captured in sufficient numbers to depict their role in defining community structure in each area.

Trophic Analysis

Six species (Fig. 4) were sufficiently abundant in time and space to allow a comparative trophic analysis to be undertaken. Collectively, they exceeded 98% of the total number of individuals captured during this study. Prey taxa were defined on the basis of 39 categories (Table 4). All but two—miscellaneous (MISC) and unidentified (UID)—were mutually exclusive. These two did not exceed 17% of the total diet composition of any one species and were generally much lower than this amount. The dietary relationships of these six species are summarized across all sampling strata by the dendrograms appearing in Figure 4. With the exception of summer flounder, *Paralicthys dentatus*, sufficient numbers of individuals were captured to also allow partitioning by size classes. Such ontogenetic summaries are shown in Figure 5.

Although more than 2,600 specimens were examined for diet composition, sample sizes were not sufficient in the first year of the study to examine details of seasonal nor spatial food utilization in all species except spot (O'Neil 1983). In addition, several species were only abundant in a restricted area (Table 1) or attained peak abundance in a relatively narrow time frame, precluding dietary comparison of dominant species (Fig. 6).

Diet overlap was greatest between white perch and hogchoker (Fig. 4). Dietary items shared by these species included clam siphons, *Leoptochirus plumulosus*, and other gammarid amphipods. Both predators were generally habitat-specific, with young-of-year white perch more abundant in the creeks and hogchoker prevalent on the river shoals (Table 1). Largely because of fish (TEL) included in the diet of larger individuals, white catfish displayed somewhat less overlap in its diet compared with the former species, but because of its partial piscivorous habits shared this similarity with the major fish predator captured in our trawl samples—the summer flounder. Both small summer flounder and white perch (<61 mm) also consumed substantial quantities of the mysid shrimp *Neomysis americana*.

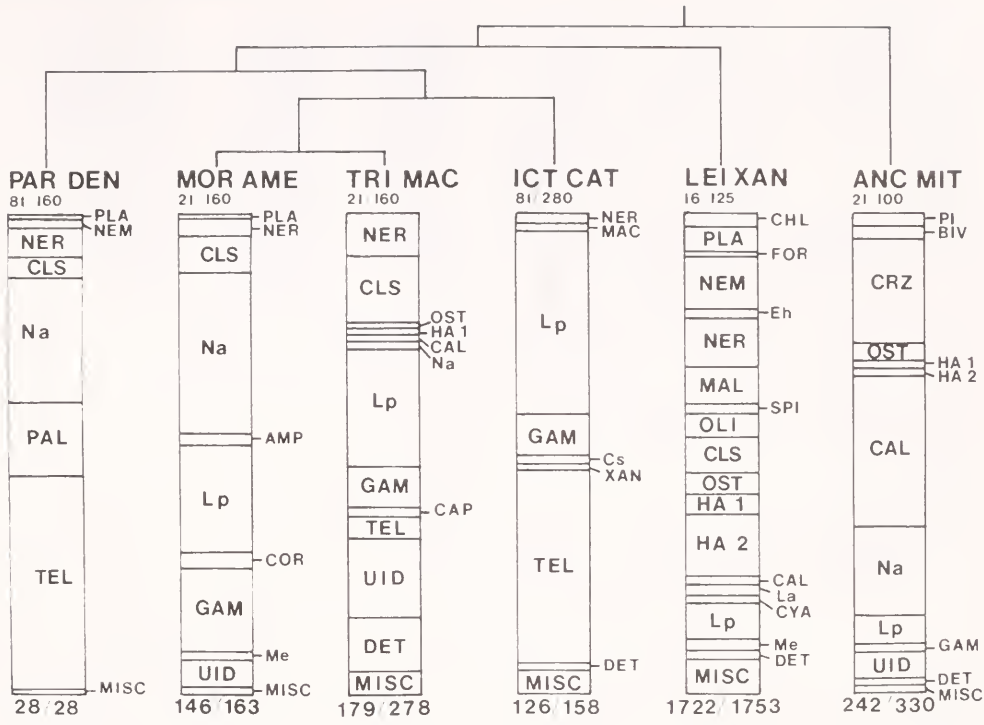

FIGURE 4.—Trophic comparisons among dominant predators (those comprising >98% of the total number of individuals captured), pooled across all sampling strata. PAR DEN = *Paralichthys dentatus*; MOR AME = *Morone americana*; TRI MAC = *Trinectes maculatus*; ICT CAT = *Ictalurus catus*; LEI XAN = *Leiostomus xanthurus*; ANC MIT = *Anchoa mitchilli*. Ratios appearing below histograms represent stomachs with food as a proportion of total stomachs. Values above histograms are size ranges (standard lengths). Diet composition was compared using Canberra metric and unweighted-pair group-average clustering strategy, data untransformed. Prey designations are defined in Table 4.

TABLE 4.—Prey categories used for trophic comparisons. All but unidentified (UID) and miscellaneous (MISC) are mutually exclusive feeding categories.

AMP	Amphipoda	La	*Leucon americanus*
BIV	Bivalves	Lp	*Leptocheirus plumulosus*
BRA	Branchipoda	MAC	*Macoma* sp.
CAL	Calanoids	MAL	Maldanidae
CAP	Caprellidae	Me	*Monoculodes edwardsi*
CLS	Clam siphons	MISC	Miscellaneous
CHI	Chironomidae	Na	*Neomysis americana*
CHL	Chlorophyta	NEM	Nematoda
COR	Corophiidae	NER	Nereidae
Crs	*Crangon septemspinosa*	OLI	Oligochaeta
CRZ	Crab zoea	OST	Ostracods
Cs	*Callinectes sapidus*	PAL	Palaemonidae
CYA	Cyathura	PI	Polydora ligni
DET	Detritus	PLA	Plant matter
Eh	*Eteone heteropoda*	POL	Polychaeta
Et	*Edotea tribola*	SPI	Spionidae
FOR	Foraminifera	TEL	Teleostei
GAM	Gammaridae	UID	Unidentified remains
HA1	Harpacticoid 1	XAN	Xanthidae
HA2	Harpacticoid 2		

Among the six species examined, spot and bay anchovy displayed the least dietary overlap, with the former exhibiting the greatest dietary diversity (consisting mainly of benthic prey items), and the latter including a greater percentage of planktonic food items in its diet. However, the large variety of prey items consumed by all species indicates that each is a trophic opportunist (Darnell 1958, 1961; Carr and Adams 1973; Sheridan and Livingston 1979; Livingston 1982).

Ontogenetic shifts in diet were evident for each of the species examined (Fig. 5). In spot, dietary importance of calanoid copepods declined in fish >20 mm SL, while harpacticoid copepods increased in importance in fish 21-80 mm SL. Concurrently, the percentage of various polychaetes and gammarid amphipods slowly increased in their diet. Nematodes also became less important with increasing size. Interestingly, spot stomachs at all sizes contained clam siphons and maldanid tails, indicating that specific parts of larger prey were important dietary items.

Ostracods and crab zoea were abundant food items for small (<21 mm SL) bay anchovy; larger

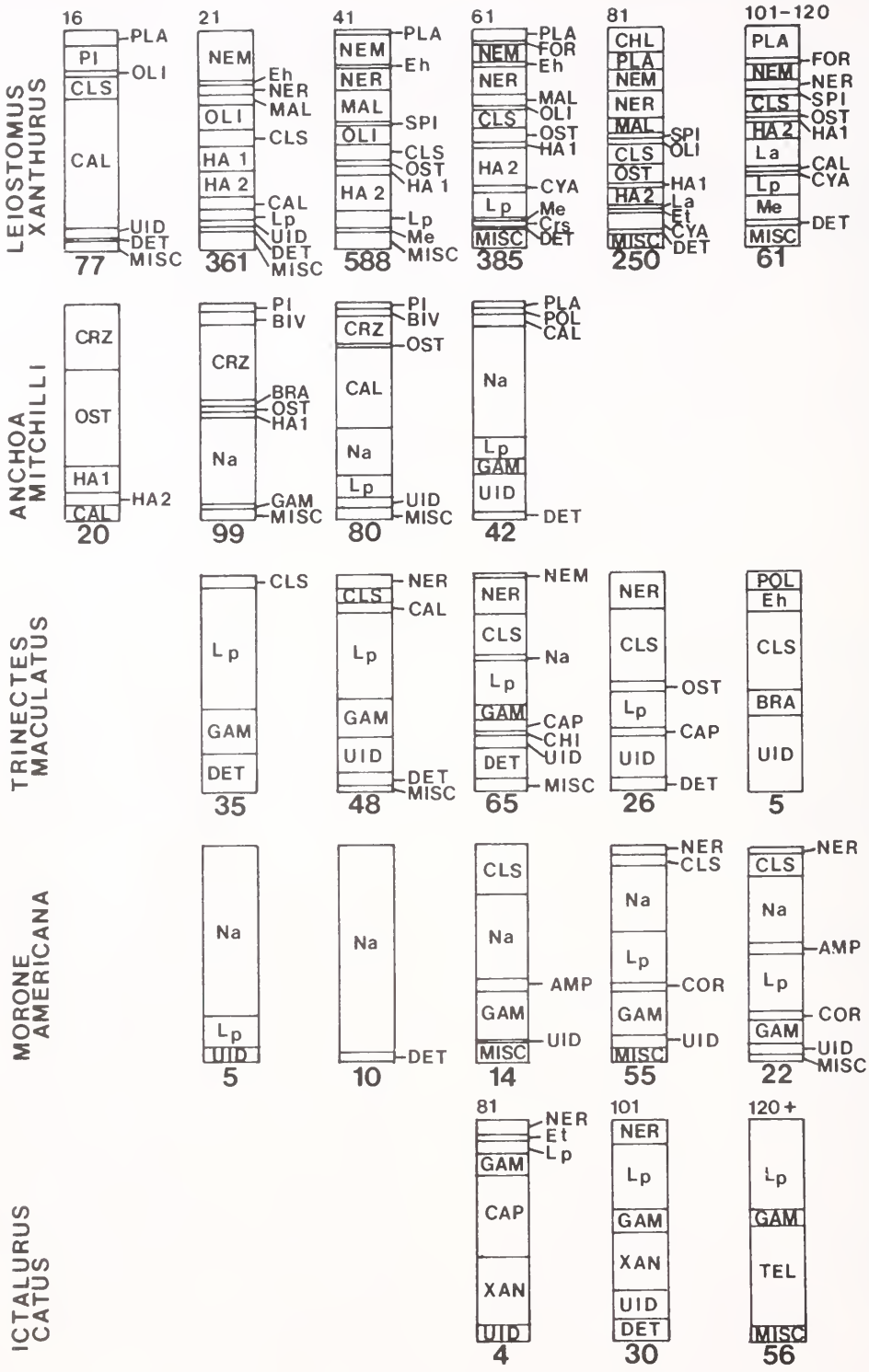

FIGURE 5.—Ontogenetic comparisons in diet among the five most dominant species captured in this study. Sample size (stomachs with food) appear below histograms, size increment (standard length) above. Prey designations are defined in Table 4.

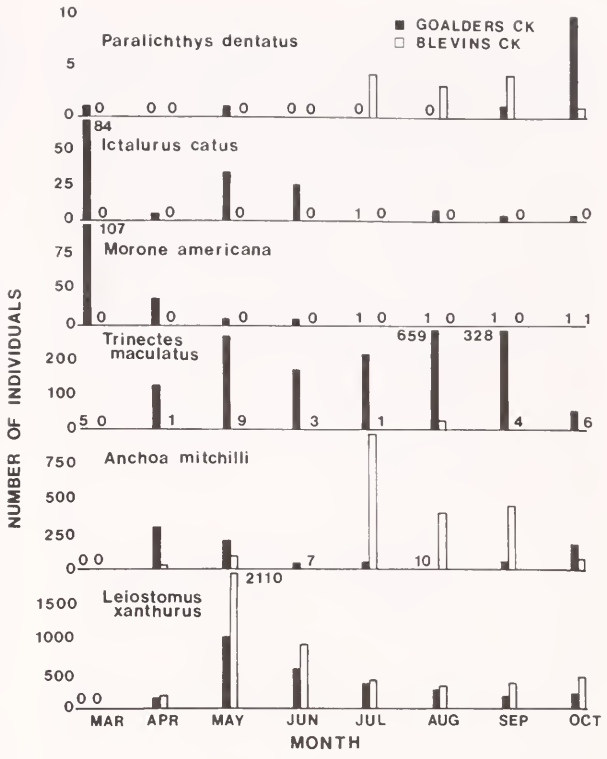

FIGURE 6.—Seasonality of selected taxa at tidal creek and shoal stations, York River estuary, Va. Numbers on x axis are sample sizes too small to plot.

individuals incorporated more *Neomysis americana*, calanoid copepods, and gammaridean amphipods into their diet. In hogchokers, however, gammarids predominated in smaller individuals, <61 mm SL, but with increasing size became somewhat less important and were replaced by nereid polychaetes and clam siphons. Hogchokers had the highest proportion of unidentified remains (UID) of any predator examined due to the high level of maceration characteristic of this species.

Neomysis americana was clearly the dominant prey item of small (<60 mm SL) white perch, but became less important in the diets of larger individuals which fed increasingly on gammarid amphipods and clam siphons. White catfish <120 mm SL also fed conspicuously on amphipods but, uniquely among the predators examined, also fed upon xanthid crabs, and at larger sizes incorporated a substantial proportion of fishes into their diet.

Relative fullness indices displayed varying trends on a species-specific basis (Table 5). Values declined in the later part of the study for white perch and white catfish, whereas no apparent trends were observed for other species.

TABLE 5.—Monthly relative fullness index (RFI) for six dominant fishes in the York River estuary, Va. Values are means for all individuals examined.

Species	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
Anchoa mitchilli		0.66	2.73	1.60	2.16	2.72	2.43	1.03
Ictalurus catus	2.53	2.20	1.84	1.50		1.19	1.74	1.00
Leiostomus xanthurus		2.45	2.45	2.62	2.59	2.77	2.51	1.98
Morone americana	2.65	1.59	1.14	1.00		1.00		0.50
Paralichthys dentatus	2.60				3.33	2.50	3.50	4.00
Tnnectes maculatus		1.82	1.91	1.45	1.47	1.60	0.88	1.30

DISCUSSION

Species Composition and Abundance

Along with other recent studies of shallow-water nekton (Orth and Heck 1980; Weinstein and Brooks 1983; Heck and Thoman 1984), the present effort provides additional information on the use of inshore habitats of the lower Chesapeake Bay. A striking characteristic of the marsh nekton community in the lower Chesapeake Bay is the generally low diversity of the constituent fauna and the high level of dominance of only a few species. On both the eastern shore of Virginia (Delmarva Peninsula) (Weinstein and Brooks 1983) and in the

York River estuary, no more than two species comprised >90% of the total number of individuals captured at polyhaline tidal creek stations. On the average, spot comprised 71.8% of this total. Only in the oligomesohaline Goulders Creek was species dominance shared by more than two species (Table 1), but once again, spot predominated with 65.4% of the total. By comparison, Hackney et al. (1976) reported a mean of seven species totaling >90.0% at four trawl stations in their study of a mesopolyhaline tidal creek in Georgia, while in several studies in South and North Carolina (Cain and Dean 1976; Bozeman and Dean 1980; Weinstein et al. 1980) three to nine species ($\bar{x}$ = 7) comprised this total. Species richness was significantly greater in Goalders Creek than in the polyhaline Blevins Creek system. This is somewhat surprising since previous studies have often shown that diversity decreases for both fishes and invertebrates in the upstream direction (Dahlberg 1972; Boesch 1977; Gainey and Greenberg 1977; Weinstein et al. 1980). The absence or scarcity of stenohaline marine species derived largely from the seasonally abundant southern Carolinian ichthyofauna may partially explain this difference in the York River estuary. In North Carolina, for example, these taxa increased species richness in polyhaline tidal creeks, especially near the estuary mouth (Weinstein 1979; Weinstein et al. 1980). Also present in estuaries below the Chesapeake Bay are species with warm-temperate affinities which share dominance with spot and bay anchovy, including *Mugil cephalus, M. curema, Lagodon rhomboides, Paralichthys lethostigma, Bairdiella chrysura*, and the brown shrimp, *Penaeus aztecus*. These species are much less common in the Chesapeake Bay.

Another noteworthy finding is that species replacement does not occur from regional and northerly taxa. For example, *Ophidion marginata, Stenotomus chrysops, Urophysis regia*, and *Centropristis striata* were only rarely encountered in our studies (Weinstein and Brooks 1983). In the present investigation, these species were restricted to shoal stations outside of the tidal creek mouths (Table 1). Thus, there appears to be an underutilization of shallow nursery habitats by transient marine fishes in the Chesapeake Bay compared with the lower latitude estuaries (for more detailed discussion see Weinstein and Brooks 1983 and Heck and Thoman 1984). This difference is perhaps due partly to the unique location of the Chesapeake Bay in the transition zone between faunal provinces (Briggs 1974) with neither taxonomic group able to adapt fully to conditions (primarily temperature regimes and their variance?) associated with this transition zone. The recent geological and evolutionary history of northern estuaries, including the Chesapeake Bay (Shubel and Hirschberg 1978), may also play a role in determining the degree of estuarine dependency of local faunas.

A unique aspect of this study was the opportunity to compare utilization of the tidal creeks with adjacent shoal areas. Previously, these comparisons had to be made among collections with different gears (and their associated selectivity and efficiency) or in different years or by different investigators (Chao and Musick 1977; Markle 1976). The results for spot are of interest because of the general dominance of this species in many estuaries along the Atlantic and Gulf coasts.

Recently, Weinstein and Walters (1981), Weinstein and Brooks (1983), and Weinstein (1983) described the importance of marshes, specifically tidal creeks, to this species and the relationship between productivity and energy export via several fish vectors—from the marshes ultimately to the marine environment (Weinstein 1981). Spot were recruited into upstream marshes of the York River estuary earlier than to downriver sites and tended to remain there longer (Fig. 3). Once recruited into the marshes (by June) spot reside here until fall, when they emigrated into deeper water, and finally (for most individuals) return to the marine environment. As expected, however, there is an upstream limit to utilization in oligohaline tidal creeks where we found densities of spot decreased (Table 2) as salinities became more variable (approaching 0‰) and where temperature regimes became more unstable (Hackney et al. 1976). Whether the lower abundance of spot outside of the creeks is due to differential mortality and/or habitat selection remains unknown. Other taxa, e.g., young-of-year Atlantic croaker, weakfish, and hogchoker, apparently prefer the shoals and generally deeper water. There is little question that they are more abundant outside of the marshes (Chao and Musick 1977; Orth and Heck 1980; Weinstein and Brooks 1983; Middleton, unpubl. data). If, as many would argue, predation is a major regulator of local abundance and ultimately community structure, what protection would the homogenous, relatively unstructured shoals and flats afford these species? Considering the apparent physical and behavioral similarities, as well as recruitment dynamics between spot and Atlantic croaker, there does not seem to be any

significant adaptive feature of the latter that would provide better survivorship in open waters (at least with regard to predation). Just how this species and others minimize the effects of predation in open waters is an important research question for the future.

Trophic Comparisons

The six species examined in detail are clearly trophic opportunists and overlap in many food categories. In addition, each goes through distinct ontogenetic stages in feeding which include significant shifts in the portions of the water column searched. The prey taxa have been categorized by Darnell (1961), Qasim (1972), and Chao and Musick (1977) according to their vertical occurrence in the water column from open waters to the bottom: fishes, macrozooplankton (e.g., *Neomysis americana*), microzooplankton (e.g., calanoid copepods), epibenthos (e.g., harpacticord copepods), infauna, and organic matter. At sizes <21 mm SL all five of the species examined apparently spent considerable periods foraging in the water column. Between 21 and 40 mm SL several species continued to feed on "pelagic" prey, although by this size the transition to benthic feeding was nearly complete in spot and hogchoker.

Whether resource partitioning or dietary specialization (Chao and Musick 1977) occurs in these taxa as a means of reducing interspecific interactions is a matter of speculation. Without question, there are differences in feeding localities of the fishes examined—e.g., white perch and white catfish are generally restricted to oligohaline habitats, while Atlantic croaker and hogchoker are more abundant on the shoals. Also noted are differences in seasonal abundance (Fig. 6), size related feeding distributions reflecting ontogenetic shifts (Fig. 5), morphological differences among predators (Chao and Musick 1977), etc. But whether or not any of these traits reflect past or present competitive pressures remains unknown. Food that is generally limiting for several of these species and others is currently an area of controversy. Currin et al. (in press) have suggested that predation, not resources, limits production rates of spot and Atlantic croaker in shallow marsh embayments in Albermarle Sound, N.C. In contrast, Weisberg and Lotrich (1980) found that growth rates of the mummichog, *Fundulus heteroclitus*, could be altered by manipulating fish density. Increased growth rates were also demonstrated with food enrichment experiments in subtidal areas. Similar findings were reported by Miklas and Reed (in press) for *F. heteroclitus* populations in a tidal tributary of the Rhode River, Del. Our own findings of a seasonal decline in relative fullness index values in several species, along with a parallel decline in benthic biomass (T. Fredette[6]), tend to support the possibility of periodic food scarcity.

Trophic opportunism has often been cited in studies of estuarine fishes (Darnell 1958, 1961; Livingston 1982). Several investigators have pointed to the importance of omnivorous and ontogenetic progressions in feeding stages (Sheridan 1979; Stoner 1980; Livingston 1982) as obscuring distinct trophic relationships in nektonic food webs. Along with these difficulties are problems associated with the "snapshot" view often gained of the system. Numerically abundant species are likely to play the major role in conversion and production of organic materials in estuaries (and are, therefore, mainly responsible for the construct of food webs and energy flow therein), yet the identification of these species often comes from the sampling program itself.

Thus, although the dominant species in this study, spot, is undoubtedly important in this regard, the selective nature of our sampling effort does not allow us to place this importance in proper perspective. It is probable that dominance, expressed in numbers and/or biomass of those species captured in this study, is shared and sometimes surpassed by other local species not sampled quantitatively by this program. These include young-of-year bluefish, *Pomatomus saltatrix*; various cyprinodonts, especially *F. heteroclitus*; anchovies; and silversides. On an estuary-wide basis, we also do not completely "track" species distributions in time and space (Purvis 1976) so that our already distorted view of local habitats cannot easily be extrapolated to system-wide considerations. Such difficulties occur in most studies and must be recognized and eventually accounted for in considerations of fish community ecology in estuaries.

SUMMARY

Tidal creeks of the York River estuary were characterized by distinct nekton communities displaying low diversity and dominated by relatively

[6]T. F. Fredette, Marine Scientist, Department of the Army Corps of Engineers, P.O. Box 631, Vicksburg, MS 39189, pers. commun. September 1982.

few taxa. Of the many transient marine species (Weinstein 1979; Weinstein et al. 1980) that utilize marsh creeks along the Atlantic coast, only the spot, *Leiostomus xanthurus*, seemed to actively select this habitat. Within creeks there also was an apparent upstream limit in abundance of this species at low salinities. Although not captured quantitatively in this study, Atlantic menhaden, *Brevortia tyrannus*, were often observed in large numbers in the creeks, especially upstream. Other species, particularly Atlantic croaker, weakfish, and hogchoker were captured in greater numbers in low salinity shoal waters (<5 m) adjacent to marshes. Compared with the polyhaline marshes and shoals, stations sampled upstream in oligo-mesohaline waters were more diverse and had a larger variety of taxa apparently utilizing this area as a primary nursery habitat. In addition to the species mentioned above, white perch; striped bass, *Morone saxatilis*; and white catfish were seasonally present as young-of-year in the area.

Dietary composition of the six species examined in detail reflected that of trophic opportunism, with maximum dietary diversity displayed by spot. Ontogenetic progressions in diet also were observed in all species. Two species, summer flounder and white catfish, were piscivorous at larger sizes, feeding mainly on *Anchoa* spp. The apparent absence of specialization in any of these predators may reflect the general adequacy of food supplies in the primary nurseries.

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DISTRIBUTION, ABUNDANCE, AND GROWTH OF JUVENILE DUNGENESS CRABS, *CANCER MAGISTER*, IN GRAYS HARBOR ESTUARY, WASHINGTON[1]

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ABSTRACT

Dungeness crabs, *Cancer magister*, were collected biweekly or monthly from May 1980 to July 1981 in Grays Harbor, Washington. Age of each crab was estimated from width-frequency analyses, and the population density and growth rate were monitored for each age class over the 14-month period. In April 1980 and 1981, crabs entered the estuary either as megalops larvae that metamorphosed to first instar postlarvae or directly as first instars. Intertidal mudflats with beds of eelgrass (*Zostera* spp.) were important habitats for the first few postlarval stages. Some crabs may have emigrated from the estuary during their second year of life, whereas others dispersed throughout the estuary and appeared to emigrate at sexual maturity (about 2 years). No gravid females were ever found in the bay. Population size was estimated to range from 3.3 million crabs (winter) to 39.0 million crabs (summer); 74% of the summer population were early instars. Growth of early instars was rapid and resulted in a 282-fold increase in dry weight from May to September, but little growth occurred during the remainder of the year. Based on summer population abundance, it is estimated that this estuary could account for a substantial portion of recruitment to the offshore commercial fisheries.

The biology of the Dungeness crab, *Cancer magister*, has been studied by numerous investigators for several decades (Weymouth and MacKay 1936; MacKay 1942) because of its importance to commercial fisheries and its position as a benthic predator in estuaries and offshore communities (Gotshall 1977; California Department of Fish and Game 1981). Previous studies of *C. magister* biology have been conducted largely along the open coast (MacKay 1942; Cleaver 1949; Butler 1960, 1961; Gotshall 1978b, c). The few studies of crab populations in estuaries or shallow-water habitats (Butler 1956; Tegelberg and Arthur 1977; Gotshall 1978a; California Department of Fish and Game 1981) have indicated that such areas may be extremely important nursery grounds, but the size and dynamics of estuarine populations have not been statistically determined and, furthermore, the contribution of estuarine habitats to offshore stocks has not been adequately assessed. Orcutt et al. (1978) estimated that 50-80% of crabs caught by the fishery in the Gulf of the Farallones spend some of their life cycle in the San Francisco-San Pablo Bay complex. Benefits derived from estuarine early life history may include enhanced growth rates, more abundant food, and refuge for postlarval and juvenile crabs from larger, older age classes that act as competitors and predators (Botsford and Wickham 1978).

Quantitative studies of *C. magister* in major estuaries are timely and imperative. The demise of the San Francisco fishery prompted a 5-yr investigation of *C. magister* biology in that region (California Department of Fish and Game 1981), and hypotheses for the decline include alterations of estuarine habitat and water quality. In addition, channel dredging practices in west coast estuaries kill hundreds of thousands of crabs annually (Stevens 1981). Armstrong et al. (1982) estimated that a proposed channel modification project in Grays Harbor, Wash., could entrain and kill 2.5 million crabs over a 2-yr period. Knowledge of estuarine crab population dynamics and ecology of juveniles is required to gauge the relative importance of such habitat to the species, and to mitigate impacts of estuarine development on juvenile stages.

MATERIALS AND METHODS

Study site

Grays Harbor is a shallow drowned river basin

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estuary with an extensive littoral zone and a wide variety of substrate types (Fig. 1). Sampling stations were established primarily along the existing navigation channel in accord with a concurrent study to assess the impact of dredging on Dungeness crabs (Armstrong et al. 1982). Habitats represented include deeper sandy channels (stations 1-3), shallow sand (station 4), sand-mud (stations 6 and 7), mud (stations 8-12), and those adjacent to eelgrass (*Zostera marina* and *Z. noltii*) beds (station 5) (Table 1; Fig. 1). Fifteen sublittoral strata were established for the purpose of estimating population abundance, and sampling stations were located approximately at the center of each (Fig. 1). However, strata 14 and 15 contained no regularly sampled stations because these areas were outside the primary focus of our contract. The boundaries of each stratum were defined by the midpoint between sampling stations, or the bottom contours at −5.5 m or 0.0 m (for detailed

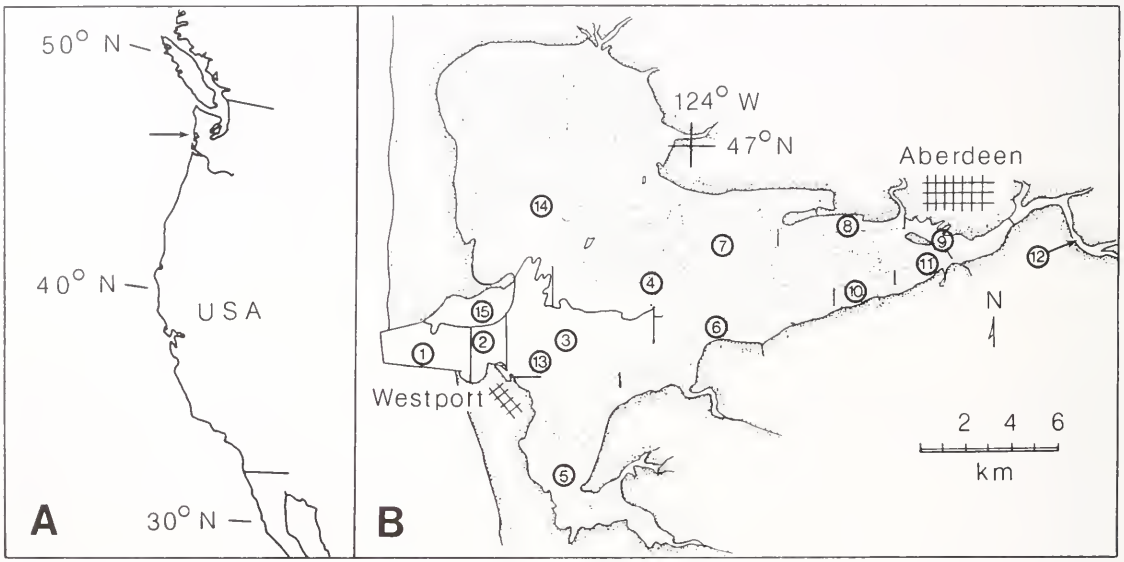

FIGURE 1.—A. West coast of North America. Arrow indicates site of Grays Harbor, Wash.; B. Map of Grays Harbor, showing sites of *Cancer magister* collection (1-13). Stations 14 and 15 represent unsampled strata. Lines separating strata were defined arbitrarily for use in determining crab population size.

TABLE 1.—Location and description of sampling sites for *Cancer magister* in Grays Harbor, Wash.

Station no.	Area (ha)	Gear type[1]	Latitude N	Longitude W	Depth (m)	Bottom type	Comments
1	837	T	46°54'30"	125° 9' 0"	15-18	Sand, cobble	Not sampled in 1981 due to rough water conditions.
2	496	T	46°55'15"	124° 7'20"	13-15	Hard sand	Dredged sediment disposal site.
3	1,507	T	46°55'15"	124° 4'20"	10-15	Sand	Outer harbor channel bottom.
4	1,120	T	46°56'40"	124° 1'10"	3-5	Sand, mud	Shallow outer harbor habitat.
5	658	T	46°51'55"	124° 4'15"	5-8	Sand, mud	Adjacent to extensive eelgrass beds.
6	680	T	46°55'40"	123°59' 5"	6-8	Sand, mud, leafy debris	Near mudflats without eelgrass.
7	656	T	46°57'30"	123°59' 0"	11-14	Mud, sand	Adjacent to eelgrass beds.
8	418	T	46°58'10"	123°55'20"	11-15	Mud	Inner harbor channel bottom.
9	221	T	46°57'40"	123°50'50"	12	Mud	Numerous snags; adjacent to shipping terminals, inner harbor.
10	96	RN	46°56'20"	123°54'15"	3-4	Mud, snags	
11	86	RN	46°57'12"	123°51'15"	3-4	Mud, snags	
12	—	RN	46°57'37"	123°46'18"	3-4	Mud, cobble	Along shore of deep (20 m) river channel.
13		T	46°54'45"	124° 5'15"	0-3	Sand	Intertidal sand flat; no eelgrass.
14	2,653					Mud, sand, eelgrass	Not sampled. Used for population estimate.
15	414					Sand	Not sampled. Used for population estimate.

[1]T = otter trawl; RN = ring net.

descriptions see Stevens 1982). The area of each stratum was determined by planimetry at the level of mean lower low water (NOAA Chart No. 18502 Grays Harbor, 1979 edition).

Sampling Design

Crabs were sampled at stations 1-9 and 13 with a 4.9 m, 4-seam, semiballoon otter trawl net, having 38 mm stretch nylon mesh throughout and a 6 mm cod end liner. Working width of the net was about 3.0 m. Distance towed was measured between buoys placed at the beginning and end points of each trawl, by compass triangulation to stationary objects whose positions were predetermined and located on 7.5-min topographic maps (U.S. Geological Survey). Distances were then converted to area swept and catches expressed as crabs/ha. At stations 10-12, underwater snags prevented trawl operation so crabs were collected by setting collapsible ring nets (76 cm diameter) covered with 12 mm mesh. A "set" consisted of 4 baited nets set 50 m apart and fished for 20 min. Catches were expressed as crabs/net. Trawls and ring net sets were made within 1-2 h of slack low tide in daylight. Occasional plankton tows were made with a 0.5 m diameter conical net of 500 μm mesh, in the spring of 1980 and 1981, to determine if crabs entered the bay as larvae.

Stations 3, 6, 8, and 9 were sampled biweekly from May through October 1980 and at intervals of 4-5 wk thereafter through July 1981. Other stations were generally sampled monthly except when weather or boat problems precluded operations. Most stations were sampled on 13-19 occasions during the 14-mo field study (May 1980 to late June 1981), with the exception of stations 1 and 2 (6 and 10 samples, respectively). Station 13 was sampled quarterly on a diel basis, and complete results from that diel study are reported elsewhere (Stevens and Armstrong 1984). No samples were taken at stations 14 and 15 which were used only to calculate crab populations based on data from adjacent areas (see below).

All crabs were measured to the nearest millimeter across the carapace between the notches just anterior to the 10th anterolateral spines ("carapace width" or cw), sexed, and released. Subsamples were used for width frequencies only in May and June of 1980 and 1981, when early instars were collected in large quantities. Surface and bottom-water samples were collected during each trawl with a modified Van Dorn bottle; temperature was measured to 0.1°C, and salinity determined with a refractometer at room temperature.

Growth Analysis

Cumulative width frequencies of all crabs caught during a given week were plotted on probability paper, and width limits were subsequently defined as the curve inflection points (arbitrarily nonoverlapping) to delimit the size range of each year class through time, according to the method of Cassie (1954). These were compared with frequency graphs for verification. Values were interpolated during weeks in which too few crabs were caught for accurate analysis. Each crab was then assigned to an age-group on the basis of the width limits for each sampling week. Age was defined as the number of years since metamorphosis. Mean widths were calculated for each age group (0+, 1+, 2+, and 3+) and plotted by sampling week. Eighty-seven males (12-132 mm cw) and 74 female crabs (15-115 mm cw) were frozen and returned to the University of Washington where they were opened at the epimeral line and dried to constant weight at 60°C (48-72 h). Only hardshell intermolt crabs were used. Log_{10} dry weight (g) was plotted against $\log_{10}$ carapace width (mm) and regression equations determined for each sex. Mean weights for each age group of crabs were calculated at monthly intervals from mean widths using the regression equation (the 1977 year class was omitted because the regression equation did not represent these larger animals). Weight-specific growth rates (k) per month were calculated by use of the equation

$$W_t = W_0\, e^{kt}.$$

The monthly percent weight increase was calculated as $e^k - 1$.

Crab Density Analysis

Because counts of benthic invertebrates usually show a contagious distribution (Elliott 1977), all density data were transformed prior to analysis of variance or regression by

$$X_t = \text{Log}_{10}\,(\text{density} + 1),$$

where X_t is the transformed variable.

Density was plotted against bottom-water salinity, temperature, and estimated Chehalis River flow by a stepwise multivariate procedure (SPSS REGRESSION) for all trawl and ring net samples.

The effects of season and location on crab density were examined by analysis of variance (SPSS ANOVA procedure). The sampling year was divided into two seasons: spring-summer (March-August) and fall-winter (September-February). The navigation channel was divided into two areas: the outer estuary (stations 2, 3, and 4: station 1 deleted due to lack of winter data points), and the inner estuary (stations 7, 8, and 9). A two-way ANOVA was performed with these two seasons and two station groups as the independent variables, and crabs/ha as the dependent variable.

Population Estimation

Two basic assumptions were made concerning the trawl data: 1) Sampling efficiency of the net was not 100% and varied for each age class of crabs. Efficiency was estimated to be 0.33 for the 0+ age class during summer, and 0.25 in winter, based on comparisons between net catches and visual counts of young instars on mudflats at low tide (see Discussion). Sampling efficiency was estimated to be 0.50 for all other age groups in accordance with Gotshall (1978a). 2) Sampling efficiency was assumed to remain constant and not to vary as a function of changes in crab behavior (e.g., burial or diel activity variations).

Data on crab densities were used from a 12-mo period, June 1980 to May 1981, which was divided into three "seasons": summer (June-August 1980), fall-winter (September 1980-February 1981), and spring (March-May 1981). Population estimates were made for three age groups (0+, 1+, and 2+, the latter including all 3+ animals which were identifiable only in summer 1980) in each of the three defined seasons. A stratified random technique was used, using the following variables (see Cochran 1953):

h	= stratum of harbor
C_{ih}	= catch of crabs in tow i, stratum h
a_{ih}	= area (ha) covered by tow i, stratum h
n_h	= number of tows in stratum h
x_{ih}	= individual estimates of crabs ha^{-1}, from tow i, stratum h
$\bar{x}_h$	= mean catch (crabs ha^{-1}) in stratum h for a given season
A_h	= area of harbor in stratum h (ha)
$s^2_{(x_h)}$	= variance of mean $\bar{x}_h$ in stratum h
T	= total number of crabs in harbor.

Data used for population estimates were not transformed as done for ANOVA comparisons because that would have led to complications in the determination of confidence intervals, but only minor changes in the resultant mean densities of crabs. Mean crab density in each stratum was calculated for each age group and season by

$$\bar{x}_h = \frac{\sum_{i=1}^{n} (c_{ih}/a_{ih})}{n_h} .$$

The total number of crabs in each stratum was calculated as $T_h = A_h\ (\bar{x}_h)$, and the total for the harbor by the sum of all stratum totals,

$$T = \sum_{h=1}^{15} T_h .$$

For strata 1-9, the variance of each stratum total was calculated by

$$V_{(T_h)} = \frac{A_h^2 s^2(\bar{x}_h)}{n} ,$$

and the variance of the total was calculated by summing the individual variances

$$V_{(T)} = \sum_{h=1}^{9} V_{(T_h)} .$$

Confidence intervals for T were approximated at the 95% level by

$$T \pm t_{(\mathrm{df},\ 0.05)} V_{(T)}^{1/2} .$$

Crab abundances in strata which were not sampled by trawl (10, 11, 14, and 15) were calculated using mean density values from nearby strata of similar ecological characteristics. Data were used from strata 6 (for 10 and 11), 5 (for 14), and 3 (for 15). Totals by age group and season for those strata were added to totals for strata 1-9, to obtain totals for the entire estuary. The estuary totals were divided by the estimated trawl efficiency factors to obtain final corrected estimates of crab abundance by age group and season. Confidence intervals for these final estimates could not be computed.

RESULTS

Temperature-Salinity Profile

Grays Harbor has a strong horizontal salinity gradient (Fig. 2). Temperature and salinity were

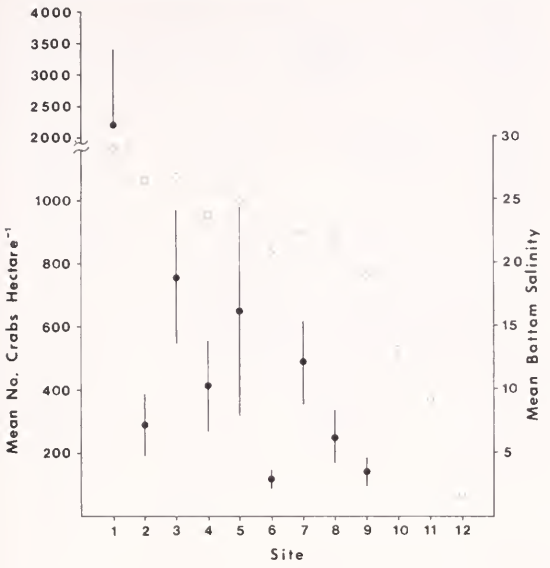

FIGURE 2.—Temperature-salinity profile for crab sampling sites 1-12, Grays Harbor, Wash. Filled circles indicate mean density +1 SE of crabs for the entire study, as determined by trawl; open circles indicate mean bottom salinity at low tide. Crab densities are not plotted for stations 10-12 where ring nets were used.

more stable in the outer estuary, but less so as distance increased eastward from the harbor mouth. At station 3, bottom temperatures ranged from 7°C (winter) to 14°C (summer), while at station 9 they ranged from 5° to 18°C. Vertical stratification was greater toward the head of the estuary and less so in the outer estuary as a result of turbulent mixing. Greatest vertical salinity difference measured during the study was 17‰ at station 9. Grays Harbor receives 70-100 in of rainfall annually, and stratification was greatest during November-March, the period of peak rainfall. Flow rates of the Chehalis River, which contributes 80% of the freshwater inflow, varied from 22.3 m^3s^{-1} in August 1980 to 2,322 m^3s^{-1} in February 1981 (data provided by U.S. Geological Survey).

Spatial Distribution of Crab Population

Complete records (width, sex, age) were obtained for 14,556 crabs. Coefficients of variation averaged 0.53 for the trawls and 0.46 for the ring nets, implying that both techniques had a similar degree of precision.

Mean density of crabs during the 14-mo sampling period was greatest at station 1 (2,190 crabs ha^{-1}), and catches declined with increasing distance from the estuary mouth and decreasing bottom salinity (Figs. 2, 3A). Notable exceptions to this pattern were low densities at stations 6 and 2 (120 and 290 crabs ha^{-1}, respectively; Fig. 3). Station 2 was concurrently being used as a dredged sediment disposal site by the U.S. Army Corps of Engineers.

Crabs caught by ring net were more abundant at station 11, near the eastern (upstream) end of the estuary than at station 10, and averaged 22.9 and 12.7 crabs net^{-1}, respectively, from June to October (Fig. 3F). No crabs were caught at station 12 except in August and September 1980.

Temporal Distribution of Crab Population

Megalops larvae were found as early as 1 April 1980 at station 6, and in densities up to 810/1,000 m^3 at station 5 on 22 April 1980.

Crab densities at all stations were greatest from May to August 1980 (Fig. 3A-E) and declined from September 1980 through January 1981. Lowest densities occurred in October and November 1980, none being >200 crabs ha^{-1} except at station 1. Although monthly variation was great at each station, this general decline in crab density during fall-winter occurred throughout the estuary.

Crab abundance at the three ring-net stations (10, 11, and 12) increased dramatically from June through October 1980, then dropped in November 1980 to a low of <1.0 crabs net^{-1} at all three stations (Fig. 3F). No crabs were caught at station 12 except during August and September 1980, when the salinity reached 9 and 7‰, respectively. Salinity at station 12 was 1.0‰ or less during all other sampling periods.

The *F*-tests showed that mean crab density in the outer estuary (stations 2, 3, and 4) was significantly greater ($P = 0.011$) than in the inner estuary (stations 7, 8, and 9; Table 2). Crab density at all six stations (2, 3, 4, 7, 8, and 9) was significantly greater ($P = 0.001$) in spring-summer than in fall-winter 1980-81. Regression analysis of $\log_{10}$-transformed density data on bottom salinity, temperature, and Chehalis River flow rate showed no significant dependence of trawl catches on these variables, but salinity alone was responsible for about 40% of the variance in crab abundance at the ring net stations (10, 11, and 12; $r^2 = 0.398$, $P = 0.001$).

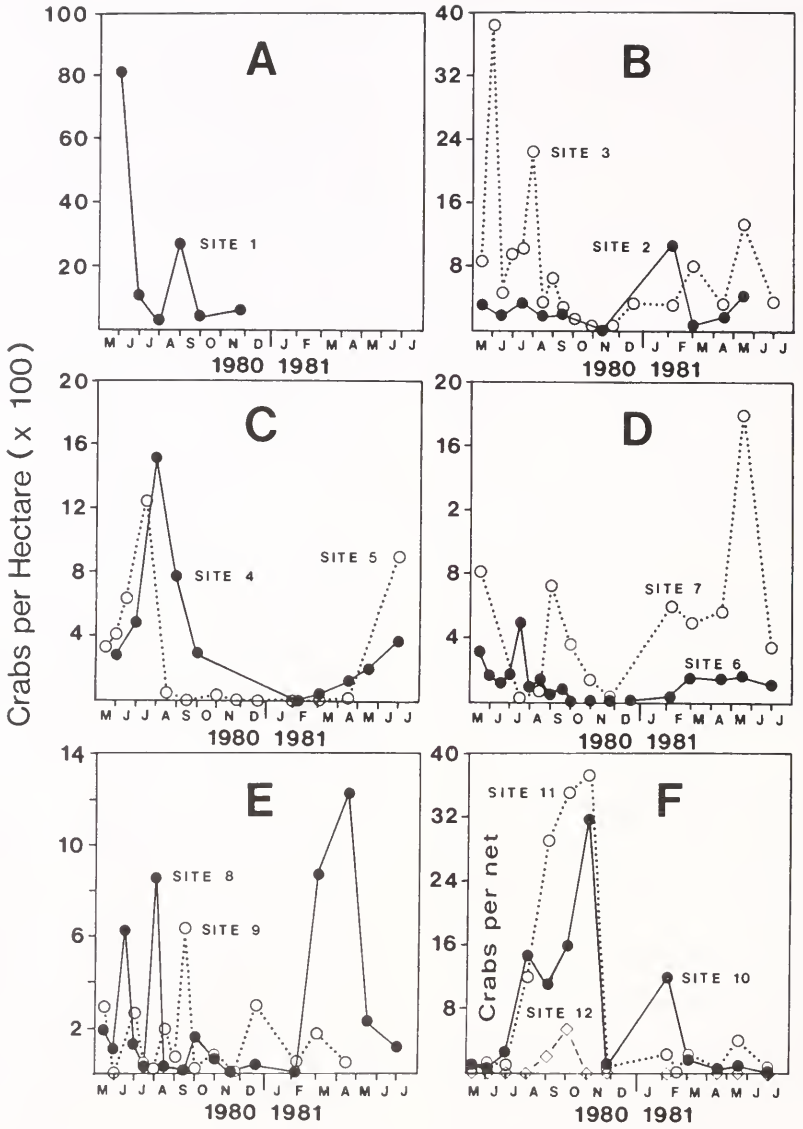

FIGURE 3.—Crab density for all sampling sites in Grays Harbor, Wash., sampled in 1980-81. Trawl sampling sites 1-9 are shown as crabs ha^{-1}; ring-net sampling sites 10-12 are shown as crabs per ring net. Each point represents a single sample.

Age-Structure of Crab Population

Width-frequency distributions for all crabs caught by trawl in the estuary are presented by sampling week in Figure 4. Width limits for each age class were selected so as to be nonoverlapping (Table 3).

The distribution of crabs within the estuary varied with age group. Animals in the 0+ age group were commonly found from station 2-8 at an average of 46 crabs ha^{-1}, and represented 16.6% of total crabs caught in the estuary throughout the entire 14-mo sampling period (Fig. 5). The greatest annual mean density of this age group occurred at station 5 near an area of dense eelgrass. The density of this age group was very low during October-December.

Summer populations of 0+ crabs were about twice as dense at station 5 than at any other (Fig. 6). Visual inspection of mudflats adjacent to this

TABLE 2.—Mean densities of *Cancer magister* in Grays Harbor, Wash., areas and seasons compared by ANOVA. Values are means of original data expressed as crabs ha^{-1}, ± SE, with n in parentheses. F tests were performed on log-transformed data.

Mean densities:	Outer harbor (sites 2-4)	Inner harbor (sites 7-9)	Season means
Spring-summer (March-Aug.)	658 ±146 (29)	358 ±73 (32)	500 ±81 (61)
Autumn-winter (Sept.-Feb.)	229 ±104 (10)	120 ±42 (16)	162 ±47 (26)
Area means	548 ±114 (39)	279 ±53 (48)	

Results of F-tests:

Comparison	df	F-value	Probability level
Seasons	1/83	15.181	0.001
Areas	1/83	6.744	0.011
Interaction	1/83	0.607	0.438

site in May 1982, and at a similar site in stratum 14 in May 1981, revealed that first instar crabs were abundantly distributed on the mudflats at low tide in slight depressions, buried just beneath the sediment surface and in burrows of *Callianassa* spp. Estimated densities were 1-5 crabs m^{-2}, based on random visual observations within an area of the mudflats measuring about 100 m^2. This density was 1-2 orders of magnitude greater than that calculated from trawl catches of this age group. Therefore, it is likely that 0+ crabs were grossly underrepresented in the trawl catch, especially at stations near mudflats such as 4 through 8. The 0+ age group formed <1% of the catch at station 1 and were virtually absent from the ring net stations (10-12).

Crabs in the 1+ age group were by far the most

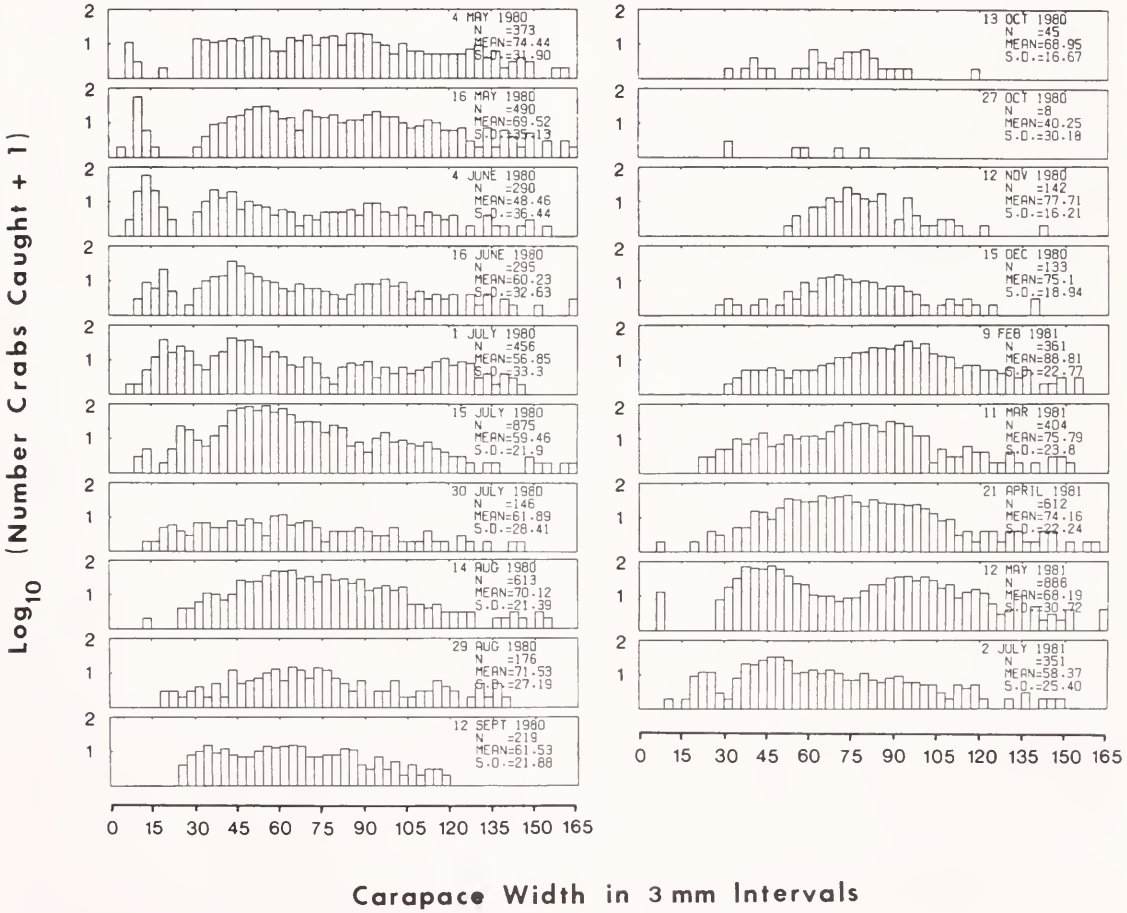

FIGURE 4.—Carapace width frequencies of all crabs caught by trawl at stations 1-9 in Grays Harbor, Wash., 1980-81. Numbers expressed as $\log_{10}$ (catch +1). Box for each sampling period shows date, number of crabs measured, mean carapace width overall (mm), and standard deviation.

TABLE 3.—Upper limit of carapace width range (mm) of *Cancer magister* in Grays Harbor, Wash., for each age/sex group. Selection method was cumulative probability (P) or interpolation (I). The upper limit for age 2+ crabs (lower limit of 3+) was not distinguishable in fall-winter due to low numbers caught. nd = not distinguishable.

	Males				Females			
		Age groups				Age groups		
Date	Method	0+	1+	2+	Method	0+	1+	2+
5/4/80	P	25	60	115	P	30	60	120
5/16/80	I	26	65	120	I	28	69	124
6/4/80	P	27	70	124	P	25	77	127
6/16/80	I	29	70	132	I	27	79	126
6/21/80	P	30	70	136	P	28	80	126
7/1/80	I	32	75	136	I	31	87	127
7/15/80	P	34	85	136	P	37	90	130
7/30/80	I	37	88	134	I	36	91	nd
8/14/80	P	40	92	132	P	36	92	nd
8/29/80	I	43	92	nd	I	41	93	nd
9/12/80	I	45	94	nd	I	45	94	nd
9/26/80	P	46	96	nd	P	50	95	nd
10/13/80	P	46	105	nd	P	50	96	nd
10/27/80	I	46	106	nd	I	52	98	nd
11/12/80	P	46	107	nd	P	54	100	nd
12/15/80	P	46	101	nd	P	52	104	nd
1/17/81	P	44	121	nd	P	55	125	nd
2/9/81	I	44	121	nd	P	54	126	nd
3/11/81	P	45	121	nd	P	61	126	nd
4/4/81	P	47	120	nd	P	56	133	nd
4/21/81	I	15	55	nd	I	15	63	120
5/21/81	P	26	70	127	P	29	75	120
7/1/81	P	29	75	nd	P	29	86	nd

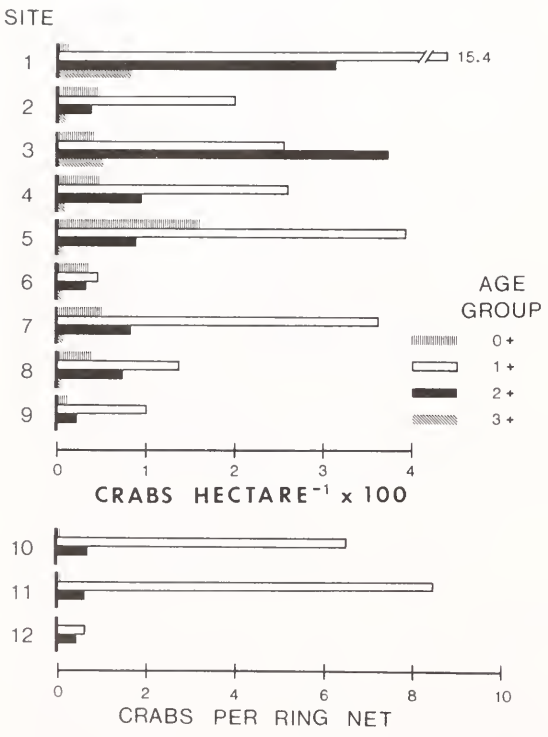

FIGURE 5.—Mean number of crabs per hectare (sites 1-9) and crabs per ring net (sites 10-12) in Grays Harbor, Wash., over the entire study period, by age group.

abundant at all stations except 3, averaging 268 crabs ha^{-1} and 54.7% of all crabs over the entire sampling period. Greatest densities occurred at station 1, but these crabs were also abundant at stations 3, 4, 5, and 7 (Fig. 5), i.e., the outer estuary. This group was least abundant at stations 6, 8, and 9, but comprised the largest proportion (73-78%) at the ring net stations (10-12).

The average density of the 2+ age group was 121 crabs ha^{-1} (stations 1-9) equal to 21.3% of all crabs caught. Greatest densities occurred at stations 1 and 3 (Fig. 5). This group was the most abundant at station 3, the only area where the 1+ age group did not predominate.

The 3+ age group was difficult to separate from the 2+ group because the former were caught in low numbers. Of all samples taken during the study, they represented 3% with an average density of 17 crabs ha^{-1}. This group occurred primarily at stations 1-3, with greatest densities at station 1 (Fig. 5).

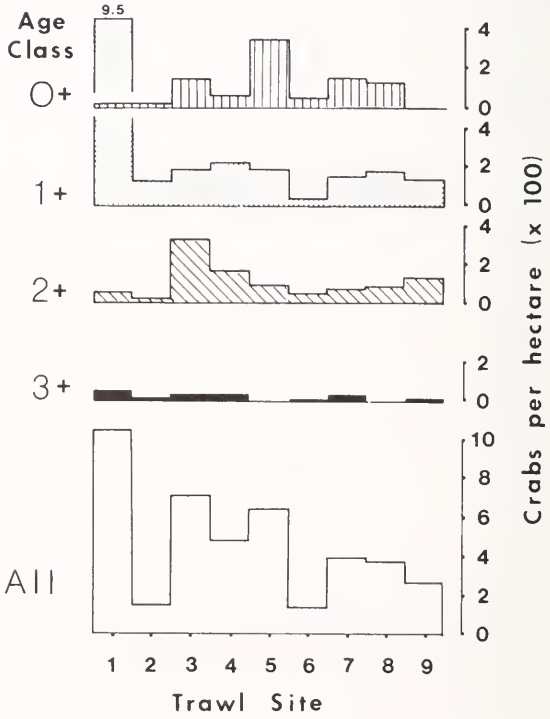

FIGURE 6.—Actual density of crabs caught by trawl at sites 1-9 in Grays Harbor, Wash., June 1980, by age class. Sites 2, 5, and 7 sampled on 4 June; sites 1, 4, and 9 sampled on 16 June; sites 3, 6, and 8 sampled on both dates and averaged. Note greatest abundance of 0+ age group at site 5.

Growth: Width

Crabs in the 0+ age group (1980 year class) increased in width by a factor of 4, from 10 mm in May to 40 mm in October 1980, but growth slowed from then to the following April 1981 when they were about 50 mm wide (Fig. 7). The same pattern of rapid growth during spring and summer was evident among the 1+ and 2+ age groups (1979 and 1978 year classes, respectively), although measurable increases in carapace width were recorded into winter 1981 for these older crabs. Crabs of the 1979 year class grew from 45 to 73 mm between May and October 1980 (factor of 1.6), while the 1978 year-class crabs grew from 84 to 118 mm during the same period, an increase of 1.4. Females had slightly greater mean widths than males up to about 125 mm cw, but the differences were minor (Table 3).

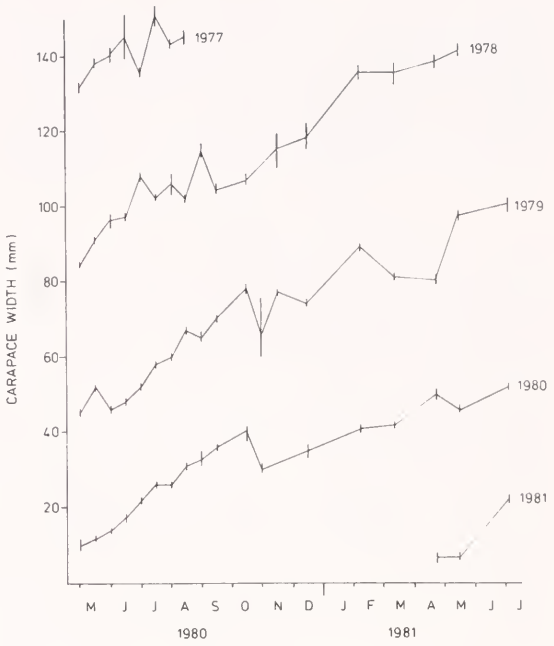

FIGURE 7.—Mean width of four age groups of crabs (0+, 1+, 2+, 3+) in Grays Harbor, Wash., 1980-81. Mean width (+1 SE) shown for each sampling period was determined by graphical analysis of width-frequency data or interpolation (see Table 3).

Growth: Weight

Regression equations for $\log_{10}$ dry weight (g) on $\log_{10}$ carapace width (mm) were derived separately for male and female crabs, but were not significantly different. Therefore, a pooled regression equation was calculated for both sexes combined:

$$\text{Log}_{10}\ \text{Weight (g)} = -4.064 + 2.832\ (\text{Log}_{10}\ \text{Width, mm})$$

or

$$\text{Weight (g)} = (8.63 \times 10^{-5})\ \text{Width}^{2.832}$$

($r^2 = 0.985$, $P = 0.0001$; Fig. 8).

Differences in width/weight and width/age relationships between male and female crabs would probably increase at sexual maturity, which occurs about 2 yr after metamorphosis, and at widths of 93-122 mm for males and 100-105 mm for females (Butler 1960, 1961; Poole 1967). Growth data presented herein are probably valid only for male crabs <132 mm and female crabs <115 mm width.

Changes in mean weight with time (Fig. 9) probably represent a continuous curve, but there appeared to be an inflection point in late August that separated spring-summer and fall-winter growth stanzas. Therefore, k values were calculated for the periods May-August and September-April.

Monthly weight-specific growth rates were greater in spring-summer than in fall-winter for all age groups but decreased with size (Fig. 9). Specific growth rates were greatest for 0+ age group crabs in their first summer during which the average monthly weight increase was 206% (Table 4). Growth decreased to an average 15.8% per month during the winter. Growth rates increased again for age 1+ crabs in their second summer (31% per month), but were lower than experienced in their first year. This pattern was found for all age groups. Crabs in the 2+ age group (probably at sexual maturity) increased in weight 25% per month in the summer of 1980, but only 6.5% per month during the following winter (Table 4). First

TABLE 4.—Weight-specific growth rates (k) and percent weight increase of three year classes of *Cancer magister* in Grays Harbor, Wash. Weight calculated from mean carapace widths of each year class by regression equation (see Figure 8). Growth per month calculated for spring-summer (May-August) and fall-winter (September-April) growth stanzas (see also Figure 9).

				Mean growth per month			
	Dry weight (g)			Spring-Summer		Fall-Winter	
Year class	4 May 1980	29 Aug. 1980	22 Apr. 1981	k	% weight increase	k	% weight increase
1980	0.02	1.75	5.56	1.118	206	0.147	15.8
1979	4.02	11.75	21.46	0.268	31	0.075	7.8
1978	24.30	59.70	98.71	0.225	25	0.063	6.5

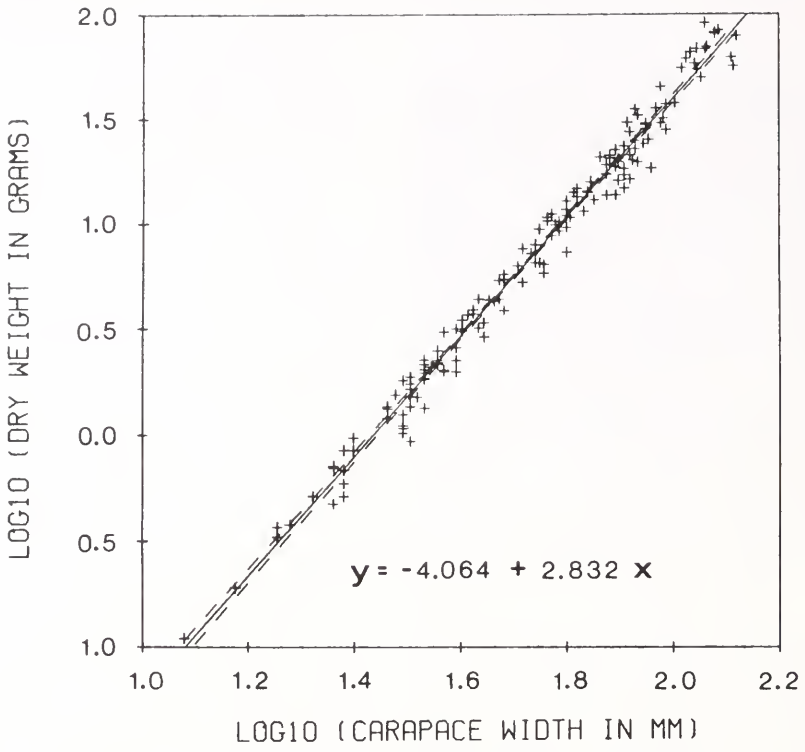

FIGURE 8.—Regression of $\log_{10}$ dry weight (g) on $\log_{10}$ carapace width (mm) for 87 male (12-132 mm) and 74 female (15-115 mm) *Cancer magister* from Grays Harbor, Wash. Observations (+), regression line (solid), and 95% confidence interval about the regression line (dashed) are shown.

instar crabs (7 mm cw) of 0.02 g dry weight increased in dry biomass 282 times by the time they reached the 6th or 7th instar (about 50 mm cw), weighing 5.7 g the following April (Fig. 9). Some may have reached 70 mm by that time, weighing 14.7 g, an increase of over 700-fold. Second-year crabs increased in dry biomass 5.3 times, from 4.0 to 21.5 g. Third-year crabs increased from 24 to 99 g, a dry biomass increase of 4.1 times.

DISCUSSION

Recruitment and Distribution in the Estuary

Megalops larvae probably metamorphosed to the first postlarval stage in Grays Harbor, since trawl collections included second instars on 4 May 1980 and first instars in April and May 1981. Cast exuviae of these stages were abundant on beaches of the outer estuary in early May 1982. Larval densities in the estuary were at the low end of the range of densities found by Lough (1976) off the Oregon coast in 1970-71 (100-8,000/1,000 m^3). In contrast, no megalops larvae were found in San Francisco-San Pablo Bays during 4 yr of surveys by the California Department of Fish and Game, which concluded that crabs entered that estuarine system only after metamorphosis (Orcutt et al. 1975, 1976).

Once inside Grays Harbor, *C. magister* showed an ontogenetic change in habitat selection, i.e., centers of abundance changed with age. Eelgrass beds may be the preferred habitat of the first postlarval stages, because catches of 0+ crabs were most abundant near those areas (Figs. 5, 6). Butler (1956) also found that the most abundant concentrations of early instars along the northern shore of Graham Island, Canada, were associated with the presence of *Zostera marina* in sheltered inlets. However, this age class was widely distributed from stations 1 to 9.

Crabs in the 1+ age group (size range 50-90 mm cw) were the most abundant. Although their dis-

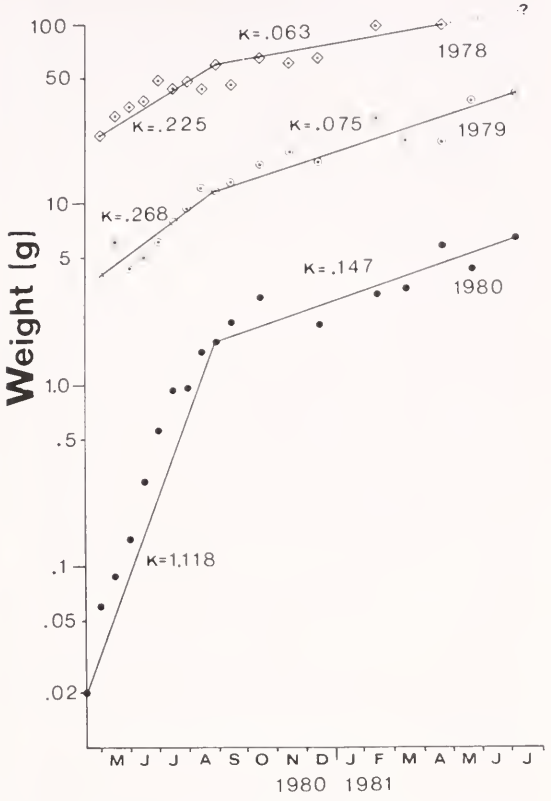

FIGURE 9.—Growth rates of *Cancer magister* from Grays Harbor, Wash. Points represent $\log_{10}$ mean dry weight calculated from mean width by regression equation. Straight lines (fitted visually) show slope of growth curve (k) for summer and winter growth stanzas of 1980 (0+), 1979 (1+), and 1978 (2+) year classes. Growth stanzas arbitrarily separated at 28 August 1980.

tribution greatly overlapped that of the 0+ age class, age 1+ crabs showed proportionally less use of low-salinity stations such as 6, 8, and 9. Although this group was also abundant near eelgrass beds, they were restricted to the subtidal channels and showed only intermittent use of mudflat areas during high tides, whereas many crabs of the 0+ group remained in the littoral zone at low tide.

The 2+ age group, consisting of sexually mature crabs (Poole 1967), was abundant only at the outer estuary stations (1, 3, 4, 6, and 7). Many crabs probably migrate out of the harbor before reaching age 3+. This hypothesis is supported by the scarcity of age 3+ crabs east of station 3 and the total absence of gravid females from trawls taken in the estuary, although many trawls were made during the spawning season (October-March). Apparently, most mature females leave the harbor to spawn. Stressful salinity and temperature, high larval predation in the estuary, or inadequate larval food supplies might have created selection pressures for spawning females to seek water offshore with the proper environmental conditions for higher egg and larval survival.

Crab Population Estimates

A more important question than that of local crab densities at several stations is that of total population abundance throughout the estuary, determined for different seasons and age classes. Such a calculation is of interest in order to gauge 1) the potential use of the estuary by the species and the 0+ age class in particular; 2) the theoretical contribution made by the estuarine population to the commercial fishery; and 3) the potential impacts of estuarine development (e.g., dredging and landfill) on resident populations. The former two points are addressed in this discussion.

Trawl Efficiency Estimates

In order to extrapolate crab density values at each station to abundance within the corresponding stratum, some measure of trawl efficiency was needed. Examinations of mudflat areas (stations 5 and 14) in May of 1981 and 1982 showed very high densities of 0+ age crabs, ranging from 1 to 5 crabs m^{-2}. This estimate was conservatively reduced to 1 crab m^{-2}, and we assumed that only 50% of the available estuarine bottom (Fig. 1B) was utilized by early instars (excluding the inner estuary and perimeter which had lower salinities and had produced few or no crabs of this age group). This "corrected" density of 0.5 crabs m^{-2} (5,000 crabs ha^{-1}) was about 30 times the mean summer density of age 0+ crabs at station 5 (162 crabs ha^{-1}) as estimated by trawl; thus trawl efficiency in that season was about 0.033 (more recent studies have shown early instar densities to equal or exceed 10 m^{-2} in 1983; D. Armstrong, unpubl. data). In winter and spring, 0+ age group crabs were large enough to be sampled more effectively, but probably not as effectively as larger crabs; thus a factor of 0.25 was used in both of those seasons. An efficiency factor of 0.5 was applied to all other age groups, in accordance with Gotshall (1978a).

Abundance Calculation

For the nine strata of Grays Harbor sampled by

trawl, the total number of trawl-catchable crabs present in 1980-81, ±95% confidence intervals, were summer, 4.3 ± 1.7 million crabs; winter, 1.3 ± 0.7 million crabs; and spring, 2.6 ± 1.2 million crabs (Table 5). However, stratum 1 (837 ha) was excluded from the spring estimate due to lack of data, but was reincluded later, using density estimates from adjacent stratum 3. Totals for the other nonsampled strata (10, 11, 14, and 15) were added to totals for the trawl-sampled strata, and the sums for each age group were divided by the trawl efficiency estimates described above. Final calculated numbers for the total crab population were summer, 39.0 million crabs; fall-winter, 3.3 million crabs; spring, 7.8 million crabs (Table 5).

The 1980 year class, which was extremely abundant in the summer of 1980, virtually disappeared during the following winter, and reappeared in spring of 1981. Some hypotheses for this decline and recovery include winter hibernation, migration to nonsampled areas (e.g., stratum 14), and temporary egress from the estuary. Natural mortality probably contributed substantially to the decline as well.

Due to the speculative nature of these estimates and the underlying assumptions concerning trawl efficiency and proportion of habitat utilized, it was not possible to compute confidence limits on these final estimates. The estimates of total population abundance in the estuary suggest a tremendous increase in summer with the influx of 0+ crabs as megalopae and first instars, and an increase in 1+ animals as well. This estimate of 39 million crabs is the highest estuarine crab population abundance yet reported. The only other reported estimate, that of 9.3 million crabs in the San Francisco-San Pablo estuary complex during 1975 (Orcutt 1978), is based on a much less systematic survey than ours and does not correct for poor gear efficiency in regards to the small size of early instars. Furthermore, this latter estuarine system represents an area (500 km²) five times that of Grays Harbor.

The accuracy of our estimates of population abundance can be qualitatively assessed by comparison of trawl density data with that of other studies (Gotshall 1978a; Orcutt et al. 1975, 1976; Orcutt 1977, 1978; Table 6). Generally, there is great seasonal variation, but densities estimated in Grays Harbor are in accord with values for Humboldt Bay and San Francisco Bay. Extrapolations to total abundance indicate that large populations of juvenile crabs may use other coastal estuaries as well. Even relatively small estuaries in Oregon, such as Tillamook, Netarts, Yaquina, and Coos Bay, could support large populations of 0+ crabs, considering their small biomass (0.2 g dry weight). The principal benefits of these estuaries are probably refuge from larger cannibalistic conspecifics (Botsford and Wickham 1978; Stevens et al. 1982), more abundant food, and possibly accelerated growth as a result of food supplies and warmer temperatures than offshore waters.

TABLE 5.—Estimation of *Cancer magister* population in Grays Harbor, Wash., for 1980-81. All values are numbers of crabs except efficiency factors and percentages. C.I. = confidence interval.

Season/ Age Class[1]	Strata sampled by trawl (sites 1-9) n (×10³)	Variance of n (×10⁹)	df	C.I.[2] (×10³)	Strata not sampled[3] (n ×10³)	Sum of crabs (×10³)	Efficiency factor	Total crabs (×10³)	% of total
Summer									
0+	485	9	36	188	470	955	0.033	28,942	74.2
1+	2,979	555	36	1,511	982	3,961	0.5	7,922	20.3
2+	851	19	36	279	228	1,079	0.5	2,160	5.5
Total	4,315	687	36	1,681	1,680			39,024	100.0
Winter									
0+	182	14	28	244	6	188	0.25	753	23.0
1+	1,070	82	28	588	87	1,157	0.5	2,311	70.7
2+	97	10	28	65	7	104	0.5	207	6.3
Total	1,349	123	28	720	100			3,271	100.0
Spring									
0+	146	8	13	189	87	233	0.25	931	11.9
1+	1,176	181	13	918	307	1,483	0.5	2,965	38.0
2+	1,246	342	13	1,262	707	1,953	0.5	3,904	50.1
Total	2,568	290	13	1,163	1,101			7,800	100.0

[1]See Table 3 and Figure 7 for size of these age classes throughout the year 1980-81.
[2]Values for $t_{(0.05)}$: summer = 2.029, winter = 2.048, spring = 2.160.
[3]See text for explanation of estimates based on data of adjacent trawl stations.

TABLE 6.—Comparison of *Cancer magister* densities in Grays Harbor, Wash. (this report); Humboldt Bay, Calif. (Gotshall 1978a); and San Francisco-San Pablo Bay, Calif. (Orcutt et al. 1975, 1976; Orcutt 1977). Data are not corrected for gear efficiency.

Bay	Season	Year	Transect		No. crabs/ha
			Method	Area (m^2)	
San Francisco-	Summer	1975-77	Trawl	[1]1,500	90-340
San Pablo, Calif.	September	1977-78	Trawl	1,500	13-170
Humboldt Bay, Calif.	January	1967	Trawl	2,400	4,910
	August	1967	Trawl	2,400	300
	April	1968	Trawl	2,400	140
	August	1968	Trawl	2,400	1,280
	October	1968	Trawl	2,400	930
		(Mean of trawl samples, 1967-68 = 890)			
	August	1967	Scuba	140	520
	April	1968	Scuba	140	0
	August	1968	Scuba	140	4,480
	October	1968	Scuba	140	280
		(Mean of scuba samples, 1967-68 = 1,080)			
Pacific Ocean, near	October	1968	Trawl	[2]6,667	0-9,400
Humboldt Bay, Calif.	November	1968	Trawl	6,667	0-36,000 ($\bar{x}$ = 800)
Grays Harbor, Wash.	June	1980	Trawl	variable	200-1,000
Outer Harbor	December	1980	Trawl	1,400	310
	May	1981	Trawl	2,000	1,320

[1]Distance estimated as 50 m/min.
[2]Area estimated as distance (given) × ⅔ (headrope length).

Growth

Dry weight increased 282 times between first instar (0.2 g) and sixth instar (5.7 g) during the first year. Other authors have not presented growth data as changes in weight, but rather as increases in carapace width. Crabs in Grays Harbor grew from about 7 mm to 50+ mm cw during 1980-81, which is similar to values reported by Cleaver (1949) and Butler (1961). However, Poole (1967) concluded that crabs in Bodega Bay, Calif., reached 75 mm (range 50-100 mm) by 1 yr after metamorphosis. This would represent fairly rapid growth, but close to the upper limits of crab growth rates in Grays Harbor.

In contrast to Grays Harbor, Tasto (1983) stated that juvenile crabs spend only 1 yr in San Pablo Bay, and reach 100 mm by the end of that time (twice the growth rate of ocean crabs and Grays Harbor crabs). He concluded that the estuarine population was a single year class and was almost completely replaced by a new year class each spring, a situation very different from Grays Harbor where at least three year classes are present constantly. The San Francisco data may have been misinterpreted, perhaps caused by use of collecting gear (mostly ring nets) that selected larger crabs and resulted in a frequency mode near 100 mm cw that may have actually represented older 1+ age group crabs.

Unfortunately, growth data are not available for 0+ age Dungeness crabs that metamorphose directly offshore for comparison with estuarine populations. Presumably, colder bottom-water temperatures offshore (8°-10°C) would cause metabolic, growth, and general energetic depression of these animals relative to rates in warmer (14°-18°C) estuaries. Studies of offshore juvenile populations are much needed in this regard.

Importance of Grays Harbor to Commercial Fisheries.

The potential contribution of Grays Harbor to the commercial landings of *Cancer magister* was calculated by assigning various mortality rates to the 1980 year class for a period of 3.5 yr, i.e., until recruitment to the fishery. Jow (1965) estimated annual natural mortality of adult male crabs to be 15% per year (M = 0.165, exponential). Mortality rates for juveniles are unknown, so we have assumed a range of 0.5-0.8. From an initial population (N_0) of 28.9 million juvenile crabs in summer of 1980, the number surviving 3.5 yr (N) was calculated from the equation

$$N = N_0 e^{-zt}$$

where z represents the annual mortality rate and t is the time interval. Values of z used were 0.8 for the first half year (t = 0.5), 0.5 for the second half year, and 0.2 (as above) for the remaining 2.5 yr necessary to reach legal size, assuming crabs enter the fishable population at that age, as suggested by Cleaver (1949). At these mortality rates, about 9.2 million adult crabs might remain by

December 1983, of which about half, 4.6 million, would be males subject to the commercial fishery. If an equivalent number of crabs were available from the 1980 recruitment to Willapa Bay, a large bay equaling or exceeding Grays Harbor in area and located about 20 km south, then about 9.2 million legal male crabs of estuarine origin might be available to the commercial fishery in 1984-85 from larvae and early instars that utilized these two Washington estuaries in 1980-81.

Washington coastal crab landings for the period 1971-80 have averaged 3,500 t/yr (PMFC 1981), or about 3.85 million crabs (at 0.9 kg/crab). Thus, these two bays could theoretically serve as nursery grounds for more than enough crabs necessary to maintain a viable commercial fishery in Washington. However, landings over the past 40 yr have fluctuated from 1,000 to 8,000 t, with a 9-12 yr period, so it is impossible to predict how the estimated contribution of the 1980 year class will compare to 1984 commercial landings.

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AGE, GROWTH, AND MORTALITY OF GRAY TRIGGERFISH, *BALISTES CAPRISCUS*, FROM THE NORTHEASTERN GULF OF MEXICO

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ABSTRACT

Age, growth, and mortality of gray triggerfish, *Balistes capriscus*, from the northeastern Gulf of Mexico were estimated from sections of the first dorsal spine of 1,746 fish. The oldest female was estimated to be 12 years old and the oldest male was 13 years old. The von Bertalanffy growth equations, using weighted means, were as follows: males, $l_t = 491.9\ (1 - e^{-0.382(t-0.227)})$ and females, $l_t = 437.5\ (1 - e^{-0.383(t-0.150)})$, where l = fork length in millimeters and t = age in years. The mean annual mortality rate as determined by four methods of analyses (based on number of fish at age) ranged from 0.32 to 0.53. The weight-length relationships of gray triggerfish were males, $W = 6.71505 \times 10^{-6}\ L^{3.187}$, and females, $W = 1.3939 \times 10^{-5}\ L^{3.065}$, where W = weight in grams and L = fork length in millimeters.

Exploitation of fish from the northeastern Gulf of Mexico by recreational and commercial fishermen has created a demand for underutilized fish resources. One of the abundant fish resources that is being subjected to exploitation is the gray triggerfish, *Balistes capriscus*. A dramatic increase in demand for this species can be seen in the commercial landings on the west coast of Florida: 7.8 t in 1967 and 26.7 t in 1977 (Anonymous 1967, 1977).

This species is known to occur in the western and eastern Atlantic. In the western Atlantic, its range is from Nova Scotia to Argentina, including the Gulf of Mexico (Briggs 1958; Moore 1967). In the Gulf of Mexico, the gray triggerfish is a primary reef fish inhabiting the area between 12 and 42 m in depth (Smith 1976), except for its first year of life when it is planktonic and associated with *Sargassum* (Dooley 1972).

The harvest of the gray triggerfish in the northeastern Gulf of Mexico and its utilization of reef habitats has created a need to know more about the biology of this species, especially age, growth, and mortality. Age and growth of gray triggerfish, using the first dorsal spine, has been reported only for the southwestern coast of Africa (Anonymous 1980; Caveriviere et al. 1981). This paper reports the results of our investigation on age, growth, and mortality, using the first dorsal spine of gray triggerfish from the northeastern Gulf of Mexico.

METHODS AND MATERIALS

The hook and line fishery for gray triggerfish off Panama City, Fla., was sampled from May 1979 to March 1982. During this period, 2,808 fish were sampled and from each the fork length in millimeters and total weight in grams measured and recorded. The sexes of the fish were also recorded when determinable by gross examination of the gonads. First dorsal spines were available from 1,746 of the 2,808 fish in the collection. Total length (TL), standard length (SL), and fork length (FL) were measured in millimeters from 100 fish to develop length conversion formulas.

The first dorsal spines were processed for examination as follows: 1) removing the first 5 mm of spine shaft above the condyle with a Dremel[2] tool; 2) placing the shaft section on a mounting tag using Lakeside No. 70c thermoplastic cement and sectioning the shaft using the method described by Berry et al. (1977); 3) removing three 0.18 mm thick serial sections from the cement with 50% isopropanol; and 4) mounting the clean sections in 20% Piccolyte cement (20% Piccolyte, 80% xylenes) on glass slides.

Spine cross sections were examined and measured using a closed-circuit television using a 50

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

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mm 3.5 macro lens which projected an image of the section on to a monitor screen at 20× magnification. Illumination was by transmitted light. Translucent (light) bands on the cross sections were counted and the distances (in millimeters) from the center of the spine to the distal edge of each band was measured. The spine radius (R) was defined as the maximum distance (in millimeters) from the center of the section (appears as a small hole) to the posterior distal edge (Fig. 1).

Additionally, before the spines were sectioned, the anterior-posterior thickness (T) of 200 dorsal spines was measured to the nearest 0.01 mm at the sectioning site.

The type of growth (opaque = dark, translucent = light) of the margin of each section was noted. The sections were read three times.

The relationships of R, T, and body weight to FL and the relationships between TL, SL, and FL were determined by least squares methods following the suggestions of Ricker (1975). A computer program by Abramson (1971) was used to fit weighted back-calculated mean length at age to von Bertalanffy growth curves. The growth equation (von Bertalanffy 1938, 1957) and values were as follows:

$$l_t = l\,(1 - e^{-K(t-t_0)})$$

where l_t = length at age t,
l = asymptotic length,
K = growth coefficient,
t_0 = time when length would theoretically be zero.

Estimates of annual mortality (a), annual survival (s), and instantaneous mortality (i) were developed for the total collection (2,808 fish) (Ricker 1975). Length-frequency data were converted to age-frequency distribution (N_y = number of fish caught in age class y) by applying age-length keys. Ages III through IX of the resultant catch curves were analyzed by the methods of Heincke (1913), Jackson (1939), Robson and Chapman (1961) and by finding the slope (m) of a regression line fitted to $l_n(N_y)$ and y and substituting the equation $a = 1 - e^m$.

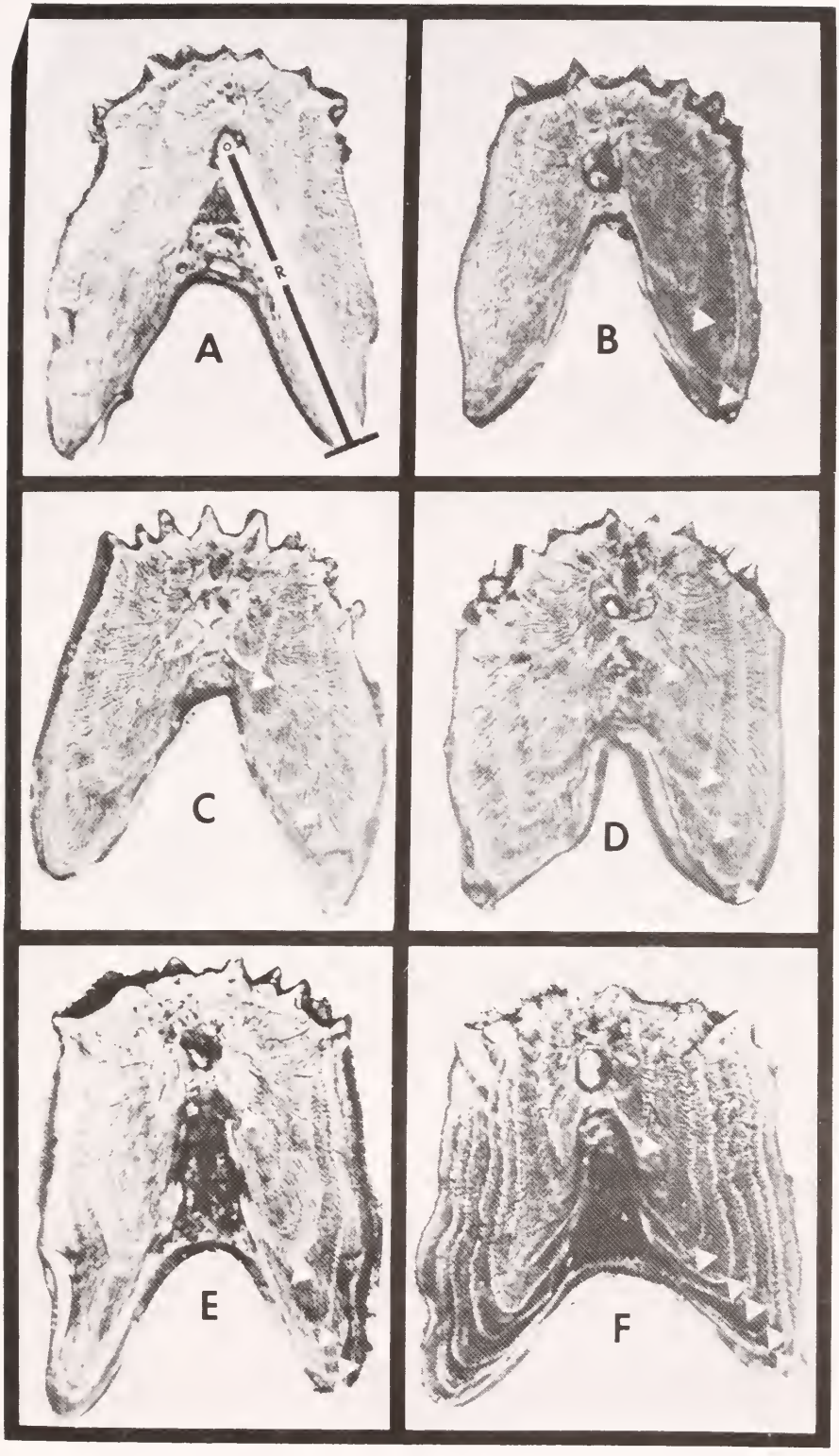
FIGURE 1.—Sections of gray triggerfish first dorsal spines from fish collected off Panama City, Fla. (A) Spine section from a 1-yr-old male (263 mm FL) collected 4 September 1980 with spine radius R labeled. (B) Spine section from a 2-yr-old female (336 mm FL) collected 11 September 1980. (C) A 3-yr-old female (315 mm FL) collected 8 August 1980. (D) A 4-yr-old male (350 mm FL) collected 13 August 1980. (E) A 5-yr-old female (331 mm FL) collected 24 September 1980. (F) A 6-yr-old male (477 mm FL) (seventh mark forming on margin) collected 25 June 1980.

RESULTS

A positive relationship was found between the growth of the first dorsal spine and FL. The relation between FL and R was as follows: FL = $4.58\ R^{0.951}$ with a correlation coefficient (r) of 0.84. The relation between FL and T was as follows: FL = $24.87\ T^{1.422}$ with r = 0.89. The variation in the two relationships probably resulted from the slight tapering of the spine in the area from which the sections were taken and the effect of sectioning. The FL-R relationship was used for back-calculation of sizes at previous ages. The spine sections possessed distinct dark-light banding patterns (Fig. 1) and the agreement between readings as to the numbers of bands was 98% [Beamish and Fournier's (1981) index of average error was 0.0072]. The translucent (light) band formation occurred during spring and summer (April to October with a peak during June-July), and the mean marginal opaque increment was least during this period of time (Table 1). We thus considered the translucent bands on the first dorsal spines to be annular

TABLE 1.—Percent frequency of dorsal spines with translucent (light) margins and mean marginal measurements of opaque (dark) margins in millimeters for gray triggerfish from northeast Gulf of Mexico, 1979-82.

	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
Percent of fish with translucent margins	0.00	0.00	0.00	52.27	41.86	56.70	53.59	23.79	2.40	0.90	0.00	0.00
Mean opaque marginal increment for fish												
2 light bands	—	—	1.40	1.24	1.09	0.74	0.82	0.64	1.00	1.70	—	—
3 light bands	—	0.79	0.49	0.59	0.60	0.58	0.56	0.36	0.50	—	—	—
4 light bands	—	0.56	0.47	0.43	0.52	0.48	0.56	0.38	0.60	—	—	—
5 light bands	—	0.44	0.24	0.26	0.06	0.24	0.37	0.037	—	—	—	—
Total number of fish	6	19	83	88	215	194	209	248	250	111	97	13


A
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deposits and suitable for age determination. Lengths varied within age classes and length ranges overlapped between age classes (Tables 2, 3, 4). For example, males with three annuli (translucent bands) ranged from 258 to 537 mm FL and those with four annuli ranged from 250 to 549 mm FL. There was, however, a general trend of increasing modal length with increase in age.

The gray triggerfish is a moderately long-lived species. The oldest male was estimated to be 13 yr old (544 mm FL) and the oldest female was 12 yr old (561 mm FL).

The back-calculated and empirical sizes at age are presented in Tables 5, 6, and 7. The average mean back-calculated length at age for males was slightly (5-50 mm FL) larger than that for females at age 1-9, after which the females were larger. Only three fish were collected that were older than 9 yr; thus the reversal of the trend is probably an artifact caused by few samples.

The von Bertalanffy growth parameters varied slightly between males, females, and all fish. The von Bertalanffy equations were:

$$\text{males } l_t = 491.9(1 - e^{-0.382(t-0.227)}),$$

$$\text{females } l_t = 437.5(1 - e^{-0.383(t-0.150)}),$$

$$\text{all fish } l_t = 466.0(1 - e^{-0.382(t-0.189)}).$$

TABLE 2.—Length composition, in percent, of male gray triggerfish by age groups from northeast Gulf of Mexico, 1979-82.

Length group (FL mm)	Age in years										Total number of fish
	0	1	2	3	4	5	6	7	8	9	
150-199	50.00	50.00									2
200-249		50.00	50.00								18
250-299		14.46	44.58	36.14	3.62	1.20					135
300-349		0.66	26.32	42.10	25.66	2.63	1.97	0.66			307
350-399			9.26	35.80	32.72	18.52	3.70				339
400-449			1.48	18.52	29.62	25.19	15.56	5.93	3.70		233
450-499			11.02	12.24	26.53	29.59	16.34	9.18	4.08	1.02	155
500-549				3.30	27.47	30.77	27.47	8.79	1.10		121
550 and larger						66.67	8.33	16.67		8.33	24
Total	1	23	184	371	339	229	117	47	19	4	1,334

TABLE 3.—Length composition, in percent, of female gray triggerfish by age groups from northeast Gulf of Mexico, 1979-82.

Length group (FL mm)	Age in years												Total number of fish
	1	2	3	4	5	6	7	8	9	10	11	12	
200-249	41.67	33.33	25.00										19
250-299	5.04	42.86	33.61	15.97	0.84	1.68							207
300-349	0.47	14.08	44.61	26.29	7.98	4.69	1.41	0.47					453
350-399		4.64	23.84	35.76	23.18	10.60	1.98						304
400-449			15.38	27.69	21.54	18.46	9.23	3.08	4.62				122
450-499		2.63	7.89	21.06	28.95	26.32	7.89		5.26				74
500-549			4.55	22.73	22.73	18.18	9.09	9.09	13.63				40
550 and larger				20.00	40.00	20.00						20.00	9
Total	20	175	374	321	168	107	35	10	17	0	0	1	1,228

TABLE 4.—Length composition, in percent, of gray triggerfish (all fish) by age groups from northeast Gulf of Mexico, 1979-82.

Length group (FL mm)	Age in years													Total number of fish
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	
150-199	50.00	50.00													2
200-249		47.83	39.13	13.04											32
250-299		9.13	42.47	35.16	11.42	0.91	0.91								365
300-349		0.47	18.27	41.69	26.93	7.72	3.75	0.94	0.23						848
350-399			7.12	31.05	34.47	19.09	6.84	1.43							691
400-449			0.90	16.59	28.70	25.11	16.59	7.17	3.14	1.38	0.45				418
450-499			1.36	10.20	26.53	28.57	19.73	8.84	2.73	2.04					244
500-549				4.23	27.37	28.20	24.79	8.36	2.58	4.37				0.10	172
550 and larger					5.00	50.00	15.00	10.00	5.00	10.00			5.00		36
Total	1	53	373	805	737	445	249	92	29	22	1	0	1	1	2,808

The weight-length relationships for gray triggerfish computed for the equation $W = aL^b$, where W is weight in grams and L is FL in millimeters, were as follows:

males $W = 6.7105 \times 10^{-6} L^{3.187}$, $r = 0.97$, $n = 169$,

females $W = 1.393 \times 10^{-5} L^{3.065}$, $r = 0.93$, $n = 167$,

TABLE 5.—Back-calculated fork lengths (mm) at age for male gray triggerfish from the northeastern Gulf of Mexico, 1979-82.

Age group	Mean length ± 1SD at capture	N	Average back-calculated FL at age												
			1	2	3	4	5	6	7	8	9	10	11	12	13
I	250.0 ± 29.0	18	137.7												
II	313.4 ± 41.8	99	123.9	248.0											
III	357 4 ± 55.8	192	119.2	243.0	319.6										
IV	407.8 ± 66.6	186	124.1	244.2	322.8	376.3									
V	450.6 ± 56.2	134	128.2	245.1	324.7	381.8	427.0								
VI	461.9 ± 56.0	72	132.2	245.3	309.7	364.3	409.8	443.2							
VII	474.5 ± 51.5	28	126.3	231.8	301.2	350.7	390.7	430.5	458.7						
VIII	462.5 ± 27 4	10	134.0	236.5	307.4	344.3	372.8	399.5	429.7	448.6					
IX	511.5 ± 78.5	2	165.8	293.1	323.0	362.0	389.8	424.7	468.7	489.9	504.0				
XIII	544 0 ± —	1	91 0	308 5	395.0	452.7	461.5	479.0	492.1	496.5	500.8	509.5	513.8	526.8	535.4
Weighted mean			124.9	244.3	319 6	373.7	415.5	436.2	452.9	458.7	502.9	509.5	513.8	526.8	535.4
± 1SD			± 41.0	± 49.4	± 55.5	± 60.9	± 60.1	± 56.8	± 48.6	± 32.3	± 54.5	—	—	—	—
N			742	724	625	433	247	113	41	13	3	1	1	1	1
Annual increment			124.9	119.4	75.3	54.1	41.8	20.7	16.7	5.8	44.2	6.6	4.3	13.0	8.6

TABLE 6.—Back-calculated fork lengths (mm) at age for female gray triggerfish from the northeastern Gulf of Mexico, 1979-82.

Age group	Mean length ± 1SD at capture	N	Average back-calculated FL at age											
			1	2	3	4	5	6	7	8	9	10	11	12
I	259.0 ± 34.0	12	155.6											
II	300.4 ± 35.2	93	120.1	241.4										
III	330.8 ± 46.2	187	117.0	227.8	298.3									
IV	360.1 ± 57.5	161	117.9	226.3	292.4	335.6								
V	398.5 ± 64 0	85	128.2	226.5	291.7	340.7	378.5							
VI	402.5 ± 63 6	55	113.5	218 4	276.0	320.1	357.5	387.1						
VII	419.8 ± 73.6	16	124.9	205.3	260.9	307.2	345.9	379.0	405.1					
VIII	448.8 ± 79 6	5	109.0	193.3	262.3	305.7	342.4	376.8	415.1	437.4				
IX	457.8 ± 71 2	10	101.8	208.1	264.8	306.9	340.2	373.7	402.5	431.0	447.9			
XII	561.0 ± —	1	121.2	258.2	390.4	463.2	481.2	494.6	516.8	525.7	534.6	547.8	552.2	556.6
Weighted mean			119.4	227.3	291.1	332.0	366.1	384.7	409.3	438.9	455.8	547.8	552.2	556.6
± 1SD			± 37.8	± 43.1	± 45.1	± 53.3	± 61.1	± 62.4	± 70.0	± 71.4	± 73.6	—	—	—
N			625	613	520	333	172	87	32	16	11	1	1	1
Annual increment			119.4	107.9	63.8	40.9	34.1	18.6	24.6	29.6	16.9	92.0	4.4	4.4

TABLE 7.—Back-calculated fork lengths (mm) at age for all gray triggerfish collected from the northeastern Gulf of Mexico, 1979-82.

Age group	Mean length ± 1SD at capture	N	Average back-calculated FL at age												
			1	2	3	4	5	6	7	8	9	10	11	12	13
I	259.3 ± 29.7	34	140.9												
II	308.6 ± 42.3	210	121.7	247.4											
III	343.9 ± 52.1	424	118.0	235.4	308.9										
IV	384.0 ± 66.1	398	122.0	235.3	307.3	356.1									
V	425.8 ± 70.7	243	128.1	236.6	309.1	361.8	403.9								
VI	434 7 ± 67.1	141	123.9	232.6	295.0	346.0	386.6	417.7							
VII	541.0 ± 64.6	49	123.6	221.0	286.7	334.8	373.2	409.0	435.7						
VIII	464.8 ± 54.2	16	134.2	227.1	296.3	335.3	372.2	401.3	432.6	452.2					
IX	478.1 ± 72.3	14	117.4	233 5	282.6	324.1	354 4	388.8	420.1	448.4	468.6				
X	439.0 ± —	1	108.3	204.0	251.5	274.8	286.3	309.2	331.9	354.9	384.1	420.8			
XII	561.0 ± —	1	212.2	258.2	390.4	463.2	481.2	494.6	516.8	525.7	534.6	547.8	552.2	556.6	
XIII	544.0 ± —	1	91.9	308.4	395.0	452.7	461.5	479.0	492.1	496.5	500.8	509.5	513.8	526.7	535.4
Weighted mean			112.8	236.5	305.8	354.1	392.9	412.9	432.8	451 2	460.4	492.7	533.0	541.7	535.4
± 1SD			± 40.0	± 47.8	± 52.6	± 61.0	± 65.9	± 66.0	± 64.0	± 61.8	± 72.0	± 65.1	± 27.2	± 21.1	—
N			1,523	1,498	1,288	864	466	223	82	33	17	3	2	2	1
Annual increment			112.8	123.7	69.3	48.3	38.8	20.0	19.9	18.4	9.2	32.3	40.3	8.7	−6.3

all fish $W = 2.146 \times 10^{-5} L^{2.992}$, $r = 0.96$, $n = 175$.

Conversions between different length measures were linear and expressed as follows:

FL vs. TL: FL = 29.704 + 0.774 TL, $r = 0.97$, $n = 100$,

FL vs. SL: FL = 22.823 + 1.171 SL, $r = 0.99$, $n = 100$,

TL vs. SL: TL = 9.666 + 1.446 SL, $r = 0.96$, $n = 100$.

Estimates of mortality (a, s, and i) varied slightly between estimation methods (Table 8). Full recruitment to the fishery was considered to be at 3 yr for both sexes. Estimates of a were between 0.32 and 0.53 with i between 0.39 and 0.75 (Table 8).

TABLE 8.—Estimated annual mortality (a), annual survival (s), and instantaneous mortality (i) by estimation technique for gray triggerfish from the northeastern Gulf of Mexico, 1979-82.

	Estimation technique			
	Heincke (1913)	Jackson (1939)	Robson and Chapman (1961)	Regression analysis
Males				
a	0.33	0.32	0.44	0.53
s	0.67	0.67	0.56	0.47
i	0.40	0.39	0.57	0.75
Females				
a	0.36	0.32	0.45	0.47
s	0.64	0.68	0.55	0.53
i	0.45	0.38	0.59	0.64
All fish				
a	0.34	0.33	0.44	0.49
s	0.66	0.64	0.56	0.51
i	0.41	0.40	0.58	0.67

DISCUSSION

The variation in length at age and overlays of length ranges between ages found in gray triggerfish is not unusual in fish from southeastern U.S. waters. Many species such as king mackerel, *Scomberomorus cavalla*; Spanish mackerel, *S. maculatus*; red grouper, *Epinephelus morio*; sailfish, *Istiophorus platypterus*; and black sea bass, *Centropristis striata*, have large variations in size within age groups (Beaumariage 1973; Powell 1975; Moe 1969; Jolley 1977; Waltz et al. 1979).

Our gray triggerfish growth rates are similar to growth information from the Gulf of Mexico, but not information from Africa. Beaumariage (1969) reported growth rates for three tagged fish (250, 270, and 332 mm TL) from the northeastern Gulf of Mexico. His fish grew at a rate of 187.2, 153.6, and 51.6 mm/yr. If one considers Beaumariage's fish to be 2, 2, and 3 yr old, respectively, then his growth increments are similar to ours (Table 7). Gray triggerfish age and growth have been reported from southwestern Africa (Ivory Coast-Ghana-Togo area) by Anonymous (1980). We took the information in Anonymous' figure 11 and converted it to mean length at capture per age which gave the following approximate values: age I, 148 mm; age II, 203 mm; values are about 100 mm less than ours for each age (Table 7). Caveriviere et al. (1981) provided comprehensive information on the age and growth of gray triggerfish off Senegal and the Ivory Coast. Two hypotheses with regard to band formation were suggested: A) one band per year, and B) two bands per year. The sizes (FL) at age (in years) for Senegal fish by hypotheses were age I, 153 mm for hypothesis A, 90 mm for B; age II, 231 mm for A, 170 mm for B; age III, 285 mm for A, 238 mm for B; age IV, 322 mm for A, 290 mm for B; age V, 348 mm for A, 324 mm for B. Sizes at age of our Gulf of Mexico fishes (Table 7) were larger after the first year than predicted by both of the above hypotheses for Senegal fish. The sizes at age for Ivory Coast fish were smaller than both the Senegal and the Gulf of Mexico fish using the hypothesis of one band formed per year. These differences may be the result of different environments, biology, methods of capture, or aging. Anonymous (1980) suggested that the African fish have a seasonal offshore migration to avoid the cold coastal water (during the third quarter of the year) which is the result of upwelling. Gulf of Mexico fish are not known to have migratory habits, and thus might not be subject to the energy expense such movements incur. More information on the life histories and environments of these groups of gray triggerfish is needed to explain the observed variations.

The K values (growth coefficient) of gray triggerfish varied between 0.382 and 0.383. These values were similar to, but higher (about 0.1) than, those reported for other demersal marine fish from the southeastern United States (see Manooch 1982 and Pauly 1978 for a listing of values). The K values estimated for gray triggerfish may be high because of the low asymptotic lengths that were found. Additional investigation of the larger and older fish is needed to evaluate the growth coefficients of this species. The esti-

mates of mortality (Table 8) were similar to those of demersal marine fish such as the white grunt, *Haemulon plumieri*, where a = 0.37-0.51 and the red porgy, *Pagrus pagrus*, where a = 0.32-0.55 (Manooch 1976; Manooch and Huntsman 1977) that inhabit similar habitats. The mortality rates for gray triggerfish probably reflected the exploitation level on this species in the northeast Gulf of Mexico. Nelson and Manooch (1982) reported similar values (i = 0.39-0.50) for red snapper, *Lutjanus campechanus*, from the Carolinas and Florida coasts where the fishing pressure is light to medium and much higher values (i = 0.78-0.94) from the fishery off Louisiana where the commercial fishing pressure is high. The effect of fishing on gray triggerfish populations were therefore assumed to be similar to the effects of fishing on these other reef fish resources.

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THE EFFECT OF DISTURBANCE ON HARBOR SEAL HAUL OUT PATTERNS AT BOLINAS LAGOON, CALIFORNIA[1]

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ABSTRACT

We studied harbor seals at Bolinas Lagoon, California, from May 1978 to June 1979. Field observation and two time lapse motion picture cameras were used to monitor the numbers of seals and of disturbances, and to provide information on tidal height. Peak numbers occurred during the summer. During nonbreeding seasons, high numbers occurred at low tides, and during the breeding season they occurred in early afternoon except when haul out areas were flooded. Seals were disturbed by humans on 71% of days monitored; people in canoes were the primary source of disturbance. Human activities closer than 100 m caused seals to leave haul out sites more than activities at greater distances.

Several studies exist on the haul out patterns of harbor seals, *Phoca vitulina*, in undisturbed locations (Scheffer and Slip 1944; Venables and Venables 1955; Richardson 1975[4]; Pitcher 1977[5]; Loughlin 1978), but the effects of human activities on haul out patterns have been examined infrequently (Newby 1971; Paulbitsky 1975; Chapman 1979[6]). We report here how daily and seasonal haul out patterns of harbor seals can be modified by human activity in a small estuary, Bolinas Lagoon, Calif. The data also provide a baseline against which the effects of pending increased levels of human activity could be compared.

Since 1970, a state quarantine has reduced human activities in the contaminated waters of Bolinas Lagoon. Human use has been confined to bird watching, some boating, illegal clam digging, beach combing, and recreational bait fishing. When the quarantine is lifted, many of these activities will increase. Increased human activity could also result from provisions included in the General Management Plan of the Golden Gate National Recreation Area (June 1979) for a walk-in camp site and parking area along the lagoon.

Little information exists on harbor seals at Bolinas Lagoon. Carlisle and Alpin (1966, 1971) estimated numbers as part of a statewide aerial count, but their figures for Marin County were low compared with preliminary data collected by Gary W. Page (unpubl. data). More recently, Mate's (1977)[7] monthly statewide counts failed to detect any seals in Bolinas Lagoon.

STUDY AREA AND METHODS

Bolinas Lagoon, a 448 ha estuary 24 km north of San Francisco, is a Marin County Nature Preserve and is part of the Golden Gate National Recreation Area. Triangular in shape, it is bordered by paved roads, pasture land, the small community of Bolinas, and a 3 km long sand spit covered with houses. At the end of the spit there is a 60 m wide opening to the ocean. The major channel used by the seals passes by Kent Island (KI) and Pickleweed Island (PWI) and cuts north along the northeastern shore (Fig. 1). KI and PWI remain above water when tides exceed 1.7 m above mean low water level and are the two main seal haul out areas.

Movie cameras recorded the activity of seals and humans in the vicinity of KI and PWI. A Canon[8]

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

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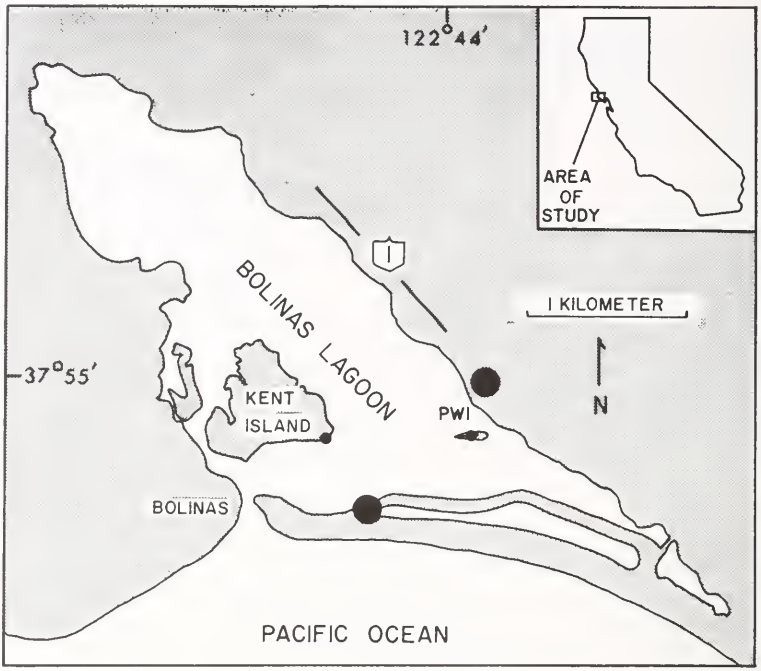

FIGURE 1.—Study area showing the two major haul out sites, Kent Island (KI) and Pickleweed Island (PWI), Calif., (small solid circles), and the location of the two cameras (large solid circles).

"814 XL Super 8" with a 7.5 to 60 mm zoom lens was focused on KI from a private residence on the sand spit about 400 m away. A photocell activated the camera at day break and deactivated it at sundown; an intervalometer exposed one frame of film every minute. Another camera, a Eumig "880 Super 8" with a 7 to 56 mm zoom lens, positioned in a weatherproof box on private property along State Route 1, was focused on PWI, about 300 m away. The built-in intervalometer also triggered 1 frame/min. An electrical timer activated the camera during daylight hours. The film used (Kodachrome ASA 40) contained 3,000 frames/roll and lasted a week except during summer, when film was changed every 4 d due to increased day length.

We used a Kodak "Moviedeck model 475" projector to analyze film. We noted time, tide level, and the number of seals once every hour of photographic time. Any major change in seal numbers within the 1 h interval was also noted, as well as any disturbance. A stake marked with 0.3 m increments was placed near the major channel by KI and in line of the Canon's viewfinder. This provided a photographic record of tidal change. Actual time for the first frame each day was extrapolated from tables for sunrise and sunset; on several mornings and evenings we compared these times with the actual time that camera operation began or ceased. Extrapolated times were accurate to within 1.0 h.

Twelve (once per month) day-long watches and 211 (124 breeding, 47 summer, and 40 winter) incidental sightings validated camera counts, detected sources of disturbance outside the camera field, estimated disturbance distance from the herd, identified additional haul out sites, and accurately counted pups, which were difficult to detect on film.

When analyzing data, the year was divided into three seasons: winter (November through February), breeding (March through June), and summer (July through October); seasonal averages are expressed with ± 1 standard deviation. Correlation coefficients were calculated to compare camera and field counts as a test for camera reliability, and to examine the relationship of seal numbers to tide level within each hour (Snedecor and Cochran 1967). For daily use per season graphs of hourly means were compared; the "runs up and down test" (Bradley 1968) was used to test the sequence of hourly means for randomness.

All human activities (including dogs off leashes) in the area were divided into two types: actual disturbance and zero-seal disturbance. Actual disturbances, or any activity occurring when at least one seal was present, were further subdivided into type I, where at least one seal left the area, and

type II, where no seals left the area. A zero-seal disturbance was any activity occurring in the area when seals were not hauled out but which may have prevented seals from doing so.

To investigate the effect of actual disturbance on the seals at KI, disturbances were classified by four criteria: 1) seal response (yes, at least one seal left; no, no seals left); 2) distance between the seals and the disturbance source (≤100 m, 101-200 m, 201-300 m); 3) day of week (weekend/holiday, weekday); and 4) disturbance type (person/dog, nonpower boat, power boat). Due to the low number of disturbances during the breeding and winter seasons, season was not used as a variable. Only the 156 instances where disturbance type and distances were known were used in the analysis. The result was a $2 \times 3 \times 2 \times 3$ contingency table. We used log-linear models to examine the effects of 2, 3, and 4 (explanatory variables) on 1 (response variable). Log-linear models are used to analyze multidimensional contingency tables and can be used to study two- and three-way interactions between variables (Bishop et al. 1975). We asked the question: "Is seal response independent of the other variables?" We then asked: "If not, what variables affect seal response?" Exploration of models was done by backward and forward selection of models (models were fit with iterative proportional fitting). Both methods produced the same final model; only the backward selection method is presented in the paper.

Backward selection starts with a model that fits the data. All interaction terms that are found to be not significantly different from zero by using a conditional likelihood ratio test (Fienberg 1981) are removed from the model. The final model is found when all nonsignificant terms are deleted. Models were adjusted for marginal zeros (Bishop et al. 1975: Ch. 3), and are displayed here using a shorthand notation (Fienberg 1981). For example, seal response independent of all other variables is denoted [1] [234], and seal response dependent on one of the variables, such as distance, is denoted [12] [234]. Once the final model is selected, weights or "u-terms" are calculated from the data, and are given to each of the levels of each variable included in the final model. The sign of the weight indicates the effect of the explanatory variable [2, 3, or 4] on the response variable [1]. The relative magnitude of the weight indicates the importance of the explanatory variable.

The average time it took for seals to recover from disturbance was based on the elapsed time between when the seals were flushed to when 50% of the original number had rehauled. A chi-square test determined the significance of tide level on the ability of seals to recover from disturbance at KI (Snedecor and Cochran 1967). Correlation coefficients were used to detect the importance of PWI as an alternate haul out site.

RESULTS

Camera Reliability

A correlation of KI camera counts with field counts revealed that the camera was not a reliable indicator of the actual number of seals present but was reliable for information on daily trends. Correlation coefficients by season were as follows: winter, $r = 0.92$, $n = 19$; breeding, $r = 0.55$, $n = 40$; summer, $r = 0.75$, $n = 28$. Discrepancies between the two count methods were caused by seals shifting along the haul out area and, therefore, out of the camera's viewfinder, the inclination of females with pups to haul out on the fringe of the herd, and the difficulty in identifying pups. On the other hand, the camera was very reliable at PWI for the summer ($r = 0.94$, $n = 25$) and breeding ($r = 0.97$, $n = 13$) seasons because seals could not shift out of viewfinder range. Also, this camera was slightly elevated, allowing for better detection of seals hauled out close together. During much of the winter season the PWI camera was broken. Both cameras readily detected boats and people on foot disturbing seals, but could not detect aircraft. Dogs were seen on film twice and on 13 occasions during field counts.

Seasonal and Spatial Use Patterns

Seals used the lagoon on 95-100% of the days each month. More seals hauled out on KI during the breeding and summer seasons than during winter. Numbers on field counts averaged 31.2 ± 28.1 seals during the breeding season (range 0-101, $n = 78$), 53.5 ± 28.5 during the summer (range 0-105, $n = 48$), and 19.6 ± 19.3 during the winter (range 0-58, $n = 28$). The same trend was apparent from field counts on PWI; the number of seals averaged 10.6 ± 15.1 for the breeding season (range 0-77, $n = 107$), 10.0 ± 18.4 for summer (range 0-48, $n = 41$), and 7.7 ± 12.5 for winter (range 0-55, $n = 43$). The PWI means were much lower than those for KI, indicating that KI was the preferred haul out site.

During the breeding season, mother-pup pairs hauled out on PWI and on exposed sand bars along

the major channel, but on 83% (125 d) of 150 camera monitoring days, seals were present on KI. Ten and 12 pups were counted in 1978 and 1979, respectively. After the breeding season in July, seals were present on 97% (111 d) of 114 camera days. By contrast, seals were counted on PWI on 56% (54 d) of 96 camera census days during the breeding season and 73% (74 d) of 102 d in the summer. After October, when the population declined, the level of use was still high at KI with seals present on 81 of 92 camera census days.

Daily Use

Peak numbers of seals usually occurred in early afternoon at both sites except at KI during winter when a constant number were present until late afternoon (Table 1, Figs. 2, 3). All the daily trends were significantly different from randomness except for PWI during winter [$P = 0.02$ for KI winter, $P = 0.008$ for KI breeding, $P = 0.007$ for KI summer; $0.24 < P < 0.06$ for PWI winter, and $P < 0.001$ for PWI breeding and summer ("runs up and down test")]. The greater use of KI during the summer and breeding seasons is also reflected in the elevated hourly means (Fig. 2).

Correlation coefficients revealed a positive correlation between low tides and seal numbers (Table 2). The daily temporal use pattern (Table 1) was affected by tide level during winter (range of $r = 0.54 - 0.75$) and summer (range of $r = 0.49 - 0.69$) for KI and to a lesser extent during the summer for PWI (range of $r = 0.11 - 0.62$). No tidal effect was apparent at either site during the breeding season.

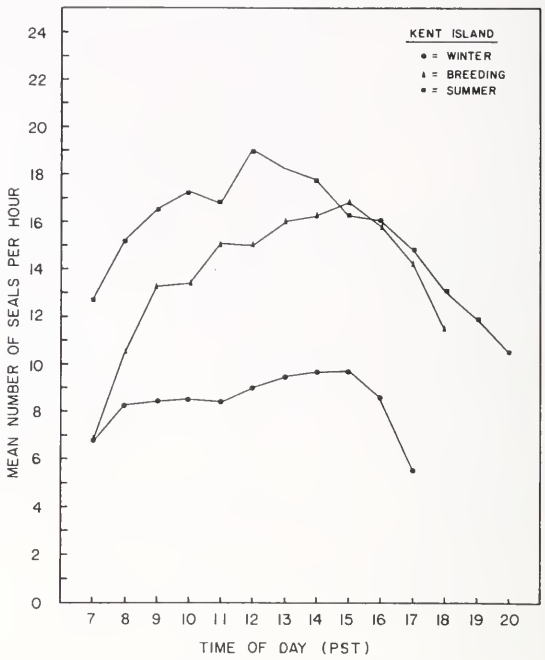

FIGURE 2.—Graph of time of day and the mean number of seals hauled out per time period for winter, breeding, and summer seasons at Kent Island.

Disturbance

Camera and field observations of KI recorded 539 actual and zero-seal disturbances. Of those with identifiable cause, 33.1% were nonpower boats, 10.0% people on foot, 7.8% power boats, 3.4% clam diggers or bait harvesters, 2.8% dogs, and

TABLE 1.—The relationship between time of day and the number of seals hauled out per season on Kent Island (KI) and Pickleweed Island (PWI); $\bar{x}$ is the mean number of seals per hour, SD is the standard deviation, and n is the sample size.

		Time													
Season		0700	0800	0900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000
Winter															
KI	$\bar{x}$	6.8	8.3	8.4	8.5	8.4	9.0	9.5	9.8	9.8	8.7	5.6			
	SD	9.5	11.6	11.9	11.6	11.7	11.4	12.0	12.5	12.0	11.5	8.9			
	n	84	83	84	84	87	88	87	88	87	87	12			
PWI	$\bar{x}$	0	0.8	3.5	6.9	6.3	5.5	6.2	5.4	2.2	2.2				
	SD	0	2.1	4.9	6.7	6.2	6.6	6.8	6.0	3.9	3.6				
	n	9	8	10	10	11	11	10	10	10	10				
Breeding															
KI	$\bar{x}$	6.9	10.6	13.3	13.4	15.1	15.1	16.1	16.4	16.9	15.9	14.3	11.6		
	SD	10.2	13.8	16.5	16.0	16.8	16.3	16.8	16.1	16.5	16.2	15.3	13.8		
	n	105	108	112	114	118	119	118	119	116	116	116	94		
PWI	$\bar{x}$	1.2	1.9	2.6	3.3	4.0	4.2	4.7	4.9	4.9	3.8	3.3	0.1		
	SD	3.1	4.8	5.8	6.6	7.3	8.0	8.3	8.4	8.5	7.3	6.5	0.3		
	n	87	89	86	89	91	89	92	91	91	90	83	37		
Summer															
KI	$\bar{x}$	12.7	15.2	16.5	17.3	16.8	19.1	18.3	17.8	16.4	16.1	14.8	13.1	12.0	10.6
	SD	14.4	15.9	17.4	17.7	16.5	18.0	18.2	18.2	17.8	16.8	15.3	14.9	15.1	15.3
	n	77	83	92	98	104	102	101	105	105	103	86	51	27	
PWI	$\bar{x}$	0.4	1.2	2.1	3.5	4.7	5.4	5.0	4.5	3.6	2.4	1.3	0.8	0.6	0.7
	SD	1.0	4.0	5.5	9.2	10.8	12.0	12.8	11.1	10.6	7.4	3.9	3.0	2.5	2.2
	n	91	90	91	94	101	101	99	99	98	98	98	92	70	14

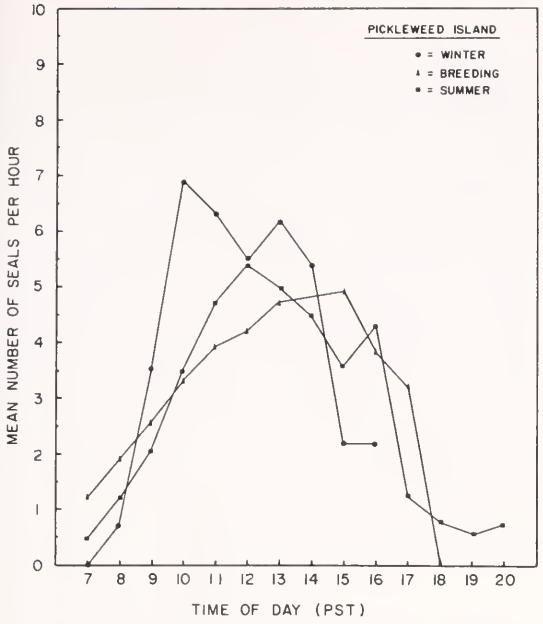

FIGURE 3.—Graph of time of day and the mean number of seals hauled out per time period for winter, breeding, and summer seasons at Pickleweed Island.

0.7% helicopters. The camera did not record the cause in 40% of the disturbances. During December, January, and February, commercial bait harvesters accounted for 25.7% of the disturbances. Disturbances from aircraft were detected only in field observations. The seals were disturbed at least once on 71% of 356 d when the KI camera was functioning, and during these days, 72.7% of 539 disturbances caused the seals to disperse (Table 3). On 211 d during which the PWI camera was functional, seals reacted to 57% of 236 disturbances (Table 3). The frequency of actual disturbances per day averaged highest during the summer for both KI and PWI.

Of the actual disturbances of known cause, most occurred within 100 m of the KI site and resulted more from nonpower boats than from any other source (Table 4). The deletion of terms [13] and [14] from the log-linear model in backward selection, however, indicated that only the distance of a disturbance significantly affected seal behavior (Table 5). Seals did not react differentially to any disturbance type and did not react more to disturbances during weekend/holidays than during weekdays. The relative magnitude of the weights associated with the distance/seal response interaction term [12] denoted that seals responded to

TABLE 2.—Correlation coefficients between tide level and the number of seals hauled out at hourly intervals per season at Kent Island (KI) and at Pickleweed Island (PWI), from camera data; n = number of censuses. Insufficient data were available for PWI during the winter. A positive correlation indicates a positive relationship between seal number and low tide, and a negative correlation indicates a negative relationship between seal number and high tide.

	Winter	Breeding		Summer	
Time	KI (n = 27)	KI (n = 26)	PWI (n = 16)	KI (n = 24)	PWI (n = 21)
0800	0.54**	0.35	0.23	0.49**	0.36
0900	0.75**	0.34	0.17	0.69**	0.20
1000	0.67**	0.42*	−0.17	0.55**	0.62**
1100	0.71**	0.31	−0.30	0.57**	0.52**
1200	0.64**	0.14	0.06	0.68**	0.48*
1300	0.65**	−0.12	0.34	0.54**	0.45*
1400	0.58**	−0.15	0.42	0.62**	0.37
1500	0.55**	0.001	0.22	0.67**	0.23
1600		0.20	0.11	0.67**	0.11

* Significant at $P = 0.05$.
**Significant at $P = 0.01$.

TABLE 3.—The frequency of disturbances on Kent Island (KI) and Pickleweed Island (PWI) by season; n is the number of days the camera was functional, A is the number of actual and zero-seal disturbances combined, $A1$ is the number of actual disturbances type I, A/n is the mean number of all disturbances per day, and $A1/n$ is the mean number of the actual disturbances per day.

	KI					PWI				
Season	n	A	$A1$	A/n	$A1/n$	n	A	$A1$	A/n	$A1/n$
Breeding	150	216	158	1.4	1.1	96	101	54	1.1	0.6
Summer	114	215	167	1.9	1.5	102	121	75	1.2	0.7
Winter	92	108	67	1.2	0.7	13	14	6	1.1	0.5
Totals	356	539	392	1.5	1.1	211	236	135	1.1	0.6

TABLE 4.—Data from the Kent Island camera used in log-linear model analysis (Bishop et al. 1975). The numbers in the table are the number of disturbances where seals were present for each category. Y = response (at least one seal left site); N = no response (no seals left site).

	Weekday						Weekend/holiday					
Distance:	≤100 m		101-200 m		201-300+ m		≤100 m		101-200 m		201-300+ m	
	Y	N	Y	N	Y	N	Y	N	Y	N	Y	N
People/dog	12	0	1	0	0	0	12	0	2	0	0	0
Nonpower boat	35	2	8	5	1	7	32	1	5	1	1	6
Power boat	7	1	3	3	1	0	8	0	0	1	1	0

TABLE 5.—Backward selection of log-linear model using data in Table 4; model variables are 1 (response), 2 (distance), 3 (day of week), and 4 (disturbance type). An asterisk indicates a term that is significantly different from zero.

Model	G	df	P	Term deleted
[12] [13] [14] [234]	11.15	8	>0.10	
[12] [13] [234]	15.4	13	>0.25	[14]
[12] [14] [234]	12.18	9	>0.25	[13]
[13] [14] [234]	57.52	14	<0.01	[12] *
[12] [234]	16.91	14	>0.25	[14]
[14] [234]	58.98	11	<0.01	[12] *
[1] [234]	70.38	16	<0.01	[12] *
Final model = [12] [234]				

disturbances at ≤100 m more than at distances 101-200 m and 201-300 m, and were least reactive to disturbances at 201-300 m (Table 6).

TABLE 6.—Weights associated with the distance/seal response interaction term [12] of the log-linear model that fits the data in Table 5. Relative magnitude of weight indicates importance of the variable. Sign of the weight indicates direction of effect (+ is more, − is less).

Distance (m)	Seal response	
	Yes	No
0-100	[1]1.116	−1.116
101-200	−0 201	0.201
201-300	−0.915	[2]0.915

[1]Seals were most reactive to disturbance.
[2]Seals were least reactive to disturbance.

After actual disturbances (type I), the number of seals that eventually rehauled was always lower than the original number. On KI, the average time it took seals to rehaul regardless of season, was 28 ± 20.8 min (range 5-100, $n = 187$). In 96 instances, no seals rehauled, primarily due to tidal height. During rising tides, they rehauled only 16.2% of the time ($n = 37$ disturbances), at low slack tide, 55.6% of the time ($n = 124$), and on falling tides 61.5% of the time ($n = 26$; $\chi^2 = 13.82, P < 0.001$).

Disturbances were of short duration and seals rehauled after the disturbance source had left the area, except for disturbance from commercial bait harvesters, who remained in the vicinity for entire low tide cycles. Bait harvesters likely prevented seals from hauling out at all (zero-seal disturbance). During December, January, and February, we recorded the presence of the harvesters on 13 d. After being disturbed, seals did not return to the haul out site on eight of those days. They were disturbed briefly by the harvesters and then rehauled on 3 d, and there was no change in seal numbers on 2 d.

PWI apparently was not an important alternative site when KI was disturbed. A weak correlation between seal numbers at PWI after they were disturbed from KI existed during the winter ($r = -0.42, n = 7$) and summer ($r = -0.40, n = 152$), but not during the breeding season ($r = -0.14, n = 123$). In 45 of these instances, however, (winter 3, breeding 14, and summer 28), disturbances occurred simultaneously at KI and PWI, thereby precluding seal movement to PWI. During field observations, the movement from KI to PWI after disturbance was actually observed on 11 occasions.

DISCUSSION

The population of harbor seals at Bolinas Lagoon is much higher than previously recognized, and in contrast to seasonal peaks during the breeding season at other seal haul out sites (Fancher 1979; Johnson and Jeffries 1977[9]; Loughlin 1978; and Allen and Huber 1983[10]), the peak at Bolinas Lagoon occurred during summer after the pupping season. The peak at Bolinas may be caused in part by an influx of seals, possibly from San Francisco Bay, only 24 km south, or from Double Point, 10 km north, where numbers decline after the pupping season (Risebrough et al. 1978[11]; Allen and Huber 1983 footnote 9). The summer increase also coincides with a marked increase in fish abundance in Bolinas Lagoon and Bolinas Bay; fish abundance and species diversity are greater in the lagoon from May to September than from November to February (J. Gustafson[12]). Scheffer and Sperry (1931), Spalding (1964), and Pitcher (1977 footnote 5), suggested that harbor seals are opportunistic, preying primarily upon small schooling fish. In a study by Brown and Mate (1983), peak abundance of seals in Netarts Bay, Oreg., also occurred in the fall and coincided with the seasonal abundance of chum salmon. Movement to Bolinas Lagoon at a time of high food availability may be a consequence of the seal's opportunistic feeding strategy.

Time of day and tide were important factors that influenced daily haul out patterns of seals. The peak in numbers during early afternoon is consistent with studies on the Farallon Islands (Ainley et al. 1977[13]) and in San Francisco Bay (Fancher 1979). Though seals were seen hauled out on KI at night on 10 occasions, the sharp drop in numbers during late afternoon suggests that diurnal hauling out is preferred. The diurnal pattern may also

[9]Johnson, M. L., and S. J. Jeffries. 1977. Population evaluation of the harbor seal (*Phoca vitulina richardi*) in the waters of the State of Washington. U.S. Dep. Commer., N.T.I.S. PB-270 376, 27 p.

[10]Allen, S. G., and H. R. Huber. 1983. Pinniped assessment in the Point Reyes/Farallon Islands National Marine Sanctuary, 1982-83. Annual Report to U.S. Department of Commerce, Sanctuary Programs Office, 64 p.

[11]Risebrough, R. W., D. Alcorn, S. G. Allen, V. C. Alderlini, L. Booren, R. L. DeLong, L. E. Fancher, R. E. Jones, S. M. McGinnis, and T. T. Schmidt. 1978. Population biology of harbor seals in San Francisco Bay, California. U.S. Dep. Commer., N.T.I.S. PB81-107963, 67 p.

[12]J. Gustafson, Environmental Consultant, Resources and Ecology Projects, Mill Valley, CA 94941, pers. commun. August 1979.

[13]Ainley, D. G., H. R. Huber, R. P. Henderson, T. J. Lewis, and S. H. Morrell. 1977. Studies of marine mammals at the Farallon Islands, California, 1975-76. U.S. Dep. Commer., N.T.I.S. PB-266 249, 32 p.

be related to seal feeding habits as discussed by Antonelis and Fiscus (1980) and Spalding (1964) who noted that seals fed primarily in the late afternoon. The weak inverse correlation between tide level and seal numbers during the breeding season is likely related to the tendency of females with pups to haul out at irregular times to nurse.

These patterns were interrupted by disturbance from boats, pedestrians, dogs, and aircraft. People in nonpower boats were the greatest source for disturbance possibly because they are more mobile than people in power boats or on foot. Distance of disturbance, however, rather than type or season was the significant element at KI since at distances >100 m seals tended not to leave the hauling out site. The response of seals at distances >100 m may have been precipitated by the nature or unpredictability of the disturbance source. For example, a boat advancing directly toward the seals or lingering nearby caused flight more often than a boat moving by.

The source of current disturbances is a small but stable resident and tourist human population; however, a variety of changes in the seal's behavior may be expected if disturbance levels increase. Both Paulbitsky (1975) and Woodhouse[14] documented a change from diurnal to nocturnal hauling out patterns in seals at Strawberry Spit, Tiburon, and at Atascadero State Beach, Morro Bay, Calif., which was believed to be a response to an increase in the local human populations. The response of seals to the prolonged activities of commercial bait harvesters on Bolinas Lagoon is indicative of the potential disruption of seal haul out patterns.

Excessive disturbance may also lead to increased pup mortality. According to Kenyon (1972), 7 of 18 Hawaiian monk seals, *Monachus schaunislandi*, died before weaning on heavily disturbed pupping grounds on Midway Atoll, Hawaii. In contrast, for harbor seals at a relatively undisturbed pupping ground in British Columbia, Bigg (1969) estimated that pup mortality was only 12%. We do not know to what extent disturbance is affecting pup mortality rates at Bolinas Lagoon. In 1979, 3 of 12 pups were found dead; at least 1 of those 3 was killed by a dog.

Site abandonment is a third possible response to increased disturbance. Newby (1971) attributed harbor seal abandonment of a site in Puget Sound in part to increased disturbance from recreational boating. Kenyon (1972) postulated for the monk seal that site abandonment results in overall population losses because other traditional haul out sites probably cannot absorb the emigration. The same could apply to harbor seal populations in Marin County, if other sites are currently filled to capacity.

[14]C. Woodhouse, Santa Barbara Museum of Natural History, 2559 Puesta del Sol, Santa Barbara, CA 93105, pers. commun. May 1977.

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REPRODUCTION OF WEAKFISH, *CYNOSCION REGALIS*, IN THE NEW YORK BIGHT AND EVIDENCE FOR GEOGRAPHICALLY SPECIFIC LIFE HISTORY CHARACTERISTICS

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ABSTRACT

Reproduction characteristics for weakfish, *Cynoscion regalis*, in the New York Bight were examined. Spawning in 1980-81 occurred from May to early July with spawning time dependent on parental size. Maturity for both sexes occurred by age 1 but at a greater size in females. Annual fecundity estimates were compared with literature values for North Carolina weakfish and were found to be considerably lower at size, yet cumulative fecundities were nearly equivalent. The latitudinal variations in fecundity may be a behaviorally and environmentally induced phenomena, and influence the long-term population stability of weakfish.

Weakfish, *Cynoscion regalis*, are a member of the family Sciaenidae and are a common inshore species occurring between Cape Cod, Mass., and southern Florida. The species undergoes a spring migration from offshore waters of Virginia and the Carolinas to appropriate estuarine spawning areas, then a return migration in late fall to overwintering grounds (Nesbit 1954). The center of greatest abundance occurs within the Middle Atlantic Bight in quantities sufficient to support a recreational and commercial fishery. In 1979 commercial fishermen landed 13,000 metric tons (t) of weakfish and nearly 5,000 t were caught by recreational anglers (Wilk 1981). Abundance has, however, undergone some dramatic fluctuations over the last several decades. Commercial landings averaged 8,800 t from 1940 to 1949, then dropped to 2,915 t by 1950, and remained at these low levels until the mid-1970's (Wilk 1981). The exact cause of these variations remains a mystery, although speculations include overfishing, DDT-induced mortality, and environmentally induced recruitment failure (Massman 1963; Joseph 1972; Merriner 1976). To adequately assess the mechanisms controlling recruitment success or failure, we must first have a thorough understanding of the reproductive biology of weakfish.

Merriner (1976) has examined reproduction of weakfish in North Carolina, and Daiber (1957) mentioned spawning behavior of weakfish in Delaware Bay, but the reproductive biology of weakfish in their northern range has never been fully investigated. Furthermore, there is reason to believe that reproduction may vary throughout the geographic range. Leggett and Carscadden (1978) have shown latitudinal variations in reproduction and growth of American shad, *Alosa sapidissima*, and White and Chittenden (1977) have likewise shown geographic differences in another sciaenid, the Atlantic croaker, *Micropogonias undulatus*. Growth differences have already been established for weakfish between the New York Bight and North Carolina (Perlmutter et al. 1956; Shepherd and Grimes 1983), so there is reason to suspect possible reproductive differences. The purpose of the study was to investigate weakfish reproduction in the Middle Atlantic region, to determine if any geographic variations exist, and to consider possible reasons for geographically specific characteristics.

METHODS AND MATERIALS

Sample Collection

Samples (n = 1,208) were collected during the National Marine Fisheries Service (NMFS) groundfish survey from 1980 to 1983 at stratified random stations north of Chesapeake Bay (Fig. 1). Fish were collected with a #41 Yankee trawl in spring and a #30 Yankee trawl in summer and fall at depths between 5 and 200 m (Grosslein 1969). NMFS samples were supplemented by 461 fish collected between May 1980 and June 1981 from commercial pound nets in Gardiners Bay, N.Y., (n = 61) and Sandy Hook Bay, N.J., (n = 115) and

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from pair and otter trawl fisheries in Delaware Bay (n = 285).

At each NMFS station, weakfish catches were stratified into 10 cm size intervals and 10-15 fish sampled per interval. Total length to the nearest centimeter, sex, and maturity stage were recorded. Weakfish from Gardiners Bay were randomly sampled, total length measured to the nearest millimeter, sex, and maturity stage recorded, and gonads removed and weighed to the nearest 0.1 g. Sandy Hook and Delaware Bay samples were collected by random selection of 50-lb (22.5 kg) boxes in each market category available from the catch, and total length to the nearest millimeter and weight (whole and gutted) to the nearest gram recorded. Gonads and livers were also removed and weighed to the nearest 0.1 g. Gonads were preserved in modified Gilson's solution (Bagenal and Braum 1971) for several weeks, then removed, washed with distilled water and stored in 95% isopropyl alcohol.

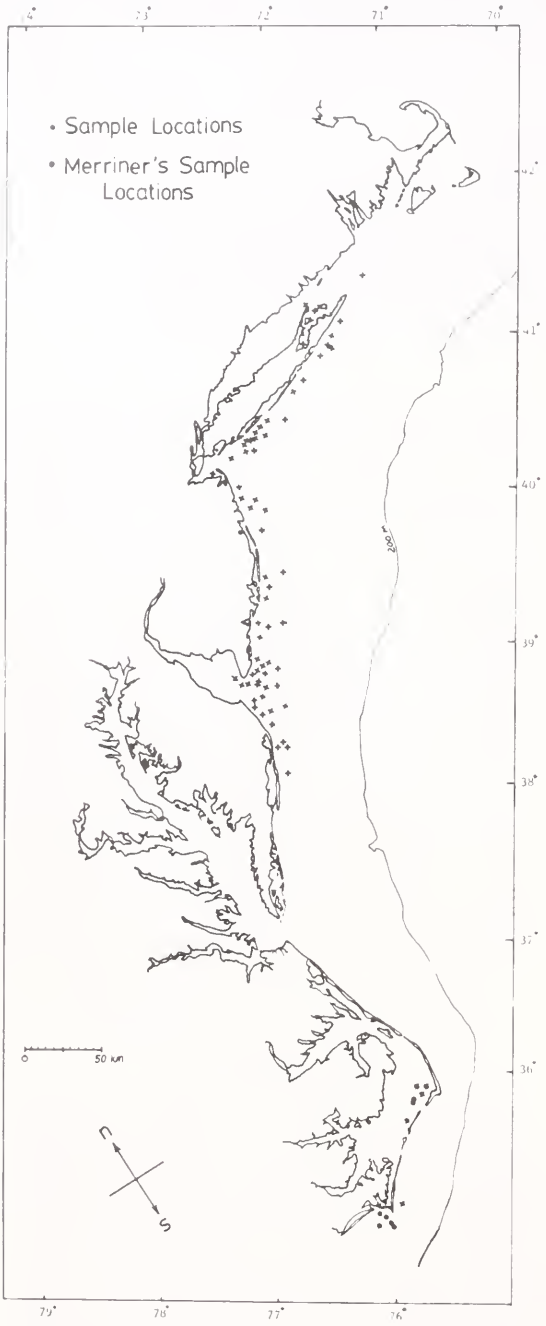

FIGURE 1.—Sampling locations for weakfish, *Cynoscion regalis*, in the New York Bight and North Carolina site of Merriner (1976).

Maturity and Fecundity Methods

The maturity stage of each sample was categorized as immature, developing, ripe (spawning), spent, or recovering as modified from Nikolsky (1963). The maturity stages were further subdivided as mature or immature for calculation of length at 50% maturity using probit analysis (Finney 1971).

Seasonality of reproduction was determined from changes in the gonad condition. A gonosomatic index (GSI) was calculated to show changes in gonad weight relative to somatic weight (gutted body weight). The index was computed as

$$\text{GSI} = (\text{gonad weight/somatic weight}) \times 100.$$

To examine physiological changes associated with spawning, liver condition was assessed using a hepatosomatic index (HSI) computed by substituting liver weight for gonad weight in the above relationship (Htun-Han 1978). The differences in monthly mean HSI between sexes were analyzed statistically using a Wilcoxon test (Patzner and Adam 1981).

The number of spawnings in the season were investigated by analyzing the seasonal frequency distribution of oocyte diameters (Hickling and Rutenberg 1936). In each of 15 samples collected between 5 May and 22 July 1980-81 in Delaware and Gardiners Bays, three subsamples were taken per ovary and about 500 oocyte diameters were randomly measured using an ocular micrometer.

Fecundity estimates were determined from 28 fish macroscopically classified as developing,

which were captured during May 1981 in Delaware and Gardiners Bays. An oocyte diameter of 0.20 mm was determined from diameter frequency distributions and the degree of yolk accumulation as the size between oogonia and developing ova, and was used as the lower size limit of ova in the fecundity estimates. Each sample was diluted with distilled water, stirred, then several aliquots removed from the solution to provide a density of about 10,000 ova in a 6 × 6 cm gridded petri dish. About 800-1,000 ova were counted from six randomly selected squares, then adjusted for a total subsample count. Two subsamples were counted per sample and three if the ova sample was from a large fish (>60 cm). The sample and subsample were oven dried at 40°C for a minimum of 24 h then weighed to the nearest 0.001 g on a Mettler[3] balance. Total fecundity was calculated as

Total fecundity = [number in subsample × (sample wt/subsample wt)] + number in subsample.

Predictive equations of fecundity from length and weight were fit to a geometric mean (GM) functional regression (Ricker 1975) following log-log transformation.

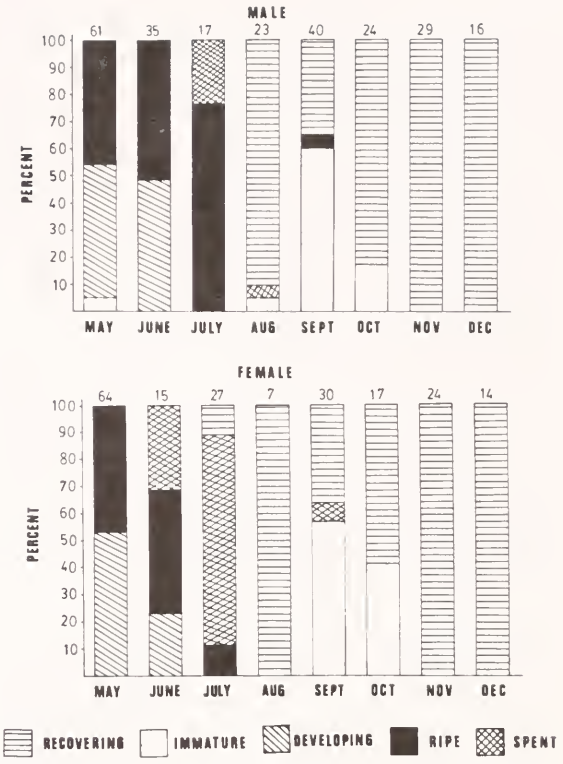

FIGURE 2.—Changes in visual maturity stage of weakfish, *Cynoscion regalis*, in 1980-81 for the New York Bight. *N* indicated for each month.

RESULTS

Seasonality

The changes in maturity stages during the year indicate spawning takes place from May to mid-July for weakfish in Delaware Bay and north to Long Island (Fig. 2). In May, all 122 mature fish examined of both sexes were in the developing or ripe stage of gonad development. The 50 fish that were inspected in June included 100% of the males and 70% of the females in a developing or ripe stage. Several of the ovaries examined in a June sample from Gardiners Bay had the appearance of being partially spent. The ovary was flaccid, slightly hemorrhaged and the lumen filled with fluid, but a few transparent ova were still visible. Spawning weakfish in Delaware Bay were captured as late as 12 July, when 11% of the females and 76% of the males were classified as ripe. In the same month, 84% of the females were in spent condition. By August, all of the fish examined at all locations were in postspawning condition. Weakfish from Sandy Hook Bay were not available until June and all the samples examined from this area were in postspawning condition, either spent or recovering.

This seasonality of spawning at each of the sample locations was suggested by seasonal changes in the GSI. Mean GSI values (percent gonad weight relative to somatic weight) ± 95% C.I. (Confidence Interval) of all females rose from 5.75 ± 1.29 in May to a peak value of 6.04 ± 1.43 in June, then declined to 1.76 ± 0.40 by July (Fig. 3). Male GSI were at a yearly high of 4.88 ± 1.45 in May but declined to only 2.51 ± 0.85 by July. The mean GSI values for females were consistently higher in all months except July. Gonad size reached the lowest levels for both sexes in August with mean GSI values of 0.71 ± 0.07 and 0.19 ± 0.02 for females and males, respectively. The GSI values remained low until the last samples were collected in November.

Specific spawning time, as reflected in GSI, was dependent on the size of the individual fish (Fig. 4).

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

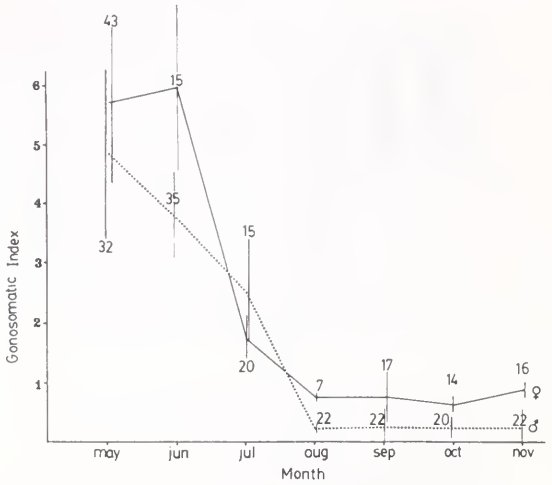

FIGURE 3.—Mean monthly gonosomatic indices ±95% C.I. of weakfish, *Cynoscion regalis*, for 1980 in the New York Bight. *N* values at each point.

Mean index values and lengths ±95% C.I. for developing fish in Delaware and Gardiners Bays during May was 2.48 ± 0.67 at a mean length of 551 ± 47.0 mm for females and 1.13 ± 0.85 at a length of 391 ± 98.9 mm for males. Spawning fish captured during May had GSI of 8.65 ± 1.64 at mean length of 702 ± 25.2 mm for females and 6.49 ± 1.58 at mean length of 619 ± 33.1 mm for males. In June, spawning fish had mean GSI values of 6.72 ± 1.83 with mean length of 544 ± 95.6 mm for females and 4.54 ± 1.04 with mean length of 570 ± 56.3 mm for males. These index variations confirmed observations of earlier spawning by large fish.

Seasonal variation in mean HSI of Delaware and Sandy Hook Bay samples indicates that changes in liver weight occurred at the time of spawning and prior to fall migration (Fig. 5). Mean HSI values ±95% C.I. for females decreased from a high in May of 2.80 ± 0.35 to a low in September of 0.87 ± 0.30. The index values for males followed the same pattern declining from 1.89 ± 0.27 in May to 0.96 ± 0.18 in September, but the maximum values occurred in November with a mean HSI of 2.57 ± 0.29. The indices were tested for differences between sexes and the differences were found to be significant in May and June ($P < 0.001$) with the values for females being greater (Table 1). No significant differences were found in a comparison of the July through November samples.

Frequency distributions of oocyte diameters from 15 fish, ranging from 55 to 81 cm and collected between 6 May and 22 July show one seasonally progressing mode of developing ova (Fig. 6). The position of the mode varied according to the development stage of the individual ovary. A sample from 5 May had a mode between 0.02 and 0.45 mm and was skewed toward a prominent peak at 0.12 mm. In the 13 May sample, a second mode appeared around 0.35 mm and this mode increased to a size of 0.63 mm in the 20 June sample. The 22 July sample contained only oogonia. Maximum ova diameter observed was 0.95 mm from a sample on 26 May. That ovum was filled with fluid between the yolk and chorion, indicative of an ova immediately prior to release (Bagenal 1967). This corresponds to the size of weakfish eggs, 0.870-0.975 mm, which have been identified in the water column (Harmic 1958).

TABLE 1.—Wilcoxon (Mann-Whitney) test comparing hepatosomatic indices between sexes of weakfish, *Cynoscion regalis*, from the New York Bight for June through November 1980 and May 1981. S = Wilcoxon test statistic, Z = critical value.

	S	*N*	Z	Probability level
1980				
June	622.0	50	5.081	0.0001***
July	194.0	34	−1.767	0.0865
August	106.0	28	0.265	0.7928
September	274.0	37	−0.904	0.3658
October	252.0	35	0.017	0.9867
November	283.5	40	−1.215	0.2318
1981				
May	332.0	48	−3.782	0.004***

*** = highly significant differences.

Maturity, Sex Ratio, and Fecundity

Length ±95% C.I. at which 50% of the total sampled population reached maturity was similar for both sexes. Females attained 50% maturity at 25.6 ± 1.2 cm, while males were slightly lower at 25.1 ± 1.1 cm (Table 2). The corresponding age at maturity for both sexes was 1 yr. The smallest mature male and female was 20 cm. The maximum size of immature weakfish was 40 cm for females and 33 cm for males.

The overall population sex ratio approached equality (Table 3). The sex ratio of the population, divided into 5 cm length intervals, was 48:52 females to males and was not significantly different from 50:50 as determined from a chi-square analysis ($\chi^2 = 1.81$, $\chi^2_{0.05} = 3.84$, $n = 1{,}669$). Sex ratio at size data did reveal significant differences from 50:50 for several length intervals. At 40 cm, the ratio was 52:48 female to male but increased to

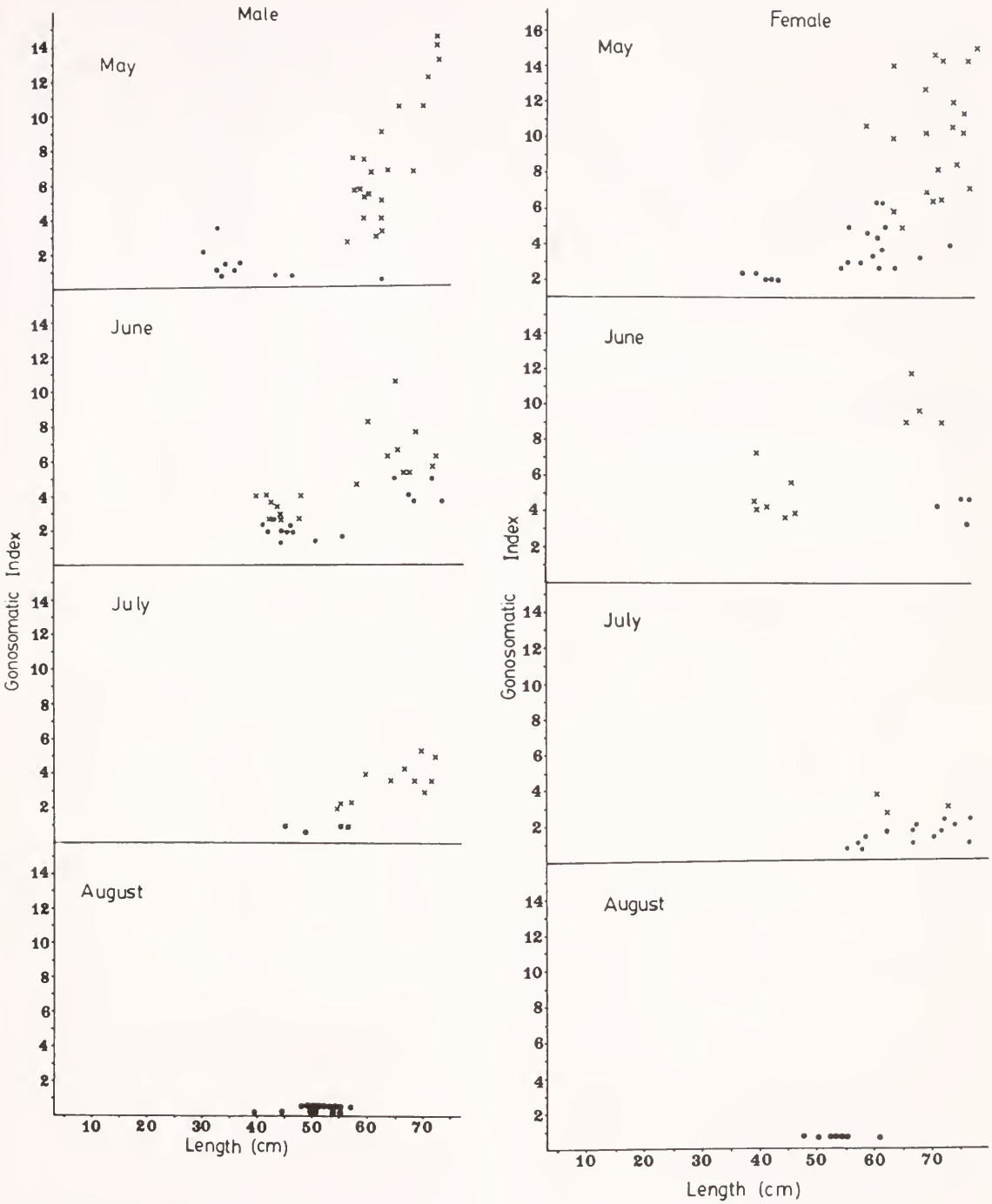

FIGURE 4.—Monthly gonosomatic indices of individual weakfish, *Cynoscion regalis*, by sex for 1980. Spawning fish indicated by ×.

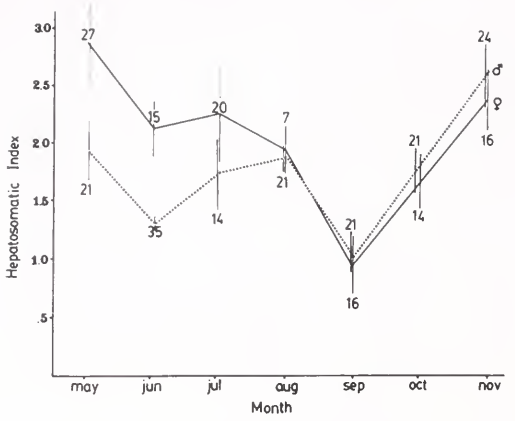

FIGURE 5.—Mean monthly hepatosomatic indices ±95% C.I. of weakfish, *Cynoscion regalis*, for 1980 with *N* indicated at each point.

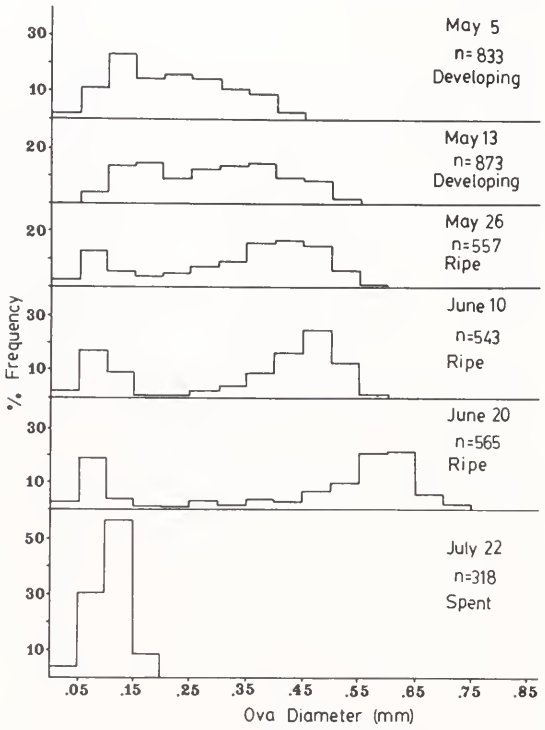

FIGURE 6.—Monthly frequency of oocyte diameters for weakfish, *Cynoscion regalis*, in the New York Bight for 1980-81.

60.5% ($\chi^2 = 5.25$, $\chi^2_{0.05} = 3.84$, $n = 119$) and 63.8% ($\chi^2 = 7.19$, $\chi^2_{0.01} = 6.64$, $n = 94$) males at 45 and 55 cm, respectively. The sex ratio of combined length intervals above 55 cm had a ratio of 58.5:41.5 which was significantly dominated by females ($\chi^2 = 7.45$, $\chi^2_{0.01} = 6.64$, $n = 260$).

Regression models indicated that length and weight were equally predictive of fecundity. The relationships between total length or gutted weight, and fecundity were best described by a power curve. The GM functional regression (Ricker 1975) of the $\log_e$ transformed data ± standard error of the regression were

TABLE 2.—Length at maturity for weakfish, *Cynoscion regalis*, from 1980 to 1983.

Length (cm)	Female		Male	
	N	% mature	*N*	% mature
18	15	0.0	16	0.0
19	7	0.0	11	0.0
20	8	12.5	11	9.1
21	11	18.2	5	40.0
22	8	37.5	9	33.3
23	13	53.8	16	31.3
24	11	45.5	12	50.0
25	13	46.2	12	75.0
26	14	71.4	15	86.7
27	17	88.2	14	71.4
28	10	80.0	20	65.0
29	17	82.4	22	63.6
30	19	100.0	17	82.4
31	18	88.9	14	85.7
32	16	93.8	20	85.0
33	10	90.0	17	94.1
34	14	85.7	15	100.0
35	7	85.7	3	100.0
36	10	80.0	8	100.0
37	9	77.8	12	100.0
38	15	100.0		
39	14	85.7		
40	13	92.3		
41	4	100.0		
42	10	100.0		
43	10	100.0		
Total	313		269	
Size at 50% mature	25.6		25.1	
95% Confidence Interval	24.4-26.8		24.0-26.2	

TABLE 3.—Sex ratios (female:male) of weakfish, *Cynoscion regalis*, in the New York Bight.

Length[1]	Ratio	χ^2
15	27:40	2.52
20	72:73	0.01
25	149:174	1.93
30	148:157	0.27
35	72:73	0.01
40	71:65	0.26
45	42:72	5.25*
50	35:40	0.33
55	34:60	7.19**
60	36:35	0.01
65	35:27	2.00
70	31:28	0.15
75	28:17	2.69
80	18:1	15.21***
85	4:0	4.0*
Total	807:862	1.81

[1]Midpoint of length interval (12.5 to 17.5, etc.).
* = significant difference $P < 0.05$.
** = significant difference $P < 0.01$.
*** = significant difference $P < 0.001$.

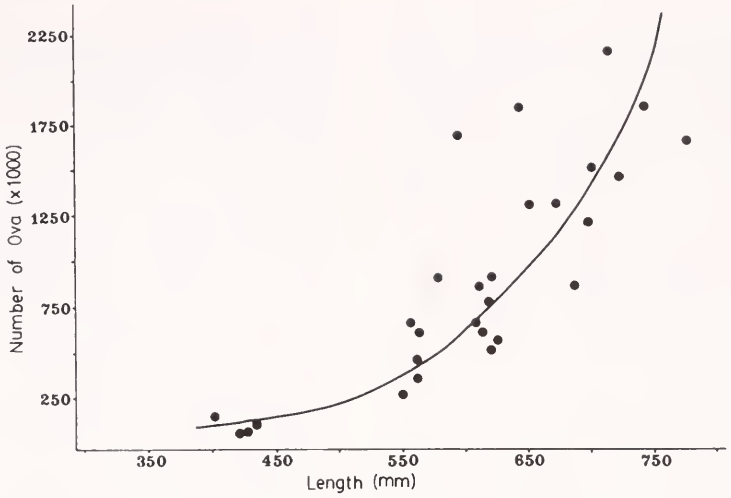

FIGURE 7.—Fecundity as a function of length for weakfish, *Cynoscion regalis*, in New York Bight for 1981.

$$\ln \text{fecundity} = -16.322 + 4.659 \ln \text{total length (mm)} \pm 0.368$$
$$r^2 = 0.835 \quad n = 28 \quad \text{Figure 7}$$
$$\ln \text{fecundity} = 1.975 + 1.542 \ln \text{gutted weight (g)} \pm 0.364$$
$$r^2 = 0.839 \quad n = 28.$$

Fecundities were also estimated for six weakfish collected in June from Gardiners Bay which appeared to be spent, although they had ova remaining in the gonad. These ova were 0.55 to 0.65 mm which were similar in size to those present in a ripe ovary. All six samples were significantly different ($P < 0.001$) than expected values based on a Students t-test (Table 4). These June samples were 60-75% lower than the predicted fecundities at length.

TABLE 4.—Difference between expected fecundity (based on ln fec = −16.322 + 4.659 ln TL) and observed fecundity for 6 weakfish, *Cynoscion regalis*, collected 27 June 1981, in Gardiners Bay, N.Y.

Total length (mm)	Fecundity estimate		% Difference
	Expected	Observed	
590	650,171	196,891	69.7
613	777,718	93,579	88.0
615	789,675	105,919	86.6
704	1,487,262	438,909	70.5
737	1,843,210	650,600	64.7
644	979,893	313,054	68.1
			$\bar{x}$ = 74.6

DISCUSSION

Weakfish spawning in northern estuaries is a seasonal event which occurs following the spring inshore migration. (Welsh and Breder 1923; Hildebrand and Schroeder 1928). Our study found the spawning period for weakfish in Delaware Bay and Gardiners Bay, as determined from maturity stages, to be from May to mid-July. Ichthyoplankton surveys have found weakfish eggs and larvae present in New York Bight from May to July (Colton et al. 1979). The spawning period was further substantiated by changes in GSI. The mean GSI values reached a maximum in May for males and in June for females, then both declined to minimum values by August. The gonad weights were maintained at this low level until the fish disappeared from the coast in late November. The spawning period of weakfish in North Carolina is somewhat longer, extending from March to September with the peak period from April to June (Merriner 1976). The duration of the ripe maturity stage in Delaware and Gardiners Bays was greater for males, with ripe males captured as late as 22 July. The protracted spawning season of males was also evident in the GSI values. July was the only month in which male indices were greater than those of females, indicating that the gonad weight per unit body weight was larger in males. In other months, female GSI values were as much as 2.8% greater than males.

Sex differences were also evident in physiological changes associated with spawning. HSI values were near maximum in May, during spawning season, and as expected higher in females. Devel-

opment of ovaries demands higher energetic costs than testicular development (Nikolsky 1963); therefore, the necessary energy reserves in the liver would be proportionately larger in females (Timashova 1982). After spawning, the sexual dimorphism disappears and HSI values for both sexes increase similarly prior to the fall migration.

The peak spawning period in the New York Bight estuaries varied with different size weakfish. Generally, among migratory fishes, the larger individuals will return to an estuary prior to their smaller counterparts (Briggs 1955; Nikolsky 1963). Weakfish exhibit a similar behavior, as the largest individuals or "tiderunners" enter the bays in early May and spawn by mid-May, whereas the smaller weakfish arrive later and reach peak spawning during June. The GSI values for fish >60 cm generally decline from May to June, while smaller fish increase to maximum values in June. This differential spawning based on parental size results in two spawning peaks and the subsequent appearance of bimodal length-frequency data for juvenile weakfish (Daiber 1954; Thomas 1971; Shepherd and Grimes 1983).

Sex Ratio, Maturity, and Fecundity

The overall sex ratio of the population is not different from 1:1, but one sex was dominant at certain length intervals. We believe the deviations from a 1:1 ratio at various lengths were attributable to differential growth between sexes (Wenner 1972). Female growth begins to exceed male growth at about 45-55 cm (Shepherd and Grimes 1983), at which point the sex ratio becomes dominated by males. Females grew beyond that size interval faster and occupied the majority of the 60-85 cm length intervals. Although males have growth potential equal to females, the numbers attaining maximum size were greater for females.

In northern waters, the size at which weakfish attained 50% population maturity was similar for both sexes. Females matured by 25.6 cm at age 1 while males attained maturity at 25.1 cm, also at age 1. Apparently, greater differences exist between northern weakfish (Delaware Bay and north) and southern weakfish (North Carolina). Although ages were similar, southern females spawned at 23 cm and males by 18 cm (Merriner 1973).

Estimates of fecundity for New York Bight weakfish differ from estimates for southern weakfish. Weakfish in North Carolina did not reach sizes much beyond 45 cm but had fecundities, relative to length, several times higher than northern weakfish (Merriner 1976) (Table 5). For example, at 50 cm TL female weakfish from New York Bight produced 306,159 ova, while the fecundity of southern fish of the same size was 2,051,080 ova. In spite of these large differences, lifetime fecundity would be approximately equal. Southern weakfish can potentially reproduce until age 5 and produce about 9,913,080 ova (based on the equation, fecundity = $0.152\ TL^{2.6418}$, from Merriner 1976), whereas northern weakfish reproducing for 10 yr have nearly equivalent total ova production of 10,008,167.

Batch spawning, involving two distinct groups of ova, was found for weakfish in North Carolina (Merriner 1976). In samples examined in 1980-81 from Delaware and Gardiners Bays, multiple spawns were not evident. The ova diameter frequencies of developing and ripe ovaries contained two modes, one consisting of reserve oocytes and another of developing ova. The developing ova had a wide size range (≈0.3 mm) and may have been released during consecutive spawning events, but did not constitute separate batches within an ovary. Furthermore, all ova produced annually by weakfish may not be released during spawning. A study of Delaware Bay weakfish in 1954 proposed batch spawning, but spent ovaries were not examined to determine if all ova were released (Daiber 1954). Ovaries classified as spent which we examined still contained 25-40% of the ova expected for a fish of that size. These results suggest fertility may be 60-75% of estimated potential fecundity. Foucher and Beamish (1980) reported similar conclusions from studies of Pacific hake, *Merluccius productus*. We did not examine

TABLE 5.—Comparison of fecundity for weakfish, *Cynoscion regalis*, between Cape Hatteras (Merriner 1976) and New York Bight.

	Fecundity comparisons			
	Cape Hatteras		New York Bight	
Age	SL	Fecundity	TL	Fecundity
0	159	149,429		
1	225	391,688	203	4,593
2	286	762,258	323	39,978
3	357	1,410,550	479	250,685
4	421	2,229,220	578	601,544
5	562	4,969,940	638	953,027
6			677	1,256,487
7			701	1,477,902
8			728	1,762,445
9			758	2,127,278
10			763	2,193,448
Cumulative fecundity		9,913,085		10,667,387

enough spent weakfish ovaries to determine if this phenomenon was consistent from year to year.

The variable reproductive and age and growth characteristics for weakfish in different geographic areas suggest specific physiological responses to different environmental conditions. North Carolina weakfish had smaller sizes at maturity, smaller length at corresponding age after age 1, reduced longevity and maximum size, and higher relative fecundity than New York Bight weakfish. However, the lifetime reproductive potential was nearly equal for both groups. These life history characteristics for weakfish are similar to clinal variations between Labrador and Florida described for American shad (Leggett and Carscadden 1978), differences in reproductive characteristics between Atlantic herring, *Clupea harengus harengus*, in the Norway and the Baltic Sea (Schopka 1971), and north to south variations in North American populations of Pacific herring, *Clupea harengus pallasi* (Paulson and Smith 1977).

The different reproductive strategies in weakfish may result from varying environmental demands. When weakfish spawning occurs in northern estuaries, water temperatures are unpredictable and subject to sudden drops which are potentially lethal to eggs and larvae (Harmic 1958). Table 6 shows minimum estuarine temperatures during the spawning season in northern waters may drop below the temperature limits of 12°-16°C necessary for successful hatching (Harmic 1958). The higher probability of prereproductive mortality of progeny in northern estuaries results in a "bet-hedging" strategy in which fewer eggs are produced each year, but the possible number of annual spawnings are increased (Stearns 1976; Giesel 1976), thus maximizing potential contributions to the gene pool throughout a fish's lifespan. In contrast, southern weakfish spawn in a more predictable estuarine environment (Table 4) and, consequently, there is less chance of environmentally induced prereproductive mortality. However, southern fish are faced with greater postreproductive mortality (longevity observed by Merriner (1973) was 5 yr). Greatest reproductive success in this situation requires maximizing annual gamete production in the few years possible. In addition, weakfish migrating to northern estuaries (Nesbit 1954) may utilize energy reserves otherwise available for gonad growth, whereas southern fish having less distance to travel may reallocate energy towards reproduction.

TABLE 6.—Surface water temperatures (°C) for April-July in Plum Island, N.Y.; Cape May, N.J.; Gloucester Point, Va; and Beaufort, N.C.[1]

	April	May	June	July
Plum Island, N.Y.				
$\bar{x}$	5.6	9.7	14.6	18.8
Max	9.0	18.0	20.0	24.0
Min	2.0	4.0	9.0	15.0
$\bar{x}$max	7.7	13.4	17.7	21.4
$\bar{x}$min	3.3	6.4	11.4	16.3
Cape May, N.J.				
$\bar{x}$	10.2	14.5	20.0	22.6
Max	17.0	21.0	25.0	28.0
Min	6.0	9.0	12.0	18.0
$\bar{x}$max	14.6	18.9	23.8	25.6
$\bar{x}$min	7.0	10.8	15.7	19.9
Gloucester Point, Va.				
$\bar{x}$	13.1	19.1	23.8	26.5
Max	21.0	26.0	30.0	32.0
Min	7.0	13.0	17.0	21.0
$\bar{x}$max	17.1	22.4	27.0	29.0
$\bar{x}$min	9 6	15 6	20.4	24.1
Beaufort, N C.				
$\bar{x}$	17.2	21.4	25 2	27.4
Max	21.0	26.0	32.0	30.0
Min	14.0	14 0	18.0	24.0
$\bar{x}$max	20.3	24.2	28.3	29.2
$\bar{x}$min	14.3	17.5	21.9	25.8

[1]National Ocean Survey. 1972. Surface water temperature and density; Atlantic coast, North and South America. 4th ed. NOS Publ. 31-1, p. 1-109.

Consequences of the area specific reproductive characteristics may be a reduced population stability for weakfish in the northern end of the range. Apparently, northern fish have a strategy to cope with potentially higher egg and larval mortality by spreading reproduction over more years and reducing annual fecundity, i.e., a "bet-hedging" strategy (Stearns 1976). Therefore, to fulfill their reproductive potential they must avoid premature adult mortality. If adult mortality (natural and fishing) in weakfish becomes excessive, the larger, most fecund individuals will be lost or reduced, thus shifting the burden of spawning to the smaller, less fecund fish. When the value of b in the fecundity equation $F = a\mathrm{TL}^b$ is >3, as in New York Bight weakfish, then truncation of the size/age structure in a spawning population will also result in a reduction of population fecundity (Hempel 1979). Concurrent high adult mortality and high prereproductive mortality could contribute to a decline in population abundance. The large fluctuations which have occurred in weakfish populations over the last several decades (Wilk 1979) may be due in part to these circumstances (i.e., high adult and prereproductive mortality). Although the correlation between population fecundities and recruitment is not usually strong for marine fishes (Cushing 1977), a decrease in population fecundity may eventually

reduce any buffer that weakfish have of withstanding natural fluctuations in egg, larval, and juvenile survival. Therefore, if management practices are to effectively regulate the weakfish resources, geographic variations in reproductive potential should be considered.

ACKNOWLEDGMENTS

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FIELD AND LABORATORY OBSERVATIONS ON DIURNAL SWIM BLADDER INFLATION-DEFLATION IN LARVAE OF GULF MENHADEN, *BREVOORTIA PATRONUS*

D. E. Hoss[1] and G. Phonlor[2]

ABSTRACT

Diurnal swim bladder inflation-deflation in gulf menhaden larvae was studied at sea and in the laboratory. At sea, the larvae filled their swim bladders at night and deflated them during the day. Laboratory experiments in which the larvae were either prevented or allowed to reach the air-water interface demonstrated that the larvae fill their swim bladder each night by swallowing air. These results agree with the findings of other investigators and suggest that diurnal swim bladder inflation may be a common characteristic in the late stage larvae of clupeoid species.

The swim bladder in fishes has been assigned various functions, the most widespread being the regulation of buoyancy. Recent work on clupeoid species, however, has shown that the function of the swim bladder changes with ontogeny. In adults of at least two clupeoids—Atlantic herring, *Clupea harengus*, and Atlantic menhaden, *Brevoortia tyrannus*—the swim bladder is thought to serve as a reserve of gas for the adjustment of hydrostatic pressure in the gas-filled bulla, allowing the bulla membrane to maintain acoustic sensitivity independently of depth. The swim bladder's role as a buoyancy regulating organ is secondary (Blaxter and Hunter 1982). During the late larval stages of some clupeoids, however, buoyancy provided by an inflated swim bladder may have an important function. Hunter and Sanchez (1976), working with the pelagic larvae of the northern anchovy, *Engraulis mordax*, proposed that an observed diurnal inflation and deflation of the swim bladder by larvae is an energy-sparing mechanism. In this case, one function of the inflated swim bladder is to provide buoyancy that allows the larvae to "rest" during the night when they are unable to see to feed. This diurnal inflation and deflation of the swim bladder has also been reported for other larval clupeoids by Uotani (1973).

The objective of this study was to determine if a diurnal swim bladder inflation-deflation rhythm exists in larval gulf menhaden, *Brevoortia patronus*, under natural conditions and, if so, to evaluate the mechanism of inflation in the laboratory.

The swim bladder in gulf menhaden is similar to that described for Atlantic menhaden by Hoss and Blaxter (1981). In the Atlantic species the anlage of the swim bladder is present at 10 mm standard length (SL), and the pro-otic bullae first appear at 12.5 mm and may contain gas soon after. The swim bladder first contains bubbles of gas in 13 mm SL larvae, and the lateral line first appears in larvae of about 17 mm. In the fully developed system, narrow ducts connect the swim bladder to the gas-filled bullae which are close to the labyrinth of the inner ear. The bullae-swim bladder system is in turn connected to the extensive lateral line on the head of adult fish through a membrane in the skull. As in other clupeoid species (Blaxter and Hunter 1982), menhaden apparently swallow air to initially fill both the bullae and the swim bladder. As there is no evidence for gas secretion in menhaden, it is also assumed that they replace lost gas by regularly swallowing air into the alimentary canal and then by transferring it to the swim bladder through the pneumatic duct. The swim bladder is deflated by diffusion and by reversing gas movement in the above pathway. Unlike some clupeoids, menhaden have no direct connection between the swim bladder and the anal opening (Tracy 1920).

METHODS

At Sea

Gulf menhaden larvae were obtained in the northern Gulf of Mexico off Southwest Pass, La.,

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at the mouth of the Mississippi River in December 1981 (RV *Oregon II* cruise 123) and December 1982 (RV *Oregon II* cruise 131). On cruise 123, larvae were collected by oblique or surface tows of either a multiple-opening closing net and environmental sensing system (MOCNESS) (Wiebe et al. 1976), a neuston net, or an opening-closing paired BFN-1 net[3]. The sampling scheme was modified on cruise 131 in that only the MOCNESS system was used and duplicate samples were taken at fixed depths (1, 8, and 20 m) during a 24-h period of time. On board the ship, menhaden larvae were removed from the samples, measured to the nearest 0.1 mm SL, and examined for the presence of gas in the swim bladder. Gas in the swim bladder was easily observed before pigmentation of larvae (Fig. 1). In inflated bladders, a light-refractive bubble is obvious while a deflated bladder appears under the microscope as a flattened sac (Doroshev et al. 1981). Maximum width and length of the swim bladder (with or without gas) was measured to the nearest 0.02 mm, and volume was calculated by the equation for a prolate spheroid, $V = 4/3\ \pi ab^2$, where a is half the maximum bladder length and b is half the maximum bladder width (Hunter and Sanchez 1976). Approximate changes in volume of the swim bladder due to increased pressure at increased depth of capture were calculated from Boyle's law $\frac{P_1}{P_2} = \frac{V_2}{V_1}$ where P is pressure and V is volume, and temperature is assumed to be constant. After being measured, larvae were preserved in 5% Formalin[4].

In the Laboratory

Experiments to determine if larvae filled the swim bladder by gulping in air at the water surface utilized larvae hatched from eggs in the laboratory (Hettler 1983). Larvae were reared on the rotifer *Brachionus plicatilis*, also cultured in the laboratory. As larvae grew older, their diet was supplemented with newly hatched *Artemia* nauplii. Before being used, larvae were held in 80 l tanks at a water temperature of 20°C, salinity of ca. 25‰, and a 12 h light-12 h dark photoperiod without a dawn or dusk transition.

Three hours before the start of the experiment, 15-20 larvae were transferred from the rearing tanks to each of eight 10 l tanks, and 10 larvae were measured and observed for the presence of gas in the swim bladder. A 500 μm screen was then placed below the water surface (Fig. 2) in four of the experimental tanks to prevent access of the larvae to the air-water interface. In the other four tanks, larvae had access to the air-water interface. During the experiment, the 12-h-light photoperiod was continued. Larvae sampled at ca. 1800, 2100, 0630, 0900, and 1230 h were measured and observed for gas in the swim bladder.

[3]Tarez and Co., 8460 S.W. Street, Miami, FL 33143.

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

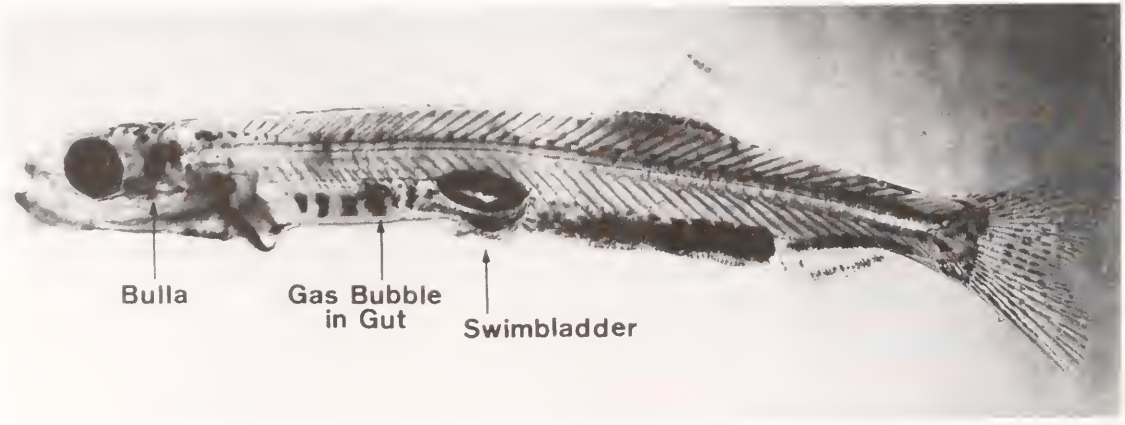

FIGURE 1.—Larval gulf menhaden, *Brevoortia patronus*. Inflated swim bladder, gas-filled bullae, and gas bubble in foregut are indicated by arrows.

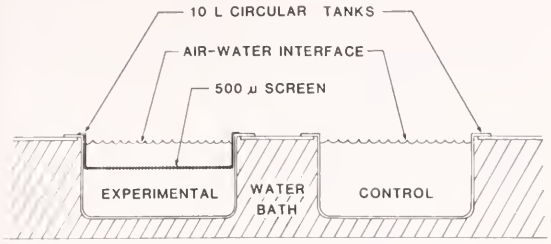

FIGURE 2.—Cross section view of tanks used in laboratory experiments to determine if larvae of gulf menhaden, *Brevoortia patronus*, fill the swim bladder at the water surface.

RESULTS

At Sea

The percentage of larvae having gas in the swim bladder was much greater at night than during the day (Fig. 3). The number of larvae with gas increased within an hour of sunset and decreased within an hour of sunrise (i.e., within the twilight periods). Although sample size was sometimes small (8-10 fish), the combined data for the two cruises were consistent.

The volume of gas in the swim bladder of larvae captured at night was greater than the volume of gas in larvae captured during the day (Table 1). There was a significant difference between the day and night volumes, where sample size was sufficient to allow testing. Sunrise and sunset samples were not significantly different (t-test, $P > 0.05$) from daylight samples.

Gulf menhaden larvae showed a diurnal pattern of depth distribution that seemed to contrast the pattern of swim bladder inflation (Table 2). Night sampling (1700-0600) indicated that larvae were present from the surface down to at least 20 m, the deepest samples taken. Maximum water depth at

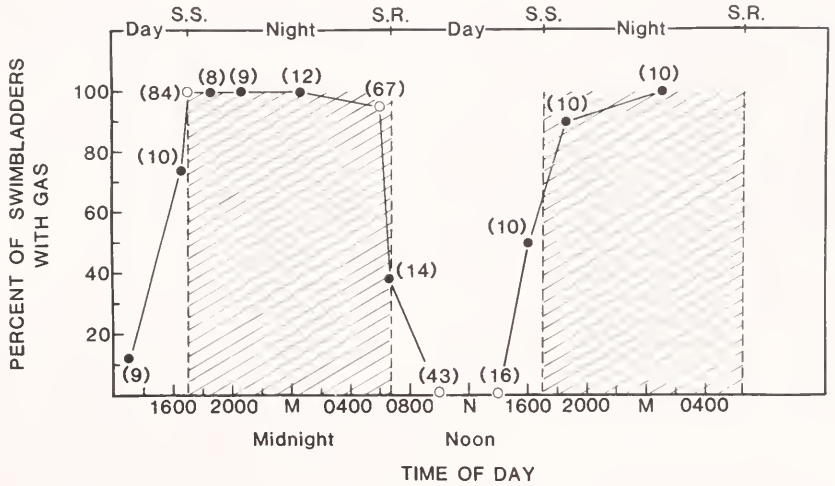

FIGURE 3.—Diurnal change in percent of gulf menhaden, *Brevoortia patronus*, larvae with gas in their swim bladders (S.S. = sunset, S.R. = sunrise). Numbers of fish examined are in parentheses. Data from two cruises (Dec. 1981, open circles; Dec. 1982, closed circles) are combined and presented in chronological order.

TABLE 1.—Swim bladder volume of gulf menhaden, *Brevoortia patronus*, larvae measured immediately after capture. Samples are from oblique and surface net tows.

Length class (mm)	Night samples N	Night samples Swim bladder vol. (mm^3) (mean ± 2 SE)[1]	Day samples N	Day samples Swim bladder vol. (mean ± 2 SE)[1]	t	df	P
<14.9	7	0.44 ± 0.19	1	0.03	—	—	—
15-16.9	13	0.89 ± 0.21	9	0.05 ± 0.02	7.97	20	<0.001
17-18.9	18	1.71 ± 0.52	12	0.17 ± 0.10	5.81	28	<0.001
>19.0	11	1.78 ± 0.75	8	0.32 ± 0.19	3.77	17	<0.01

[1]SE = standard error of the mean.

TABLE 2.—Swim bladder volume of gulf menhaden, *Brevoortia patronus*, larvae captured in MOCNESS tows and measured immediately after capture. Volumes were corrected for expansion of the swim bladder due to the change in pressure (0.1 atm/m of water).

Water depth (m)	Night samples N	Night samples Swim bladder vol. (mm^3) (mean ± 2 SE)[1] At surface	Night samples Corrected for pressure change	Night samples % with gas	Day samples N	Day samples Swim bladder vol. (mm^3) (mean ± 2 SE)[1] At surface	Day samples Corrected for pressure change	Day samples % gas
1	55	0.422 ± 0.148	NA	97	54	0.033 ± 0.013	NA	0
8	75	0.593 ± 0.136	0.329 ± 0.075	99	3	([2]) —	—	0
20	21	0.336 ± 0.123	0.126 ± 0.044	97	0	— —	—	—

[1]SE = standard error of the mean.
[2]Swimbladder volume of the three fish captured was not measured.

this station varied between 23 and 27 m. During the day nearly all the larvae were taken at the surface and only three larvae were captured as deep as 8 m. Without exception, fish examined from daylight samples did not have gas in the swim bladder, while almost all of the fish from the night samples contained some gas. In some cases, the volume of the swim bladder was such that it constricted the gut (Hunter and Sanchez 1976) or burst through the body wall.

The volume of gas in the larval swim bladder would, of course, be reduced due to increased pressure as the larvae moved deeper in the water. As the volume of the swim bladder decreased, its capacity as a buoyancy organ would decrease, causing the larvae to expend more energy in swimming or to sink more rapidly. Since our measurements were all made at the surface, we corrected the volumes of the swim bladders in larvae collected at 8 and 20 m to reflect the increased pressure at these depths (Table 2). Since swim bladder volume is related to size of the fish, a *t*-test was used to compare the mean standard length of the larvae from each depth. This test showed no significant difference in lengths of fish captured at the three depths (*t*-test, $P > 0.05$).

In the Laboratory

Swim bladder volume was much greater in tanks where the larvae had direct access to air (Fig. 4). Swim bladder volume of the larvae without access to air remained essentially the same throughout the experiment. It appears from this experiment that gulf menhaden larvae, like a number of other clupeoid species, fill their swim bladders by swallowing air at the surface.

DISCUSSION

Our findings for swim bladder inflation in larval gulf menhaden generally agree with the findings of Hunter and Sanchez (1976) and Uotani (1973) for other clupeoid species. Our field studies showed conclusively that gulf menhaden inflate their swim bladders at night and deflate them during the day. Hunter and Sanchez (1976) suggested that nighttime swim bladder inflation in larvae of the northern anchovy is an energy-sparing mechanism that allows larvae to reduce swimming activity during nonfeeding periods while maintaining their depth in the water column. These authors further suggest that a reduction in swimming activity may reduce predation, since some predators of larval fish (e.g., chaetognaths) use the water movement caused by swimming activity to detect their prey.

In the laboratory we found that larvae were unable to fill their swim bladders when they were prevented from reaching the air-water interface. This too agrees with the previous hypothesis on

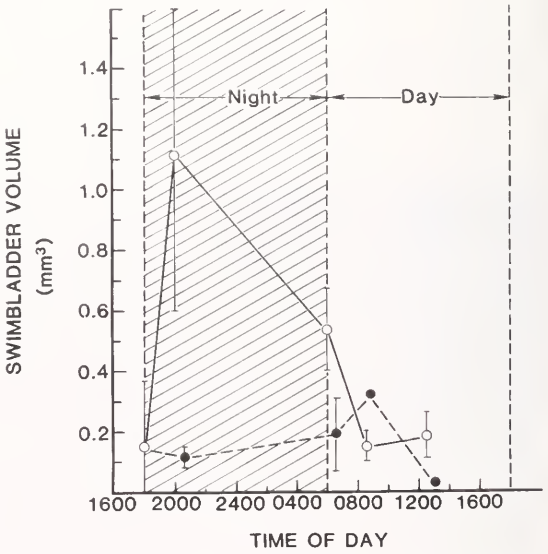

FIGURE 4.—Swim bladder volume (X ± 2 SE) of gulf menhaden, *Brevoortia patronus*, held in the laboratory with access (solid line) and without access (dashed line) to the air-water interface.

how larvae of physostomatous clupeoid fishes initially inflate the swim bladder (Blaxter and Denton 1976).

Under field conditions, gulf menhaden larvae began to fill and empty their swim bladders during the approximately 45 min of twilight preceding sunset and sunrise. The numbers of fish with gas in their bladders increased and decreased gradually (i.e., it is not an all or none phenomenon) prior to darkness (or daylight). This observation suggests to us that larvae are responding as individuals to gradually changing light levels. This response is probably better developed in larger larvae.

The relation of diurnal vertical migration to swim bladder inflation that we found is different from the generally accepted position that larvae are near the sea surface with well-inflated swim bladders at night and are deeper in the water with deflated swim bladders during the day. We captured menhaden larvae at three discrete depths at night (down to 20 m) and over 95% of the larvae captured at 8 and 20 m had gas in their swim bladders. On four previous cruises, collections in the same location also showed that menhaden larvae were distributed throughout the water column at night but concentrated at the surface during the day (unpubl. data[5]).

In conclusion, the swim bladder of the larval stages of gulf menhaden acts as a buoyancy regulator that allows the fish to maintain a position in the water column at night without movement. By day the swim bladder is deflated, and the larvae must actively swim to maintain their position near the water surface. At some point during development, the swim bladder's primary function switches to that of a pressure-adjusting mechanism for the otic bullae.

[5]Sogard, Susan M., Donald E. Hoss, and John J. Govoni. In prep. Density and depth distribution of larval fishes at selected sites in the northern Gulf of Mexico. Southeast Fish. Cent. Beaufort Lab., Natl. Mar. Fish. Serv., NOAA, Beaufort, NC 28516-9722.

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COMPARISON OF AMERICAN EEL GROWTH RATES FROM TAG RETURNS AND LENGTH-AGE ANALYSES

Estimates of growth rates of American eel, *Anguilla rostrata*, have been largely indirect, based on projections from length-age regressions or comparisons of mean lengths at particular ages (Smith and Saunders 1955; Boëtius and Boëtius 1967; Ogden 1970; Bieder 1971; Gray and Andrews 1971; Hurley 1972; Harrell and Loyacano 1980; Kolenosky and Hendry 1982). Although valid for many fish species, these two approaches may be questionable in eel studies because of high variability in lengths at given ages and because of considerable overlap in lengths among ages (e.g., Bertin 1956; Fahay 1978; Facey and LaBar 1981; Moriarty 1983). Testing the accuracy of a length-age regression as an estimator of growth rate requires a simultaneous mark-recapture study. Our objective was to mark and recapture eels in a Georgia estuary and to compare growth data from recaptures with growth estimates derived from length-age regressions and mean-length-at-age calculations for eels from the same population captured at the same time. We also sought information on seasonal growth patterns and differences in growth rates among size classes.

Materials and Methods

All American eels were captured in tidal Fridaycap Creek (lat. 31°21′N, long. 81°24′W) which enters the South Altamaha River, Ga., about 11 km from the river mouth (see Helfman et al. 1983). Salinities and water temperatures ranged from 0 to 22‰ and 5.5° to 31°C, respectively. Baited eel traps were set at or before sunset and pulled shortly after sunrise the next day. Animals were anesthetized in an ice slurry or in tricaine methanesulfonate, measured (total length), weighed, tagged with 25 mm long Floy[1] FD-68B anchor tags, and released where captured. We tagged 659 animals on eight occasions between October 1980 and December 1982. Growth data from eels at large <20 d were not used because of possible confusion with measurement error, which averaged ± 1 mm (range = 0-5 mm, $N = 35$ measurements of seven eels).

Age determinations are based on sagittal otolith analyses from 305 eels captured concurrently with tagged animals. Most otoliths had distinct opaque and transparent zones, with few apparent supernumerary zones. Seasonal analysis of otolith margins indicated that presumed annuli were deposited on an annual basis and were a reasonable chronicle of age (Helfman et al. in press). Fish used in the mark-recapture study of growth were not collected for histological examination of gonads, and we therefore could not determine if sex-related differences in growth occurred (Tesch 1977).

Results

We recaptured 101 individuals, for an overall recapture rate of 15%. Time at large ranged from 8 to 493 d. Recapture frequencies were 84 fish recaptured once, 14 recaptured twice, 2 recaptured three times, and 1 recaptured four times.

Growth rates of recaptured eels were variable but fell into two apparent seasonal categories (Table 1): 1) Slow growth from November through February (0.0-0.08 mm/d, $\bar{x} = 0.026$, SD = 0.024, $N = 13$ recaptures) and 2) fast growth during spring, summer, and fall (0.01-0.63 mm/d, $\bar{x} = 0.221$, SD = 0.152, $N = 78$ recaptures); fast period growth was significantly greater (t-test, $P < 0.001$). Combining averages, and assuming a slow period of 4 mo, yield an average annual growth

TABLE 1.—Growth rates of recaptured American eels as a function of season and year. Values in the body of the table are numbers of animals with particular growth rates. Intervals for fastest and slowest rates are subdivided by 0.05 mm/d; other intervals are 0.10 mm/d.

	Slow growth period (Nov.-Feb.)[1]	Fast growth period (Mar.-Nov.)	
Growth (mm/d)	1980-81	1981	1982
0.00-0.05	12	2	4
0.06-0.10	1	5	12
0.11-0.20		10	9
0.21-0.30		7	9
0.31-0.40		3	4
0.41-0.50			7
0.51-0.60		1	4
0.61-0.65			1
$\bar{x}$ growth (mm/d)	0.026	0.182	0.246
SD	0.024	0.107	0.172

[1]An additional 26 eels at large from late November 1982 to early May 1983, i.e., encompassing primarily the slow growth period, grew an average of 0.054 mm/d (SD = 0.034 mm/d).

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

rate of 57 mm for eels 270-500 mm long over the 2-yr studied (95% C.I. [confidence interval] = ±8.4 mm, growth periods treated as independent random variables, Bliss 1967). Growth as percent increase in length for an average eel 347 mm long was 16%.

Accuracy of the extrapolated annual estimate can be tested against independent, long-term growth data from animals whose recapture intervals included both growth periods. Seven animals had recapture intervals of 6-16 mo (Table 2); average growth was 62 mm/yr (95% C.I. = ±20.1 mm) or a 17% increase in length.

TABLE 2.—Annual growth rates of eels in Fridaycap Creek, Ga., based on long-term recaptures. Data are from eels that were at large for more than a 180-d interval that included both fast and slow growth periods.

Eel no.	Date: First capture	Date: Second capture	Days at large	Length (mm): Initial	Length (mm): Final	Growth rate (mm/yr)	Percent increase
[1]	26-X-80	27-VIII-81	313	353	429	83	23
1	26-II-81	24-II-82	363	362	460	98	27
2	26-X-80	30-IV-81	186	328	351	45	14
3	7-III-81	24-II-82	353	378	450	74	20
4	26-X-80	27-VIII-81	306	487	511	24	5
5	19-II-81	24-II-82	369	307	352	45	15
6	7-III-81	24-II-82	354	433	504	73	17
7	7-III-81	13-VII-82	492	393	492	56	14
		$\bar{x}$		381		62	17
		SD		58		24	7

[1]Eel No. 1 was captured four times; growth between first and third and between second and fourth captures were analyzed separately.

When the data are grouped into 50 mm size classes, animals in the 350-400 mm class grew faster than smaller animals (Fig. 1); 95% confidence intervals for other size classes overlapped, although some overlap may result from small samples of larger animals. Similar trends in relative growth (percent increase in length) were apparent (Fig. 1): values overlapped in the smaller size classes, and the largest size class grew slower than the fast-growing 350-400 mm group.

Growth rates during fast growth periods (Table 1) suggest that animals grew faster in 1982 than in 1981 (t-test, one tail, df = 76, $P < 0.05$). Maximum growth rates also differed: the 5 fastest growth rates, as well as 13 of the 15 fastest rates, occurred in 1982 (Table 1).

Information on weight gain is less complete but shows a similar seasonal trend. Average weight increase between recaptures was 0.223 g/d (SD = 0.222, $N = 47$) for the fast growth period; limited data suggest lesser gains for the slow growth period (0.017-0.144 g/d, $N = 2$). When seasonal data are summed and a 4-mo slow growth period is assumed, annual weight increase was 63 g. Long-term weight change data from two animals at large 299 and 371 d indicate an average weight increase of 76 g/yr (range = 67 to 86 g/yr).

Mean lengths at different ages were

Age class (yr):	*II*	*III*	*IV*	*V*	*VI*	*VII*
$\bar{x}$ length (mm)	242	310	361	403	442	460
Range (mm)	197-278	214-446	233-548	256-570	297-559	386-500
N	6	51	134	78	32	5

The mean values project an average annual increase of 44 mm (range = 39-68 mm). The related length-age regression for all eels aged at this locale during the study period was length = 183.3 + 43.5 × age ($N = 305$, $r = 0.492$, $P < 0.01$) which also projects an average annual increase of 44 mm (95% C.I. = ±8.7 mm) for an average eel 370 mm long.

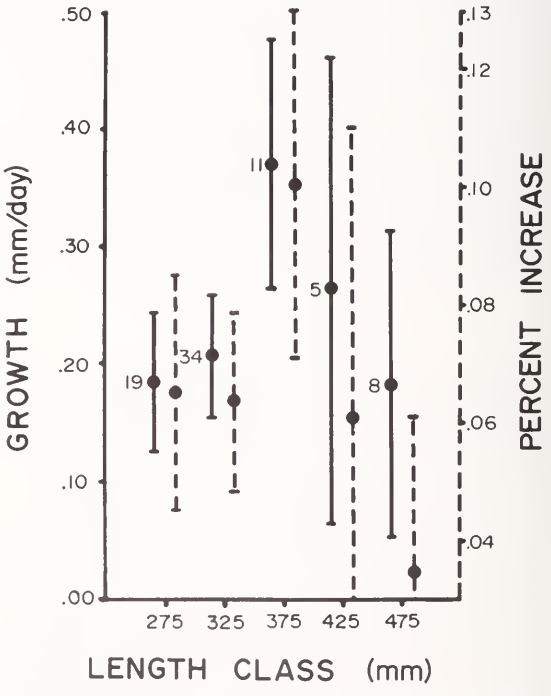

FIGURE 1.—Growth rates of recaptured American eels as a function of size at initial capture, Fridaycap Creek, Ga., October 1980-November 1982. Growth is expressed as the actual daily rate of increase (solid vertical lines, means ±95% confidence intervals) and the percent increase as a function of initial length (dashed vertical lines, means ±95% confidence intervals). Data are from fast growth periods, 1981 and 1982 combined. Numbers beside each mean are the total animals comprising each 50 mm size class. Midpoints of length classes are shown on x-axis.

Discussion

Comparisons of Growth Measures

Different procedures yielded different estimates of growth rate. The two independent, direct measures based on recaptures—seasonal summation and long-term recaptures—produced similar values (57 mm/yr and 62 mm/yr, respectively). The indirect measures—length-age regression and mean-length-at-age analysis—both projected annual growth rates of 44 mm/yr. All estimates are complicated by extreme variability in growth, with overlap in lengths among four to six year classes common (Smith and Saunders 1955; Ogden 1970; Gray and Andrews 1971; Hurley 1972). Growth rate estimates based on recapture data were apparently higher than those derived from length-at-age analyses, but confidence intervals overlapped among all estimates. However, we feel that the direct measures are more accurate. First, the sample size for the length-age analyses was more than three times larger than for the seasonal summation analysis, but the confidence intervals were very similar (17.4 mm and 17.8 mm, respectively), suggesting less variability in the recapture data. Second, growth rates derived from recaptured animals are based on actual growth between captures; variability in calculated growth rates should therefore reflect real variability in growth among animals. In length-age analyses, age classes are commonly resolved at no finer than an annual level. Consequently, growth subsequent to day 1 of each year increases the variance around the estimate rather than increasing the accuracy of the estimate. Finally, the accuracy of age determinations from otoliths in some eel populations is questionable (Moriarty and Steinmetz 1979; Deelder 1981; Casselman 1982), placing length-age analyses in doubt unless annulus formation can be verified.

Limited growth data from other mark-recapture studies of American eels are available. Hurley (1972) tagged 1,418 American eels in Lake Ontario, Canada, and reported recapture intervals for 13 large individuals (730-874 mm), which increased an average of 34 mm/yr. At two Louisiana freshwater locales, Gunning and Shoop (1962) tagged 43 American eels; only four recaptures provided usable data, indicating an average growth of 140 mm/yr (growth range = 46-325 mm, initial lengths = 255-915 mm). R. L. Haedrich[2] tagged 148 American eels in a Massachusetts estuary. Four individuals (initial lengths = 500-700 mm) had an average annual growth rate of 6% (range = 4.1-8.4%). An inverse latitudinal trend in growth is suggested (see also Harrell and Loyacano 1980), but direct comparison is complicated by different initial lengths, small sample sizes, and high variability in growth.

Length-related differences in growth have also been found for other populations. A shift from allometric to symmetric growth occurred at 800 mm for American eels in Lake Ontario (Hurley and Christie 1982). Those authors, as well as Smith and Saunders (1955), related such a growth change to physiological preparation for maturation and migration. Gray and Andrews (1971) found that American eels in New Brunswick, Canada, estuaries grew slowly after age XI. Helfman et al. (in press) suggested that maturation of Fridaycap Creek eels occurred at around age IV (mean length = 387 mm). An apparent decrease in growth rates of Fridaycap Creek animals longer than 400 mm (Fig. 1) supports their interpretation.

Causes of Seasonal Differences

Seasonal and annual differences in growth rate can be linked to fishing success as affected by climate. Eel fishing in Georgia estuaries is typically poor at water temperatures below 10°C and above 24°C. In 1980-81, estuarine water temperature fell below 10°C during December 1980, but average 1981-82 monthly temperatures were higher and did not reach the 10° minimum until January 1982. In addition, rainfall in 1981 was 45 cm below average, and mean water temperatures were 2°C higher during June through September than in 1982 (R. Arnsdorff[3] and T. E. Targett[4]). The winter slow growth period may therefore result from colder water temperatures and reduced feeding. Faster growth in 1981 than in 1982 may have resulted from elevated temperatures during much of the fast growth period of 1981. High water temperatures—leading to reduced feeding, interrupted growth, and poor fishing—occurs in European eels, *Anguilla anguilla* (Deelder 1981). Interrupted summer growth may

[2]R. L. Haedrich, Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland, Canada A1B 3X9, pers. commun. April 1983.

[3]R. Arnsdorff, Georgia Department of Natural Resources, Environmental Protection Division, 270 Washington St. S.W., Atlanta, GA 30334, pers. commun. October 1982.

[4]T. E. Targett, Skidaway Institute of Oceanography, P.O. Box 13687, Savannah, GA 31406, pers. commun. October 1982.

have occurred in our study population, but because we lack growth data from midsummer only, we cannot test for it.

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DESCRIPTION OF EARLY STAGE ZOEAE OF *SPIRONTOCARIS MURDOCHI* (DECAPODA, HIPPOLYTIDAE) REARED IN THE LABORATORY

Larvae of *Spirontocaris murdochi* Rathbun have not been described in the literature. During studies on rearing larvae in the laboratory for descriptive purposes, I succeeded in rearing zoeae of *S. murdochi* through Stage III. The first three zoeal stages of *S. murdochi* are described, illustrated, and compared with descriptions of morphologically similar hippolytid zoeae.

Methods and Rearing Results

I obtained an ovigerous female *Spirontocaris murdochi* carrying late-stage embryos while sampling pandalid shrimp in Auke Bay, Alaska, for toxicity studies. The female was caught 2 April 1979 at a depth of 18 m at lat. 58°21.6′ N, long. 134°39.3′ W. Stage I zoeae released from the female were reared in 250 ml jars containing about 200 ml of filtered seawater. The jars were checked daily for exuviae, and a few zoeae were preserved every other day. The zoeae were offered live plankton strained through a 0.333 mm mesh, but there was no evidence that the zoeae ate the plankton. (For a more complete description of the methods, see Haynes 1982.) Most of the zoeae molted to Stage II, but only two zoeae molted to Stage III.

Techniques of measurement and illustration are those of Haynes (1976, 1979). At least five zoeae of Stages I and II were used to verify segmentation and setation.

Description

The terms used in the descriptions and nomenclature of appendages are from Haynes (1976, 1979). Only those morphological characteristics useful for readily identifying each stage are given. Setation formulae are the number of setae per segment from the distal to the proximal segment. The telsonic setae are numbered as pairs beginning with the inner (medial) pair. For clarity, setules on setae are usually omitted, but spinulose setae are shown.

The following characteristics apply to zoeal Stages I, II, and III. The rostrum is slender, spiniform, without teeth, about one-fourth the length of the carapace, and projects horizontally. The ventral and posterior margins of the carapace are smooth except for pterygostomian spines. Mandibles are without palps; there is no proximal setose seta on the maxillule; and the maxillipeds are without epipodites. Abdominal somites 4 and 5 have posterolateral spines (the fifth pair is slightly longer than the fourth pair in Stage I, but both pairs are nearly the same length in Stages II and III). An anal spine is present.

Stage I Zoea

Mean total length of Stage I zoea (Fig. 1A), 3.4 mm (range 3.2-3.6 mm; six specimens). Eyes sessile. Carapace with two minute rounded prominences: One at posterior edge, other at base of rostrum.

ANTENNULE (Fig. 1B).—Protopodite of first antenna, or antennule, simple, unsegmented, tubular, with heavily plumose seta terminally. Conical projection tipped with four aesthetascs: Three long, one of intermediate length.

ANTENNA (Fig. 1C).—Second antenna, or antenna, with inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum unsegmented, slightly shorter than scale, styliform, tipped by plumose seta and shorter spine. Antennal scale distally divided into five joints (distal joint incomplete) and fringed with 10 heavily plumose setae along terminal and inner margins. Tip of antennal scale curved toward outer margin. Protopodite with spine only at base of flagellum.

MANDIBLES (Fig. 1D).—Incisor process of left mandible has four teeth in contrast to triserrate incisor process of right mandible. Both left and right mandibles with movable premolar denticle (lacinia mobilis). Left mandible with subterminal tooth.

MAXILLULE (Fig. 1E).—First maxilla, or maxillule, with coxopodite, basipodite, and endopodite. Coxopodite (proximal lobe) with seven spines: Five spinulose, two simple. Basipodite (median lobe) with 10 short, smooth spines terminally. Two-segmented endopodite originates from lateral margin of basipodite: Proximal segment with two spinulose spines, distal segment with three spinulose spines.

MAXILLA (Fig. 1F).—Second maxilla, or maxilla, has platelike exopodite (scaphognathite) with five plumose setae along outer margin and

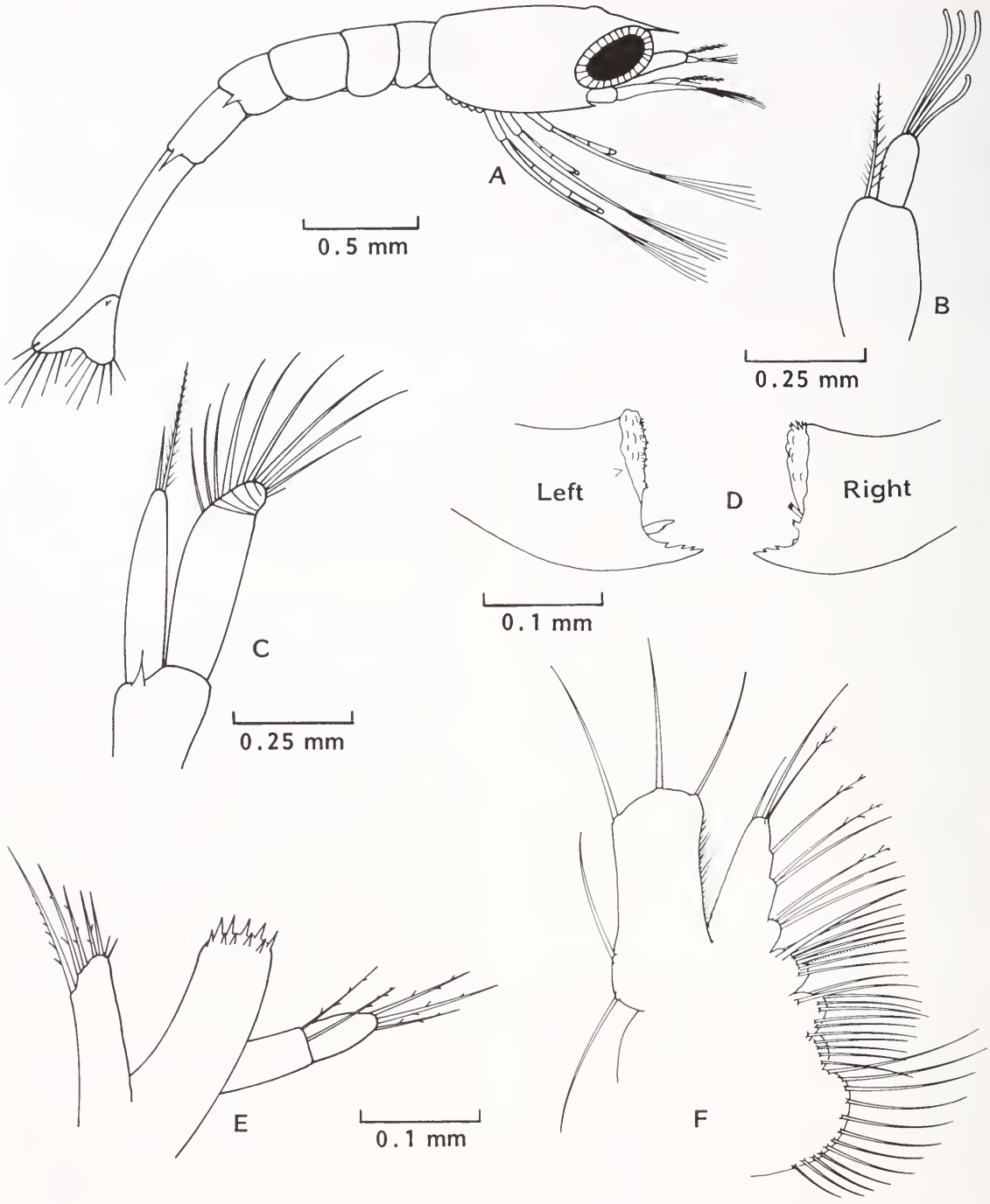

FIGURE 1.—Stage I zoea of *Spirontocaris murdochi*: A, whole animal, right side; B, antennule, dorsal; C, antenna, ventral; D, mandibles (left and right), posterior; E, maxillule, ventral; F, maxilla, dorsal.

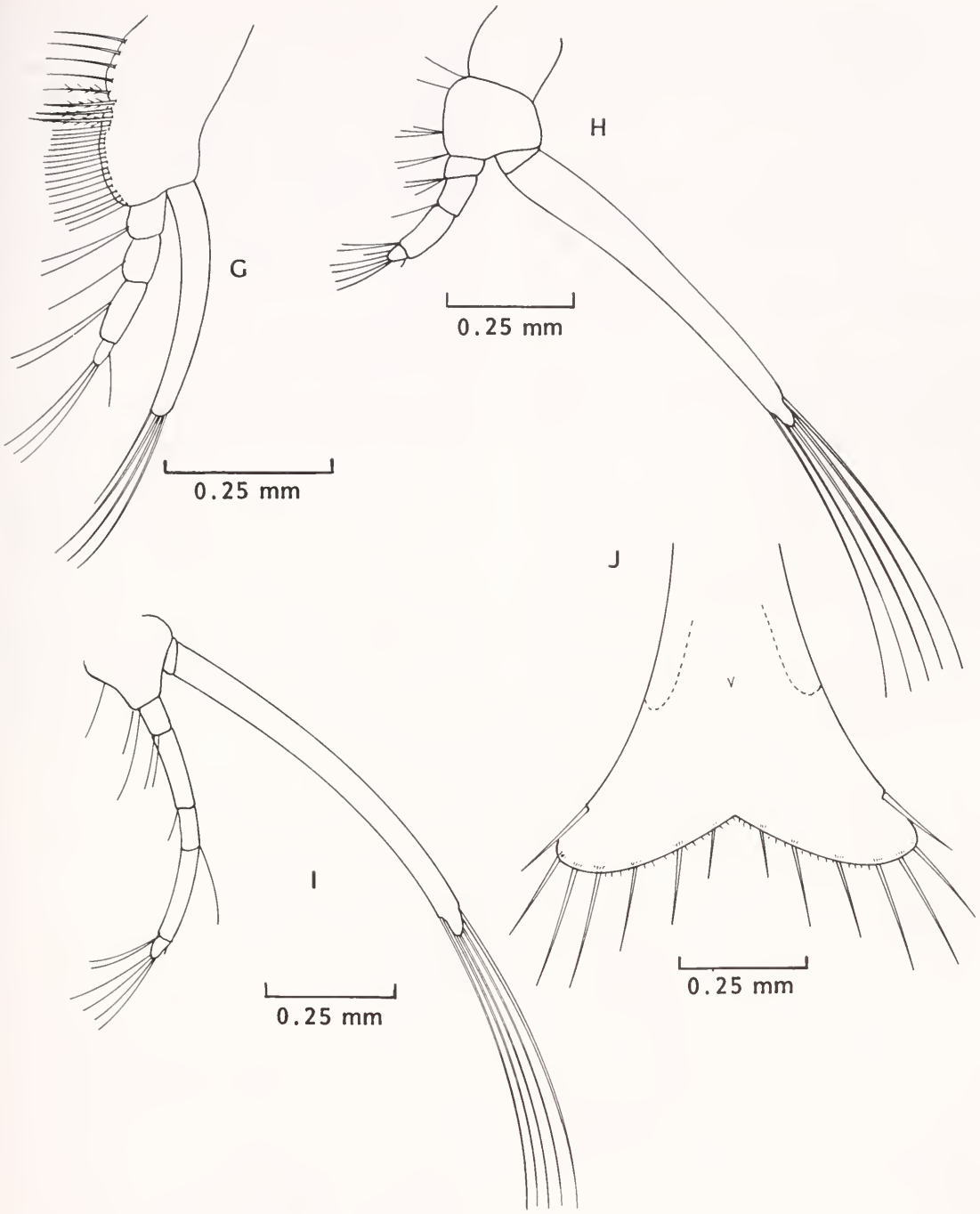

FIGURE 1.—*Continued*—G, first maxilliped, lateral; H, second maxilliped, lateral; I, third maxilliped, lateral; J, telson, ventral.

hairs along medial margin. Unsegmented endopodite with nine setae (four setae slightly spinulose). Coxopodite and basipodite bilobed. Coxopodite with eight setae on each lobe. Basipodite with 16 setae: 4 on distal lobe, 12 on proximal lobe.

FIRST MAXILLIPED (Fig. 1G).—Most setose of natatory appendages. Bilobed protopodite with 5 setae on proximal lobe, 20 setae on distal lobe (three of setae on distal lobe spinulose). Endopodite four-segmented; setation formula 4, 2, 1, 2. Exopodite (a long, slender ramus jointed at base) has four natatory setae.

SECOND MAXILLIPED (Fig. 1H).—Protopodite bisegmented: Distal segment with seven setae, proximal segment without setae. Endopodite four-segmented; setation formula 6, 2, 1, 3. Exopodite with five natatory setae.

THIRD MAXILLIPED (Fig. 1I).—Unsegmented protopodite with three setae. Five-segmented endopodite about two-thirds length of exopodite; setation formula 5, 2, 1, 1, 2. Exopodite with five natatory setae.

PEREOPODS.—Poorly developed, anteriorly directed under body.

PLEOPODS.—Absent.

ABDOMEN AND TELSON (Fig. 1A, J).—Abdomen with pair of posterolateral spines on somites 4 and 5, pair on somite 4 somewhat shorter than pair on somite 5. Telson emarginate posteriorly, fused with abdominal somite 6. Telson with 7 + 7 densely plumose setae, minute spinules at base of each seta except outermost pair, larger spinules along terminal margin of telson between bases of four inner pairs of setae. Uropods visible and enclosed.

Stage II Zoea

Mean total length of Stage II zoea, 3.7 mm (range 3.5-4.0 mm; three specimens). Eyes stalked. Carapace identical to Stage I carapace.

ANTENNULE (Fig. 2A).—Two-segmented, with large outer flagellum and smaller inner flagellum on terminal margin. Flagella not segmented; inner flagellum conical, with long spine terminally; outer flagellum with four aesthetascs terminally. Proximal segment with large spine projecting slightly downward from ventral surface. Both proximal and distal segments have two plumose setae each.

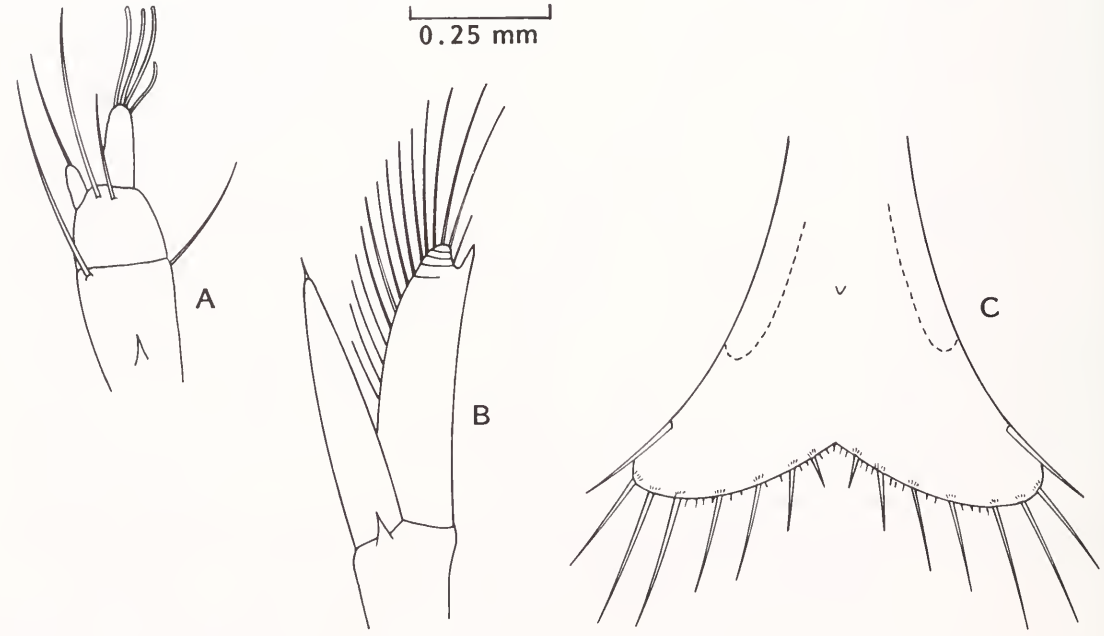

FIGURE 2.—Stage II zoea of *Spirontocaris murdochi*: A, antennule, ventral; B, antenna, ventral; C, telson, ventral.

ANTENNA (Fig. 2B).—Flagellum styliform, about same length as antennal scale, tipped by short spine. Antennal scale about 3.5 times as long as wide, fringed with 15 plumose setae along terminal and medial margins. Antennal scale with four joints distally (proximal joint incomplete), lateral projection on distal portion. Tip of antennal scale not curved laterally as in Stage I. Protopodite with spine at base of flagellum.

MANDIBLES.—Same as in Stage I except have slightly developed molar lip.

MAXILLULE, MAXILLA, AND MAXILLIPEDS.—Similar to Stage I except scaphognathite of maxilla has six setae; exopodites of maxillipeds 1-3 have 5, 8, and 10 natatory setae, respectively.

PEREOPODS.—Slightly larger than in Stage I, extend somewhat vertically, have naked exopodites on pereopods 1 and 2.

PLEOPODS.—Absent.

ABDOMEN AND TELSON.—Posterolateral spines on abdominal somites 4 and 5 nearly same length. Telson (Fig. 2C) still fused with abdominal somite 6, has 8 + 8 densely plumose setae. Enclosed uropods somewhat longer than in Stage I.

Stage III Zoea

Mean total length of Stage III zoea, 4.1 mm (range 3.9-4.3 mm; two specimens). Carapace identical to Stage II carapace, except has supraorbital spine.

ANTENNULE.—Similar to Stage II antennule except outer flagellum has subterminal seta, proximal segment with four setae around distal joint and three plumose setae laterally, distal segment with four large plumose setae.

ANTENNA, MANDIBLES, MAXILLULE, AND MAXILLA.—Similar to Stage II but with following differences. Antennal scale, without joints terminally, has 20 plumose setae along terminal and medial margins; subterminal spine extends just beyond tip of scale. Mandibles with a few additional teeth between incisor and molar processes. Maxillule with 9 spinulose spines on coxopodite and 12 short smooth spines on basipodite. Scaphognathite of maxilla has 9-12 plumose setae.

MAXILLIPEDS.—Exopodites of maxillipeds 1-3 have 5, 10, and 10 natatory setae, respectively.

PEREOPODS (Fig. 3A, B).—Exopodites only on pereopods 1 and 2; chelae present but undeveloped; endopodites of pereopods 1 and 2 with terminal seta.

PLEOPODS.—Present as buds.

ABDOMEN AND TELSON.—Telson (Fig. 3C),

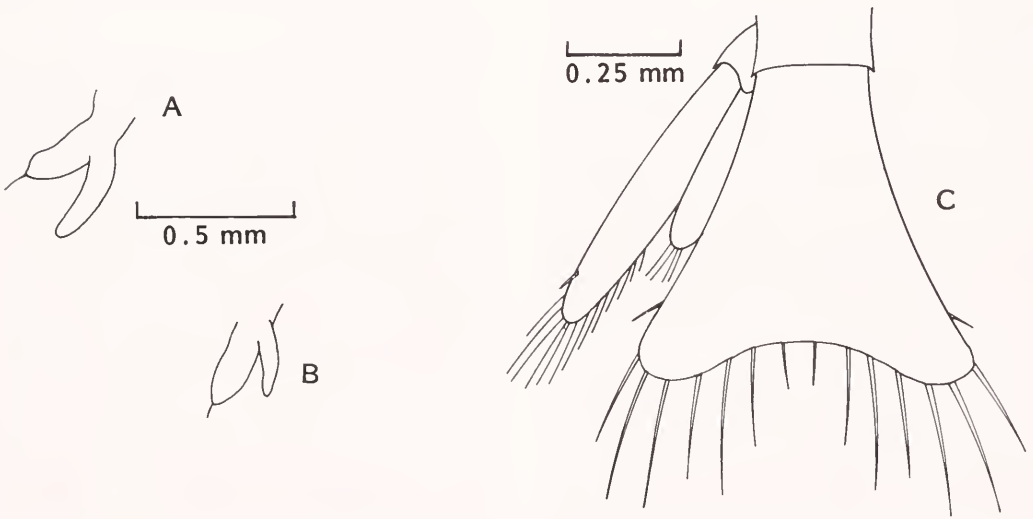

FIGURE 3.—Stage III zoea of *Spirontocaris murdochi*: A, pereopod 1, lateral; B, pereopod 2, lateral; C, telson, dorsal.

jointed with abdominal somite 6, has 8 + 8 densely plumose setae. Most of spinules at setal bases and along terminal margin absent. Uropods free. Endopodite of uropod about one-half length of exopodite, has four setae along terminal margin. Exopodite usually with 13 distal marginal setae and an outer subterminal spine.

Comparison of Zoeal Stages with Descriptions by Other Authors

Of the described *Spirontocaris* zoeae, those of *S. murdochi* are most similar to zoeae of *S. spinus* (Sowerby), *S. spinus intermedia* Makarov, and *S. phippsii* (Krøyer): all have relatively long, spiniform rostrums; exopodites on pereopods 1 and 2; and posterolateral spines on abdominal somites 4 and 5. However, larvae of *S. spinus* (described by Pike and Williamson 1961) and *S. spinus intermedia* (described by Ivanov 1971) are distinguishable from larvae of *S. murdochi*: *S. spinus* and *S. spinus intermedia* have a tuft of setae on the dorsal surface of abdominal somite 4; *S. murdochi* does not. Furthermore, in Stage I zoeae of *S. spinus* and *S. spinus intermedia*, the posterolateral spine on abdominal somite 5 is as short as, or shorter than, the spine on abdominal somite 4; whereas, in Stage I zoeae of *S. murdochi*, the posterolateral spine on abdominal somite 5 is noticeably longer than the posterolateral spine on abdominal somite 4.

Pike and Williamson (1961) described a Stage II specimen of *S. phippsii* whose identity is assumed from the distribution of adults in the northwestern Atlantic Ocean. The specimen is described as being nearly the same as Stage II *S. spinus* except somewhat larger (6.0 mm). Also, the posterolateral spines on abdominal somites 4 and 5 of *S. phippsii* are "more prominent", the dorsal tuft of setae on abdominal somite 4 is absent, the telson is "broader", and the second pair of telsonic spines are about three-fourths the length of the third pair. This description is inadequate to distinguish between Stage II *S. phippsii* and Stage II *S. murdochi*, except for total length: Stage II *S. murdochi* average 3.7 mm total length compared with 6.0 mm for *S. phippsii*.

The Stage III zoeae described as "*Spirontocaris* larva Nr. 2" by Stephensen (1916) from Greenland waters are assumed to be *S. phippsii* (Pike and Williamson 1961). When the figures and description of Stephensen's Stage III zoeae are compared with my description of Stage III *S. murdochi*, *S. murdochi* are smaller and noticeably less developed. Stephensen's zoeae are 6.5 mm long, the carapace has an antennal spine, the pleopods and the chelae of pereopods 1 and 2 are clefted, and telsonic setal pairs 3 and 4 are the same length. My Stage III zoeae average 4.1 mm long, the carapace does not have antennal spines, the pleopods and chelae of pereopods 1 and 2 are not clefted, and the third pair of telsonic setae are noticeably shorter than the fourth pair of telsonic setae.

It should be noted, however, that this comparison of zoeae of *S. murdochi* and *S. phippsii* is based on specimens from different geographical areas as well as specimens of *S. phippsii* that are of unproven identity. Confirmation of morphological development of *S. phippsii* larvae from the North Pacific Ocean is desirable.

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INCIDENCE OF MOLTING AND SPAWNING IN THE SAME SEASON IN FEMALE LOBSTERS, *HOMARUS AMERICANUS*

The reproductive cycle in female lobsters, *Homarus americanus*, normally covers 2 yr. Molting and mating occur first, primarily during the summer months. Laying of eggs (spawning) takes place about a year later. Hatching of eggs, followed by molting and mating again, takes place another year later (Aiken and Waddy 1980). However, departures from the normal cycle occur. One such departure is molting and egg laying in the same year (Aiken and Waddy 1980; Ennis 1980). Ennis (1980) noted that new-shelled ovigerous females obtained in fall sampling at various Newfoundland localities ranged towards the lower end of the size range of all ovigerous specimens and suggested that those females that molt and spawn in the same year are spawning for the first time. Aiken and Waddy (1980) similarly suggested that this phenomenon probably occurs primarily in the Adult-I year (i.e., first spawning).

In this paper I present data on the incidence of this phenomenon in a Newfoundland lobster population and illustrate its relationship to size of lobster.

Materials and Methods

Annually, since 1975, research fishing for lobsters has been carried out in autumn, following the summer molting/spawning period, in the area of Arnold's Cove, Placentia Bay, on the southeast coast of Newfoundland. The main purpose of this fishing is to tag legal lobsters to obtain estimates of standing stock during the following spring fishing season. All lobsters caught are measured, sexed, and examined for shell condition to determine whether molting has occurred recently and for the presence of external eggs. Since hatching of eggs laid the previous year occurs during July-August in this area, all ovigerous specimens present in the autumn carry recently laid eggs.

To determine the relationship between percent molting and laying eggs in the same season, it was necessary to convert the observed postmolt carapace length (CL) of new-shelled ovigerous specimens to premolt carapace length. This was done using a premolt-postmolt carapace length relationship for Arnold's Cove lobsters (Ennis 1978). The data for all years were pooled. The total number of ovigerous specimens examined and the number which had molted prior to laying eggs at each 1 mm CL interval (premolt carapace length for new-shelled specimens) were subjected to probit analysis.

Results and Discussion

All ovigerous lobsters $\leq$70 mm CL (premolt) molted prior to laying eggs. Beyond 70 mm, the percentage of animals that molt and lay eggs in the same season declined very rapidly to zero at 82 mm CL (Fig. 1).

The lobsters in which Aiken and Waddy (1976, 1980) noted the occurrence of molting and egg laying in the same individual during the same molting/spawning season came from the southern Gulf of St. Lawrence. They suggested that the high summer water temperatures that prevail in the area may be the cause of the phenomenon. However, its occurrence in several Newfoundland localities (Ennis 1980) indicates that the phenomenon may be quite widespread.

At Arnold's Cove the percentage of non-ovigerous females that molt and lay eggs in the same season declines to zero over the size range (70-82 mm CL) where functional maturity increases to 50% (Ennis 1984). This is consistent with the suggestion that this phenomenon occurs in animals laying eggs for the first time. If this is so, the incidence of this phenomenon in a population is likely to be related to the minimum legal

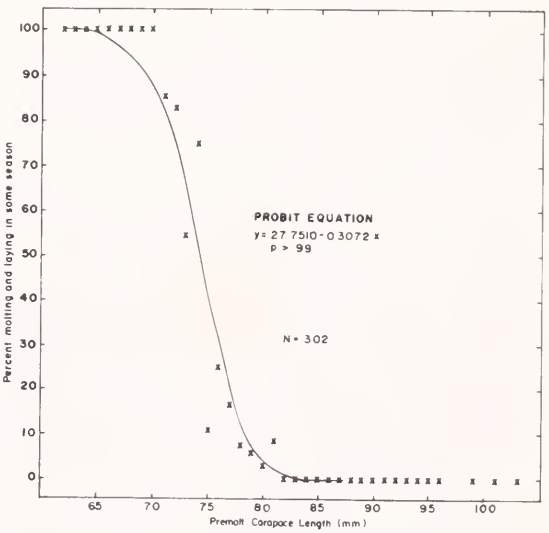

FIGURE 1.—Percentage of non-ovigerous female lobsters that molt and lay eggs in the same season in relation to size at Arnold's Cove, Newfoundland.

size (in relation to size at maturity) and exploitation rates in the fishery. In a fishery with a small minimum legal size and high exploitation rates, most of the ovigerous females in the population would be small animals laying for the first time.

The incidence of new-shelled ovigerous females in autumn sampling at Arnold's Cove has ranged from 0 to 38.5% of the total ovigerous specimens examined (Table 1). This year-to-year variability, which has also been observed elsewhere in Newfoundland (Ennis 1980), could be accounted for by variation in relative abundance of prerecruit animals caused by annual fluctuation in recruitment and exploitation rate.

TABLE 1.—Percentage of ovigerous lobsters with new shells in autumn sampling at Arnold's Cove, Newfoundland, 1975-82.

Year	No. ovigerous examined	% ovigerous with new shell	Carapace length (mm) Range of ovigerous	Carapace length (mm) Range of new-shelled ovigerous[1]
1975	75	10.7	72-103	73-83
1975[2]	16	12.5	65-92	65-71
1976	31	6.5	73-92	83-90
1976[2]	26	19.2	68-91	68-77
1977	78	38.5	71-101	76-88
1978	12	16.7	71-95	82-83
1979	31	25.8	72-99	72-90
1980	18	0.0	73-99	—
1981	31	6.5	71-101	71-81
1982	27	3.7	75-94	75

[1]These are postmolt carapace lengths.
[2]Diver-caught samples obtained during the same period as the trap-caught samples.

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PARASITES OF OLIVE ROCKFISH, *SEBASTES SERRANOIDES*, (SCORPAENIDAE) OFF CENTRAL CALIFORNIA

The olive rockfish, *Sebastes serranoides*, inhabits reefs from Del Norte County, Calif., to San Benito Island, Baja California, Mexico. Olive rockfish are large (to 64 cm TL), active predators, usually found in the water column, but occasionally hovering over or resting upon rocky substrates. Juveniles are primarily midwater feeders, preying upon zooplankton and small fishes, though some demersal feeding (e.g., isopods, caprellid and gammarid amphipods, etc.) has been noted (Hobson and Chess 1976; Love and Ebeling 1978; Love and Westphal 1981). Adults feed almost entirely on nektonic forms of squid and fish and on substrate-dwelling octopus (Love and Westphal 1981).

Little is known about the parasite fauna of olive rockfish, as previous reports are either descriptions of newly discovered species (Cressey 1969; Moser and Love 1975; Love and Moser 1976; Moser et al. 1976) or surveys of particular parasites throughout a fish community (Turner et al. 1969; Hobson 1971; Dailey et al. 1981). As part of a life-history study, we investigated the parasite population of central California olive rockfish.

Methods

Specimens were collected monthly from April 1975 to February 1976 at a group of shallow-water pinnacles, about 11 km west of Avila Beach, San Luis Obispo Co., Calif., (Fig. 1). These pinnacles, at depths of 20-30 m, are situated 100-300 m offshore from Diablo Cove and North Cove and rise to within 5-10 m of the surface.

Six hundred olive rockfish, ranging from 8.6 to 49.2 cm TL, were collected by hook and line or spear, placed in plastic bags, and frozen for later dissection. After thawing, each specimen was

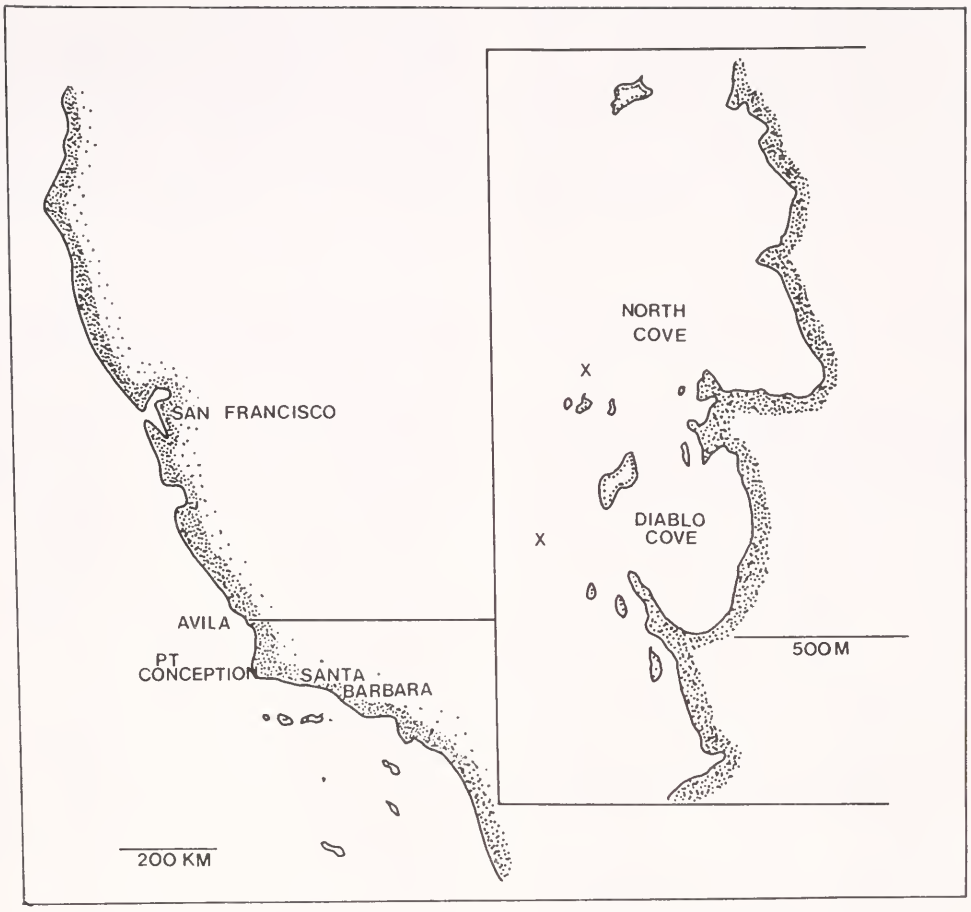

FIGURE 1.—Location of sampling sites (marked with x) for olive rockfish off Diablo Cove, Calif.

measured (total length) to the nearest millimeter and examined for parasites on external surfaces, gills, gill cavities, mouth, mesentery, heart, gallbladder, stomach, intestine, and muscle. Copepods and monogenetic and digenetic trematodes were fixed in alcohol-formaldehyde-acetic acid (AFA). The trematodes were stained with Harris' hematoxylin, cleared with xylene, and mounted. Nematodes were cleared in lactophenol. Protozoans were studied unpreserved after thawing.

Most parasites were identified to the lowest possible taxon. However, the microsporida, copepods of the genera *Caligus* and *Lepeophtheirus*, and larval cestodes, nematodes, and acanthocephalans were not identified to species. Copepods of the genera *Caligus* and *Lepeophtheirus* were only identified to genus, as an earthquake destroyed most of the specimens before they were identified to species.

To facilitate our analysis, we grouped together the relatively uncommon gallbladder myxozoans (= myxosporidans) (*Ceratomyxa sebasta, Leptotheca informis, L. longipes, L. macrospora, Myxidium incurvatum, Zschokkella ilishae*) and the hemiurid trematodes (*Lecithaster gibbosus, Parahemiurus merus, Lecithochirium exodicum*, and *Tubulovesicula lindbergi*).

We analyzed the incidence of infection of all parasites over the entire range of host lengths throughout the year. Differences in prevalence between size classes and between monthly samples were examined using the Kruskal-Wallis test.

Results

For our analyses we divided the specimens into 11 size classes. Table 1 shows the number of specimens taken per month per size class.

TABLE 1.—The number of olive rockfish taken per month per size class, April 1975-February 1976.

Month	Size class (cm TL)									
	5-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46+	Total
April	6	6	3	6	8	10	6	7	3	55
May	4	7	4	4	5	8	8	8	4	52
June	5	5	5	8	6	9	5	7	6	56
July	6	5	7	8	6	8	9	8	7	64
Aug.	4	4	7	6	10	8	7	6	5	57
Sept.	5	8	6	9	5	9	9	9	3	63
Oct.	4	7	5	4	8	7	10	5	4	54
Nov.	5	6	5	6	7	8	8	7	3	55
Dec.	4	6	6	5	7	11	8	8	5	60
Jan.	2	3	5	6	4	6	6	7	5	44
Feb.	2	1	6	4	5	8	6	4	4	40
Total	47	58	59	66	71	92	82	76	49	600

Thirty-six parasite species were recovered from olive rockfish (Table 2). Five species were found in <1% of the individuals examined. These incidental parasites were an unidentified microsporidan and the copepods *Neobrachiella robusta, Chondracanthus pinguis, Naobranchia occidentalis*, and *Sarcotaces arcticus*. Found in <10% of the hosts were *Davisia reginae, Kudoa clupeidae, Leptotheca longipes,* and *L. macrospora* (Myxozoa); *Trochopus marginata* (Monogenea); *Aporocotyle macfarlani, Lecithaster gibbosus, Lecithochirium exodicum, Parahemiurus merus*, and *Tubulovesicula lindbergi* (Digenea); *Anisakis* sp. and *Phocanema* sp. (Nematoda); *Caligus* sp. and *Clavella parva* (Copepoda); and Rhabinorhynchidae gen. sp. (Acanthocephala).

Larval cestodes were the most commonly encountered parasites, infecting 98% of all individuals >20 cm in length. Larval *Contracaecum* sp. were found in 62% and cysticanths of immature *Corynosoma* sp. in 18% of fishes >20 cm.

Of parasites which use *Sebastes serranoides* as a final host, *Microcotyle sebastis* had the highest prevalence, occurring on more than 90% of hosts >20 cm. It was most prevalent on the filaments of the first gill arch (Table 3), declining in number through successive arches ($\chi^2 = 108.1, P < 0.001$). No significant differences in infection intensities were noted between left and right arches.

Other commonly encountered ectoparasites were *Holobomolochus spinulus, Neobenedenia girellae*, and *Lepeophtheirus* sp. Adult metazoan endoparasites were not abundant, though three, *Deretrema cholaeum, Opechona sebastodis*, and *Hysterothylacium aduncum*, were often found in larger fish.

Three myxozoans, *Henneguya sebasta, Leptotheca informis*, and *Zschokkella ilishae*, were found in more than 10% of hosts. *Henneguya sebasta* was found in 93% of hosts >35 cm. Nine percent of *H. sebasta* infections were sufficiently severe to virtually occlude the bulbous arteriosus. Although no histological sections were made, no evidence of gross pathogenic effects were noted, as these heavily infected individuals were of an age and weight indistinguishable statistically (analysis of variance) from lightly or non-infected individuals.

TABLE 2.—Parasites recovered from olive rockfish, *Sebastes serranoides*, off Diablo Cove, Calif. *denotes first host records.

Parasite	Location
Protozoa (Myxozoa)	
Ceratomyxa sebasta	Gallbladder
Davisia reginae	Urinary bladder
Henneguya sebasta	Bulbus arteriosus, gallbladder (rarely)
**Kudoa clupeidae*	Muscle
Leptotheca informis	Gallbladder
Leptotheca longipes	Gallbladder
Leptotheca macrospora	Gallbladder
Myxidium incurvatum	Gallbladder
Zschokkella ilishae	Gallbladder
*Protozoa (Microsporida)	Urinary bladder
Monogenea	
**Microcotyle sebastis*	Gills
**Neobenedenia girellae*	Skin, mouth
**Trochopus marginata*	Gills
Digenea	
**Aporocotyle macfarlani*	Afferent branchial arteries
**Deretrema cholaeum*	Gallbladder
**Lecithaster gibbosus*	Stomach
**Lecithochirium exodicum*	Stomach
**Opechona sebastodis*	Intestine
**Parahemiurus merus*	Stomach
**Podocotyle* sp.	Stomach
**Tubulovesicula lindbergi*	Stomach
Cestoda	
*Tetraphyllidea (immature)	Viscera
Nematoda	
Anisakis sp. (immature)	Viscera
**Contracaecum* sp. (immature)	Viscera
**Hysterothylacium* (=*Thynnascaris*) *aduncum*	Stomach, intestine
Phocanema sp. (immature)	Muscle
Copepoda	
**Neobrachiella robusta*	Gills
Caligus sp.	Skin, gills
**Chondracanthus pinguis*	Gills
**Clavella parva*	Dorsal and anal fin rays
Holobomolochus spinulus	Gills, inner surface of gill opercula
**Lepeophtheirus* sp.	Skin, gills
**Naobranchia occidentalis*	Gills
**Sarcotaces arcticus*	Body cavity near anus
Acanthocephala	
**Corynosoma* sp. (immature)	Viscera
**Echinorhynchus gadi*	Intestine
*Rhabdinorhynchidae gen. sp.	Intestine

TABLE 3.—Position and number of *Microcotyle sebastis* on 32 olive rockfish, *Sebastes serranoides*, off Diablo Cove, Calif.

Arch number	Arch position		Total
	Left	Right	
1	114	124	238
2	60	63	123
3	29	37	66

We found numerous cases of multiple species myxozoan infections in the gallbladder, particularly in individuals >35 cm. Twenty-two percent of all infections were comprised of two species, 5.1% of three, and 1.2% of four. The occurrence of myxozoans in *Deretrema cholaeum*-infected gallbladders occurred less frequently than expected ($\chi^2 = 123.3$, $P < 0.0001$).

The species of parasites infecting olive rockfish by host length and age is shown in Table 4. *Sebastes serranoides* harbors a maximum number of parasite species between 31 and 40 cm or 4 and 10 yr of age [compared with 3-6 yr in *S. alutus* and *S. caurinus* (Sekerak 1975)]. Of the five species of parasites found in the smallest size class, four exhibited direct life cycles, whereas in fish of 20 cm (1-2 yr old) 6 of 11 species had indirect life cycles. In the largest class (41-50 cm), slightly less than half (15 of 34) of the species had indirect life cycles. By 20 cm, representatives of all the parasite groups, with the exception of microsporida, were found in olive rockfish. The prevalence rates of six parasite species and one parasite group increased significantly with increasing host length (Fig. 2). Seven species or species groups showed significant annual changes in prevalence (Fig. 3).

Discussion

Of the seven parasite species showing increasing prevalence with increasing host length, six (*Lepeophtheirus* sp., *Neobenedenia girellae, Microcotyle sebastis, Holobomolochus spinulus, Henneguya sebasta*, and the gallbladder myxozoans) had direct life cycles and one (*Hysterothylacium aduncum*) had an indirect cycle. A change in diet to-

TABLE 4.—Parasite species infecting five size classes of olive rockfish off Diablo Cove, Calif. See Table 1 for number of specimens per size class.

Host length cm TL (age in years)				
5-10 (0)	11-20 (1-2)	21-30 (1-4)	31-40 (4-10)	41-50 (7-20)
	Acanthocephala	Acanthocephala	Acanthocephala	Acanthocephala
	Corynosoma sp.	*Corynosoma* sp.	*Corynosoma* sp.	*Corynosoma* sp.
		Rhabdinorhynchidae gen. sp.	Rhabdinorhynchidae gen. sp.	Rhabdinorhynchidae gen. sp.
Cestoda	Cestoda	Cestoda	Cestoda	Cestoda
Tetraphyllidea	Tetraphyllidea	Tetraphyllidea	Tetraphyllidea	Tetraphyllidea
Copepoda	Copepoda	Copepoda	Copepoda	Copepoda
N. robusta	*H. spinulus*	*Caligus* sp.	*Caligus* sp.	*Caligus* sp.
C. parva	*Lepeophtheirus* sp.	*H. spinulus*	*C. pinguis*	*C. pinguis*
N. occidentalis		*Lepeophtheirus* sp.	*H. spinulus*	*H. spinulus*
		S. arcticus	*Lepeophtheirus* sp.	*Lepeophtheirus* sp.
			N. occidentalis	*N. occidentalis*
			S. arcticus	*S. arcticus*
	Digenea	Digenea	Digenea	Digenea
	D. cholaeum	*D. cholaeum*	*A. macfarlani*	*A. macfarlani*
	O. sebastodis	*L. gibbosus*	*D. cholaeum*	*D. cholaeum*
		L. exodicum	*L. gibbosus*	*L. gibbosus*
		O. sebastodis	*L. exodicum*	*L. exodicum*
		P. merus	*O. sebastodis*	*O. sebastodis*
		Podocotyle sp.	*P. merus*	*P. merus*
		T. lindbergi	*Podocotyle* sp.	*Podocotyle* sp.
			T. lindbergi	*T. lindbergi*
Monogenea	Monogenea	Monogenea	Monogenea	Monogenea
M. sebastis	*M. sebastis*	*M. sebastis*	*M. sebastis*	*M. sebastis*
	N. girellae	*N. girellae*	*N. girellae*	*N. girellae*
		T. marginata	*T. marginata*	*T. marginata*
	Nematoda	Nematoda	Nematoda	Nematoda
	Contracaecum sp.	*Anisakis* sp.	*Anisakis* sp.	*Anisakis* sp.
	H. aduncum	*Contracaecum* sp.	*Contracaecum* sp.	*Contracaecum* sp.
		H. aduncum	*H. aduncum*	*H. aduncum*
			Phocanema sp.	*Phocanema* sp.
	Protozoa (Myxozoa)	Protozoa (Myxozoa)	Protozoa (Myxozoa)	Protozoa (Myxozoa)
	H. sebasta	*C. sebasta*	*C. sebasta*	*C. sebasta*
		H. sebasta	*D. reginae*	*D. reginae*
		K. clupeidae	*H. sebasta*	*H. sebasta*
		L. informis	*K. clupeidae*	*K. clupeidae*
		L. longipes	*L. informis*	*L. informis*
		L. macrospora	*L. longipes*	*L. macrospora*
		M. incurvatum	*L. macrospora*	*L. sebasta*
		Z. ilishae	*L. sebasta*	*M. incurvatum*
			M. incurvatum	*Z. ilishae*
			Z. ilishae	
		Protozoa (Microsporida)	Protozoa (Microsporida)	Protozoa (Microsporida)
Total number of specimens:				
5	11	29	35	34

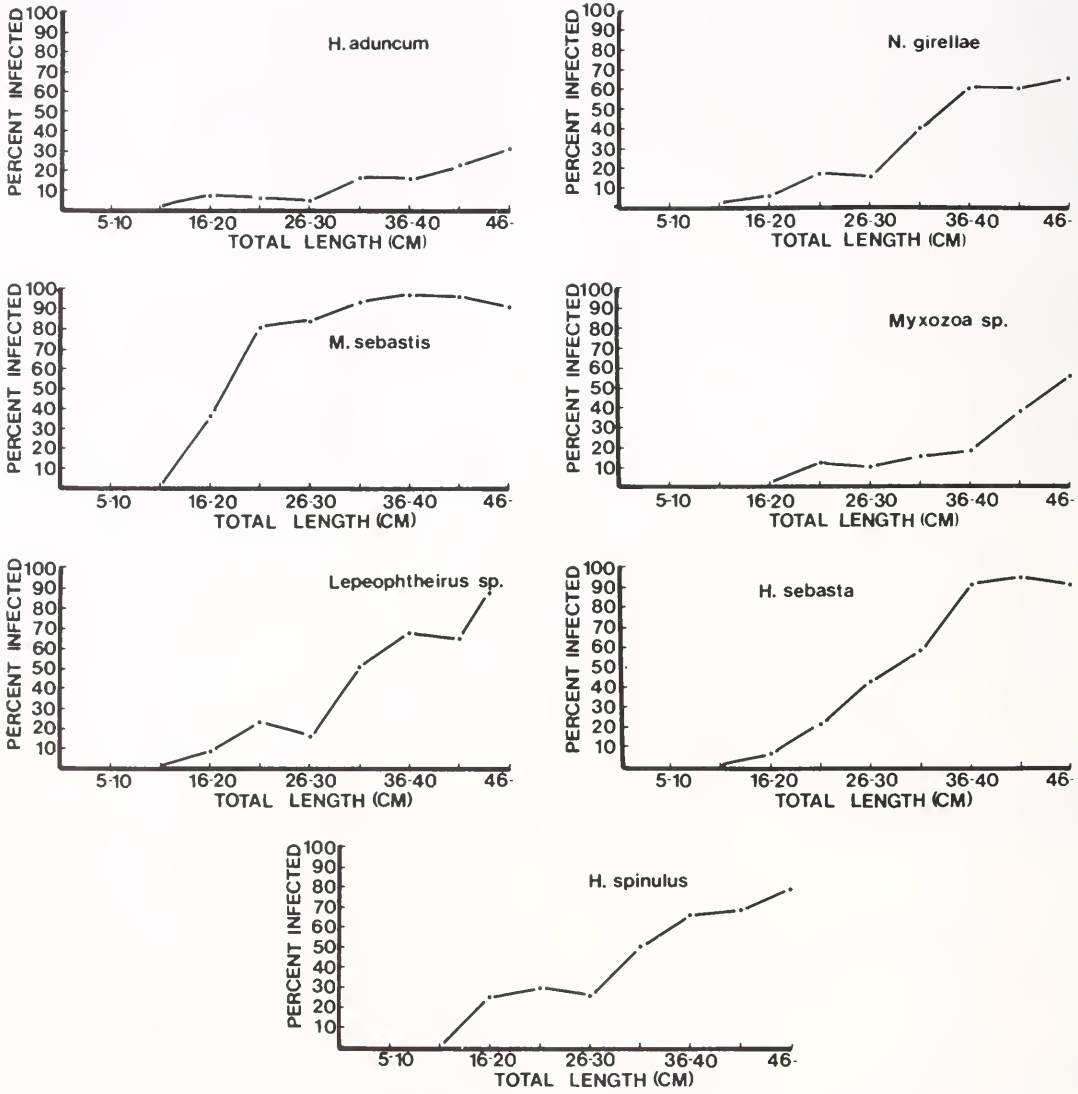

FIGURE 2.—The relationships between host length and percent prevalence of infection by seven parasite species from olive rockfish taken off Diablo Cove, Calif. All relationships show significant difference at $P \leq 0.05$. See Table 3 for numbers of fish examined in each length interval; see Table 1 for the number of specimens per size class.

ward fish and away from zooplankton (Love and Westphal 1981) probably accounts for the increase in *Hysterothylacium aduncum* infections, as fish are thought to be intermediate hosts for this species (Margolis 1970). The prevalence of *Clavella parva* was the opposite—it was found only in hosts <10 cm in length. *Clavella parva* attaches to dorsal, anal, and caudal fin rays. Perhaps structural barriers (such as ray diameter or surface characteristics) or increased water flow over the fins in larger fish prevent infection. Similar infection patterns were noted in *Sebastes alutus* and *S. caurinus* by Sekerak (1975).

Among species with seasonal patterns of infection, winter maximum infections were exhibited by *Lepeophtheirus* sp., *Holobomolochus spinulus*, the gallbladder myxozoans, and *Deretrema cholaeum*. The first three forms listed have direct life cycles. Olive rockfish are winter and early spring spawners (December-March) with internal fertilization occurring from November to February. It is possible that these parasites time their

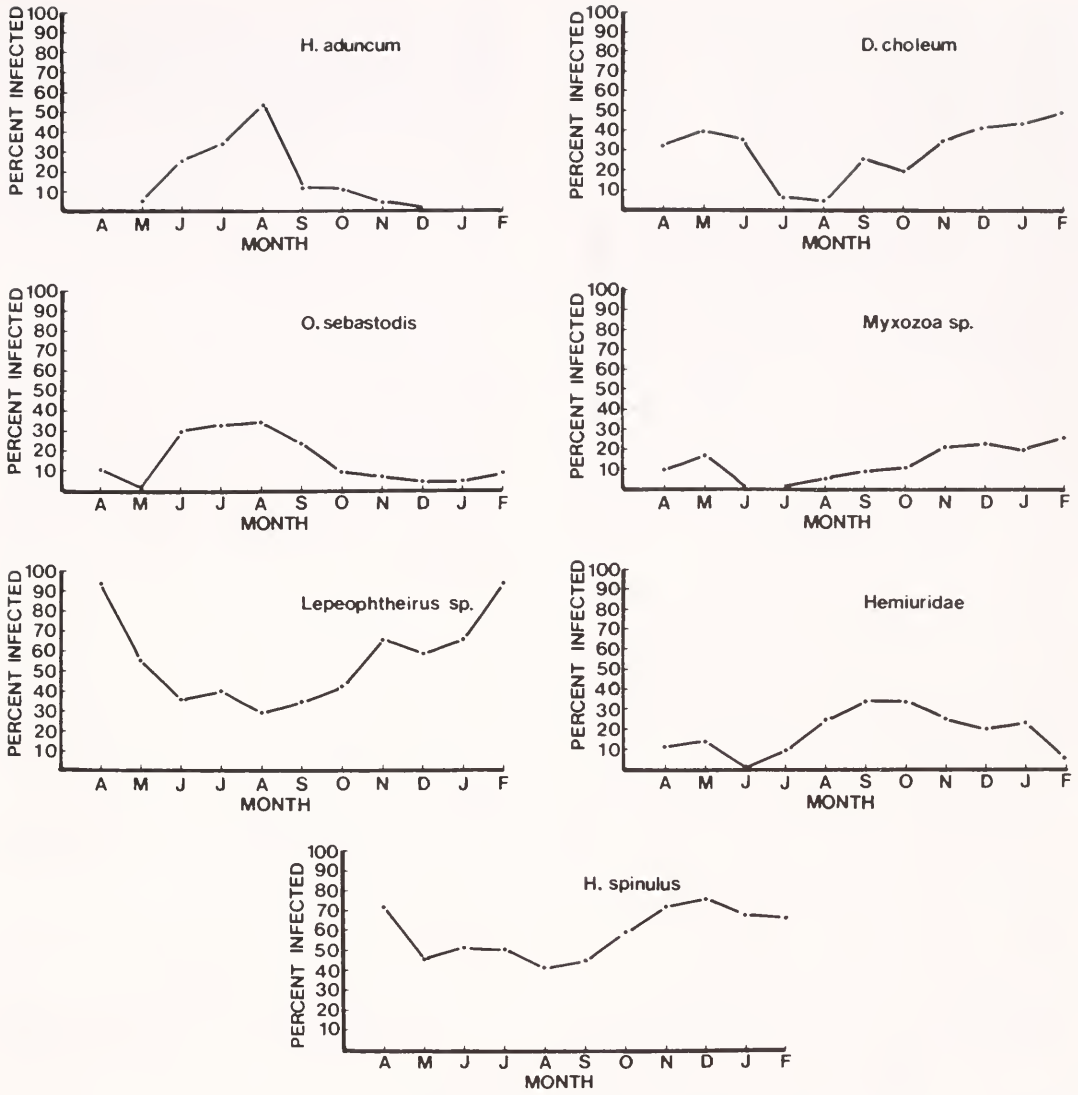

FIGURE 3.—The relationships between month of capture and percent prevalence of infection by seven parasite species from olive rockfish taken off Diablo Cove, Calif. All relationships show significant differences at $P \leq 0.05$. See Table 1 for the number of specimens per month.

movements and reproduction to coincide with that period when their hosts may be at closest proximity with each other. This phenomenon was observed between the Monogenea, *Dactylogyrus vastator* and *Mazocraes alosae*, and their respective hosts, *Cyprinus carpio* and *Alosa sapidissima* (Kennedy 1975).

Parasites with maximum prevalence during other periods all had indirect life cycles. The hemiurid trematode infections peaked in autumn, *Opechona sebastodis* in summer, and *Hysterothylacium aduncum* was most abundant in April and August. Seasonality among hemiurids has been reported by Shotter (1973) in whiting, *Odontogadus merlangus*, of the Irish Sea and in staghorn sculpin, *Leptocottus armatus*, from Oregon by Burreson and Olson (1974). In both cases infections were greatest in late summer or early fall.

The infection patterns we observed may reflect differences in the oceanographic conditions off central California. Water conditions in this region

may be divided into two periods (Bakun 1973), "upwelling" (March-August) and "oceanic" (September-February). Upwelling periods are characterized by an increase in the flow of nutrient-rich bottom water to the surface and increased plankton abundance. Olive rockfish food habits change with these seasons (Love and Westphal 1981). Zooplankton (particularly pelagic tunicates and euphausids), squids, and juvenile rockfish are eaten in greater quantity during the upwelling season, due to increased availability.

The secondary intermediate hosts for hemiurids and *Opechona sebastodis* are planktonic (Shotter 1973; Yamaguti 1971), and the prevalence increase may be due to greater seasonal predation on the planktonic intermediate host. Similarly, as fish are possible intermediate hosts of *Hysterothylacium aduncum*, its infection pattern may reflect the rockfish's heavy predation on juvenile rockfish during the upwelling period.

All of the parasite species infecting olive rockfish infect at least some other rockfish species. The genus *Sebastes* has exhibited an explosive radiation in the northeast Pacific (Kabata 1970). This rapid speciation has occurred relatively recently, probably during and after the Miocene[1]. Despite extreme morphological and behavioral differences between species, there is little species specificity among rockfish parasites, perhaps because of the rapidity of the host speciation events. Eighty-nine adult metazoan parasites have been reported from rockfishes between Alaska and California (Love and Moser 1983). Of these, 30 species have been found to infect only *Sebastes* spp. and 10 of the 89 species were unique to one host species.

Some of this specificity may be a function of host behavior or habitat preference rather than physiological differences (Kennedy 1975) between rockfish hosts. Holmes (1971) found that a rockfish's proximity to rocky reefs influenced the prevalence of the digenetic trematodes *Psettarium sebastodorum* and *Aporocotyle macfarlani*. *Aporocotyle macfarlani* was found in species associated with inshore reefs, *P. sebastodorum* in those hosts living away from rocks or in deeper waters. Olive rockfish, limited to relatively shallow reefs, occasionally harbored *A. macfarlani* but was not infected with *P. sebastodorum*.

Some parasites, particularly ectoparasites, are widespread among rockfishes. For example, *Microcotyle sebastis* has been reported from 22 species, *Naobranchia occidentalis* from 13, *Neobranchiella robusta* from 21, and *Chondracanthus pinguis* from 19. These and other parasites exhibit an extensive latitudinal range, considerably longer than some of their hosts. Further surveys of those species only lightly studied (such as *Sebastes eos*, *S. melanostomus*, *S. mystinus*, *S. rastrelliger*, and *S. semicinctus*) will show that some of those parasites infect nearly all rockfish species.

[1]W. Eschmeyer, California Academy of Science, Golden State Park, San Francisco, CA, pers. commun. 1982.

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SENSITIVITY OF THE POPULATION GROWTH RATE TO CHANGES IN SINGLE LIFE HISTORY PARAMETERS: ITS APPLICATION TO *MYA ARENARIA* (MOLLUSCA:PELECYPODA)

The question of sensitivity analyses in demographic studies was first addressed by Lewontin (1965), and since that time, Hamilton (1966), Demetrius (1969), Emlen (1970), Goodman (1971), Keyfitz (1971), and Mertz (1971) have made contributions in the area. More recently, Caswell (1978) has given general formulae for the sensitivity of the population growth rate (λ) derived from a Leslie model, to changes in single life history parameters written as formulae involving eigenvectors of the Leslie matrix. The application of such analyses to the study of the population dynamics of commercially important species can provide useful information to those interested in resource management.

The work presented here describes the sensitivity of the population growth rate to changes in the settlement rate (Brousseau et al. 1982) and in the age-specific fecundity and survivorship rates of the soft-shell clam, *Mya arenaria*, using a modified Leslie matrix model and an extension of the sensitivity formulae derived by Caswell (1978). Predictions concerning the effect that changes in these life history parameters will have on λ and the implications of these results to the management of this species are discussed.

Results

Leslie Model

The population of females is divided into n age classes. The Leslie matrix, M, has the following form:

$$M = \begin{bmatrix} a_1 & a_2 & a_3 & \dots & a_{n-1} & a_n \\ r_s b_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & b_2 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & & b_{n-1} & 0 \end{bmatrix} \quad (1)$$

Here, a_i is the mean number of female eggs produced annually by a female in class i (age $i-1$ to i); assuming a one-to-one sex ratio, a_i is one-half the total egg production. The parameter b_i is the probability of a clam in class i surviving to class 2, 3, ..., $n-1$. The survivorship from age class 1 to age class 2 is divided into 2 factors, r_s and b_1. The factor r_s is the settlement rate or the probability that an egg will survive the planktonic larval stage and develop into a clam with a 2 mm shell length (0-2 mo of age); b_1 is the probability that a clam with a 2 mm shell length will survive the remainder of the year (about 10 mo). If x is a column vector with n components such that x_i is the number of females in age class i immediately following spawning, then Mx represents the population 1 yr from now.

For benthic marine invertebrates possessing planktotrophic larval stages, the events surrounding metamorphosis and settlement are extremely

important for the development and maintenance of species populations. Settlement rates are notoriously variable in nature, however, making it impossible to determine a fixed r_s and hence a fixed λ. For this reason, we have studied sensitivities over a range of λ's (0.25-3.0). Values of a_i and b_i used for *Mya arenaria* are empirically derived (Brousseau 1978a, b).

Sensitivity Formulae

The population growth rate, λ, is the eigenvalue of M with maximum modulus. In general, λ is unique and is a positive real number. This follows from the Perron-Frobenius Theorem, which may be referenced, for example, in Demetrius (1969). The sensitivity of λ to a life history parameter is defined to be the derivative of λ with respect to that parameter.

Following Caswell (1978), let u and v be column vectors satisfying

$$Mv = \lambda v \tag{2}$$

$$u'M = \lambda u' \tag{3}$$

$$(u, v) = 1 \tag{4}$$

where u' denotes the transpose of u, and $(\cdot,\cdot)$ denotes inner product. Statement (2) indicates that v is a right eigenvector, while Statement (3) indicates that u is a left eigenvector, each associated with λ. Statement (4) is used as a normalization device. While Statements (2) through (4) do not define u and v uniquely, they are sufficient to make the sensitivity formulae below well defined. Explicit calculations for the components of vectors u and v start with

$$u_1 = 1$$

$$u_i = \sum_{j=1}^{n} a_j b_{j-1} \ldots b_i \lambda^{-(j-i+1)}, \; i > 1 \tag{5}$$

and

$$v_1 = 1$$

$$v_i = \lambda^{-i} b_{i-1} \ldots b_1 r_s, \; i > 1 \tag{6}$$

and then normalize using Statement (4) above.

With these definitions, Caswell (1978) shows

$$d\lambda/dm_{ij} = u_i v_j, \quad i,j = 1 \ldots n, \tag{7}$$

where m_{ij} is the parameter in the i,j position of the Leslie matrix M, u_i is the ith component of vector u_1, and v_j is the jth component of vector v. Of course, the components of M of interest to us are those in the first row (the fecundity parameters) and those in the main subdiagonal (the survivorship parameters). Further, since position m_{21} equals $r_s b_1$ in our notation, the sensitivity formulae become

$$d\lambda/da_i = u_1 v_i, \quad i = 1, 2, \ldots, n \tag{8}$$

$$d\lambda/db_i = u_{i+1} v_i, \quad i = 2, 3, \ldots, n-1 \tag{9}$$

$$d\lambda/db_1 = r_s \, d\lambda/dm_{21} = r_s u_2 v_1 \tag{10}$$

$$d\lambda/dr_s = b_1 \, d\lambda/dm_{21} = b_1 u_2 v_1. \tag{11}$$

In particular, notice that λ is not equally sensitive to r_s and b_1 unless the two values are equal.

For the present study, we hold a_i and b_i fixed and allow λ to vary. The settlement rate, r_s, then becomes a function of λ, specifically,

$$r_s = (\lambda - a_1)/(\lambda^{-1} a_2 b_1 + \lambda^{-2} a_3 b_2 b_1 + \ldots + \lambda^{-n+1} a_n b_{n-1} \ldots b_1), \tag{12}$$

and is used in the Leslie matrix, M. We then compute u and v satisfying Statements (2)-(4) for the given λ, and the sensitivity values Statements (8)-(11).

Relationships among the sensitivity formulae above have been derived by Demetrius (1969) and Caswell (1978). Of particular interest are

$$\begin{aligned} &d\lambda/da_i > d\lambda/da_j, \quad i < j, \lambda > 1 \\ &d\lambda/da_i < d\lambda/da_j, \quad i < j, \lambda < 1 \end{aligned} \tag{13}$$

$$b_i \, d\lambda/db_i > b_j \, d\lambda/db_j, \quad i < j \tag{14}$$

$$\frac{d\lambda/db_1}{d\lambda/da_1} = \frac{\lambda - a_1}{b_1}. \tag{15}$$

Statement (13) can actually be made stronger, as proven by Demetrius (1969, Statement (8)); Statement (14), in the case $i = 1$, and Statement (15) follow from Demetrius (1969, Statement (11)) and Caswell (1978, Statement (22)); and Statements (5), (10), and (12) above.

Calculation of Sensitivity Values

Settlement Rate.—Using the data in Table 1, the sensitivity of the population growth rate of

TABLE 1.—Life history statistics used in the derivation of the Leslie matrix for *Mya arenaria* (data from Brousseau 1978a, b).

Age (yr)	Age class	Shell length (mm)	Fecundity[1] (a_i)	Probability of survival (b_i)
0-1	1	2.0-29.9	0.0	0.177
1-2	2	30.0-44.9	3,744.0	0.912
2-3	3	45.0-59.9	17,170.0	0.904
3-4	4	60.0-64.9	31,159.0	0.952
4-5	5	65.0-69.9	39,957.0	0.949
5-6	6	70.0-74.9	50,341.0	0.969
6-7	7	75.0-79.9	62,450.0	0.984
7+	8+	80.0-84.9	76,465.0	0.911

[1]Fecundity = number of female eggs produced per individual assuming a 1:1 sex ratio.

Mya arenaria to changes in the settlement rate (r_s) can be calculated. Results are summarized in Table 2 for a range of values of λ. As expected, r_s increases as the population growth rate increases, while the sensitivity of λ to changes in r_s decreases as λ increases. The population growth rate, λ, is far more sensitive to changes in r_s than it is to changes in any other single life history parameter. A further discussion of this point is given below.

TABLE 2.—Sensitivity of various population growth rates (λ) to changes in the settlement rate (r_s). The intrinsic growth rate = $\log \lambda$.

Population growth rate (λ)	Intrinsic growth rate	Settlement rate (r_s)	Sensitivity of λ to r_s
0.25	−1.386	6.535×10^{-12}	3.291×10^{9}
0.5	−0.693	1.700×10^{-8}	2.697×10^{6}
0.75	−0.288	1.139×10^{-6}	6.822×10^{4}
1.0	0.0	[1]1.462×10^{-5}	8.562×10^{3}
1.25	0.223	7.320×10^{-5}	2.646×10^{3}
1.5	0.405	2.141×10^{-4}	1.307×10^{3}
1.75	0.560	4.618×10^{-4}	8.158×10^{2}
2.0	0.693	8.310×10^{-4}	5.765×10^{2}
3.0	1.099	3.702×10^{-3}	2.454×10^{2}

[1]r_s = Equilibrium settlement rate, $r_{s\,eq}$.

Fecundity and Other Survivorship Rates.—The sensitivity of λ to changes in fecundity are illustrated in Figure 1. Under equilibrium conditions ($\lambda = 1.0$), sensitivity to fecundity changes over the reproductive life span of the individual are slight. If the population is actually growing ($\lambda > 1.0$), the magnitude of the sensitivity to changes in the fecundity decreases with increasing age, while the reverse is true if the population is actually declining ($\lambda < 1.0$). This follows from Statement (13). For declining populations this is probably due to the combined effects of an increasing reproductive value with increasing age and a shift in the age structure to older individuals as the population declines.

The sensitivity of λ to changes in survivorship parameters other than r_s is illustrated in Figure 2, where it is evident that λ is more sensitive to changes in b_1, the survivorship of an individual from 2 mo to 1 yr of age, than to other values of b_i for $i > 1$. As above, these curves illustrate a general result. Since b_i is $> b_1$ for $i > 1$ in the *Mya arenaria* model, $d\lambda/db_1$ is $> d\lambda/db_i$ using Statement (14).

By comparing Figures 1 and 2, it seems evident that the population growth rate is more sensitive to changes in survivorship than to changes in fecundity. This result may be made precise if the population is actually growing ($\lambda > 1$), since using Statements (13) and (15) it follows that $d\lambda/db_1$ is $> d\lambda/da_i$ for all values of i. Finally, by examining Statements (10) and (11), it is clear that λ is more sensitive to r_s than to b_1 for the *Mya arenaria* model as long as r_s is $< b_1$. Hence, λ is more sensitive to r_s than to all other survivorship parameters, and, at least for growing populations, more sensitive to changes in r_s than to any other fecundity parameter as well.

Discussion

Fisher (1958) in his fundamental theorem of

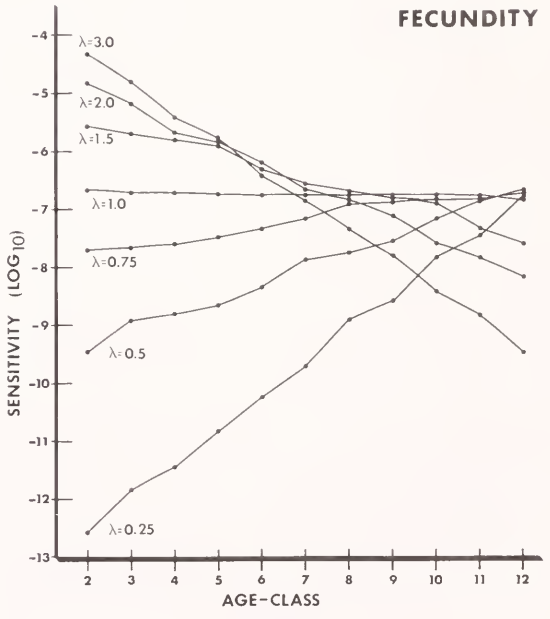

FIGURE 1.—Sensitivity of a range of λ's (0.25-3.0) to changes in the fecundity (a_i) of *Mya arenaria* in each age class. The first age class is not included since *Mya arenaria* are not mature until after the first year of age.

natural selection states that natural selection will favor genotypes which increase the population growth rate, λ. Since the λ for a population is based on the life history parameters of age-specific fecundity and survivorship, the greater the sensitivity of λ to changes in a particular life history value, the greater the potential for effecting evolutionary change through that parameter.

Existing evidence indicates that population growth rate is more sensitive to changes in survival rates than to changes in reproductive output. Cole (1954) reached this conclusion when he suggested that in species with repeated reproduction and relatively large litter size, there is little selection pressure favoring increased fecundity. Similarly, Caswell (1978) using Hartshorn's (1975) data for *Pentaclethra macroloba*, a tropical rain forest tree, illustrates by the use of models, that, for this species, population growth rate is more sensitive to changes in growth and survival than to changes in fecundity. The data reported here for *Mya arenaria* follow the same pattern; λ is relatively insensitive to changes in egg production. The most interesting results of the sensitivity analyses are produced by changes in the survivorship parameters.

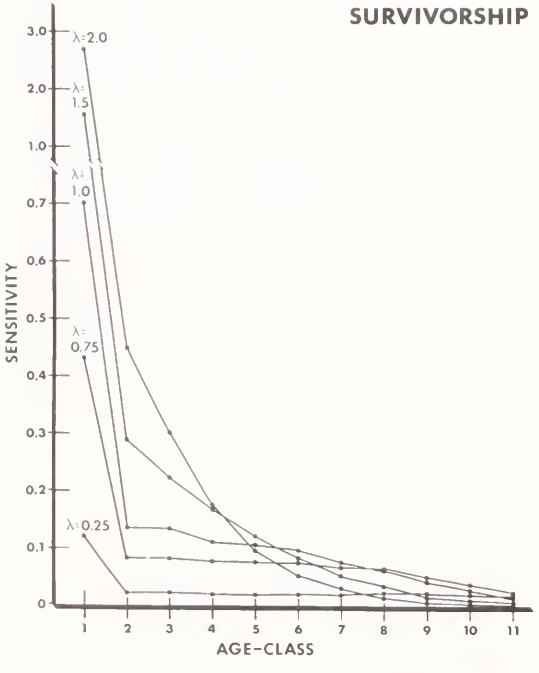

FIGURE 2.—Sensitivity of a range of λ's (0.25-2.0) to changes in the survivorship (b_i) of *Mya arenaria* in each age class.

Based on our analyses, two important generalizations can be made regarding the sensitivity of λ. First, whenever $r_s < b_1 < b_i$, the population growth rate will be more sensitive to changes in r_s than to changes in any of the other survivorship parameters. Second, in growing populations, i.e., where $\lambda > 1$, λ is always most sensitive to changes in the settlement rate. In terms of Deevey's (1947) categorization of generalized survivorship curves, the relationship $r_s < b_1 < b_i$ is probably operative in most Type III curves, which are characterized by extremely heavy mortality early in life. Consequently, these generalizations are of interest since the types of life history features exhibited by *Mya arenaria* are likely to be common to other species of marine organisms, many of which are also commercially important.

On a more practical level, the ability to identify those life history stages to which the population growth rate is most sensitive may serve as a useful tool in directing the efforts of those interested in shellfish management. For instance, the models described here indicate that larval settlement is the most critical stage in *Mya arenaria*'s life history. Developing a better understanding of the factors surrounding metamorphosis and settlement and implementing a method for inducing spatfall would probably be the single most effective way to increase clam yields.

Another area for consideration centers around the survivorship of the first year class. Since the population growth rate of *Mya arenaria* is also very sensitive to changes in the b_1 parameter, a second way to increase clam productivity is to improve the survivorship of clams 2 mo to 1 yr of age (ca. 2-25 mm shell length). This age class corresponds to that postlarval stage in *Mya arenaria* which is the most vulnerable to both biotic (predation) and abiotic (wash-out, temperature and salinity fluctuations) factors in the environment.

The practice of transplanting juvenile *Mya arenaria* from one flat to another has been used by managers since the turn of the century (Belding 1930) in efforts to 1) replenish depleted clam beds or 2) reduce densities in "overcrowded" beds. Currently, there is a renewed interest in this procedure[1] even though in the past, these efforts have met with varying degrees of success (Belding 1930; Turner 1951; Smith et al. 1955). The

[1]D. E. Wallace, Director, Department of Marine Resources, State of Maine, Boothbay Harbor, ME 04538, pers. commun. April 1983.

reasons may be related to the vulnerability of juveniles as discussed above.

To insure success with transplanting techniques, it is essential to reduce mortality among transplanted clams either by protecting them from significant sources of mortality in the field or by retaining them in protective "nurseries" until they pass this critical phase. Past attempts to protect juveniles in the field by building fences to exclude predators have proven costly, difficult to carry out, and unreliable (Smith et al. 1955). More promising are recent advances in aquaculture techniques for commercially important bivalves. By employing "nurseries" for the young and field "grow-out" procedures for adults, sources of juvenile mortality can be reduced while still utilizing natural sources of food during the greater part of the individual's growth period.

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THE OCCURRENCE OF PISCINE ERYTHROCYTIC NECROSIS (PEN) IN THE SEA LAMPREY, *PETROMYZON MARINUS*, FROM SEVERAL MAINE LOCALITIES

The sea lamprey, *Petromyzon marinus*, is an anadromous fish found in the North Atlantic Ocean from Iceland and northern Europe to northwestern Africa, and from the Grand Banks and the Gulf of St. Lawrence to Florida (Hubbs and Lagler 1949). The sea lamprey has adopted an entirely freshwater life cycle in the Great Lakes where it has seriously depleted fish populations (Everhart 1976).

The lamprey feeds on other fishes by hanging on with its sucking mouth. Once attached, it

rasps its victim with its tongue to obtain nourishment in the form of blood and other body fluids (Everhart 1976). Secretions from a pair of relatively large salivary glands below the tongue retard coagulation of host blood and also dissolve tissue (Lagler et al. 1977). Bigelow and Schroeder (1953) reported that in saltwater, lampreys have been found preying on mackerel, shad, cod, haddock, pollock, salmon, basking sharks, various anadromous herrings, swordfish, hake, sturgeons, and eels.

Piscine erythrocytic necrosis (PEN), a condition characterized by cytoplasmic inclusions and nuclear abnormalities in erythrocytes, has been shown to be of viral etiology in the Atlantic cod, *Gadus morhua*, and Atlantic herring, *Clupea harengus harengus*, from the Atlantic coast and the chum salmon, *Oncorhynchus keta*, pink salmon, *O. gorbuscha*, and Pacific herring, *Clupea harengus pallasi*, from the Pacific coast of North America (Walker 1971; Appy et al. 1976; Walker and Sherburne 1977; Philippon et al. 1977; Reno et al. 1978; Evelyn and Traxler 1978; MacMillan and Mulcahy 1979). In addition, PEN has been reported in 15 other marine teleost species from the Atlantic coast of North America, but confirmation as to viral etiology has not been made (Laird and Bullock 1969; Walker and Sherburne 1977; Sherburne 1977; Sherburne and Bean 1979). PEN has also been evident in the Atlantic mackerel, *Scomber scombrus*, (Sherburne, unpubl. data).

This report documents the first finding of PEN in a host from the most primitive group of fishes, the Agnatha.

Materials and Methods

A total of 142 lampreys, *Petromyzon marinus*, was obtained for blood analysis from 5 Maine localities (Table 1). Live lampreys were measured for total length and sexed. Slides were prepared by severing the caudal peduncle and taking the blood into a heparinized capillary tube, from which a small drop of blood was placed on a microscope slide and the smear made. Air-dried smears were Giemsa-stained and thoroughly examined for PEN using light microscopy at 1000× magnification.

Results

Of the total lampreys sampled in this study, 50.7% (72/142) had red cell lesions characteristic of PEN (Table 1). By light microscopy, PEN lesions of lamprey red cells often showed the nuclear chromatin condensed into round blebs, and there was evidence of nuclear vacuolization (Fig. 1). Red acidophilic cytoplasmic inclusions were occasionally seen in an infected cell (Fig. 2).

Individual infections were light, with only one or two infected cells evident in most smears. Among the 72 infected lampreys, the severest infection involved 2% of the red cells and it occurred in a 69 cm male from the Coopers Mills Fishway on 26 May 1980.

From a total of 139 lampreys sexed, 47.9% of the males and 53.0% of the females had PEN. The smallest infected lamprey was 62.4 cm (24.6 in) long; the largest was 81.5 cm (32.1 in).

TABLE 1.—The occurrence of piscine erythrocytic necrosis (PEN) in the sea lamprey, *Petromyzon marinus*, from several Maine localities.

Sample source	Location	Date	PEN		Mean length, SD, and range (cm) of sample
			Incidence in sample	Percent incidence	
Nequasset Lake Fishway	Woolwich	16 June 1977	0/2	0.0	67.0 ± 1.4 (66.0 – 68.0)
Kennebunk River	Kennebunk	11 May 1978	1/1	100	63.1 (63.1)
Sheepscot Pond Fishway	Palermo	9 June 1978	1/3	33.3	65.4 ± 2.7 (62.5 – 67.8)
Sheepscot Pond Fishway	Palermo	15 June 1978	0/1	0.0	65 (65)
Sheepscot River Coopers Mills Fishway	Coopers Mills	30 May 1979	5/28	17.8	72.4 ± 4.1 (62.4 – 82)
Sheepscot River Coopers Mills Fishway	Coopers Mills	26 May 1980	34/46	73.9	72.4 ± 4.6 (66 – 88.5)
Sheepscot River Head Tide	Alna	6 June 1983	7/18	38.8	71.4 ± 4.3 (64.8 – 78.8)
Sheepscot River Coopers Mills Fishway	Coopers Mills	13 June 1983	1/4	25.0	73.5 ± 2.3 (70.0 – 75.0)
Sheepscot River Head Tide	Alna	14 June 1983	5/8	62.5	70.6 ± 3.4 (66.7 – 76.0)
Sheepscot River Head Tide	Alna	15 June 1983	18/31	58.1	70.5 ± 4.0 (63.5 – 78.0)

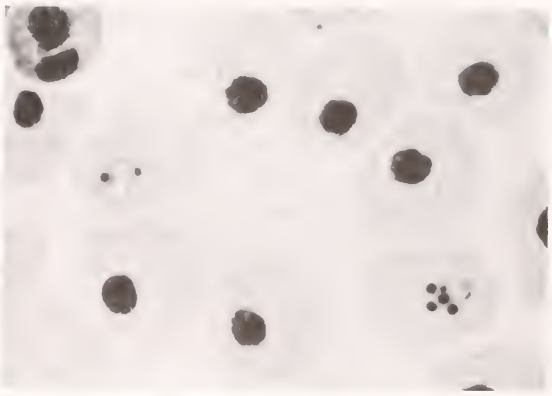

FIGURE 1.—Sea lamprey erythrocytes with PEN lesions. Infected cells show characteristic chromatin condensation with evidence of nuclear vacuolization. From a female lamprey 80 cm in total length from the Coopers Mills Fishway, Coopers Mills, Me., on 26 May 1980. Sea lamprey erythrocytes are rounded in shape in contrast to most other fish species which have elliptical shaped red cells.

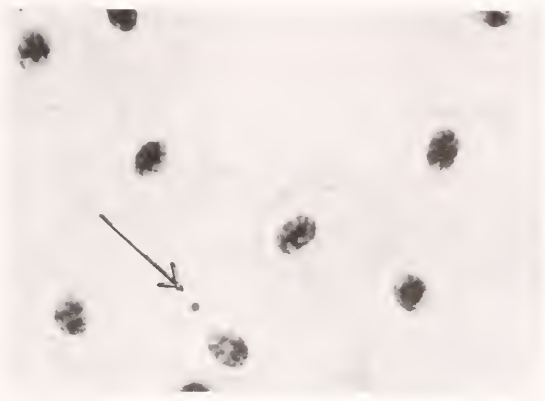

FIGURE 2.—Red acidophilic inclusions are occasionally seen in PEN infected sea lamprey erythrocytes. From a female lamprey 67.8 cm in total length from the Sheepscot Pond Fishway, Palermo, Me., on 9 June 1978.

Discussion

I prefer to use the term PEN in species where the cellular pathology has not yet been confirmed as associated with a virus, and viral erythrocytic necrosis (VEN) after confirmation. By light microscopy, PEN lesions of lamprey red cells resemble those of VEN-infected Atlantic cod. As with alewives, *Alosa pseudoharengus*, (Sherburne 1977) and smelt, *Osmerus mordax*, (Sherburne and Bean 1979), lampreys have a relatively high percentage of individuals affected with PEN, but individual infections are very light.

The blood of the sea lamprey must be examined by electron microscopy to determine if the PEN seen is an ICDV infection. Unfortunately, the individual infections observed in this study were so light as to preclude their detection by electron microscopy. Consequently, viral etiology of the condition still remains to be confirmed.

Fish obtained from lakes where alewives spawn have shown typical PEN lesions (Sherburne, unpubl. data), but whether alewives contribute to this is unknown. MacMillan and Mulcahy (1979) reported transferring VEN to chum salmon, *Oncorhynchus keta*, and brook trout, *Salvelinus fontinalis*, by waterborne virus. Perhaps infected anadromous species can transmit PEN to freshwater species via body fluids such as urine and reproductive products as well as by direct contact.

Lampreys could conceivably transmit PEN to a variety of marine and freshwater species because of their feeding habits, their diversity of prey, and their ability to become adapted to an entirely freshwater environment. The high prevalence of infection and the low intensity of infection suggest that lampreys might readily spread the infection without suffering a high mortality rate from PEN.

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ERRATA

Fishery Bulletin: Vol. 81, No. 3

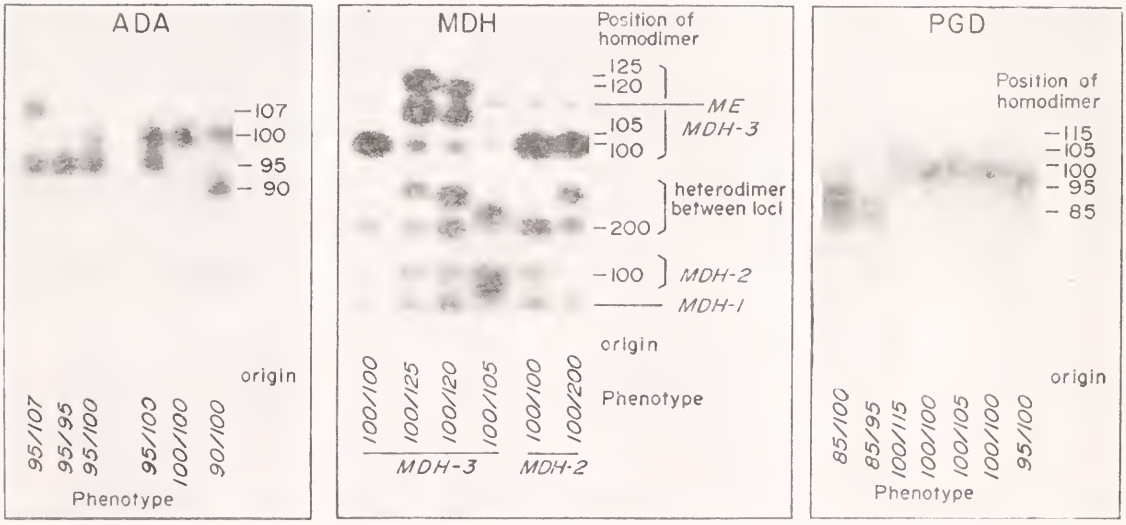
Livingston, P. A., "Food habits of Pacific whiting, *Merluccius productus*, off the west coast of North America, 1967 and 1980," p. 629-636.

Page 635, Equation (2) should read: $R = 0.0416e^{0.105T.}$

Fishery Bulletin: Vol. 81, No. 4

Grant, W. S., R. Bakkala, F. M. Utter, D. J. Teel, and T. Kobayashi, "Biochemical genetic population structure of yellowfin sole, *Limanda aspera*, of the North Pacific Ocean and Bering Sea," p. 667-677.

Page 672, Figure 2, the top portion should read:



Sherman, K., J. R. Green, J. R. Goulet, and L. Ejsymont, "Coherence in zooplankton of a large northwest Alantic ecosystem," p. 855-862.

Pages 858 and 889 should read:

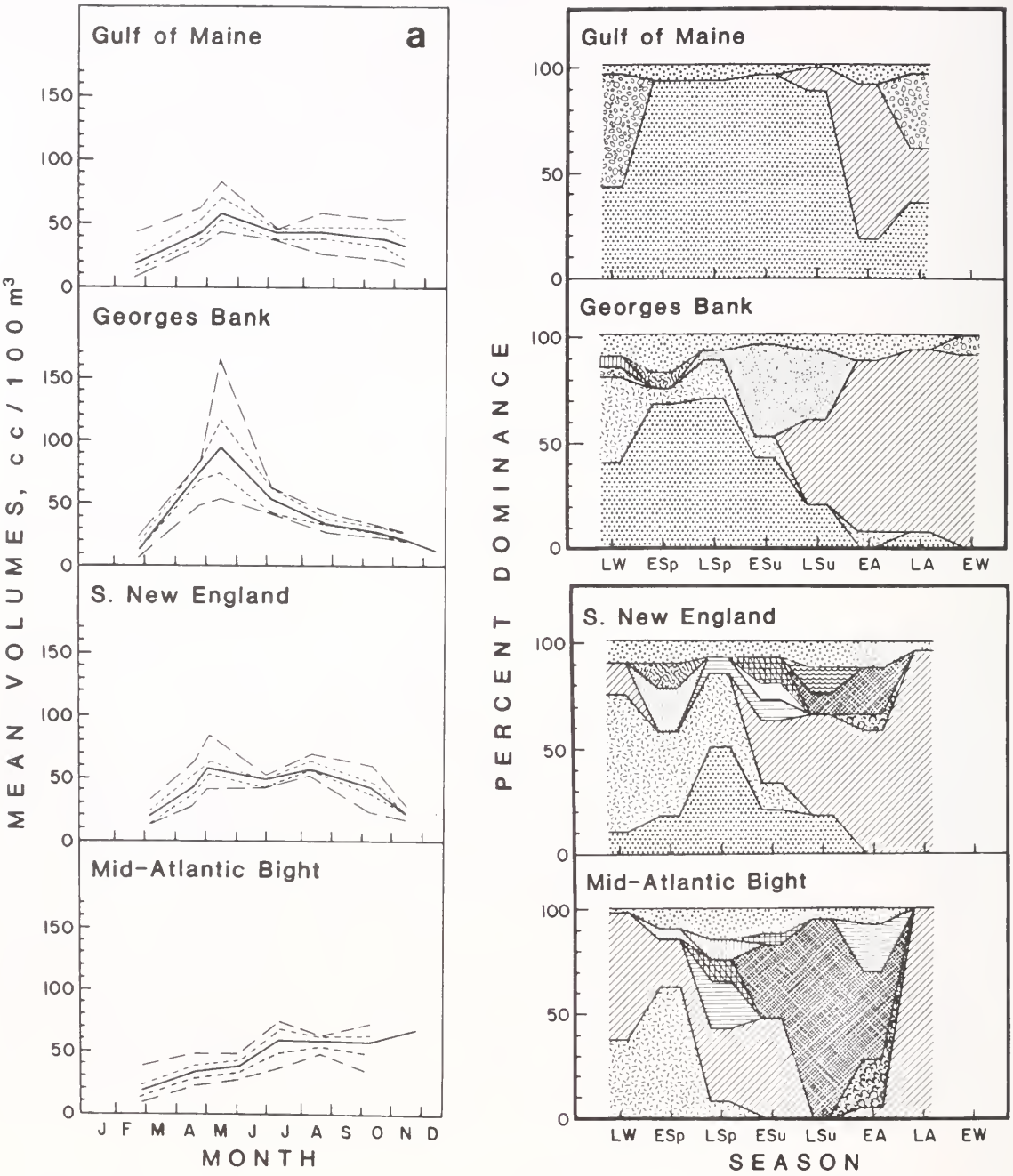


FIGURE 2.—Patterns of zooplankton in four northeastern U.S. continental shelf subareas—Gulf of Maine, Georges Bank, Southern New England, and the Mid-Atlantic Bight. (a) Seasonal patterns in mean zooplankton standing stock (cc/100 m^3) for the 5-yr MARMAP time series. Solid line represents the mean, short dashed line is one standard duration, and long dashed line is the range.

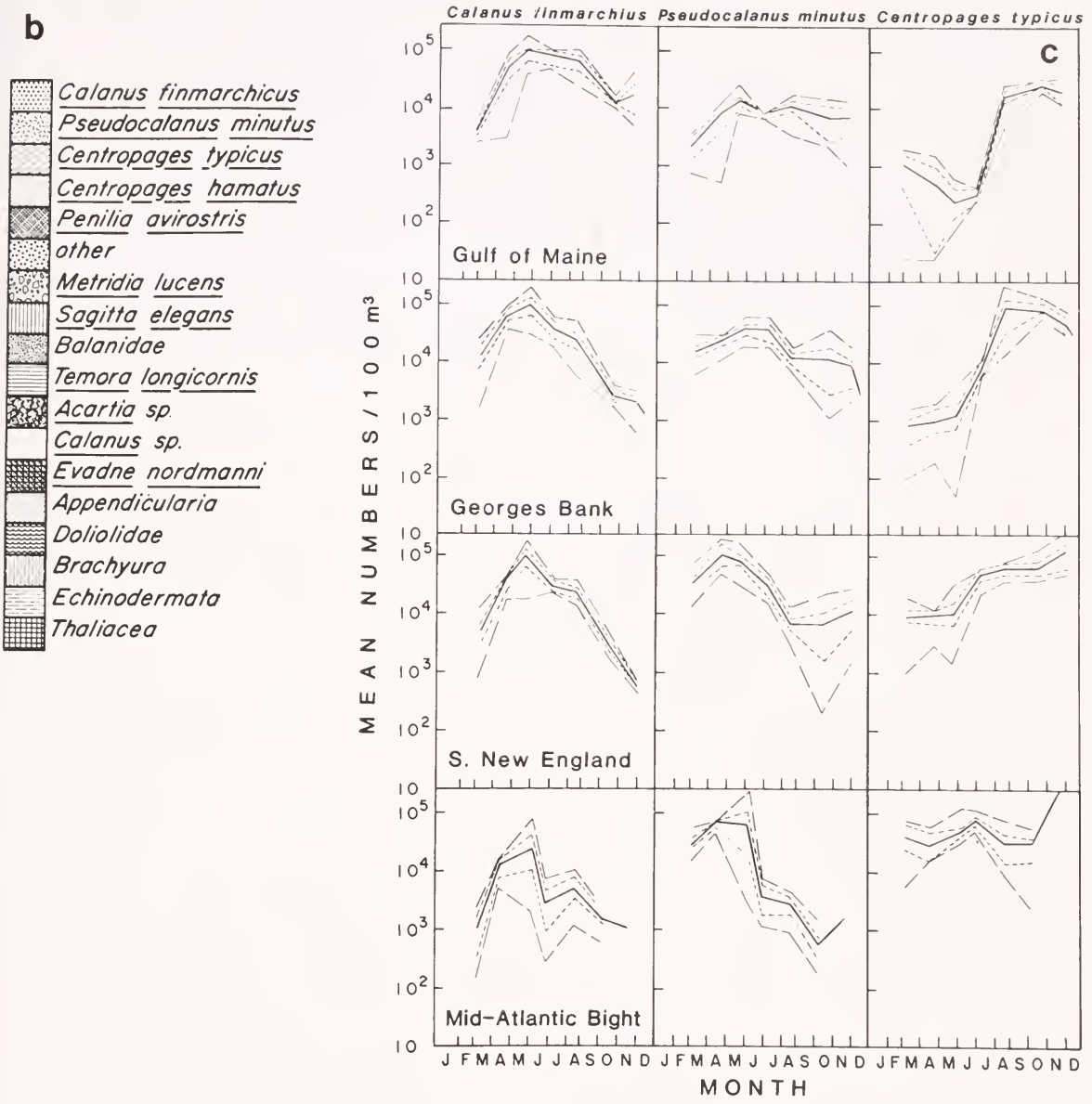


FIGURE 2.—*Continued*—(b) Seasonal patterns of dominance of zooplankters by subarea shown as a percentage of the samples with a dominant taxon in the 5-yr MARMAP time series. LW = late winter, ESp = early spring, ESu = early summer, EA = early autumn, LA = late autumn, and EW = early winter. (c) Seasonal pulses in abundance of the three dominant copepod species *Calanus finmarchicus*, *Pseudocalanus minutus*, and *Centropages typicus* (No./100 m^3) in each of the subareas for the 5-yr time series. Solid line represents the mean, short dashed line is one standard duration, and long dashed line is the range.

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CONTENTS

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MORPHOLOGY, SYSTEMATICS, AND BIOLOGY OF THE SPANISH MACKERELS (*SCOMBEROMORUS*, SCOMBRIDAE)

BRUCE B. COLLETTE[1] AND JOSEPH L. RUSSO[2]

ABSTRACT

The Spanish mackerels and seerfishes of the genus *Scomberomorus* constitute the most speciose group of the 44 genera in six families that comprise the suborder Scombroidei. As in higher scombrids, *Scomberomorus*, *Acanthocybium*, and *Grammatorcynus* have a well-developed median keel on the caudal peduncle, but there is no bony support as is present in the Sardini and Thunnini. *Acanthocybium* and *Scomberomorus* share 17 osteological characters and are considered sister-groups. The relationships of *Grammatorcynus* are not clear but it is clearly more primitive than *Scomberomorus*; therefore, we have used it as the outgroup for a cladistic analysis of *Scomberomorus*.

Scomberomorus differ from all other scombrids in having a spatulate anterior extension of the vomer. There are 18 species in the genus, nearly 40% of the 49 species of scombrids: Eastern Atlantic—*tritor* (Cuvier); western Atlantic—*brasiliensis* Collette, Russo and Zavala-Camin, *cavalla* (Cuvier), *maculatus* (Mitchill), and *regalis* (Bloch); eastern Pacific—*concolor* Lockington and *sierra* Jordan and Starks; and Indo-West Pacific—*commerson* (Lacepède), *guttatus* (Bloch and Schneider), *koreanus* (Kishinouye), *lineolatus* (Cuvier), *munroi* Collette and Russo, *multiradiatus* Munro, *niphonius* (Cuvier), *plurilineatus* Fourmanoir, *queenslandicus* (Macleay), *semifasciatus* (Macleay), and *sinensis* (Lacepède). A cladistic analysis of 58 characters shows six monophyletic species-groups in *Scomberomorus*. The *sinensis* group is monotypic and is defined by the presence of an abrupt downward curve in the lateral line under the first dorsal fin and by its retention of a swim bladder. The *commerson* species-group contains *commerson*, *niphonius*, *queenslandicus*, and *cavalla* and is defined by the presence of an intercalar spine of at least moderate length. *Scomberomorus cavalla* and *S. commerson* share two additional specializations, the pterosphenoid bones are close together and the lateral line curves abruptly downward under the second dorsal finlets. The *munroi* species-group is monotypic and is defined by the loss of the anterior process on the outer surface of the head of the maxilla. The *semifasciatus* species-group contains *semifasciatus*, *plurilineatus*, and *lineolatus*, and is defined by the presence of a greatly expanded posterior end of the maxilla. *Scomberomorus lineolatus* and *S. semifasciatus* share an additional specialization, a wide parasphenoid, but this character state appears independently in several other lines. The *guttatus* species-group contains *guttatus*, *multiradiatus*, and *koreanus* and is defined by a high supraoccipital crest. Auxiliary branches extend off the anterior part of the lateral line in *S. guttatus* and *S. koreanus*. The *regalis* species-group contains *regalis*, *tritor*, *maculatus*, *concolor*, *sierra*, and *brasiliensis* and is defined by the presence of nasal denticles. All but the most primitive species in this group (*S. tritor*) have an artery arising from the fourth left epibranchial artery. The four most advanced species (all except *tritor* and *maculatus*) have developed a long posterior process on the pelvic girdle. The three most advanced species (*sierra*, *brasiliensis*, and *regalis*) have a coeliaco-mesenteric shunt connecting the fourth right epibranchial artery with the coeliaco-mesenteric artery.

The purposes of this paper are to define the 18 species of *Scomberomorus*, to clarify their relationships, and to assess the systematic position of *Scomberomorus* within the Scombridae. The methods used are similar to those of Collette and Chao (1975) in a revision of the bonitos and of Gibbs and Collette (1967) in a revision of *Thunnus*, and rely on previous work by Kishinouye (1923), Munro (1943), Mago Leccia (1958), and Devaraj (1977).

The Spanish mackerels have been placed by Collette and Chao (1975) and Collette and Russo (1979) in a tribe (the Scomberomorini) along with *Acanthocybium* and *Grammatorcynus*, intermediate between the more primitive mackerels (Scombrini) and the more advanced bonitos (Sardini). *Acanthocybium* is clearly the specialized sister group of *Scomberomorus*, but the phylogenetic position of *Grammatorcynus* has been unclear.

Until recently, the number of valid species of

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Scomberomorus has been in doubt. In his revision of Australian species, Munro (1943) recognized 15 species in the world (excluding *Cybiosarda elegans*, a bonito, and *Lepidocybium flavobrunneum*, a gempylid). Fraser-Brunner (1950) recognized only nine species, placing five valid species in synonymy. In the course of this revision, we have discovered two previously undescribed species, *S. brasiliensis* (Collette et al. 1978), which was confused with *S. maculatus*, and *S. munroi* (Collette and Russo 1980), which was confused with *S. niphonius*.

Emphasis was placed on obtaining fresh or frozen specimens for dissection from several populations of each species. Standard counts and measurements were taken, color pattern was recorded, and a search made for parasitic copepods. Results of the copepod study have been reported by Cressey and Cressey (1980), and analysis of these data from a host-parasite point of view has been completed (Cressey et al. 1983; Collette and Russo 1985). The viscera were examined and illustrated in situ following removal of an oval portion of the ventral body wall. The viscera then were removed and drawings were made of the liver and other selected organs. The kidneys and anterior parts of the arterial system then were drawn. Counts of ribs and intermuscular bones were made and the specimen was then skeletonized, facilitated by immersion in hot water.

The base measurement for morphometric comparisons of fresh, frozen, and preserved specimens was millimeters fork length (mm FL).

This paper is divided into three major parts. The first part contains descriptions and illustrations of morphometry, meristic characters, soft anatomy, and osteology of the species of *Scomberomorus*. Comparisons with *Acanthocybium solandri* and *Grammatorcynus bilineatus* are included. All references to *Grammatorcynus* in this paper refer to *G. bilineatus*. The validity of the second species, *G. bicarinatus*, was only established recently (Collette 1983). The second part comprises separate species accounts including synonymy, types of nominal species, diagnosis (based on characters from the first section), description, size, color pattern, summaries of published information on biology and interest to fisheries, geographic distribution, and material examined. The most important references to each species are marked with asterisks in the synonymies. The third part is an analysis of the relationships of *Acanthocybium* and the species of *Scomberomorus* based on a cladistic analysis of characters described in the first part, using *Grammatorcynus* as the plesiomorphic out-group.

MATERIAL

The material examined is listed by general locality under four or five headings in the accounts for each of the 18 species of *Scomberomorus*. Comparative material of *Acanthocybium* and *Grammatorcynus* is listed at the end of this section. The numbers under these headings are not additive but are included to give some degree of confidence in the morphological data presented in the body of the paper. "Total specimens" is the total number of individuals examined whether preserved, dissected, or skeletonized. "Dissected" are fresh or frozen specimens for which data on the viscera and usually other characters were recorded. Specimens were subsequently made into skeletons. "Measured and counted" includes specimens that were subsequently dissected as well as the preserved museum specimens used for detailed morphometric and meristic examination. "Counts only" are additional museum specimens used only for meristic examination. "Skeletons" refer to all the skeletal material examined, both specimens that were dissected and additional skeletal material already in museums. Asterisks indicate type-specimens of nominal species.

Material was examined from the following institutions:

AMNH	American Museum of Natural History, New York
AMS	Australian Museum, Sydney
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
CSIRO	CSIRO Marine Biological Laboratory, Cronulla, N.S.W., Australia
DASF	Department of Agriculture, Stock, and Fisheries, Port Moresby, Papua New Guinea
FMNH	Field Museum of Natural History, Chicago
HUMZ	Laboratory of Marine Zoology, Hokkaido University, Hakodate, Hokkaido

GCRL	Gulf Coast Research Laboratory and Museum, Ocean Springs, Miss.
LACM	Los Angeles County Museum of Natural History, Los Angeles
MCZ	Museum of Comparative Zoology, Harvard
MNHN	Museum National d'Histoire Naturelle, Paris
MPIP	Museu de Pesca do Instituto de Pesca, Santos
MSUF	Museo de La Specola, Universita di Firenze, Florence
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo
NHMV	Naturhistorisches Museum, Vienna
NMC	National Museum of Natural Sciences, Ottawa
QM	Queensland Museum, Brisbane
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden
ROM	Royal Ontario Museum, Toronto
RUSI	J. L. B. Smith Institute of Ichthyology, Rhodes University, Grahamstown, South Africa
SAM	South African Museum, Capetown
SIO	Scripps Institution of Oceanography, La Jolla, Calif.
TABL	Miami Laboratory (formerly Tropical Atlantic Biological Laboratory), NMFS, Miami, Fla. [Most specimens now at UF.]
UDONECI	Universidad de Oriente, Nueva Esparta, Centro de Investigaciones, Venezuela
UF	Florida State Museum, University of Florida, Gainesville
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	United States National Museum, Washington, D.C.
WAM	Western Australia Museum, Perth
ZMA	Zoological Museum, Amsterdam
ZMH	Zoologisches Institut und Zoologisches Museum, Hamburg
ZMK	Zoological Museum, Copenhagen
ZSI	Zoological Survey of India, Calcutta

Acanthocybium solandri.—Total 47 (536-1,500 mm FL).

meas.: 26 (536-1,500): W Atlantic (8); St. Helena (1); S. Africa (3); Indian Ocean (4); Caroline Is. (6); Tuamotu Is. (1); E Pacific (3).

heads: 8 (202-380): Bahama Is. (1); St. Helena (2); Australia (1); Marshall Is. (1); E Pacific (2).

counts: 36.

diss.: 11 (943-1,420): W Atlantic (7); Indian O. (3); Revillagigedos (1).

Grammatorcynus bilineatus.—Total 52 (23.5-575 mm FL).

meas.: 34 (226-575): Red Sea (13, **Thynnus bilineatus*); Indian Ocean ? (1); Andaman Sea (3); Celebes (1); New Guinea (3); Australia (8); Philippine Is. (5, **Nesogrammus piersoni*); Solomon Is. (1); Caroline Is. (3); Marshall Is. (8); Fiji (2).

counts: 44.

diss.: 10 (382-453): Indian Ocean ? (1); Timor Sea (2); Bismarck Arch. (1); Marshall Is. (2); Queensland, Australia (4).

Grammatorcynus bicarinatus.—Total 9 (306-825 mm FL).

meas.: 9 (306-825): Western Australia (5); Queensland (4).

counts: 9.

diss.: 2 (521 and 563): Queensland.

KEY TO *GRAMMATORCYNUS*, *ACANTHOCYBIUM*, AND *SCOMBEROMORUS*

1a. Two lateral lines, the lower joining the upper behind the pectoral fin base and at the caudal fin base; interpelvic process single; teeth in jaws slender, conical, not compressed; vertebrae 31 ..... *Grammatorcynus* 2

1b. One lateral line; interpelvic process double; teeth in jaws strong, compressed, almost triangular or knife-like; vertebrae 39-64 3

2a. Gill rakers 14-15; small eye, 3-4% FL; frequently with small dark spots on lower sides of body ..... *G. bicarinatus* (Quoy and Gaimard)

2b. Gill rakers 19-24; large eye, 7-9% FL; seldom with dark spots on sides of body ..... *G. bilineatus* (Rüppell)

3a. Snout as long as rest of head; no gill rakers; 23-27 spines in first dorsal fin; posterior end of maxilla concealed un-

der preorbital bone; vertebrae 62-64 . . . . . *Acanthocybium solandri* (Cuvier)

3b. Snout much shorter than rest of head; gill rakers 1-27; 12-22 spines in first dorsal fin; posterior end of maxilla exposed; vertebrae 41-56 . . . . . *Scomberomorus* 4

4a. Lateral line abruptly curving down below first or second dorsal fin; vertebrae 41-46 5

4b. Lateral line straight or descending gradually posteriorly; vertebrae 44-56 7

5a. Lateral line abruptly curving down below first dorsal fin; total gill rakers on first arch 12-15; caudal vertebrae 21-22 . . . . . *S. sinensis* (Lacepède)

5b. Lateral line abruptly curving down below second dorsal fin; total gill rakers on first arch 2-13; caudal vertebrae 23-27 6

6a. Total gill rakers on first arch 7-13, usually 9 or more; spines in first dorsal fin 12-18, usually 15 or fewer; precaudal vertebrae 16-17 . . . . . *S. cavalla* (Cuvier)

6b. Total gill rakers on first arch 3-8, usually 6 or fewer; spines in first dorsal fin 15-18, usually 16 or more; precaudal vertebrae 19-20 . . . . . *S. commerson* (Lacepède)

7a. Total gill rakers on first arch 21-27; no bars on body . . . . *S. concolor* Lockington

7b. Total gill rakers on first arch 1-18; spots, bars, or other markings usually present on sides of body 8

8a. Anal fin rays 25-29; second dorsal fin rays 21-25, usually 23 or more; gill rakers on first arch 1-4; total vertebrae 54-56; no pattern on body . . . . . *S. multiradiatus* Munro

8b. Anal fin rays 15-24; second dorsal fin rays 15-24; total gill rakers on first arch 3-18; total vertebrae 44-53; sides of body usually with spots or other markings 9

9a. Dorsal fin spines 19-22, usually 19 or more 10

9b. Dorsal fin spines 13-19, usually 18 or fewer 11

10a. First dorsal fin black only on first 5-7 interspinous membranes, white posteriorly; intestine straight, with no folds; total vertebrae 48-50 . . . . . *S. niphonius* (Cuvier)

10b. First dorsal fin black to, or almost to, posterior end; intestine with 2 loops and 3 limbs; total vertebrae 50-52 . . . . . *S. munroi* Collette and Russo

11a. Lateral line with many small auxiliary branches anteriorly 12

11b. Lateral line without auxiliary branches or with only a few anteriorly 13

12a. Dorsal fin spines 15-18, usually 16 or more; intestine with 2 loops and 3 limbs; total vertebrae 47-52, usually 48 or more; head longer, 20.2-21.5% FL; body depth less, 22.8-25.2% FL . . . . . *S. guttatus* (Bloch and Schneider)

12b. Dorsal fin spines 14-17, usually 15 or fewer; intestine with 4 loops and 5 limbs; total vertebrae 46-47, usually 46; head shorter, 19.7-20.4% FL; body depth greater, 24.4-26.7% FL . . . . . *S. koreanus* (Kishinouye)

13a. Sides of body with spots and at least one stripe, the stripes may be short, wavy or interrupted 14

13b. Sides of body without any stripes, spots usually present 16

14a. One long stripe on sides with spots or interrupted lines above and below the stripe; total vertebrae 47-48, usually 48; total gill rakers on first arch 12-18, usually 15 or more . . . . *S. regalis* (Bloch)

14b. Sides with several short stripes; total vertebrae 44-47, usually 46; total gill rakers on first arch 9-15, usually 14 or fewer 15

15a. Sides with a series of short straight stripes and few if any spots; total gill rakers on first arch usually 11 or fewer; second dorsal fin rays 15-19, usually 18 or fewer; distance from 2D origin to caudal base 46.2-54.5% FL, $\bar{x}$ 50.0% . . . . . *S. lineolatus* (Cuvier)

15b. Sides with a series of short wavy markings plus many small spots; total gill rakers on first arch usually 12 or more;

second dorsal fin rays 19-21, usually 20 or more; distance from 2D origin to caudal base 51.8-57.5% FL, $\bar{x}$ 54.8% .. .. *S. plurilineatus* Fourmanoir

16a. Sides with bars or large spots, larger than the diameter of the eye 17
16b. Sides with small round spots, about the diameter of the eye, orange colored in life 19

17a. Sides with large spots or blotches; total gill rakers on first arch 3-9, usually 7 or fewer ..... *S. queenslandicus* Munro
17b. Sides plain or with bars; total gill rakers of first arch 6-15, usually 9 or more .. 18

18a. First dorsal fin spines 13-15; second dorsal fin rays 19-22, usually 20 or more; total gill rakers on first arch 6-13, usually 11 or fewer; total vertebrae 44-46, usually 45; base first dorsal fin 17.0-23.6% FL .... *S. semifasciatus* (Macleay)
18b. First dorsal fin spines 15-18, usually 16 or more; second dorsal fin rays 16-19, usually 17; total gill rakers on first arch 12-15; total vertebrae 46-47, usually 46; base first dorsal fin 23.8-30.4% FL ..... *S. tritor* (Cuvier)

19a. Total vertebrae 51-53; second dorsal fin rays 17-20, usually 18 or more .... *S. maculatus* (Mitchill)
19b. Total vertebrae 46-49; second dorsal fin rays 15-19, usually 18 or fewer 20

20a. Pectoral fin rays 21-24, usually 22 or more; pelvic fin short, 2.9-5.9% FL, $\bar{x}$ 4.5% .... *S. brasiliensis* Collette, Russo, and Zavalla-Camin
20b. Pectoral fin rays 20-24, usually 21 or fewer; pelvic fin longer, 3.2-6.4% FL, $\bar{x}$ 5.3% ..... *S. sierra* Jordan and Starks

COMPARATIVE MORPHOLOGY

The morphological characters useful for distinguishing the species of *Scomberomorus* and for evaluating their phylogenetic relationships are divided into six categories: lateral line, nasal denticles, morphometry, meristics, soft anatomy, and osteology.

Lateral Line

In most species of *Scomberomorus*, the lateral line runs posteriorly above the pectoral fin and then gradually descends to the middle of the body at about the level of the second dorsal fin. *Grammatorcynus* differs from *Scomberomorus*, *Acanthocybium*, and all other members of the family by having a second lateral line that joins the upper lateral line at a right angle behind the pectoral fin base and then courses ventrally and posteriorly along the ventral surface of the body to join the dorsal lateral line on the caudal peduncle. In *Acanthocybium* and three species of *Scomberomorus*, the lateral line moves abruptly downward under the first or second dorsal fin. The abrupt downward curve is under the first dorsal fin in *Acanthocybium* and *S. sinensis* (see Figure 68); it is under the second dorsal in *S. cavalla* and *S. commerson* (see Figures 50 and 52).

Scomberomorus guttatus and *S. koreanus* differ from other members of the genus in having many fine branches from the anterior part of the lateral line, both dorsally and ventrally (see Figures 54 and 56). *Acanthocybium* and *S. niphonius* (see Figure 62) may have branches from the lateral line but they are not as numerous or distinct.

Nasal Denticles

Nasal denticles (Fig. 1a, b) are small generalized teeth found within the olfactory chamber on the medial surface surrounding the posterior nares and on the skin covering the anterior surface of the lateral ethmoid. Nasal denticles are similar to the small villiform teeth present within the mouth cavity and adjoining regions of stomadeal origin and on the skin covering the cleithrum (Fig. 1c, d) and on the isthmus where they are contacted by the opercular membrane. These teeth typically fit into sockets in pads of fine spongelike bone. They point posteriorly and are aligned with presumed flow of water from the anterior naris through the olfactory chamber and out the posterior naris. Nasal denticles were found only in the six species of the *Scomberomorus regalis* species-group (*brasiliensis*, *concolor*, *maculatus*, *regalis*, *sierra*, and *tritor*). Nasal denticles are not present in *Acanthocybium* or *Grammatorcynus*. We do not know their function and are not aware of such structures in other fishes.

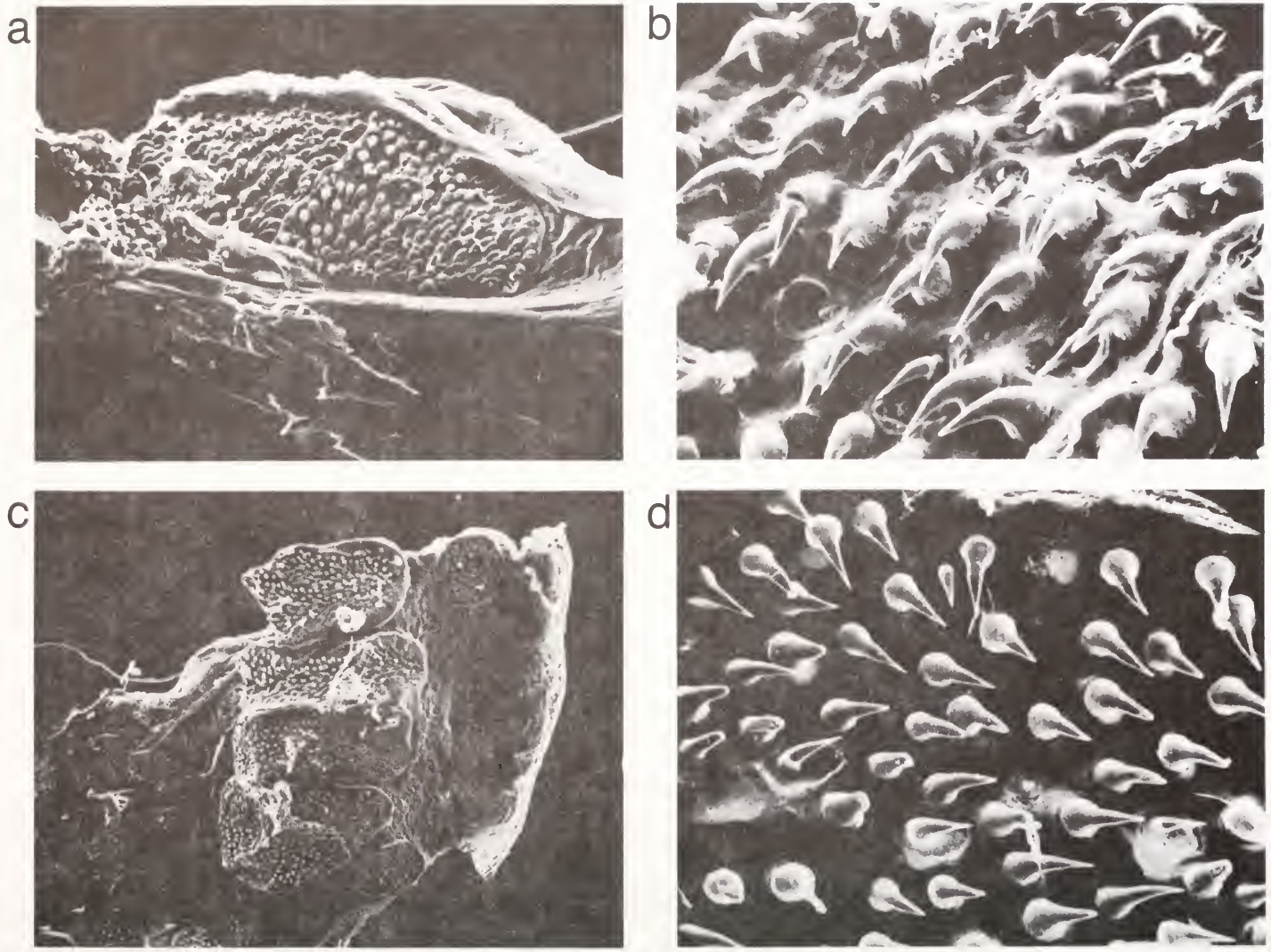


FIGURE 1.—Scanning electron photomicrographs of nasal denticles (a-b) and villiform teeth over the cleithrum (c-d) in *Scomberomorus sierra*, Gulf of California, 353 mm FL, USNM 217368. a, c. 50×. b, d. 250×.

Morphometric Characters

In addition to fork length, 26 measurements routinely were made on all specimens destined to be dissected, to insure that these data would be available if needed. Preserved material also was measured until an adequate sample was obtained. Measurements follow the methods of Marr and Schaefer (1949) as modified by Gibbs and Collette (1967) and Collette and Chao (1975). Morphometric characters can be used to separate species and populations within species. Tables showing the 26 characters as thousandths of fork length and 8 characters as thousandths of head length are presented in the systematic section of the paper (see Tables 13-30). Most of the characters are best used at the species level; therefore, only a summary table of the means of proportions (Table 1) is presented in this section. Where there was sufficient material from two or more potentially different populations, analysis of covariance (ANCOVA) was carried out on the regressions of body parts on fork length. Results are reported, under a section entitled Geographic Variation, in 11 of the 18 species accounts. Tests of significance were made by Newman-Keuls Multiple Range Test.

Meristic Characters

Countable structures are of special value systematically because they are relatively easy to record unambiguously and are easy to summarize in tabular fashion. Meristic characters that have proved valuable systematically in *Scomberomorus* include numbers of fin rays (first dorsal spines, second dorsal rays, dorsal finlets, anal rays, anal finlets, and pectoral rays), gill rakers, teeth on the upper and lower jaws, vertebrae (precaudal, caudal, and total), and lamellae in the olfactory rosettes. Olfactory lamellae are discussed as the next to last section under soft

TABLE 1.—Morphometric comparison of the species of *Scomberomorus*. Means as thousandths of fork length or head length. Species arranged alphabetically by the first three letters of their names. Ranges for the species given in Tables 13-30.

Character	bra	cav	com	con	gut	kor	lin	mac	mul	mun	nip	plu	que	reg	sem	sie	sin	tri	Min. spp.	Max. spp.
Fork length																				
Snout-A	538	539	542	524	517	493	507	536	505	546	563	502	525	548	506	537	584	533	493 kor	584 sin
Snout-2D	511	506	510	507	481	467	501	503	477	528	536	473	501	521	472	510	559	513	467 kor	559 sin
Snout-1D	242	258	243	236	239	242	252	241	249	222	248	221	234	255	245	241	291	246	221 mun, plu	291 sin
Snout-P_2	253	258	257	242	251	248	245	257	243	249	263	233	251	265	250	252	290	266	233 plu	290 sin
Snout-P_1	219	232	237	209	209	210	212	217	213	201	225	193	229	234	219	221	258	222	193 plu	258 sin
P_1-P_2	108	106	96	100	106	114	93	110	102	105	105	103	99	109	105	104	113	111	93 lin	114 kor, sin
Head length	213	223	229	202	205	208	206	212	208	198	216	193	220	223	213	212	255	217	193 plu	255 sin
Max. body depth	198	191	187	187	209	237	181	197	229	190	172	206	188	197	211	190	218	206	172 nip	237 kor
Max. body width	82	89	94	89	93	100	97	91	95	100	84	97	101	91	94	84	102	90	82 bra	104 mun
P_1 length	123	129	122	125	109	133	139	129	131	109	111	123	120	126	147	123	158	134	109 gut, mun	158 sin
P_2 length	45	65	56	50	59	60	55	52	40	54	68	51	55	56	50	53	83	60	40 mul	83 sin
P_2 insertion-vent	273	271	273	261	251	227	241	263	247	281	285	243	254	267	237	267	273	250	237 sem	285 nip
P_2 tip-vent	225	212	217	212	191	164	185	211	207	225	218	186	198	210	187	222	189	190	164 kor	225 bra, mun
Base 1D	263	245	261	254	235	218	231	256	216	307	282	240	263	257	210	260	260	262	210 sem	307 mun
Height 2D	117	109	103	111	131	166	124	125	167	112	98	148	114	114	159	123	145	126	98 nip	167 kor, mul
Base 2D	118	106	104	127	141	160	114	128	178	115	113	128	113	114	138	120	121	122	104 com	178 mul
Height anal	114	106	100	107	127	160	117	118	164	108	97	135	112	112	156	117	145	125	97 nip	164 mul
Base anal	113	108	100	134	133	154	122	123	216	105	107	125	108	110	145	119	122	120	100 com	216 mul
Snout (fleshy)	82	87	89	72	72	70	81	80	77	77	81	67	86	87	81	79	97	81	67 plu	97 sin
Snout (bony)	72	79	81	63	64	62	74	70	67	70	75	59	80	79	72	70	91	72	59 plu	91 sin
Maxilla length	123	132	131	113	108	111	113	119	125	104	120	96	125	124	119	121	147	123	96 plu	147 sin
Postorbital	95	98	104	96	96	101	91	96	86	90	102	94	102	98	95	98	117	96	86 mul	117 sin
Orbit (fleshy)	37	38	35	32	37	34	32	34	34	25	34	34	31	41	35	33	35	38	25 mun	41 reg
Orbit (bony)	54	51	49	46	53	50	48	51	52	39	47	45	49	56	51	49	52	53	37 mun	56 reg
Interorbital width	57	60	62	49	59	60	57	56	58	56	57	56	63	58	57	55	63	59	49 con	63 que, sin
2D-caudal	490	477	481	484	527	550	500	487	494	468	465	548	496	480	517	475	445	476	445 sin	550 kor
Head length																				
Snout (fleshy)	386	392	390	353	351	339	395	376	372	386	376	348	391	390	378	371	382	376	339 kor	395 lin
Snout (bony)	343	357	355	313	310	301	359	335	321	351	346	306	363	351	339	331	355	333	301 kor	363 que
Maxilla length	581	591	571	555	526	532	547	562	603	521	553	496	568	556	555	570	578	568	496 plu	603 mul
Postorbital	446	438	455	476	464	489	442	454	415	456	473	485	463	439	447	461	460	443	415 mul	489 kor
Orbit (fleshy)	175	168	147	159	174	157	156	160	165	134	150	179	142	178	162	158	138	173	129 mun	178 reg
Orbit (bony)	249	229	211	226	252	238	231	242	252	199	215	232	223	247	238	235	202	245	191 mun	252 gut, mul
Interorbital width	270	268	270	241	284	292	276	266	280	282	264	290	286	262	267	253	249	272	241 con	292 kor

anatomy. The other meristic characters are discussed in the relevant osteological sections of the paper.

Soft Anatomy

The relative position, shape, and size of the various internal organs provide valuable diagnostic characters. For purposes of discussion, the characters in the soft anatomy are divided into five sections: viscera, vascular system, urogenital system, olfactory organ, and pharyngeal muscles.

VISCERA

Emphasis was placed on the appearance of the viscera in ventral view, after removal of an oval segment of the belly wall (Figs. 2, 3). Previous papers on the viscera include Kishinouye (1923, 5 Japanese species of *Scomberomorus*, and *Acanthocybium* and *Grammatorcynus*), Munro (1943, 4 Australian species), Silas (1963, *Grammatorcynus*), Mota Alves and Tomé (1967a, *S. cavalla*), Mota Alves (1969, *S. brasiliensis*), Tongyai (1971a, *S. guttatus* and *S. commerson*), and Collette and Russo (1979, preliminary review of the genus).

The anterior end of the liver abuts the transverse septum anteriorly in the body cavity. The liver has three lobes. The left and right lobes are longer than the middle lobe in all three genera (Fig. 4). The right lobe is longest in *Scomberomorus* and *Grammatorcynus*. The left and right lobes are about equal in length in *Acanthocybium*. Two efferent (venous) vessels lead directly from the anterior surface of the liver into the sinus venosus in all species. The short esophagus leads into the stomach. The stomach is sometimes visible in ventral view but this is dependant on the amount of food present, rather than showing differences between species. The pyloric portion of the intestine arises from the anterior end of the

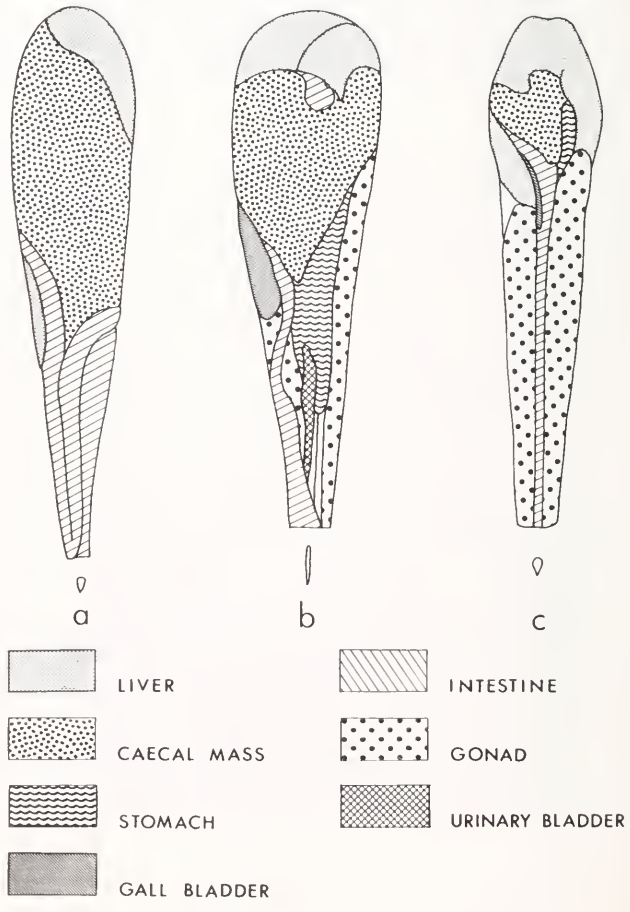


FIGURE 2.—Viscera in ventral view. a. *Scomberomorus maculatus*, Georgia, 290 mm FL. b. *Acanthocybium solandri*, Campeche Banks, Mexico, 1,280 mm FL. c. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL.

stomach. At this point the main branches of the pyloric caeca join the intestine. The caeca branch and form a dense dendritic conglomeration, the caecal mass. Cells in the pyloric caeca are histologically similar to those in the intestine and produce enzymes such as lipase, maltase, trypsin, and pepsin (Mota Alves and Tomé 1970). The intestine continues posteriorly and its course appears to be species-specific. The intestine may be a simple straight tube from stomach to anus, have two descending and one ascending arm, or have four bends with three descending and two ascending arms. The spleen is prominent in ventral view in most species but is hidden in others. The gall bladder, an elongate tubular sac which is usually green, arises from the right lobe of the liver and usually lies along the first descending arm of the intestine on the right side. A swim bladder is present in *Grammatorcynus*, *Acanthocybium*, and *S. sinensis* (Fig. 5) but is absent in the other 17 species of *Scomberomorus*.

The Spanish mackerels can be divided into three groups based on the number of folds in the intestine. *Grammatorcynus*, *Acanthocybium* (Fig. 2b, c), and *S. niphonius* (Fig. 3k) have a straight gut not folded back on itself. *Scomberomorus koreanus* (Fig. 3f) has four folds and five distinct arms. The other species all have two folds and three long arms (Fig. 3). Collette and Russo (1980) used this character to differentiate *S. munroi* from the North Pacific *S. niphonius*.

The spleen is large and centrally located in ventral view in four species: *guttatus*, *koreanus*, *munroi*, and *plurilineatus*. The spleen is smaller and distinctly on the left side in ventral view in seven species: *brasiliensis*, *commerson*, *lineolatus*, *maculatus*, *multiradiatus*, *queenslandicus*, and *sinensis*. It is not visible in ventral view in *Grammatorcynus*, *Acanthocybium*, and seven species of *Scomberomorus*: *cavalla*, *concolor*, *niphonius*, *regalis*, *semifasciatus*, *sierra*, and *tritor*.

VASCULAR SYSTEM

The only published work on the vascular system of the Spanish mackerels is on Japanese species by Kishinouye (1923). No specialized subcutaneous vascular system and no cutaneous arteries or veins are present as they are in the higher tunas, Thunnini, *Auxis* to *Thunnus* (Collette 1979). Therefore, this description will be confined to the anterior portion of the dorsal aorta and the postcardinal vein.

The efferent branchial (epibranchial) arteries and coeliaco-mesenteric artery form a unit at the anterior end of the dorsal aorta (Figs. 6, 7). Two anterior epibranchials on each side unite to form a common trunk, and these trunks join as the "Y" of the aorta beneath the posterior part of the skull or the first or second vertebra. The posterior two epibranchials of each side unite immediately before they join the aorta, usually ventral to the second or third vertebra. As the aorta proceeds posteriorly, it gives rise to the large coeliaco-mesenteric artery on the right side ventral to the second to fourth vertebrae. The coeliaco-mesenteric artery has two or three main branches which lead to the liver and other viscera.

The postcardinal vein runs along the ventral surface of the kidney (Fig. 8) from the vicinity of the first complete haemal arch anteriorly in the median line to the pectoral region. There it curves to the right and discharges into the right Cuvierian duct. Posteriorly, the postcardinal receives a pair of small veins at the level of each vertebra. The postcardinal is composed of two main branches that join anterior to the Y of the ureter. The main branch leaves the haemal arch dorsally and the small branch runs under the surface of the kidney from the urogenital area.

Five species of *Scomberomorus* (*brasiliensis*, *concolor*, *maculatus*, *regalis*, and *sierra*) have unique specializations of the right and/or left fourth epibranchial arteries (Fig. 7c-g). Each of these species has an artery arising from the fourth left epibranchial artery. Other species of the genus (e.g., *S. guttatus* and *S. tritor*, Fig. 7a, b) lack these specializations. In *S. concolor* and *S. brasiliensis* this branch is small and goes into the muscular tissue surrounding the left dorsal portion of the esophagus (Fig. 7d, f). In *S. maculatus* and *S. sierra*, this branch is large and becomes the dorsal left gastric artery (Fig. 7c, e). In *S. regalis* this branch goes into the left lobe of the liver (Fig. 7g, hepatic branch). *Scomberomorus maculatus* and *S. sierra* have lost the connection between the dorsal left gastric artery and the coeliaco-mesenteric artery. It is replaced by a connection to the fourth left epibranchial artery. In *S. regalis*, the left dorsal gastric artery seems to have been reduced.

Scomberomorus brasiliensis, *S. sierra*, and *S. regalis* share a specialization of the right fourth epibranchial artery. In these species an artery connects the fourth right epibranchial artery with a branch of the coeliaco-mesenteric artery (coeliaco-mesenteric shunt, Fig. 7e-g).

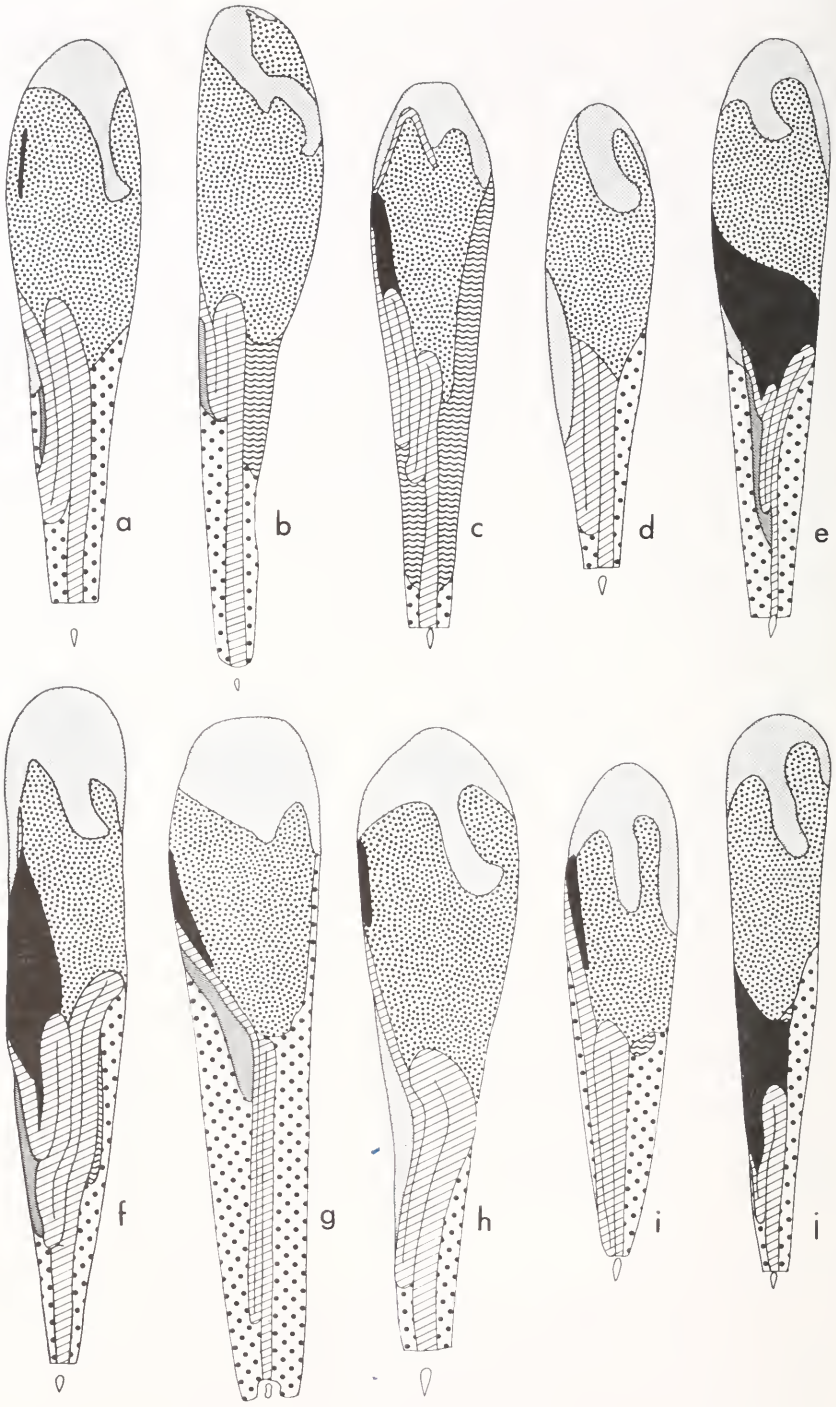
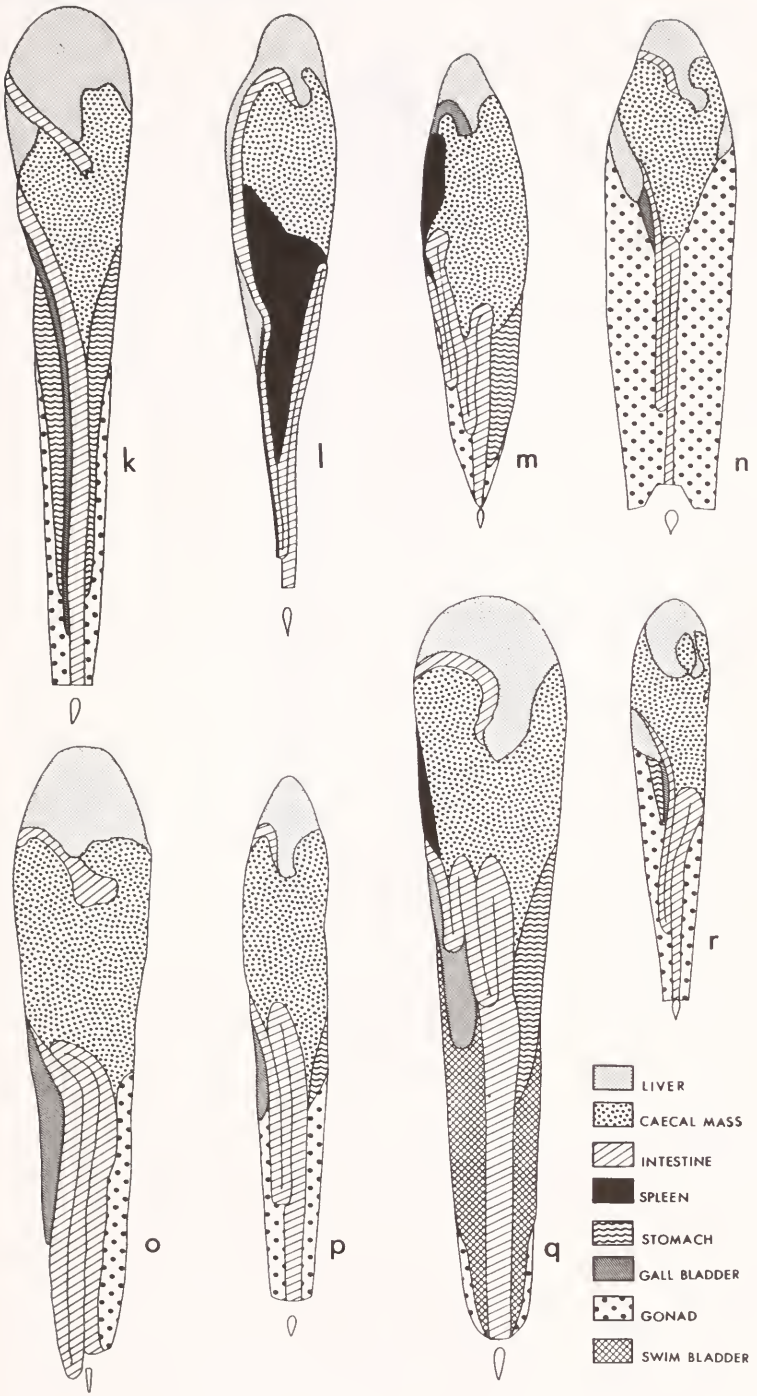


FIGURE 3.—Viscera in ventral view of representative specimens of the 18 species of *Scomberomorus*. a. *S. brasiliensis*, Belém Fish Market, Brazil, 556 mm FL. b. *S. cavalla*, off Miami, Fla., 797 mm FL. c. *S. commerson*, Gulf of Papua, 580 mm FL. d. *S. concolor*, Gulf of California, 495 mm FL. e. *S. guttatus*, Gulf of Mannar, 405 mm FL. f. *S. koreanus*, locality unknown, 812 mm FL. g. *S. lineolatus*, Cochin, India, 786 mm FL. h. *S. maculatus*, St. Andrews Bay, Fla., 323



mm FL. i. *S. multiradiatus*, Gulf of Papua, 272 mm FL. j. *S. munroi*, Gulf of Papua, 512 mm FL, USNM 219374. k. *S. niphonius*, Korea, 235 mm FL. l. *S. plurilineatus*, Durban, S. Africa, 490 mm FL. m. *S. queenslandicus*, Exmouth Gulf, Western Australia, 466 mm FL. n. *S. regalis*, Bahamas, 456 mm FL. o. *S. semifasciatus*, Gulf of Papua, 715 mm FL. p. *S. sierra*, Baja California, 516 mm FL. q. *S. sinensis*, China, 711 mm FL. r. *S. tritor*, Gulf of Guinea, 415 mm FL.

FIGURE 4.—Livers in ventral view. a. *Scomberomorus maculatus*, Florida, 712 mm FL. b. *Acanthocybium solandri*, Florida, 1,403 mm FL. c. *Grammatorcynus bilineatus*, Marshall Is., 444 mm FL.

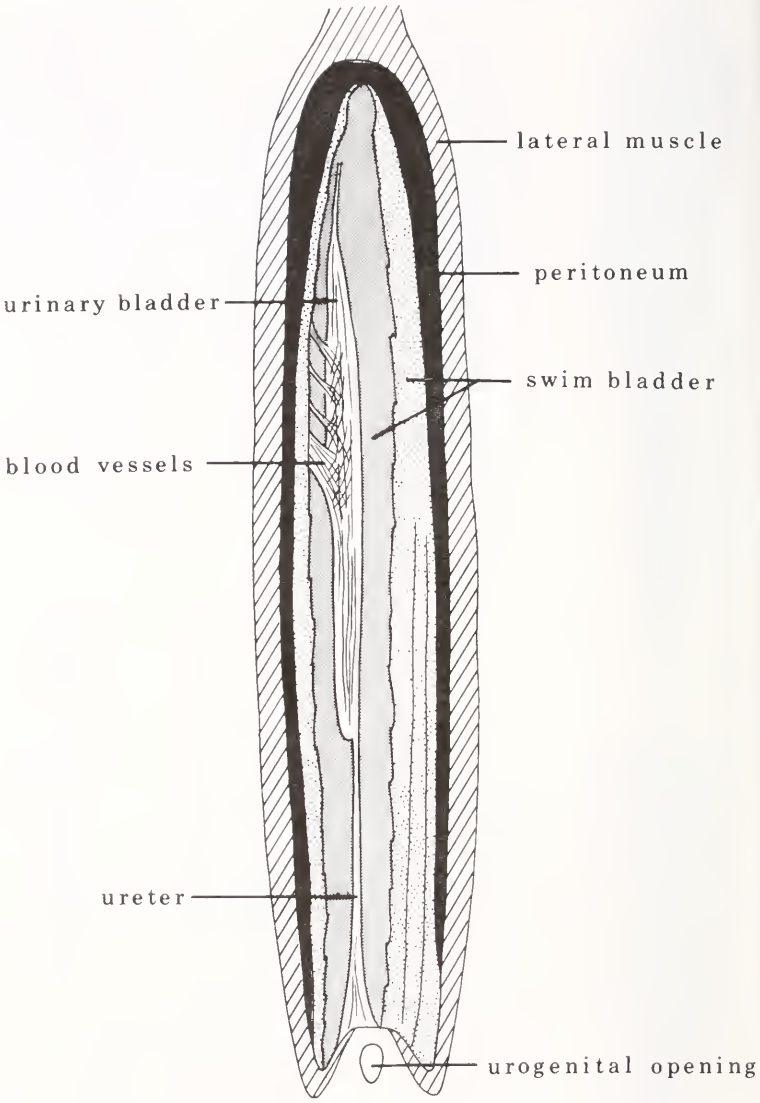


FIGURE 5.—Swim bladder and urinary bladder in ventral view of *Scomberomorus sinensis* (body wall and viscera removed), off Zhoushan Is., China, 714 mm FL, USNM 220856.

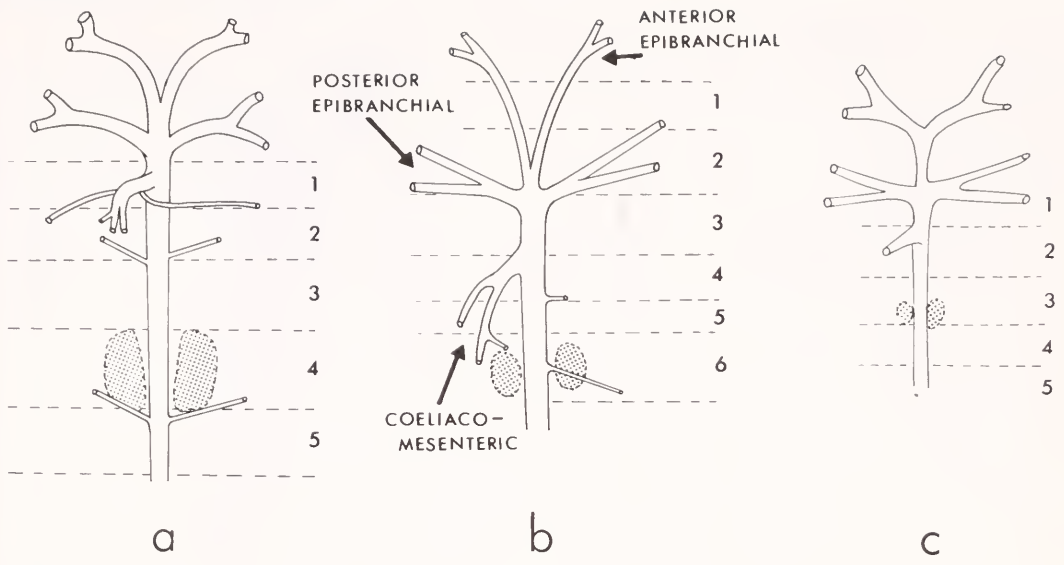


FIGURE 6.—Anterior arterial system in ventral view. Numbers indicate vertebral centra, stippled areas where pharyngeal muscles originate. a. *Scomberomorus multiradiatus*, off the Fly River, Gulf of Papua, 272 mm FL. b. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL. c. *Grammatorcynus bilineatus*, Timor Sea, 453 mm FL.

UROGENITAL SYSTEM

The only reference to the anatomy of the urogenital system in *Scomberomorus* (other than fishery biology studies of the gonads) is Kishinouye (1923) on Japanese species and *Acanthocybium*. The paired gonads lie along the dorsolateral body wall and are visible in ventral view in mature adults. The kidney lies dorsal to the layer of fibrous connective tissue which forms the dorsal wall of the peritoneum. Anteriorly, the kidney divides into a pair of narrow projections which extend along the sides of the parasphenoid and usually reach the posterior end of the "midridge" of the prootic. The anterior ends of the kidney surround the origins of the pharyngeal muscles on the vertebral column and usually separate along the middle of the vertebral column. In the vicinity of the esophagus, the kidney expands laterally and forms two projections which may extend anteriorly to the upper end of the gill slits. Posteriorly, near the posterior fifth of the body cavity, the kidney narrows to an elongate triangle (Fig. 8). The branches of the "ureter" (mesonephric ducts) join to form a common trunk just before entering the urinary bladder. The ureters enter the urinary bladder either at its anterior end or on its dorsal surface. The urinary bladder (Figs. 9, 10) is either ovoid or elongate, depending on degree of inflation, and is located in the mesenteries between the gonads in all species except *S. sinensis*. *Scomberomorus sinensis* has a specialization of the urinary bladder unique to scombrids and, so far as we know, vertebrates in general. In this species the urinary bladder has become hypertrophied and occupies the space inside the swim bladder (Fig. 5). *Acanthocybium* (Fig. 2b) has an elongate urinary bladder that extends anteriorly one-third to two-thirds the length of the visceral cavity.

OLFACTORY ORGAN

Kishinouye (1923) provided a generalized account of the olfactory organ of several scombrids. More detailed studies have been made on *Scomber scombrus* (Burne 1909), *Sarda sarda* (Tretiakov 1939), *Allothunnus fallai* (Nakamura and Mori 1966), *Katsuwonus pelamis* (Gooding 1963), *Thunnus* (Iwai and Nakamura 1964a; Gibbs and Collette 1967), and the bonitos, Sardini (Collette and Chao 1975). As in other scombrids, the olfactory cavity in *Scomberomorus* has a small anterior naris and a slitlike posterior naris. No information on the supplementary sacs, or accessory olfactory cavity (Iwai and Nakamura 1964a), was obtained from the present study comparable with that of Tretiakov (1939), who described three supplementary sacs (middle, maxillary, and rostral sacs) in *Sarda sarda*. The central axis of the

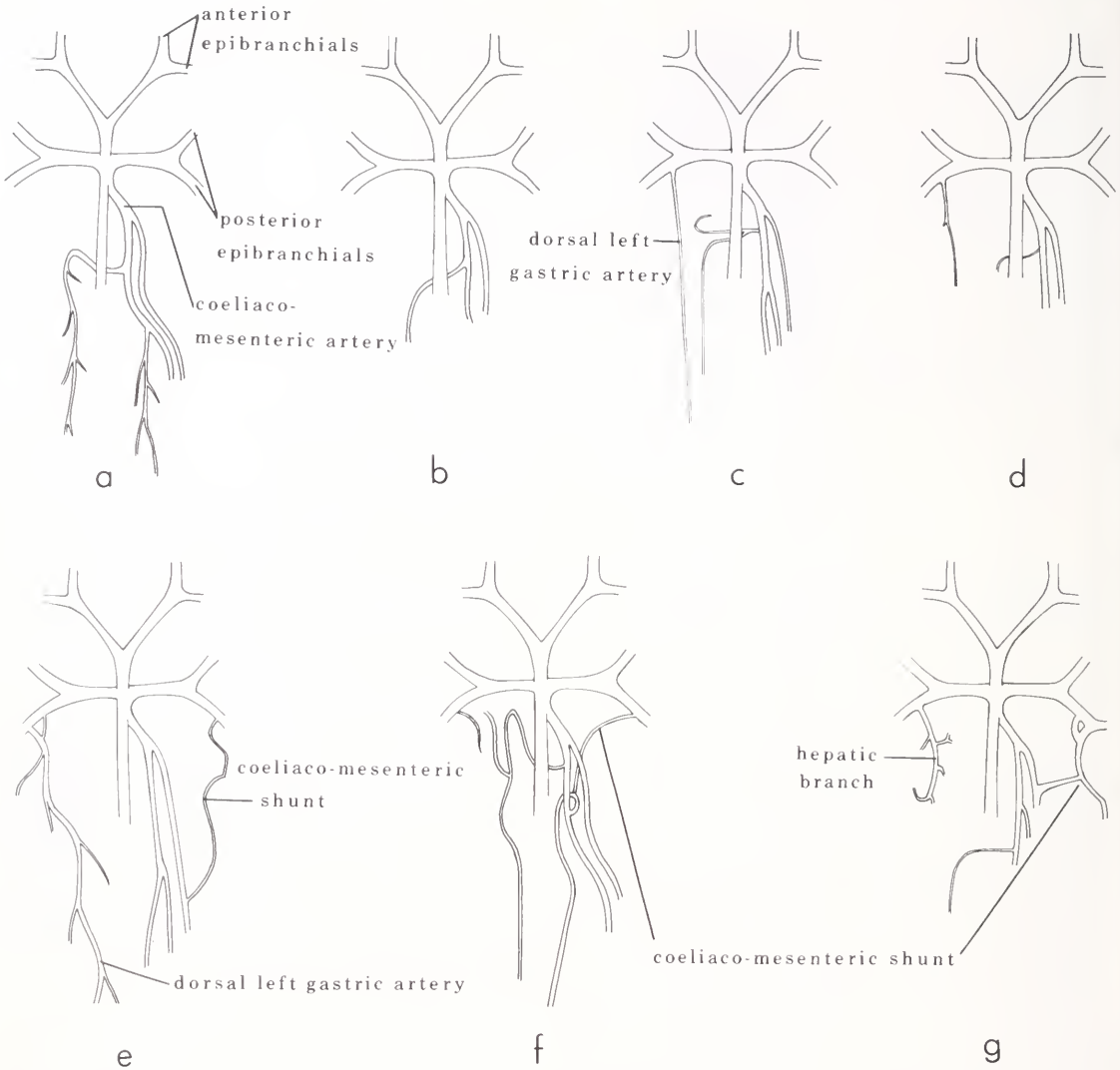


FIGURE 7.—Anterior arterial system in dorsal view of seven species of *Scomberomorus*. a. *S. guttatus*, Pakistan, 545 mm FL. b. *S. tritor*, Gulf of Guinea, 494 mm FL. c. *S. maculatus*, Chesapeake Bay, 312 mm FL. d. *S. concolor*, Gulf of California, 455 mm FL. e. *S. sierra*, Ecuador, 512 mm FL. f. *S. brasiliensis*, Belém market, Brazil, 588 mm FL, USNM 217557, paratype. g. *S. regalis*, Bahama Is., 490 mm FL.

olfactory rosette is located beneath the anterior naris. Leaflike lamellae radiate from the central axis and occupy the anterior dorsal third of the olfactory cavity. Gooding (1963) studied the morphology and histology of the olfactory organ of *Katsuwonus pelamis* and found olfactory cells on the olfactory epithelium of the lamellae. Iwai and Nakamura (1964a) found that the number of lamellae per rosette varies among specimens of species of *Thunnus* but that there were differences among species in the shape of the nasal laminae. Most species of bonitos have 21-39 lamellae in each nasal rosette but *Gymnosarda unicolor* is distinct in the group in having 48-56 (Collette and Chao 1975:532).

The number of olfactory lamellae was counted on both sides in *Scomberomorus* and a wide range of variation was observed, 24-76 (Table 2). In bonitos, the number of lamellae increases from small specimens to adults but does not appear to change after a certain size is reached, as Collette and Chao (1975:532) showed for *Gymnosarda*

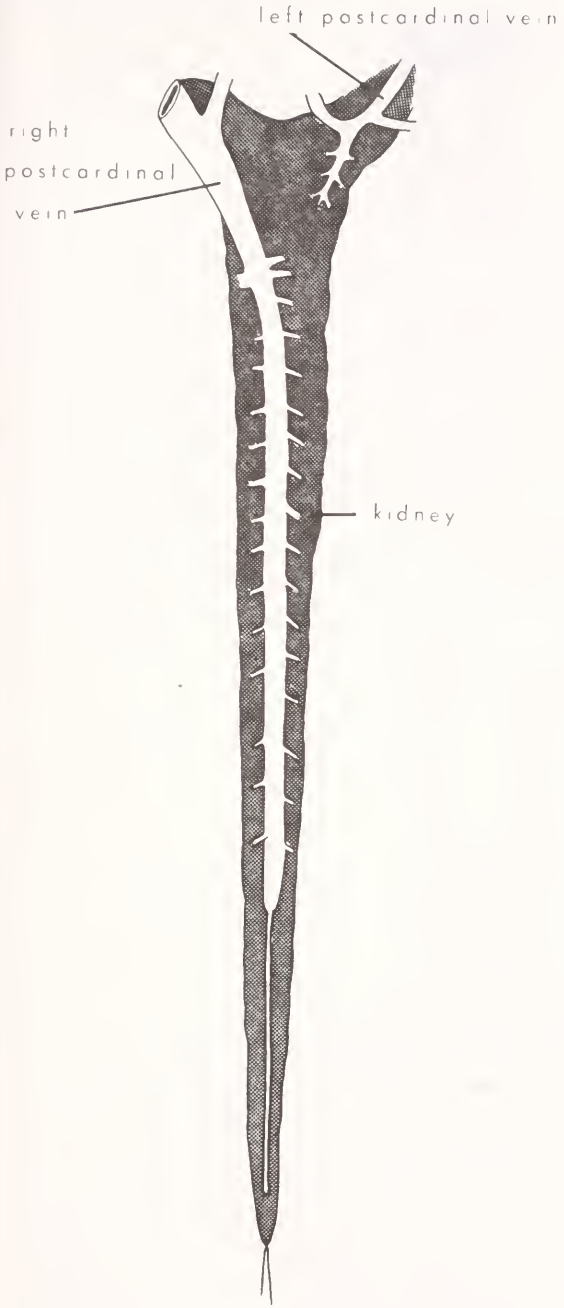


FIGURE 8.—Kidney and postcardinal vein in ventral view of *Scomberomorus queenslandicus*, Palm I., Queensland, 641 mm FL.

TABLE 2.—Number of lamella in nasal rosettes of species of *Scomberomorus*.

Species	Side	Min.	Max	$\bar{x}$	*N*	Overall $\bar{x}$	Rank
brasiliensis	L	24	40	33.67	12	33.88	6
	R	25	42	34.08	13		
cavalla	L	30	56	42.92	24	43.13	12
	R	31	55	43.35	23		
commerson	L	42	58	48.92	12	49.32	13
	R	43	60	49.80	10		
concolor	L	26	35	30.92	13	30.92	1
	R	26	34	30.92	13		
guttatus	L	30	76	53.41	27	53.43	16
	R	31	73	53.46	26		
koreanus	L	47	56	50.67	3	54.75	18
	R	48	73	57.20	5		
lineolatus	L	30	35	32.50	4	32.18	3
	R	30	34	32.00	7		
maculatus	L	25	38	33.43	14	33.44	5
	R	30	37	33.45	11		
multiradiatus	L	32	40	36.75	4	36.00	10
	R	25	44	34.50	2		
munroi	L	54	54	54.00	3	53.84	17
	R	54	57	53.67	3		
niphonius	L	25	42	33.67	15	34.41	7
	R	26	42	35.21	14		
plurilineatus	L	45	53	49.50	4	50.50	14
	R	44	56	51.50	4		
queenslandicus	L	43	59	49.75	4	50.67	15
	R	43	61	51.40	5		
regalis	L	28	41	34.00	9	35.11	9
	R	30	43	36.22	9		
semifasciatus	L	31	37	34.00	3	34.78	8
	R	31	38	35.17	6		
sierra	L	30	36	32.64	14	32.07	2
	R	28	34	31.50	14		
sinensis	L	38	38	38.00	1	42.50	11
	R	41	47	44.00	3		
tritor	L	27	48	33.40	10	32.57	4
	R	24	37	31.83	11		

unicolor and *Orcynopsis unicolor*. We have not examined many small *Scomberomorus* nasal rosettes but did find 23 lamellae in an 80 mm FL *S. guttatus*, a species for which the minimum count of lamellae for specimens larger than 100 mm was 30.

Three species of *Scomberomorus* (*koreanus*, *munroi*, and *guttatus*) had high counts, overall means 53.4-54.8. The highest counts per side were for *S. koreanus* (73) and *S. guttatus* (76). Ten species had low counts, overall means 31.0-36.0. These 10 included all 6 species of the *regalis* group as well as *lineolatus*, *multiradiatus*, *niphonius*, and *semifasciatus*.

PHARYNGEAL MUSCLES

The paired pharyngeal (retractor dorsalis) muscles originate on the ventral surface of one or two vertebrae between the third and the sixth abdominal vertebrae and insert on the upper pharyngeal bones (Fig. 2). We did not find any differences between species as Collette and Chao (1975) did for the bonitos.

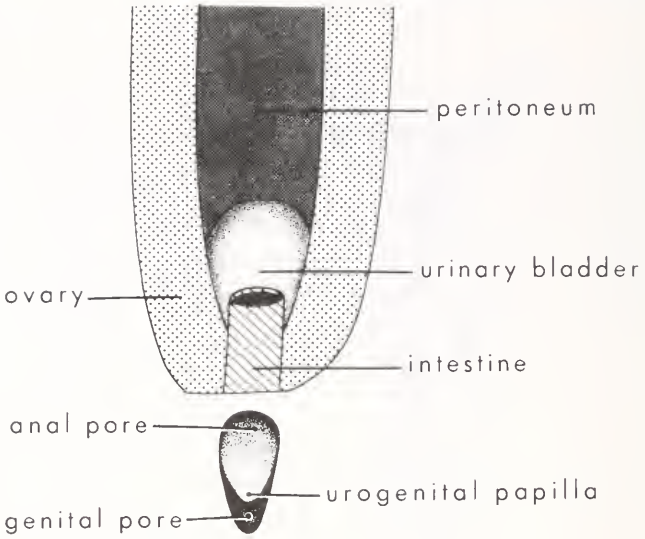


FIGURE 9.—Urogenital system in ventral view of *Scomberomorus* (body wall and viscera removed). Composite illustration.

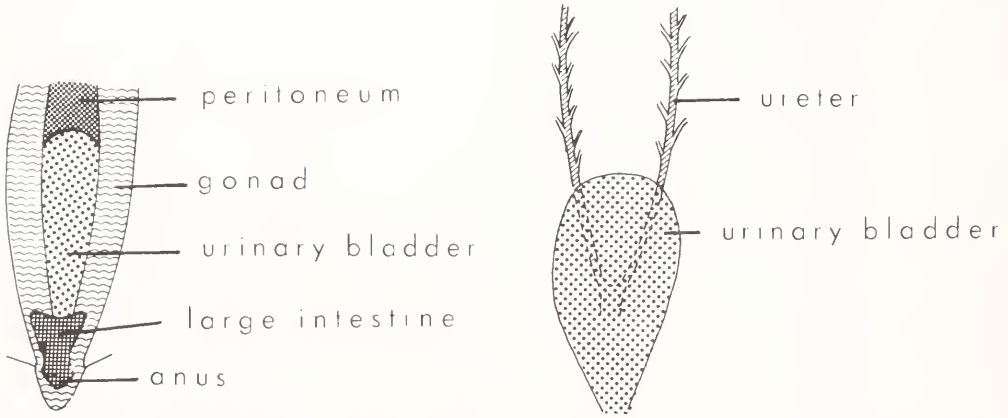


FIGURE 10.—Urogenital system in ventral view of *Scomberomorus queenslandicus*, Palm I., Queensland, 641 mm FL. a. With intestine opened. b. Urinary bladder and ureters.

Osteology

Osteological characters proved to be useful in determining relationships among the 18 species of *Scomberomorus* and between this genus and its presumed closest relatives, *Acanthocybium* and *Grammatorcynus*. The osteological portion of the paper is divided into five sections: skull, axial skeleton, dorsal and anal fins, pectoral girdle, and pelvic girdle. Osteological terminology generally follows Gibbs and Collette (1967) and Collette and Chao (1975). Organization within sections is similar to that of Collette and Chao (1975) and the two earlier papers of most importance to the osteology of *Scomberomorus*: Mago Leccia (1958) on three western Atlantic species (*cavalla*, *maculatus*, and *regalis*) and Devaraj (1977) on four Indian species (*commerson*, *guttatus*, *koreanus*, and *lineolatus*) and *Acanthocybium*.

SKULL

Description of the skull is presented in two sections: neurocranium (Figs. 11-19) and branchiocranium.

Neurocranium

Following a general description of the neurocranium, the four major regions are discussed: ethmoid, orbital, otic, and basicranial.

GENERAL CHARACTERISTICS.—In dorsal view, the neurocranium of *Scomberomorus* is more or less trapezoidal in shape. It is elongate and flat, particularly at the anterior region and is deepest at the hind end of the orbit. The dorsal surface is marked by a median ridge and three grooves on each side: dilator, temporal, and supratemporal (Allis 1903:49). These grooves are

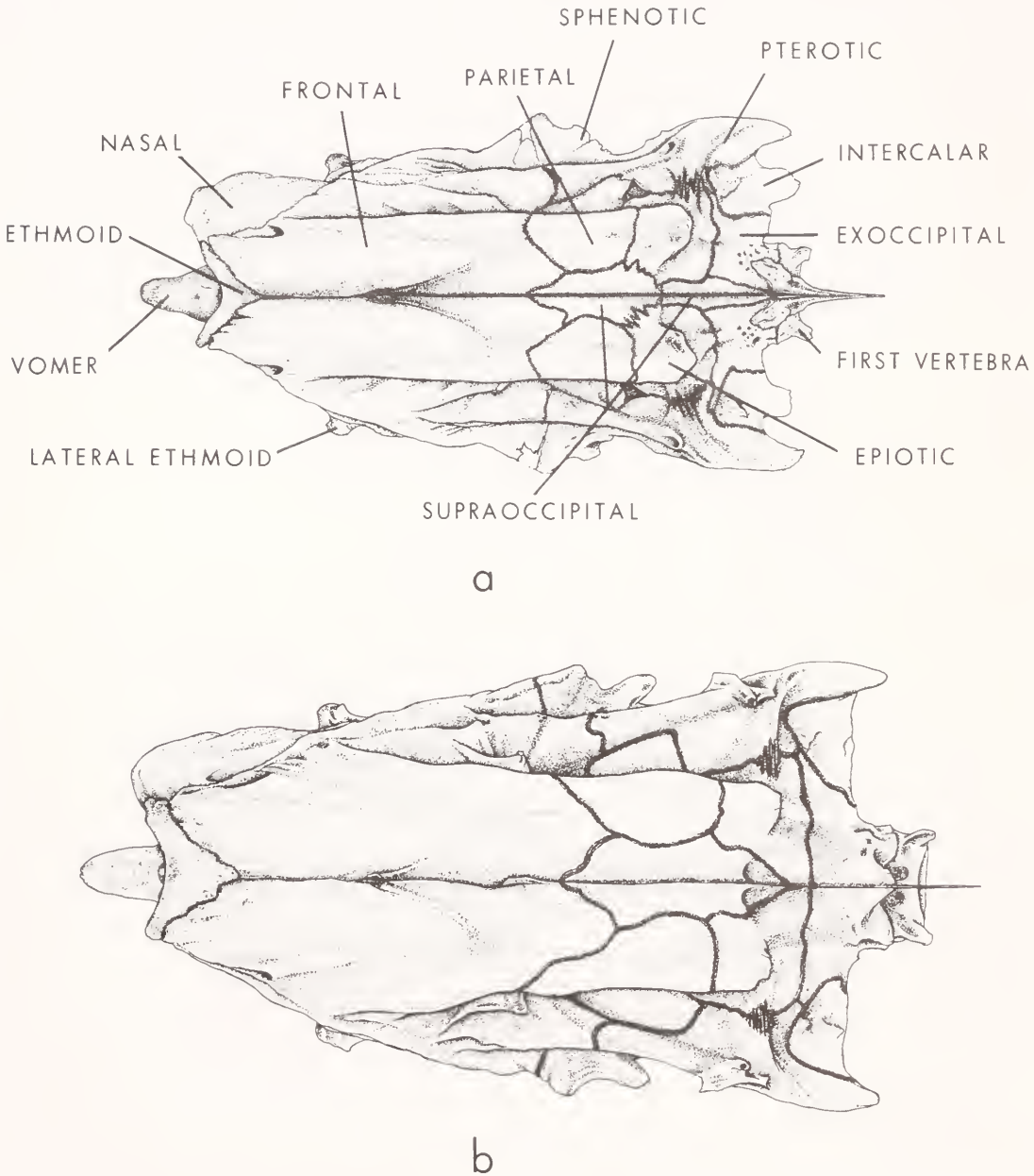


FIGURE 11.—Skulls in dorsal view. a. *Scomberomorus commerson*, Coffs Harbour, New South Wales, 1,155 mm FL. b. *Scomberomorus munroi*, Cairns, Queensland, 800 mm FL, USNM 219372, paratype.

separated from each other by ridges of bone. Thus, there are six grooves and five ridges in all. The median ridge is carried forward on the frontals to the ethmoid and is prolonged posteriorly in a large supraoccipital crest. This crest extends down over the exoccipital suture more broadly than in any other genus of the Scombridae.

The internal ridge or temporal ridge almost reaches anteriorly to the posterior portion of the nasal, and it is not interrupted above the eyes by any transverse ridge. Posteriorly, the ridge ends at the epiotic where the medial process of the posttemporal attaches.

The external or pterotic ridge extends forward to the midlevel of the orbit and develops anteriorly a small auxiliary ridge that extends laterally and posteriorly toward the temporal ridge.

The dilator groove is shorter than the other two

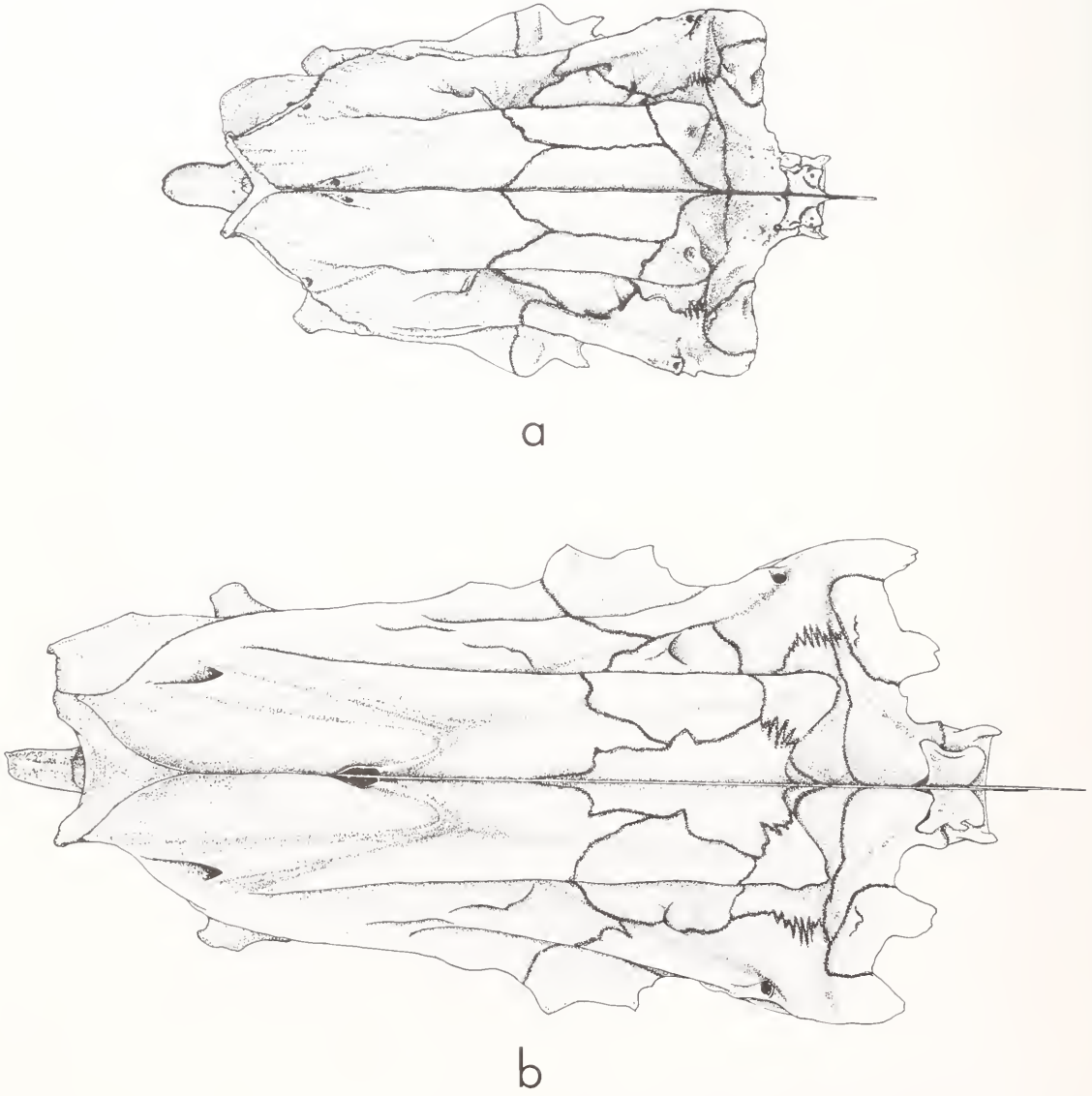


FIGURE 12.—Skulls in dorsal view. a. *Scomberomorus koreanus*, Singapore, 480 mm FL. b. *Scomberomorus concolor*, Gulf of California, 495 mm FL.

and can be detected easily in lateral view. The temporal groove is the middle one and is deeper than either of the other two. The remaining groove, the supratemporal, is the largest of the three and opens posteriorly between the supraoccipital crest and the middle portion of the epiotic.

The interorbital and otic regions are not as broad as in the more advanced genera of the Sardini (Collette and Chao 1975) and Thunnini (Gibbs and Collette 1967). The median and temporal crests are higher in *Scomberomorus* than in other scombrids. The bonitos, particularly *Orcynopsis unicolor* (Collette and Chao 1975:fig. 21),

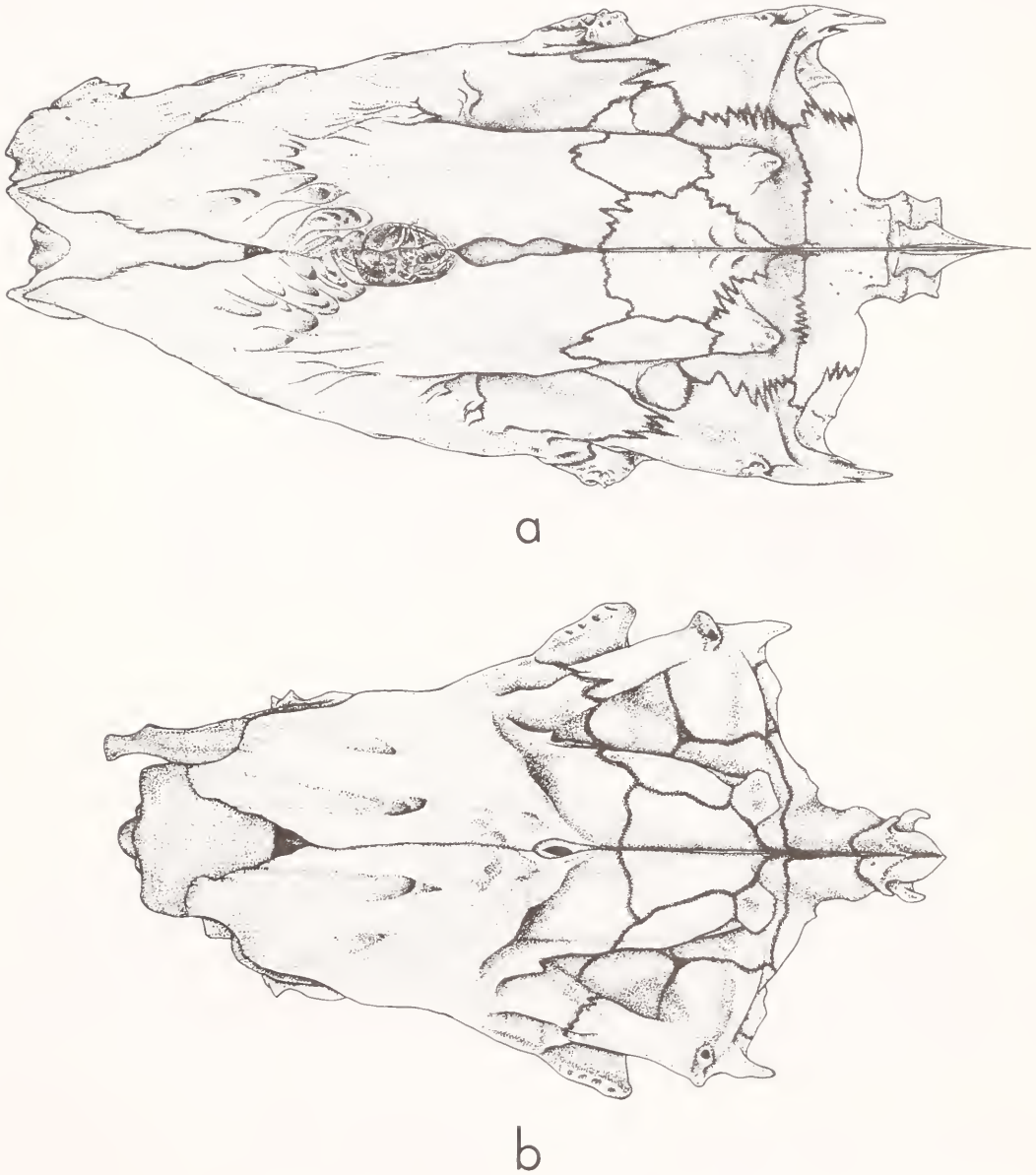


FIGURE 13.—Skulls in dorsal view. a. *Acanthocybium solandri*, Caribbean Sea, 1,240 mm FL. b. *Grammatorcynus bilineatus*, Scott Reef, Timor Sea, 453 mm FL.

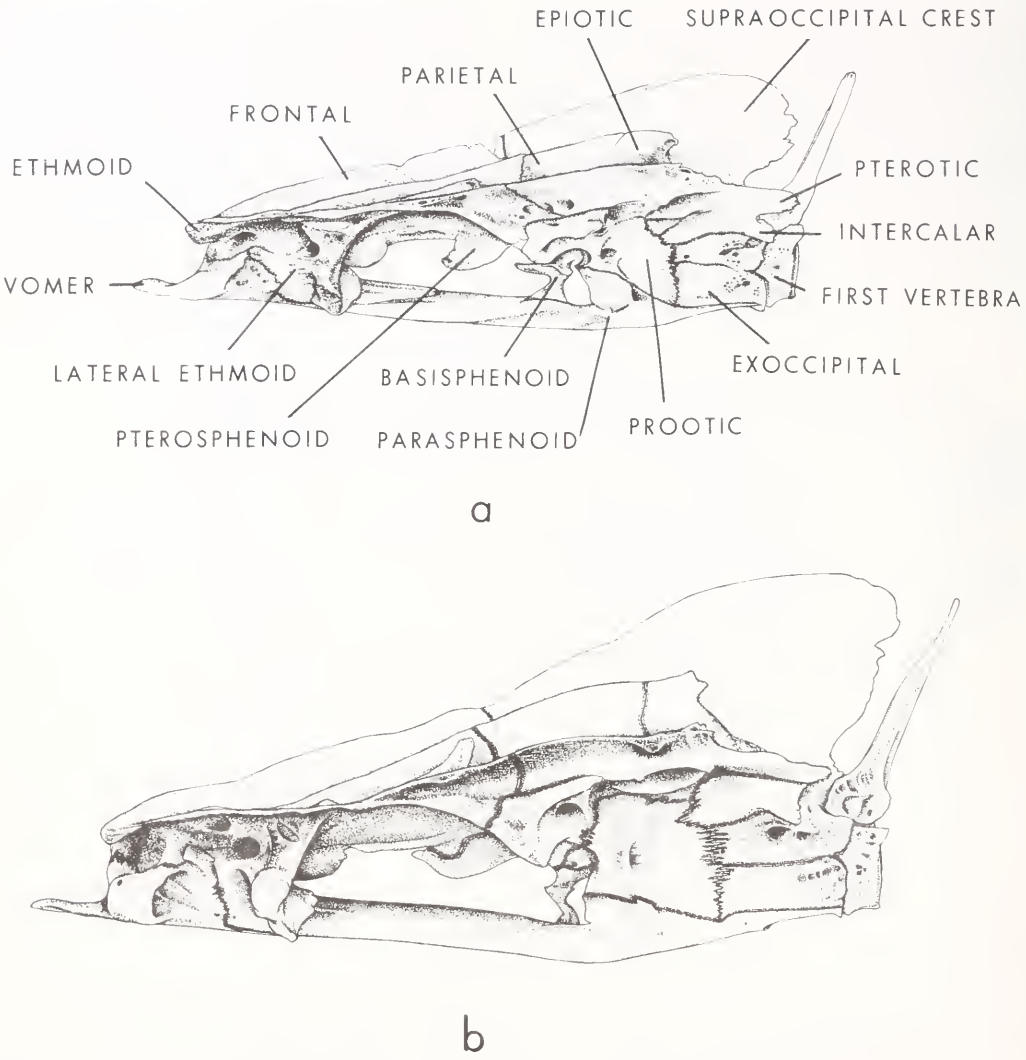


FIGURE 14.—Skulls in lateral view. a. *Scomberomorus commerson*, Coffs Harbour, New South Wales, 1,155 mm FL. b. *Scomberomorus munroi*, Cairns, Queensland, 800 mm FL, USNM 219372, paratype.

have the next highest crests.

ETHMOID REGION.—This region is composed of the ethmoid, lateral ethmoid, and vomer. The nasal bone lies lateral to the ethmoid and lateral ethmoid and, therefore, is included here.

Ethmoid.—The ethmoid (dermethmoid) is a forked median bone overlapped by the frontals above and bounded by the vomer and lateral ethmoid ventrally. The concave anterior surface articulates with the ascending process of the premaxilla. At its anterolateral aspect, the ethmoid bone supports the nasals.

In *Scomberomorus*, only the most anterior part of the ethmoid bone is exposed in dorsal view, while the rest of it is overlapped by the frontals. In *Acanthocybium*, only the lateral aspects of the bone are overlapped by the frontals and a V-shaped dorsal median portion is exposed. The ethmoid bone is longer in *A. solandri* than in *Scomberomorus*.

Lateral ethmoid.—The lateral ethmoids (par-

ethmoids) are massive paired bones which form the anterior margin of the orbit and the posterior and mesial walls of the nasal cavity. The lateral portion of each bone extends downward from the middle region of the frontals. The ventral surface of this wall mesially bears an articulating surface for the palatine and laterally another articulating surface for the first infraorbital (lachrymal). The inner walls of the lateral ethmoids come closest to each other at the ventral median line of the skull and contact the anterior edge of the parasphenoid. The median half of each lateral ethmoid extends downward about three-fourths as far as the lateral portion and has a large round foramen for the olfactory nerve which is prominently seen on the anterior surface. On the dorsal surface, they abut the nasals anteriorly, the frontals posteriorly, and articulate with the ethmoid mesially. On the anterior surface, ventral to the foramen, each lateral ethmoid bears a process

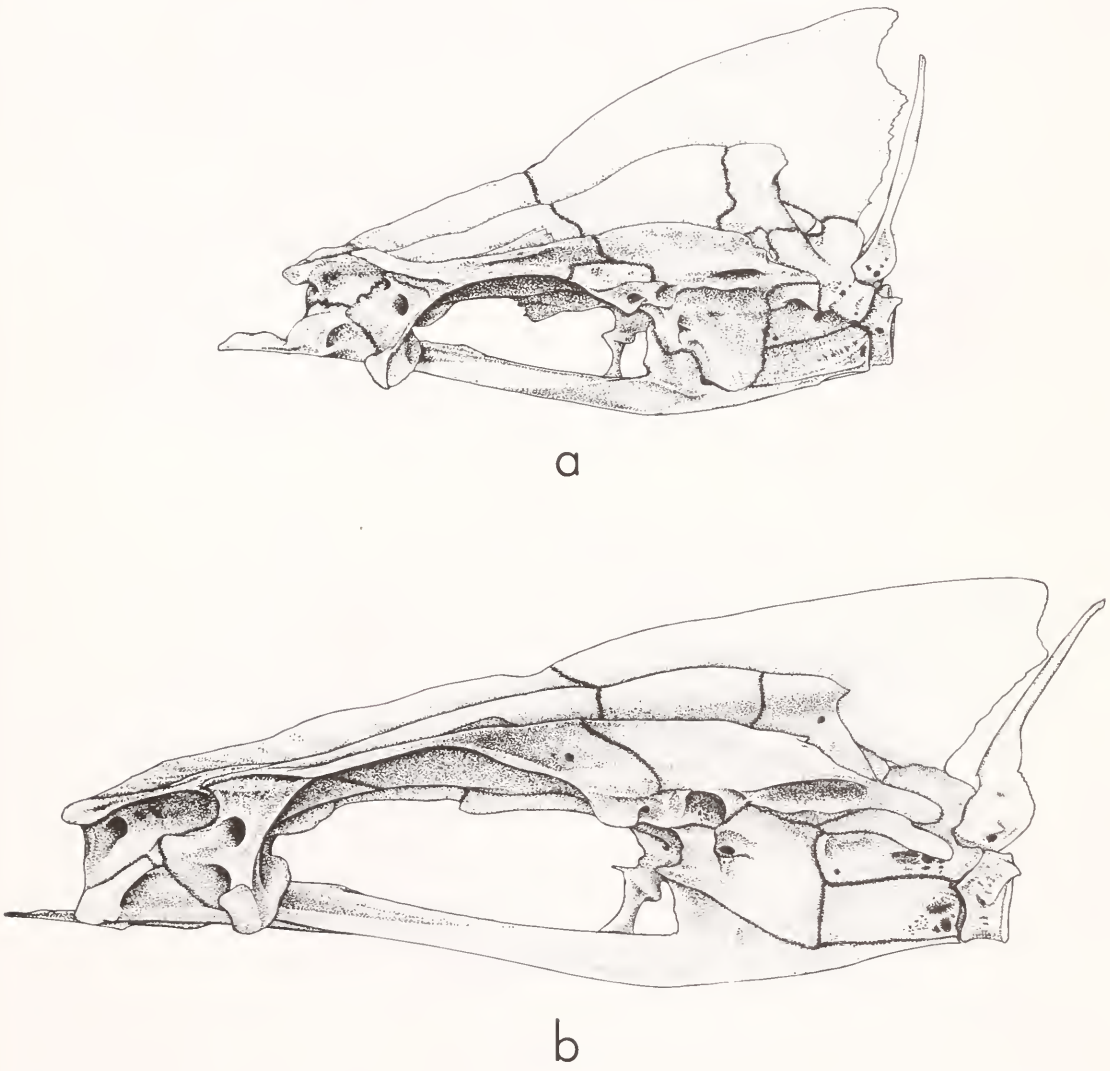


FIGURE 15.—Skulls in lateral view. a. *Scomberomorus koreanus*, Singapore, 480 mm FL. b. *Scomberomorus concolor*, Gulf of California, 495 mm FL.

that extends anteriorly and mesially to contact the dorsolateral surface of the spear-shaped posterior portion of the vomer. No appreciable difference was noted in the lateral ethmoids of the different species.

Vomer.—The vomer is the most anteroventrally located bone of the cranium. The spatula-shaped anterior process bears a large oval patch of fine teeth on its ventral surface. The vomerine tooth patch extends posteriorly as a narrow ridge in some specimens of some species, e.g., *S. concolor* (Fig. 15b). The vomer articulates with the ethmoid dorsally and lateral ethmoid dorsolaterally. The pointed posterior process is firmly ankylosed dorsally with the parasphenoid. On each side of the vomer, dorsolaterally and behind the spatulate anterior process, is a prominent articular surface for a loose articulation with the head of the maxilla. Posterior to this articular surface, facing ventrolaterally, is a prominent sulcus for a similar movable articulation with the ventral branch of the anterolateral fork of the palatine. The spatulate anterior process of the vomer is very long and extends beyond the anterior margins of the nasal and ethmoid bone in *Scomber-*

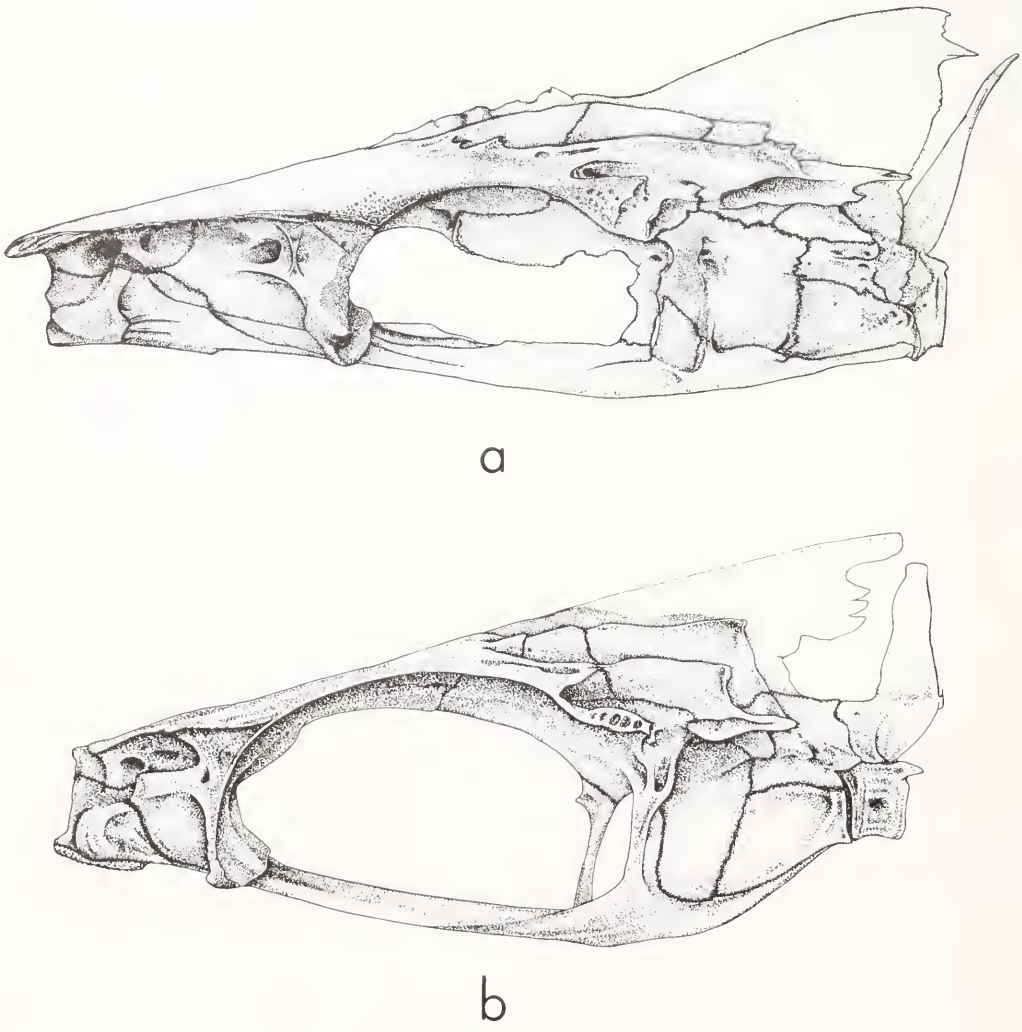
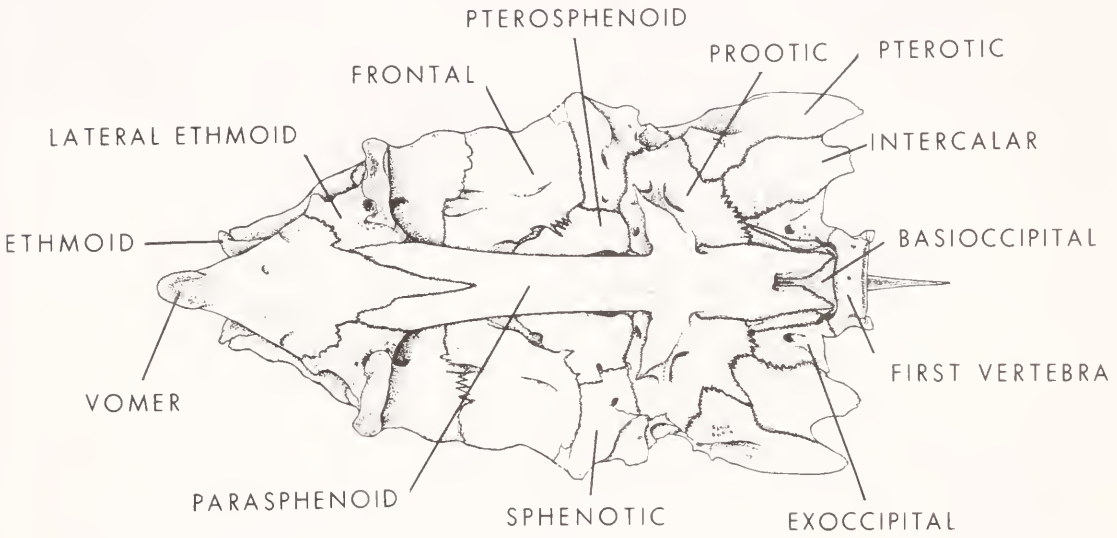


FIGURE 16.—Skulls in lateral view. a. *Acanthocybium solandri*, Caribbean Sea, 1,240 mm FL. b. *Grammatorcynus bilineatus*, Scott Reef, Timor Sea, 453 mm FL.

omorus. No other scombrid has such a spatulate anterior extension of the vomer. In fact, the vomer is either not visible in dorsal view or protrudes anteriorly slightly beyond the ethmoid in other scombrid genera.

Nasal.—The nasal bones (Fig. 20) are flat, roughly triangular bones with thickened lateral edges. The mesial edges are irregular and almost serrate in some species to form a firm immovable articulation with the lateral edge of the frontals.



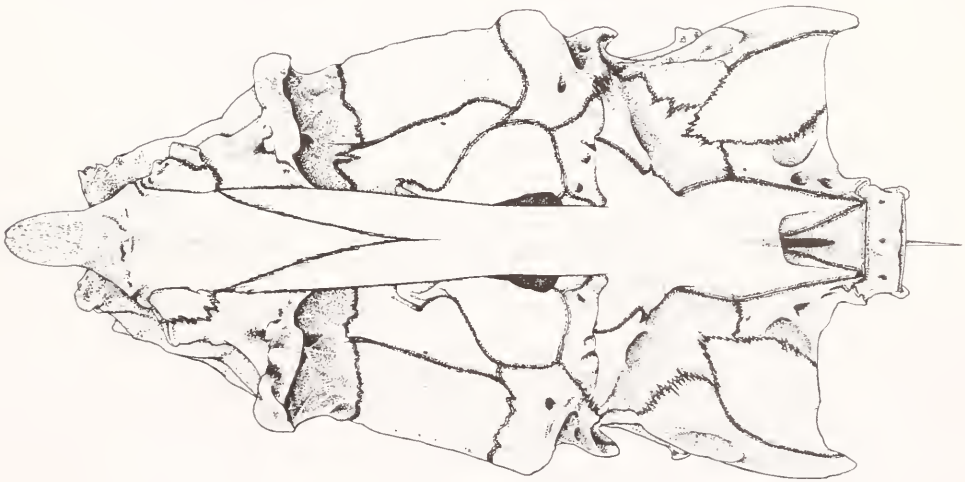


FIGURE 17.—Skulls in ventral view. a. *Scomberomorus commerson*, Coffs Harbour, New South Wales, 1,155 mm FL. b. *Scomberomorus munroi*, Cairns, Queensland, 800 mm FL, USNM 219372, paratype.

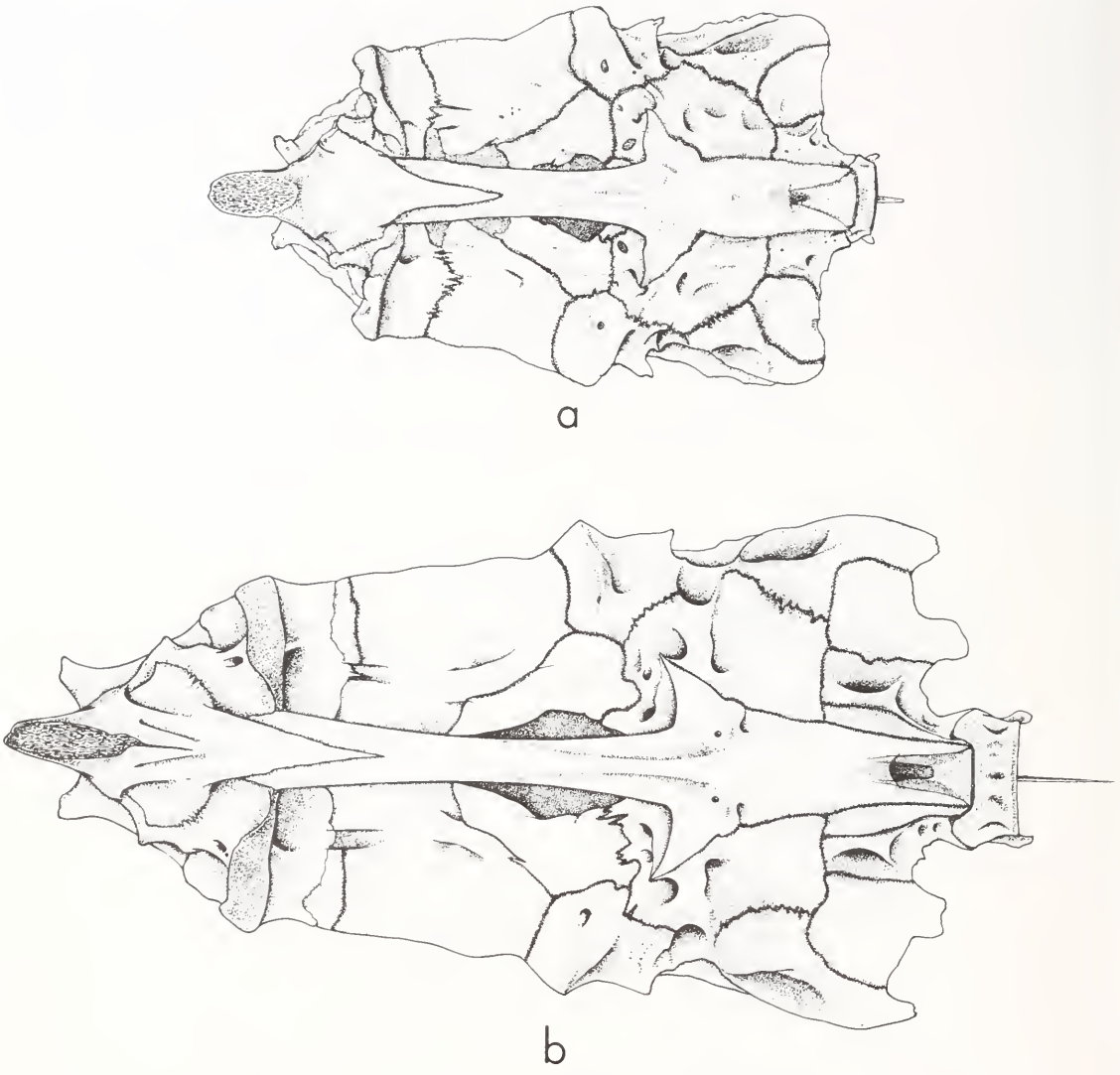


FIGURE 18.—Skulls in ventral view. a. *Scomberomorus koreanus*, Singapore, 480 mm FL. b. *Scomberomorus concolor*, Gulf of California, 495 mm FL.

The anterior margins fit neatly beside the anterior branches of the forked ethmoid bone as can be seen in the dorsal views of the skulls (Figs. 11, 12). They are nonprojecting in that their anterior margin is at the level of the ethmoid bone except in *Grammatorcynus* where they project well beyond the anterior end of the neurocranium (Fig. 13b). Length divided by width ranges from 2.0 to 4.2 in the three genera. The widest nasal bones are in *S. koreanus* (2.0-2.1) and *S. sinensis* (2.0-2.3, Fig. 20b). The most elongate nasals are in *Acanthocybium* (3.1-4.2, Fig. 20c), *Grammatorcynus* (2.8-3.4, Fig. 20d), *S. cavalla* (2.8-3.1, Fig. 20a), and *S. regalis* (2.8-3.0). The other 14 species of *Scomberomorus* are intermediate (2.0-2.9). The anterior end of the nasal bone is rounded and heavy in *Scomberomorus* and *Acanthocybium* (Fig. 20a-c). The anterior end has a short, slightly angled arm in *Grammatorcynus* (Fig. 20d).

ORBITAL REGION.—The orbit is surrounded by the posterior wall of the lateral ethmoid, the ventral side of the frontal, the pterosphenoid, sphenotic, prootic, suborbital, and lachrymal

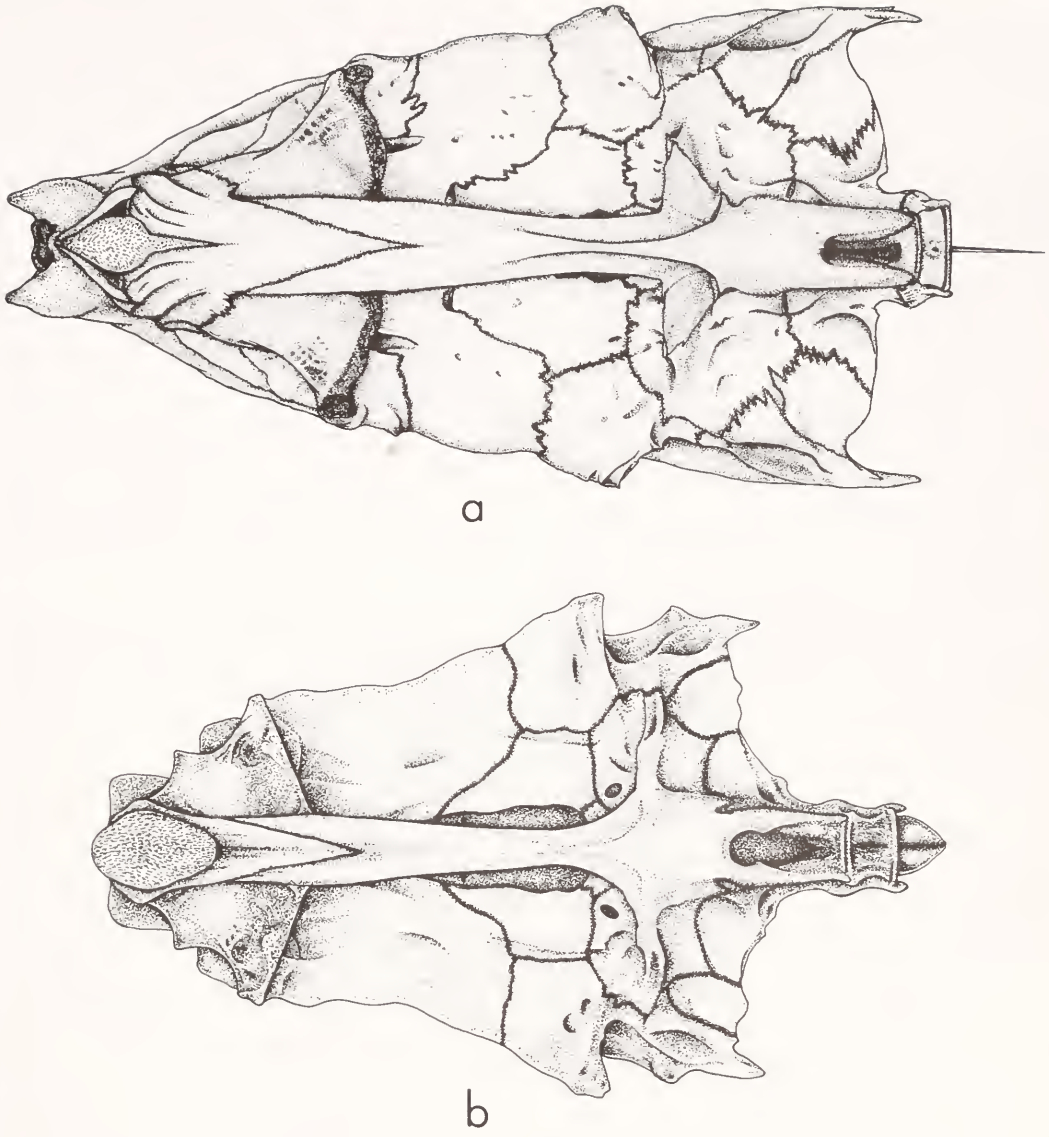


FIGURE 19.—Skulls in ventral view. a. *Acanthocybium solandri*, Caribbean Sea, 1,240 mm FL. b. *Grammatorcynus bilineatus*, Scott Reef, Timor Sea, 453 mm FL.

bones. The left and right orbits are partially separated by the basisphenoid. The sclerotic bones enclose the eyeballs.

Frontal.—The frontals are paired bones that form the largest portion of the dorsal surface of the neurocranium. Anteriorly they are pointed, and posteriorly they become expanded. Anteriorly, the frontals overlap the dorsal surface of the ethmoid bone, the inner edge of the nasals, and the dorsal surface of the lateral ethmoid. The midlateral aspect is thickened to form the orbital roof. Posteriorly, they are bounded by the supraoccipital and parietals. Posterolaterally, they overlap the pterotics and just anterior to the pterotics, cover the sphenotics. Ventrally, each frontal bears a sheet of bone, the orbital lamella, which is bounded by the sphenotic posteriorly, lateral ethmoid anteriorly, and pterosphenoid mesially. On the base of the orbital lamella may

be seen a number of small foramina for the branches of the supraorbital nerve trunk. The laterosensory canals of the frontals are evident on the pterotic crests as a series of pores.

In *Acanthocybium*, the frontals are separated from each other by the dorsomedian pineal fenestra lying just in front of the supraoccipital at the level of the pterosphenoids and another anterior fontanel just posterior to the ethmoid bone (Fig. 13a). A smaller, more oval pineal opening is present between the posterior ends of the frontals in *Grammatorcynus* (Fig. 13b). When viewed through the pineal fenestra, a part of the dorsal surface of the parasphenoid is visible through the opening of the brain chamber between the pterosphenoids. There is a deep depression on the frontals mesially, just anterior to the pineal fenestra. This depression becomes shallower anteriorly, becoming confluent with the dorsal surface of the frontals. In *Scomberomorus*, the frontals join mesially along the median line on the neurocranium where they form the anterior half of the median ridge whose posterior half is composed of the supraoccipital crest. In all but three species of *Scomberomorus*, the left and right frontals are attached very closely to each other such that there is no gap between them. However, in *S. commerson* and *S. cavalla*, there is a long narrow slit between the left and right frontals, but it is not a fenestra in the true sense, as the lower parts of the bones are very closely approximated. A third condition is found in *S. sinensis*. Here the anterior part of the median ridge is almost absent and there is a wide gap between the left and right frontals. The interorbital commissures of the lateralis system are developed a little anterior to the middle of each frontal in the form of two pores at the margin of the median ridge which lead into oblique tubes downwards and posteriorly. Another pair of commissures of the lateralis system is developed along the anterolateral margin of the frontals. These sensory canals are not developed in *Acanthocybium* and *Grammatorcynus*.

Pterosphenoid.—The pterosphenoids (alisphenoids) form the posterodorsal region of the orbit. They abut the basisphenoid and prootics posteri-

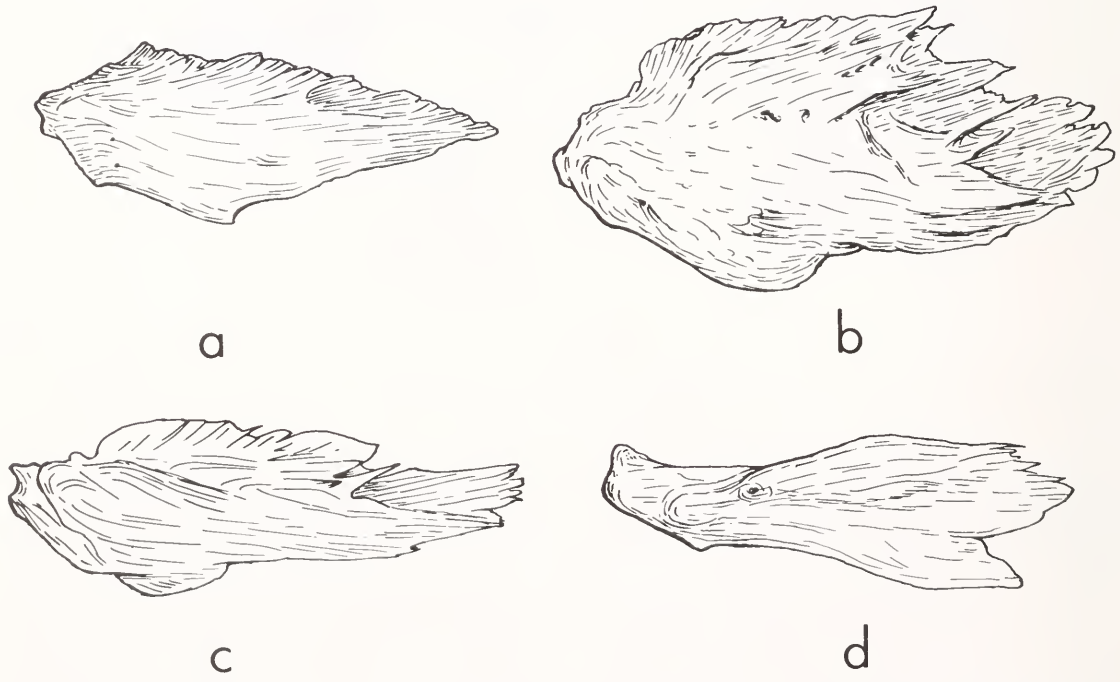


FIGURE 20.—Left nasal bones in lateral view. a. *Scomberomorus cavalla*, Miami, 797 mm FL, 2×. b. *Scomberomorus sinensis*, Tokyo, 1,850 mm FL, 1×. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL, 1.5×. d. *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 3×.

orly and the frontals and sphenotics laterally. There is a space between the left and right pterosphenoids opening into the brain chamber just anterior to the basisphenoid. In most species of *Scomberomorus*, there is an anterior medially directed lobe on each pterosphenoid. These lobes meet along the median line or at least come very close to each other in adults of three species: *commerson* (over 1,000 mm FL), *cavalla* (over 550 mm FL), and *lineolatus* (over 750 mm FL). Smaller specimens of these 3 species and all sizes of the other 15 species have a wide gap or fenestra between the left and right lobes. The gap is about equal to the width of the parasphenoid or slightly larger in three species: *brasiliensis*, *koreanus* (Fig. 12a), and *concolor* (Fig. 12b). The gap is largest in *S. multiradiatus*, so large that there is virtually no medially directed lobe. This causes the window into the brain chamber to be almost rectangular in this species.

Sclerotic.—The sclerotic bones consist of two thickened semicircular segments connected by cartilage on the inner lateral surface and by corneal membranes on the outside. The inner rim of the sclerotic bones appears elliptical externally as in the bonitos (Collette and Chao 1975) and *Thunnus* (e.g., *T. atlanticus*, de Sylva 1955:fig. 7). The sclerotic bones of *Grammatorcynus* are relatively larger, thinner, and close to circular. In *Acanthocybium*, the sclerotic bones are elliptical as in *Scomberomorus*, but they are heavier and extend further medially. The only species of *Scomberomorus* that appeared to differ from the other species is *S. sinensis*. The sclerotics are especially thick in this species and there is a thick bony lump in the middle of the posterior surface of one of the two sclerotics. Other species of *Scomberomorus* have a thickening of the bone in the same region but it does not form a distinct protrusion as it does in *S. sinensis*.

Basisphenoid.—The basisphenoid is a small, median, Y-shaped bone that connects the parasphenoid, prootics, and pterosphenoids. The compressed median vertical base bears an anterior median process but lacks a posterior process as is present in other scombrids such as *Thunnus* (Gibbs and Collette 1967) and most bonitos (Collette and Chao 1975). In most species of *Scomberomorus* there is at least a trace of a lateral ridge that extends laterally and posteriorly on each side of the anterior process. There is great variation in the length of the anterior process and in the relative degree of development of the lateral ridges. Both features are best developed in *S. commerson* where the length of the anterior process is greater than the height of the vertical axis of the bone.

Infraorbitals.—The infraorbital (suborbital) series of *Scomberomorus* consists of from 9 to 13 elements which enclose the infraorbital branch of the lateral sensory canal system (Fig. 21a). Only 9 elements were observed in *S. munroi*, *S. sierra*, and *S. sinensis*, but 13 elements were observed in *S. brasiliensis*. The canal enters the infraorbital series at what is usually considered the last element (dermosphenotic) and continues around the orbit to terminate on the first infraorbital (lachrymal).

The first infraorbital (lachrymal or IO1) is the first and largest element in the infraorbital series. Anteriorly, several canal tubes open on the laminar, platelike surface of the bone. Posteriorly, the canal tube continues directly to the second infraorbital. The first infraorbital is an elongate bone (length/height = 2.8-3.5) that covers part of the maxilla and is attached to the lateral ethmoid dorsally by a mesially directed articular process. The anterior portion is forked with a thin anterior process. This process is a point of attachment for a ligament connected to the nasal. The projection is present in all species of *Scomberomorus* except *S. lineolatus* and *S. tritor*. The portion posterior to the articular process is elongate, pointed, and longer than the anterior portion. The general shape of the first infraorbital in *Scomberomorus* is similar to that in the bonitos (Collette and Chao 1975:fig. 28), particularly *Cybiosarda elegans*, except that the anterior process is smaller and more dorsally directed than in *Cybiosarda*. *Acanthocybium* differs from *Scomberomorus* in having the posterior portion of the first infraorbital short and broad, shorter than the anterior portion (Fig. 21b). *Grammatorcynus* has a feebly forked anterior end (Fig. 21c), lacking a distinct anterior process such as is present in *Scomberomorus* and *Acanthocybium*.

As Devaraj (1977) noted, the dorsal margin of the anterior part of the first infraorbital is straight, or nearly so, in *S. cavalla* and *S. commerson* but clearly concave in the other species. Mago Leccia (1958:pl. 4, fig. 7) indicated that *S. cavalla* lacked the characteristic anterior projection, but we have found it to be present in our material. In other respects, there seems to be as much variation between individuals of a species

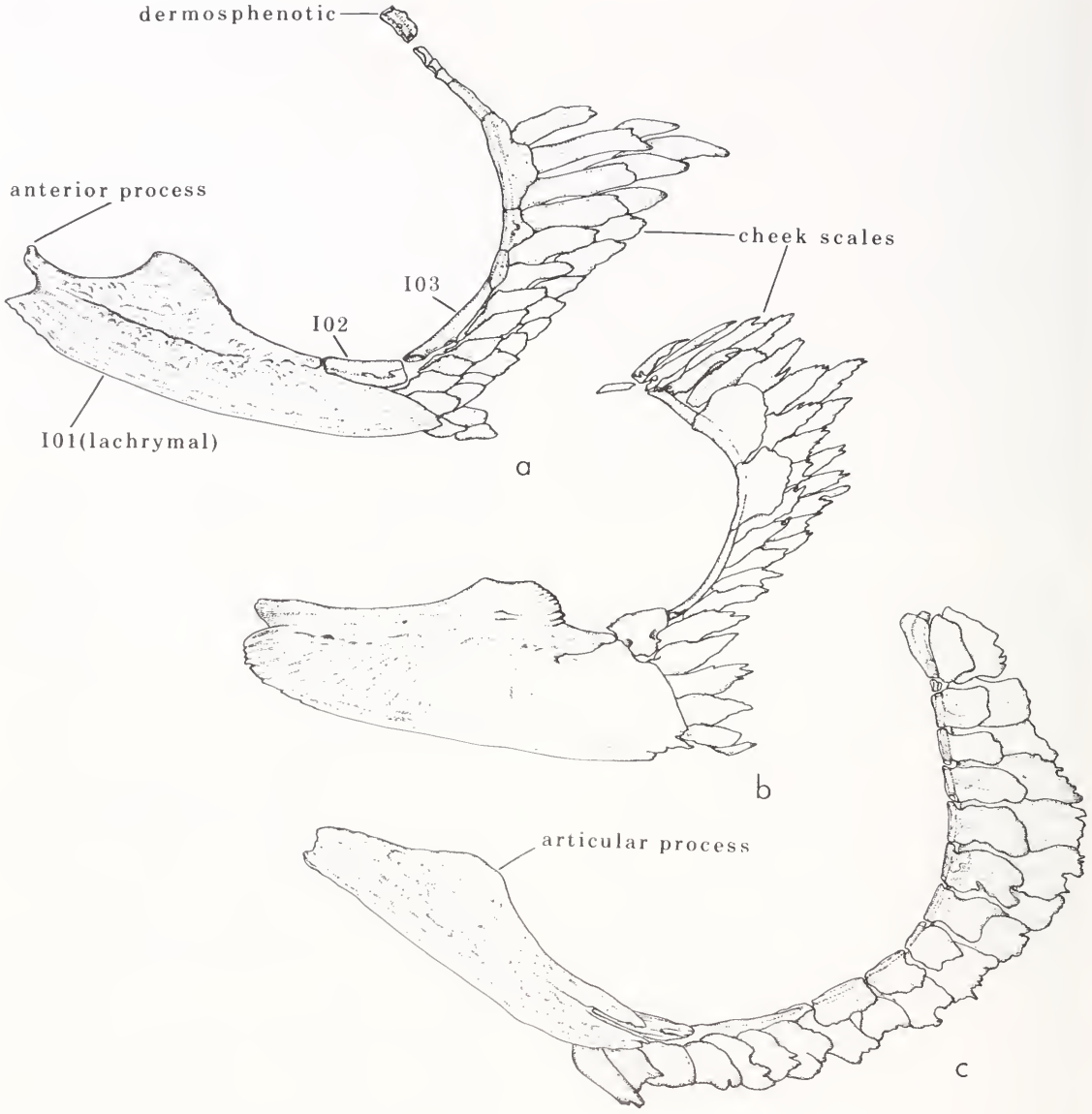


FIGURE 21.—Left infraorbital bones in lateral view. a. *Scomberomorus maculatus*, Cape Hatteras, N.C., 534 mm FL. b. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL. c. *Grammatorcynus bilineatus*, Timor Sea, 453 mm FL.

as between species in the shape of the first infraorbital.

The second infraorbital (IO2) sits firmly on the dorsal edge of the anterior portion of the first infraorbital. It is a flat, somewhat compressed bone.

The third infraorbital (IO3) is an elongate, tubular bone. It has no platelike extensions, but has a large mesial shelflike extension (subocular shelf of Smith and Bailey 1962). Although not reported by those authors, we have found this shelf to occur in all species of *Scomberomorus* as well as in all other genera of scombrids. The shape of this shelf varies among specimens of the same species as well as between right and left sides of a single specimen.

The fourth through the penultimate elements (postorbitals) usually are simple tubelike bones which may have pores accommodating canal tubes to the skin and cheek scales. The fourth

through about the seventh elements may be expanded laterally as laminar plates which cover the anterior end of the cheek scales. There may be 10-16 rows of specialized cheek scales posterior to the infraorbitals. These scales originate mesial to the infraorbital canal tubes and extend posteriorly as flat, sometimes pointed, platelike elements. These platelike scales may themselves be covered with more typical cycloid scales and exhibit the same morphology as the corselet scales of higher scombrids. The cheek scales of *Scomberomorus* may represent the primitive condition of the corselet.

OTIC REGION.—This region encloses the otic chamber inside the skull, and is formed by the parietal, epiotic, supraoccipital, prootic, pterotic, sphenotic, and intercalar (opisthotic) bones.

Parietals.—The parietals articulate with the frontals anteriorly, the supraoccipital mesially and the pterotics laterally, sphenotics ventrally, and epiotics posteriorly. The inner lateral crest that originates at the middle of the frontal bones continues through the parietals to terminate at the epiotics. This crest is typical of scombrids and is particularly well developed in *Scomberomorus*. These crests originate on the parietals, instead of the frontals, in *Acanthocybium* and *Grammatorcynus* and are not as high as in *Scomberomorus*. The parietals of all the species of *Scomberomorus* are similar.

There is a gap or fenestra on the dorsal surface of the skull where the parietal, epiotic, and pterotic bones come together. It varies in shape from roughly triangular to rectangular in most species. There is wide variation from specimen to specimen that tends to obscure potential interspecific differences. The gap is very small in some specimens of eight species: *commerson*, *concolor* (Fig. 12b), *koreanus* (Fig. 12a), *maculatus*, *munroi* (Fig. 11b), *plurilineatus*, *queenslandicus*, and *sierra*. It is usually larger in the other species and in most specimens of *S. commerson* (Fig. 11a).

Epiotics.—The epiotics are massive, irregular, and bounded by the parietals anteriorly, the supraoccipital mesially, the exoccipitals posteriorly, and the pterotics laterally. The inner lateral crests terminate at the posterior end of the epiotics. The medial process of the posttemporal bone attaches here on a rough process. There are slight differences between the species of *Scomberomorus* in the attitude of the attachment area and its roughness. In many species, the lateral crest continues posteriorly almost perpendicular to the skull. In some species such as *S. commerson* (Fig. 11a) and *S. queenslandicus*, the area of attachment is flatter. This area is flat and rough in *Acanthocybium* (Fig. 13a) and forms a separate process in *Grammatorcynus* (Fig. 13b).

Supraoccipital.—The supraoccipital forms the dorsomedial portion of the posterior end of the neurocranium and bears a well-developed crest which continues anteriorly on the frontals and is pronounced posteriorly as a strong supraoccipital crest. The supraoccipital can be divided into two parts: a thin, elongate triangular crest and a roughly hexagonal base. The crest extends down over the exoccipitals along the median line where the dorsal walls of the exoccipitals suture with each other, but it is not interposed between the exoccipitals. The hexagonal base is bounded anteriorly by the frontals and laterally by the parietals and epiotics. The crest extends posteriorly over the first vertebral centrum usually to a level past the posterior margin of the centrum (Figs. 14-16). The height of the crest varies among species of *Scomberomorus* and is highest in three species, *S. guttatus*, *S. koreanus* (Fig. 15a), and *S. multiradiatus*. Dividing the height of the supraoccipital crest (ventral margin of supraoccipital to edge of crest) by skull length (tip of vomer to posteroventral margin of basioccipital) gives a ratio of 0.46-0.57 for these three species, compared with 0.34-0.45 in the other 15 species. Low ratios are found in *S. cavalla* and *S. commerson* (0.35-0.40) and in all six species of the *regalis* group (0.34-0.42).

Prootics.—In ventral view, the prootics connect with all bones on the ventral side of the skull which compose the posterior part of the neurocranium (Figs. 17-19). Each prootic is bordered ventrally by the parasphenoid; posteriorly by the basioccipital, exoccipital, and intercalar; laterally by the pterotic and sphenotic; and anteriorly by the pterosphenoid and basisphenoid. The prootic bones are irregular in shape and meet each other along the ventromedian line of the brain case to form the anterior portion of the posterior myodome. On the ventral surface, extending from the lateral wing of the parasphenoid to the sphenotic, the prootic forms a thick bridge which strengthens the trigemino-facialis chamber (Allis 1903). A prootic foramen is present anterolateral-

ly between the tip of the parasphenoid wing and the sphenotic. There is no trace of the prootic pit characteristic of the Thunnini and *Allothunnus* (Gibbs and Collette 1967; Collette and Chao 1975). Specimens differ in the number and arrangement of foramina leading into the brain cavity from inside the anterior opening of the trigeminofacialis chamber, but these do not seem to be useful interspecific differences.

Pterotics.—The pterotics form the lateral posterior corners of the neurocranium. Posteriorly, each pterotic is produced into a truncate process or pointed spine. The pterotics articulate with the epiotics and parietals medially and with the exoccipitals and intercalars posteriorly. A ridge, the pterotic ridge, originates on the dorsal surface of the posterior third of the frontal and continues posteriorly, diverging to the posterior corner of the pterotic, just anterior to the pterotic spine. In ventral view, the pterotics articulate with the sphenotics anteriorly and the prootics and intercalars medially. Two contiguous fossae, one at the posterior half of the pterotic bone and one at its joint with the sphenotic, seat the dorsal and anterior condyles of the hyomandibula. Three closely situated lateral sensory canal pores open on each pterotic at the posteriormost region of the pterotic crest. The largest pore is the most posterior and opens dorsally; lateral to this is the next largest opening laterally on the outside of the pterotic crest; the smallest is the most anterior of the three, lying along the crest and usually more elongate in shape.

The lengths and widths of the pterotic spines vary among the species. In eight species (*brasiliensis*, *guttatus*, *koreanus* (Fig. 18a), *multiradiatus*, *plurilineatus*, *regalis*, *semifasciatus*, and *tritor*), there is essentially no pterotic spine, merely a rounded posterior area of the skull. In six species (*concolor* (Fig. 18b), *lineolatus*, *maculatus*, *munroi* (Fig. 17b), *niphonius*, and *sierra*), there is a blunt posteriorly projecting spine. *Scomberomorus sinensis* is similar to this group, but the posterior projection is broader and less like a spine. The pterotic spines are longest in three species (*cavalla*, *commerson* (Fig. 17a), and *queenslandicus*), all of which also have prominent posterior projections of the intercalars. *Grammatorcynus* (Fig. 19b) is similar to the latter group, but the spine is thinner and sharper. *Acanthocybium* (Fig. 19a) has a longer and thinner pterotic spine than do *Grammatorcynus* and the species of *Scomberomorus*.

Sphenotics.—The sphenotics form the most posterior dorsolateral part of the roof of the orbit. They continue the outer lateral shelf from the frontals and articulate with the pterosphenoid medially and the prootic and pterotic posteriorly. A segment of the articular fossa for the head of the hyomandibula is afforded by the lateral wall of the sphenotic on the ventral surface. The sphenotic is pierced by a foramen for the ramus oticus nerve (Allis 1903). When viewed dorsally, the sphenotics spread out on both sides more prominently in *Scomberomorus* than in *Acanthocybium*, as noted by Devaraj (1977). Devaraj stated that the "midlateral projection" was large in *koreanus*, *guttatus*, *maculatus*, and *regalis*; small in *lineolatus*, *cavalla*, and *commerson*; and absent in *Acanthocybium*, but we are not clear as to what he was referring.

Intercalars.—The intercalars (opisthotics) are flat bones that form part of the posterior border of the neurocranium interposed between the pterotics and exoccipitals. The anterior portion on the dorsal surface is concealed by the overlapping pterotic, thus exposing the bone on the dorsal surface less than on the ventral side. Each intercalar bears a protuberance on the dorsal surface to receive the lateral arm of the posttemporal. This protuberance is followed by a posterior projection of the intercalars in some species of *Scomberomorus* but not in *Acanthocybium* or *Grammatorcynus*.

Species of *Scomberomorus* may be roughly divided into three groups based on the size of the posterior projection from the intercalar as Devaraj (1977) noted for Indian species. Eight species lack any posterior projection or have only an insignificant projection: *guttatus*, *koreanus* (Fig. 18a), *lineolatus*, *multiradiatus*, *munroi* (Fig. 17b), *plurilineatus*, *semifasciatus*, and *sinensis*. In each of these species, except *S. multiradiatus*, the pterotic spine protrudes further posteriorly than does the intercalar region. In *S. multiradiatus*, the posterior corners of the skull are rounded and there is no pterotic spine so the intercalars project further posteriorly. Eight species have a distinct posterior projection from the intercalar: *brasiliensis*, *cavalla*, *concolor* (Fig. 18b), *maculatus*, *niphonius*, *regalis*, *sierra*, and *tritor*. The posterior projection is smaller in some specimens of *S. niphonius*, placing it somewhat between groups 1 and 2. The posterior projection is a little longer in *S. cavalla*, between groups 2 and 3. Two species, *commerson* (Fig. 17a)

and *queenslandicus*, have a prominent truncate process.

BASICRANIAL REGION.—This region consists of the parasphenoid, basioccipital, and exoccipital bones, and forms the posteroventral base of the skull.

Parasphenoid.—The parasphenoid is a long cross-shaped bone (Figs. 17-19) which articulates with the vomer anteriorly and forms the ventral axis of the skull. The lateral wing of the parasphenoid extends dorsolaterally along the ventral ridge of the prootic bones on either side, and has a pointed end which forms part of the anteroventral wall of the posterior myodome. Posteriorly, the parasphenoid bifurcates into two lateral flanges which attach dorsally to the corresponding posteroventral flanges of the basioccipital bone and surround the posterior opening of the posterior myodome. A ventrally projecting median keel is present in the area anterior to the origin of the lateral flanges. In ventral view, the general characteristic of the parasphenoid is a gradual narrowing of the bone from anterior to posterior. The broadest portion of the parasphenoid is located usually at or before the tip of the V-shaped joint with the vomer. Broad parasphenoids are also present in *Acanthocybium* and the bonitos, Sardini (Collette and Chao 1975). In lateral view (Figs. 14-16), the parasphenoid forms the ventral border to the orbits and connects with the lateral ethmoids, basisphenoid, prootics, and basioccipital bones dorsally.

The shaft of the parasphenoid is distinctly wider in seven species: *S. commerson* (Fig. 17a), *lineolatus*, *munroi* (Fig. 17b), *niphonius*, *queenslandicus*, *semifasciatus*, and *sinensis*. Devaraj (1977) included *S. cavalla* along with *S. lineolatus* and *S. commerson* as having a broad parasphenoid, based on Mago Leccia (1958). We find *S. cavalla* to have a broader parasphenoid than some members of the *regalis* species group but not as broad as in the group of seven species listed above.

Basioccipital.—The basioccipital is the most posteroventrally located bone of the skull. It is shaped like an inverted U with lateral flanges on either side of the skull and forms the roof and lateral walls of the posterior myodome. Anteriorly, the basioccipital is attached to the prootic bones and dorsally with the exoccipital bones. Its lateral flanges expand ventrally to meet the flat posterior flanges of the parasphenoid. Posteriorly, the lateral flanges fuse to form a circular margin in a slightly backward oblique position and attach to the margin of the first vertebral centrum. There are a variable number of small pores in a shallow depression on the lateral surfaces of the basioccipital. This depression is deepest in *S. sinensis* but does not approach the basioccipital depression characteristic of the bonitos, Sardini (Collette and Chao 1975).

Exoccipital.—The exoccipitals connect the skull to the first vertebra dorsally. The exoccipital articulates with the epiotic and supraoccipital bones anterodorsally, the intercalar laterally, and with the other exoccipital posterodorsally. In ventral view, the exoccipital articulates with the prootic anteriorly, basioccipital medioventrally, and intercalar laterally. In posterior view, the foramen magnum is framed by the exoccipitals. Laterally, there are two foramina. The small anterior glossopharyngeal foramen (Allis 1903) lies close to the posterior border of the prootic. The large posterior vagal foramen lies just under the overhanging shelf formed by the posterior margin of the exoccipital. Dorsally, a small foramen which opens into the brain cavity is present at the medioposterior corner of the exoccipital.

Branchiocranium

The branchiocranium is divided into five sections: mandibular arch, palatine arch, hyoid arch, opercular apparatus, and branchial apparatus.

MANDIBULAR ARCH.—The mandibular arch is composed of the upper jaw (premaxilla, maxilla, and supramaxilla) and the lower jaw (dentary, angular, and retroarticular). Teeth are borne on the premaxilla and dentary, and the number of teeth on these bones is a useful taxonomic character (see Dentition section).

Dentition.—Large, triangular, laterally compressed teeth are present in the upper and lower jaws of *Scomberomorus*. *Acanthocybium* has similar teeth that are a little blunter and more tightly packed. *Grammatorcynus* has long thin teeth that are slightly compressed laterally. Bonitos have conical teeth that are larger than the conical teeth of the higher tunas (Thunnini). Tooth replacement in *Scomberomorus cavalla* was studied by Morgan and King (1983). The number of jaw teeth in *Scomberomorus* varies widely with a range of 5-39 in the upper jaw, 4-37

in the lower jaw (Tables 3, 4). Two species of *Scomberomorus* stand out from the rest, *S. multiradiatus* with the fewest teeth (5-10, $\bar{x}$ 8.0 on the upper jaw; 5-11, $\bar{x}$ 7.8 on the lower jaw) and *S. concolor* with the most teeth (13-37, $\bar{x}$ 22.2 on the upper jaw; 12-34, $\bar{x}$ 19.7 on the lower jaw). The 18 species can be ranked from lowest to highest as follows (mean for upper jaw followed by mean for lower jaw): 1) *multiradiatus* (8.0, 7.8); 2) *queenslandicus* (13.3, 10.6); 3) *semifasciatus* (12.8, 11.2); 4) *cavalla* (14.0, 10.9); 5) *koreanus* (13.7, 11.2); 6) *commerson* (14.1, 11.3); 7) *sinensis* (13.4, 12.2); 8) *brasiliensis* (14.0, 11.9); 9) *lineolatus* (15.1, 12.9); 10) *guttatus* (16.9, 14.4); 11) *sierra* (17.3, 14.1); 12) *maculatus* (16.8, 14.6); 13) *munroi* (17.5, 15.0); 14) *plurilineatus* (17.9, 15.4); 15) *tritor* (18.6, 15.4); 16) *regalis* (19.3, 15.8); 17) *niphonius* (19.6, 15.9); and 18) *concolor* (22.2, 19.7). The species with the fewest teeth, *S. multiradiatus*, also has the fewest gill rakers (usually 2 or 3, see Table 5), and the species with the most teeth, *S. concolor*, has the most gill rakers (usually 23-25, see Table 5) but the correlation is not so good in the other 16 species (compare Tables 3 and 4 with Table 5).

Premaxilla.—The premaxilla (Fig. 22) is a long, curved bone with a stout, arrowhead-shaped, anterior end that extends dorsally and posteriorly as an ascending process. The posterior shank of the premaxilla is elongate and bears a row of 5-39 compressed triangular teeth on its ventral margin. There are two articular facets for the overlying maxilla at the junction of the posterior margin of the ascending process with the shank. The ascending processes of both premaxillae are closely approximated to each other mesially and fit into the median groove of the ethmoid bone. The ascending process forms an angle of 32°-61° with the shank, and this process is 31-48% of the total length of the premaxilla. Devaraj (1977:22) noted that *S. lineolatus* had the sharpest angle among the Indian species that he studied (23° as he measured it), and we find that it has the sharpest angle (Fig. 22b) of any of the species in the genus, 32°-36° according to our measurements. The species with the largest angle is *S. guttatus*, 60°-61°. Devaraj included *guttatus* along with *koreanus*, *regalis*, and *maculatus* as species with angles of 40°-43°. Our data for these other three species are 40°-54°. *Scomberomorus com-*

TABLE 3.—Number of teeth in upper jaw in species of *Scomberomorus*.

Species	Side	Min.	Max.	$\bar{x}$	SD	N	Overall $\bar{x}$	Rank
brasiliensis	L	6	25	14.07	3.62	68	14.00	6
	R	8	27	13.93	3.53	69		
cavalla	L	8	29	14.24	5.82	50	14.00	7
	R	6	28	13.74	5.23	46		
commerson	L	5	35	14.15	5.68	110	14.06	8
	R	7	38	13.96	5.28	109		
concolor	L	15	35	22.15	4.94	26	22.20	18
	R	13	37	22.26	5.77	23		
guttatus	L	12	36	16.78	4.13	89	16.88	11
	R	11	35	16.97	4.25	93		
koreanus	L	9	19	14.17	2.76	24	13.71	5
	R	10	16	13.25	2.11	24		
lineolatus	L	10	27	15.28	3.94	29	15.07	9
	R	9	28	14.86	4.19	29		
maculatus	L	10	32	17.04	4.06	55	16.82	10
	R	7	30	16.57	3.80	49		
multiradiatus	L	5	10	7.88	1.24	26	8.04	1
	R	6	10	8.19	1.20	26		
munroi	L	12	20	16.57	2.64	7	17.50	13
	R	12	23	18.22	3.90	9		
niphonius	L	12	26	19.53	2.71	32	19.56	17
	R	14	26	19.58	2.75	33		
plurilineatus	L	16	22	18.25	1.70	24	17.92	14
	R	12	23	17.58	2.52	24		
queenslandicus	L	8	17	13.33	2.43	30	13.29	3
	R	10	18	13.24	2.31	29		
regalis	L	9	31	19.34	5.10	47	19.29	16
	R	10	30	19.25	4.74	48		
semifasciatus	L	10	23	13.03	3.07	33	12.76	2
	R	8	21	12.48	2.92	33		
sierra	L	10	37	17.15	5.79	60	17.32	12
	R	7	39	17.48	7.34	62		
sinensis	L	10	16	13.64	1.69	14	13.43	4
	R	10	17	13.21	1.67	14		
tritor	L	11	30	18.56	3.98	32	18.58	15
	R	11	28	18.59	4.38	32		

TABLE 4.—Number of teeth in lower jaw in species of *Scomberomorus*.

Species	Side	Min.	Max.	$\bar{x}$	SD	N	Overall $\bar{x}$	Rank
brasiliensis	L	7	19	11.96	2.85	70	11.88	7
	R	7	20	11.79	3.04	67		
cavalla	L	6	24	10.94	3.84	50	10.92	3
	R	7	22	10.90	3.78	48		
commerson	L	5	29	11.37	4.40	108	11.27	6
	R	4	27	11.17	3.84	106		
concolor	L	13	30	19.46	3.96	26	19.71	18
	R	12	34	19.96	4.96	25		
guttatus	L	10	25	14.49	3.06	98	14.42	11
	R	9	23	14.34	2.70	97		
koreanus	L	8	17	11.25	2.19	24	11.21	4
	R	9	15	11.17	1.31	24		
lineolatus	L	7	28	12.72	3.69	29	12.93	9
	R	9	26	13.14	3.20	29		
maculatus	L	10	30	14.89	3.70	55	14.64	12
	R	8	26	14.37	3.02	52		
multiradiatus	L	6	11	8.00	1.20	26	7.75	1
	R	5	9	7.50	0.95	26		
munroi	L	11	29	15.88	5.62	8	15.01	13
	R	11	19	14.13	2.75	8		
niphonius	L	12	20	15.55	2.05	33	15.93	17
	R	12	20	16.30	2.05	33		
plurilineatus	L	12	22	15.83	2.08	23	15.37	14
	R	12	20	14.92	1.89	24		
queenslandicus	L	6	14	10.59	1.79	32	10.61	2
	R	7	14	10.64	1.99	28		
regalis	L	10	24	15.72	4.17	46	15.80	16
	R	8	23	15.87	4.10	47		
semifasciatus	L	7	18	11.24	2.98	33	11.23	5
	R	7	18	11.21	2.93	33		
sierra	L	7	37	13.90	5.29	61	14.05	10
	R	7	32	14.19	5.30	62		
sinensis	L	10	15	12.43	1.87	14	12.22	8
	R	10	15	12.00	1.41	14		
tritor	L	10	21	15.24	2.95	33	15.40	15
	R	10	23	15.56	3.19	33		

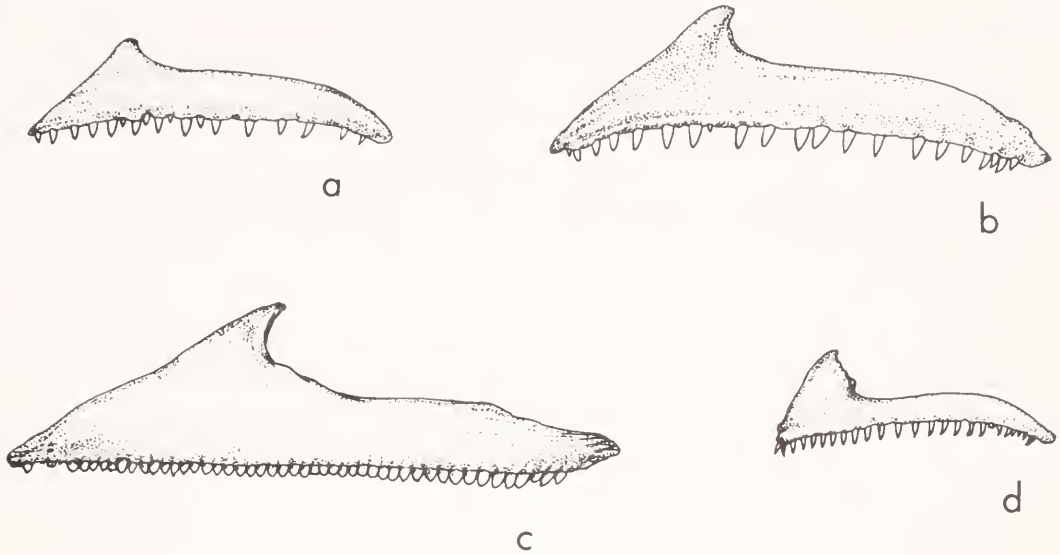


FIGURE 22.—Left premaxillae in lateral view. a. *Scomberomorus semifasciatus*, Port Moresby, New Guinea, 510 mm FL, 2×. b. *Scomberomorus lineolatus*, Cochin, India, 786 mm FL, 2×. c. *Acanthocybium solandri*, Miami, Fla., 1,403 mm FL, 1×. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL, 2×.

merson and *S. cavalla* also fall into this intermediate group with angles of 41°-54°. *Acanthocybium* (Fig. 22c) has a sharp angle (34°-37°), like *S. lineolatus*. *Grammatorcynus* (Fig. 22d) has a very large angle, 64°-67°, even greater than *S. guttatus*. The ascending process is longest in *S. lineolatus*, 46-48% of the length of the premaxilla (41-45% according to Devaraj) and *S. sinensis*, 43-46%. The process is shortest in *S. guttatus* and *S. cavalla*, 31-32%. *Acanthocybium* has a longer process than any of the species of *Scomberomorus*, 50% (according to our data and Devaraj 1977).

Maxilla.—The maxilla (Fig. 23) is a long, curved bone surmounting the premaxilla dorsolaterally by means of an anterior head and ventral sulcus. The head consists of a thick massive inner condyle and a small lateral process (see *S.*

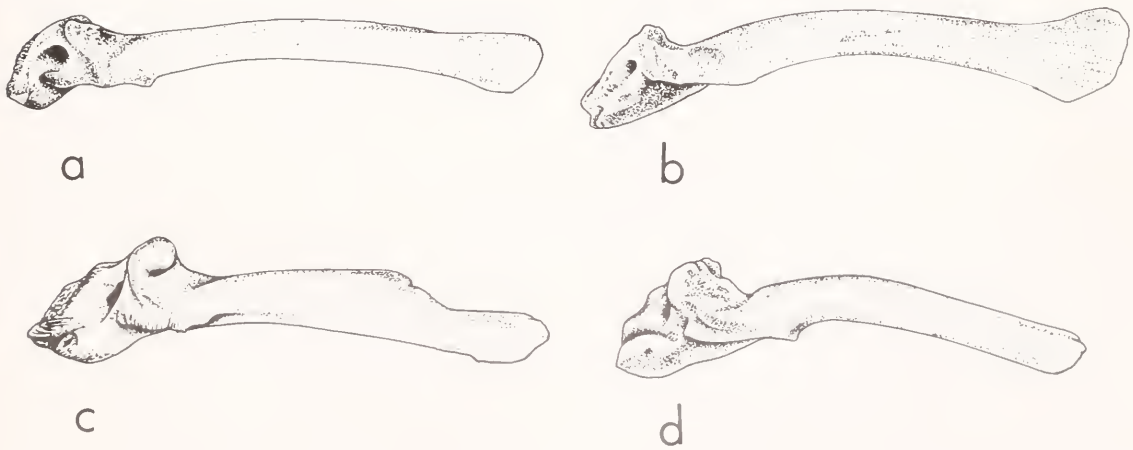


FIGURE 23.—Left maxillae in lateral view. a. *Scomberomorus semifasciatus*, Port Moresby, New Guinea, 510 mm FL, 2×. b. *Scomberomorus munroi*, New Guinea, 512 mm FL, 2×. c. *Acanthocybium solandri*, Miami, Fla., 1,403 mm FL, 1×. d. *Grammatorcynus bilineatus*, Timor Sea, 453 mm FL, 2×.

semifasciatus, Fig. 23a). The former possesses a prominent knob at its dorsolateral aspect that fits into the articular surface of the vomer and an anterior, deep concavity facing the inner wall of the premaxilla. The head is 18-25% of the total length of the maxilla. Immediately posterior to the head is a shallow depression which receives the anterior articulating process of the palatine. The shank of the maxilla is narrow and somewhat flattened. The posterior end expands into a thin, flat plate which is partially covered dorsally by the supramaxilla. The height of the plate is 8-15% of the total length of the maxilla. *Acanthocybium* (Fig. 23c) and *Grammatorcynus* (Fig. 23d) lack any posterior expansion of the maxilla. In fact, in *Acanthocybium* there is a notch in the dorsal margin of the maxilla, and the posterior end is distinctly lower than the middle of the shaft of the bone.

Scomberomorus munroi is the only species in the genus that is distinguishable from the others in characters of the maxilla; it totally lacks the anterior process on the outer surface of the head of the maxilla (Fig. 23b). Devaraj (1977:23) stated that the outer process was "flimsier" in *S. commerson*, but we find that the process varies from small to moderate in our material of the species and that *S. commerson* is not distinct in this aspect.

The head of the maxilla is shorter than in most other species, relative to total length of the maxilla, in the six species of the *S. regalis* group. Starting with the shortest maxilla head length (lowest mean percent), these six species (plus *koreanus* and *multiradiatus*) rank as follows: 1) *concolor*, 18.8; 2) *brasiliensis*, 19.0; 3) *sierra*, 19.8; 4) *tritor*, 19.9; 5) *koreanus*, 20.2; 6) *maculatus*, 20.6; 7) *multiradiatus*, 21.0; and 8) *tritor*, 21.1. The longest heads are found in *niphonius* (24.7), *semifasciatus* (24.1), and *lineolatus* (24.0). The head of the maxilla is a little longer, relative to total maxilla length, in *Grammatorcynus* (26%) and much longer (33%) in *Acanthocybium*.

The posterior expansion of the maxilla is least well-developed (lowest) relative to maxilla length in *S. multiradiatus* (8-9%) and *S. sinensis* (9-11%). The best-developed posterior expansion is in *S. plurilineatus* (15%). The other 15 species range from 11 to 14%. This range of variation is shown in *S. munroi* but the specimen illustrated (Fig. 23b) shows a relatively well-developed posterior expansion. The shape of the posterior expansion varies within and between species, but most of the expansion is usually ventral.

Dentary.—The dentary (Fig. 24) is a large forked bone which forms the major part of the lower jaw. It is laterally flattened and bears a single row of 4-37 compressed triangular teeth on the dorsal margin. Posteriorly, the dentary forms two arms. The ventral arm is relatively narrow and shorter than the dorsal arm, and its inferior margin has a groove which accepts the angular and the anterior end of Meckel's cartilage. The base of the ventral arm has an external series of pores, which seem to be the preoperculomandibular pores (Allis 1903; Mago Leccia 1958) of the lateral line system. The length of the dentary from its anterior margin to the tip of the lower arm is 86-97% of the length to the tip of the upper arm. The figures are similar for *Acanthocybium* (91-96%). However, the lower margin is longer in *Grammatorcynus*, 105-109% of the length of the upper margin (Fig. 24c). The proportions are similar in all 18 species of *Scomberomorus*, with *S. maculatus* having the shortest lower margin (87-89%) and *S. concolor* the longest (92-97%).

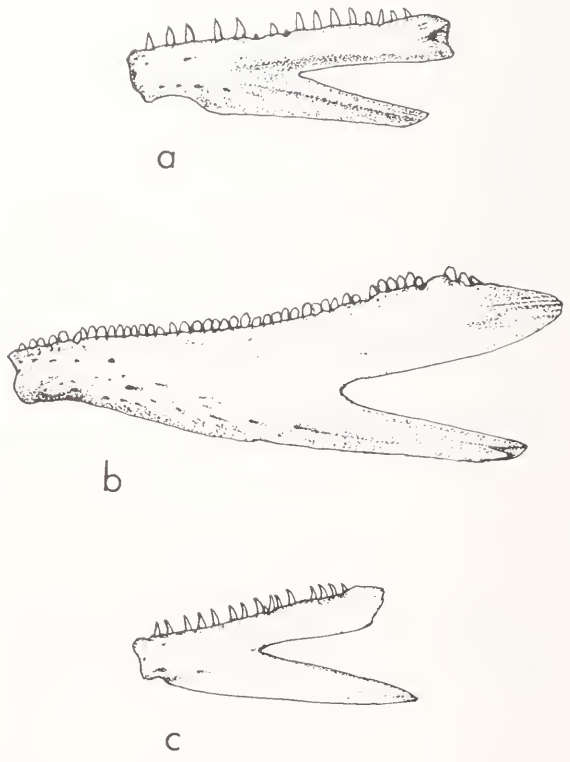


FIGURE 24.—Left dentaries in lateral view. a. *Scomberomorus semifasciatus*, Port Moresby, New Guinea, 510 mm FL, 2×. b. *Acanthocybium solandri*, Miami, Fla., 1,403 mm FL, 1×. c. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL, 2×.

All the species of *Scomberomorus* and *Grammatorcynus* have a notch on the anteroventral margin of the dentary. This notch is absent in *Acanthocybium*. The notch seems to vary as much between specimens of a species of *Scomberomorus* as between species of the genus. *Acanthocybium* has a prominent notch on the anterior margin of the dentary (Fig. 24b) which is indistinct or absent in *Scomberomorus* and *Grammatorcynus*. Devaraj (1977) stated that the anterior notch was distinct in *S. cavalla* and *S. commerson*. The notch may be a little more prominent in *S. commerson* than in the other species, but we cannot confirm this for *S. cavalla*.

Angular.—The triangular anterior end of the angular (frequently called articular) fits into the dentary anteriorly (Fig. 25). The posterior end of

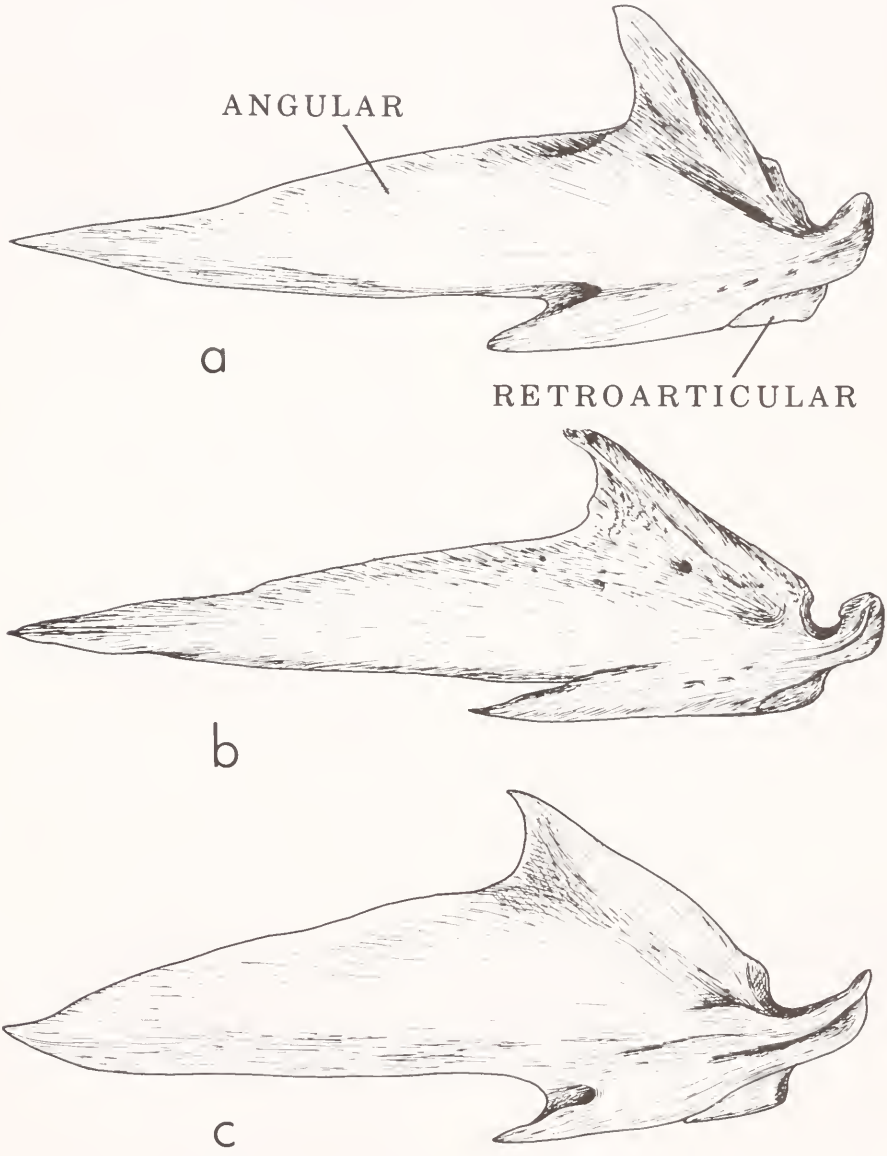


FIGURE 25.—Left angulars and retroarticulars in lateral view. a. *Scomberomorus semifasciatus*, Port Moresby, New Guinea, 510 mm FL, 3.5×. b. *Acanthocybium solandri*, Miami, Fla., 1,403 mm FL, 1×. c. *Grammatorcynus bilineatus*, New Guinea, 382 mm FL, 4.5×.

the angular bears three large processes; the dorsal process directed forward and upward, the ventral process directed forward, and the posterior process directed backward and upward. This process is hooked and carries a transverse articular facet for the quadrate. Between the dorsal and ventral processes is Meckel's cartilage which extends directly anterior into the space between the two arms of the dentary. The length of the angular to the tip of the dorsal process is 31-42% of the total length of the bone; the length to tip of the ventral process is 42-53% of the total length. The maximum width of the angular, measured from the tip of the dorsal process to the tip of the ventral process is 34-43% of the total length. Devaraj (1977) stated that the ventral process was longer and narrower in *S. commerson* and *Acanthocybium* than in other Indian species and we confirm this. The ventral process is as long or longer than the dorsal process in *S. commerson* (ventral process 99-162% of the dorsal process), *Acanthocybium* (99-148%), and also in *S. queenslandicus* (115-136%). The next longest ventral processes are in *S. cavalla* (80-104%) and *S. sinensis* (82-97%). The other 14 species of *Scomberomorus* (and *Grammatorcynus*) have shorter ventral processes, 40-85% of the length of the dorsal process. The shortest ventral process is in *S. regalis*, 40-44%.

Retroarticular.—The retroarticular bone (frequently called angular) is rhomboid and attached firmly, but not fused to the posteroventral margin of the angular (Fig. 25). No differences were found among the retroarticulars of the species of *Scomberomorus*.

PALATINE ARCH.—The palatine arch consists of four pairs of bones in the roof of the mouth: palatine, ectopterygoid, entopterygoid, and metapterygoid.

Palatine.—The palatine (Fig. 26) is forked both posteriorly and anterolaterally. The dorsal branch of the anterolateral fork is hooked, and its anterior end articulates with a facet on the maxilla, immediately ventral to the nasal. The ventral branch is cone-shaped or pointed. The exterior branch of the posterior fork carries on its dorsal surface the shank of the ectopterygoid, and the inner, flat, thin branch is attached to the anterior end of the entopterygoid. The lateral aspect of the palatine is roughly triangular and concave, and closely attached to the mesial wall of the maxilla. *Grammatorcynus* (Fig. 26d) differs from *Scomberomorus* (Fig. 26a, b) and *Acanthocybium* (Fig. 26c) in almost lacking the anteriorly directed ventral branch. *Acanthocybium* has a distinct ventral branch but it is shorter than the

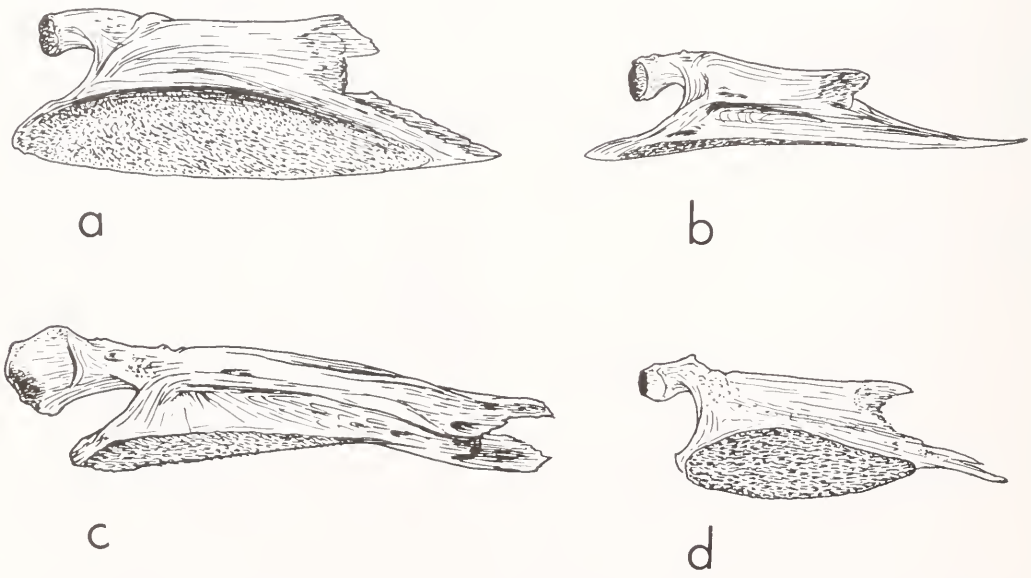


FIGURE 26.—Left palatines in lateral view, slightly rotated to better show tooth patch. a. *Scomberomorus semifasciatus*, New Guinea, 740 mm FL, 2×. b. *Scomberomorus commerson*, New South Wales, 1,155 mm FL, 1×. c. *Acanthocybium solandri*, Miami, Fla., 1,403 mm FL, 1×. d. *Grammatorcynus bilineatus*, Timor Sea, 453 mm FL, 2×.

dorsal branch, as pointed out by Devaraj (1977), whereas the ventral branch is longer than the dorsal branch in all species of *Scomberomorus*. The distance from the anterior end of the ventral branch to the end of the external branch divided by the distance from the tip of the dorsal hook to the end of the external branch is 120-123% in *Grammatorcynus*, 112-121% in *Acanthocybium*, and only 87-107% in the species of *Scomberomorus*. *Acanthocybium* differs from both *Scomberomorus* and *Grammatorcynus* in having the posteriorly directed inner branch almost as long as the outer branch. The distance from the tip of the dorsal hook to the tip of the inner branch divided by the distance to the tip of the outer branch is 97-99% in *Acanthocybium* and 54-84% in the species of *Scomberomorus* and *Grammatorcynus*. The tooth patch is long and narrow in *Acanthocybium* (Fig. 26c), short and wide in *Grammatorcynus* (Fig. 26d), and with the species of *Scomberomorus* in between these extremes. The teeth are fine in all three genera, but a little larger in *Acanthocybium* and *Grammatorcynus* than in most species of *Scomberomorus*.

The species of *Scomberomorus* show some differences in the length of the ventral branch relative to that of the length of the external branch, the relative length of the outer to the inner branch, the relative width of the tooth patch, and the size of the teeth in the tooth patch. Dividing the length of the ventral margin, from the anterior end of the ventral branch to the end of the external branch, by the length of the dorsal margin, from the tip of the dorsal hook to the end of the ventral branch, shows three species of *Scomberomorus*—*sinensis* (98-107%), *tritor* (100-102%), and *commerson* (94-102%)—to be most similar to *Acanthocybium* (112-121%). The lowest figures are for *S. niphonius* (87-88%). Dividing the length of the dorsal margin by the distance from the tip of the dorsal hook to the end of the inner branch shows four species of *Scomberomorus*—*plurilineatus* (75-84%), *munroi* (77-79%), *lineolatus* (72-74%), and *semifasciatus* (70-73%)—to resemble *Grammatorcynus* (71-75%). The lowest figures are for *S. multiradiatus* (54-56%). The tooth patch is very narrow in *S. commerson* (Fig. 26b), similar to the patch shape in *Acanthocybium* but with finer teeth. The tooth patch is also narrow in a 677 mm FL specimen of *S. sinensis* and reduced to only a single row of teeth in a 1,082 mm specimen. The teeth in *S. sinensis* are larger than in other species of the genus, at least the same size as in *Acanthocybium*. The widest tooth patch is in *S. semifasciatus* (Fig. 26a), almost as wide as in *Grammatorcynus* but with much finer teeth.

Ectopterygoid.—The ectopterygoid (Fig. 27) is a T-shaped bone, the top of the T forming its posterior end. It is joined with the entopterygoid dorsolaterally, the palatine laterally and anteriorly, and the quadrate and metapterygoid posteriorly. The dorsal arm of the ectopterygoid is shorter than the ventral arm in *Scomberomorus* and vice versa in *Acanthocybium* and *Grammatorcynus*. This relationship can be expressed by dividing the dorsal distance (from the anterior end of the bone to the tip of the dorsal arm) by the ventral distance (from the anterior end to the tip of the ventral process). The range is 85-100% in the species of *Scomberomorus* compared with greater than 100% in *Acanthocybium* (103-109%) and *Grammatorcynus* (110-116%). The shank is longer in *Acanthocybium* than in the other two genera. The posterior edge of the ectopterygoid (from the tip of the dorsal process to the tip of the ventral process) is shorter relative to the ventral distance in *Acanthocybium* (41-47%) than in the species of *Scomberomorus* (43-63%) and *Grammatorcynus* (64-68%).

The ectopterygoids of the species of *Scomberomorus* are very similar. The shortest ventral distance is in *S. sinensis*, 85-88% of the dorsal distance, the longest in *S. regalis*, 99-100%. The shortest posterior edges are in *S. niphonius* and *S. tritor* (50-51% of the dorsal distance), the longest posterior edges are in *S. koreanus* (61-63%), *S. plurilineatus* (60-63%), and *S. semifasciatus* (59-62%).

Entopterygoid.—The entopterygoid is elongate and oval in shape (width 23-46% of length) (Fig. 28). The outer margin of the entopterygoid is the thickest part of the bone and is attached to the inner margin of the ectopterygoid. The entopterygoid also connects with the palatine anteriorly and the metapterygoid posterolaterally. The mesial and posterior borders are free from contacts with other bony elements. The dorsal surface is concave and the smooth convex ventral surface forms the major part of the buccal roof. The anterior end is narrower than the posterior end in most species but a little wider in *S. guttatus* and *S. koreanus*. The entopterygoid is narrowest in *S. commerson* (width 23-28% of length, Fig. 28a) and *S. multiradiatus* (29%). The shortest and widest entopterygoids are in *sinensis* (39-46%,

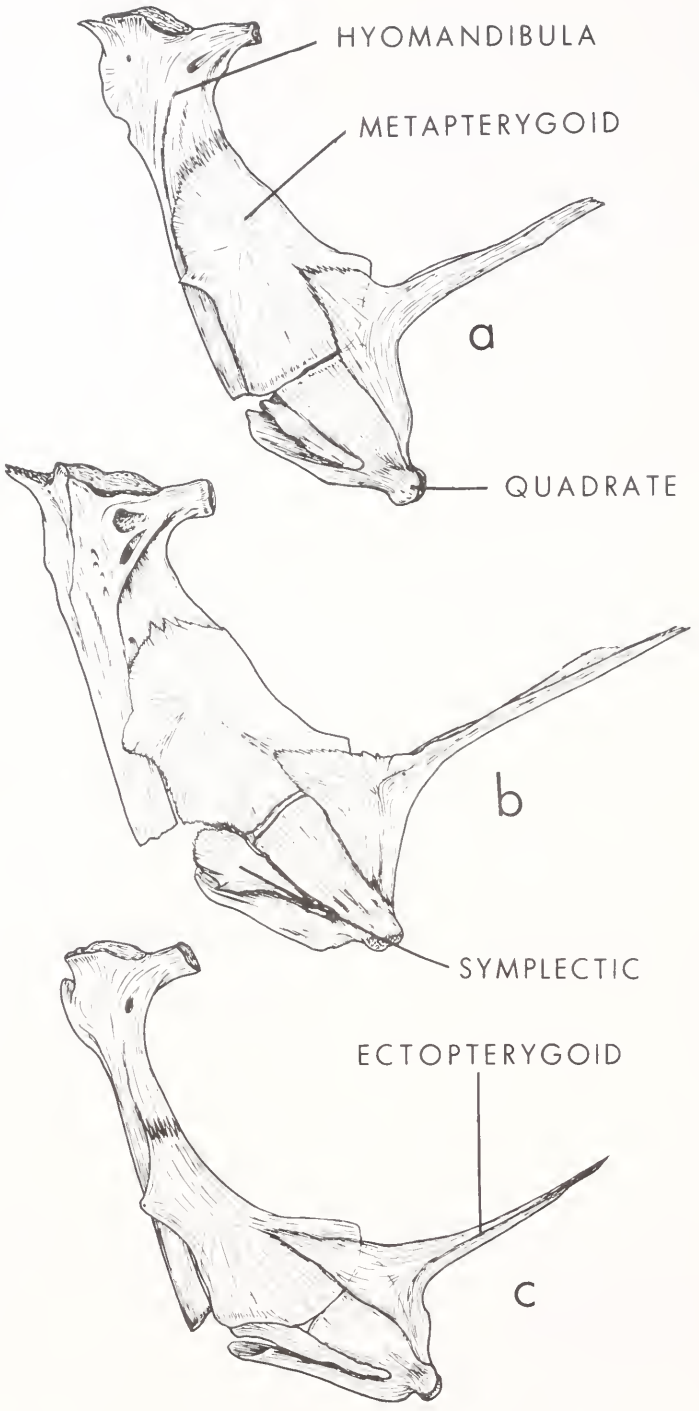


FIGURE 27.—Left suspensoria in mesial view. a. *Scomberomorus semifasciatus*, Port Moresby, New Guinea, 510 mm FL, 2.5×. b. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL, 1.5×. c. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL, 2×.

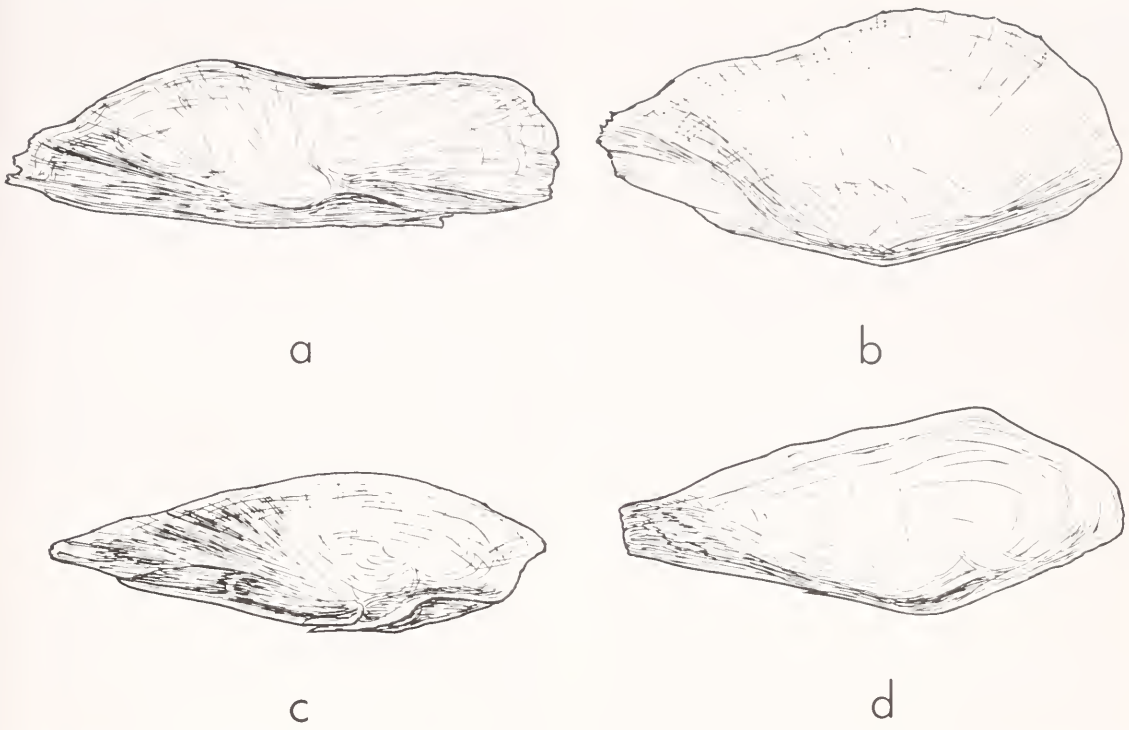


FIGURE 28.—Left entopterygoids in dorsal view. a. *Scomberomorus commerson*, New South Wales, 1,155 mm FL, 1×. b. *Scomberomorus sinensis*, Hong Kong, 677 mm FL, 2×. c. *Acanthocybium solandri*, Indian Ocean, 943 mm FL, 2×. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL, 2.5×.

Fig. 28b), *maculatus* (41-42%), and *concolor* (40-42%). *Acanthocybium* (Fig. 28c), *Grammatorcynus* (Fig. 28d), and the other 13 species of *Scomberomorus* are intermediate in width (30-40%).

Metapterygoid.—The metapterygoid (Fig. 27) is a flat, quadrangular or somewhat triangular bone. The posterodorsal margin of this bone is deeply grooved to receive the hyomandibula. The dorsal portion is strongly ankylosed to the lamellar region of the hyomandibula. The ventroposterior margin abuts the lowermost portion of the symplectic process of the hyomandibula, but does not touch the hyomandibula. There is a relatively long slit between the two bones, through which the hyoidean artery passes (Allis 1903). The ventral border is divided into two portions, the horizontal portion in contact with the quadrate and the anterior oblique portion ankylosed to the ectopterygoid. On the mesial surface, the metapterygoid possesses a triangular-shaped area which forms an interdigitating articulation with the upper arm of the ectopterygoid. The posteroventral margin of the metapterygoid articulates with the dorsal end of the symplectic in *Acanthocybium* and *Grammatorcynus* (Fig. 27b, c), but not in most species of *Scomberomorus* (Fig. 27a). The posterior horizontal part of the ventral border is longer than the anterior oblique part in *Scomberomorus* (anterior part 39-86% of posterior part), but vice versa in *Acanthocybium* and *Grammatorcynus* (anterior part 132-218% of posterior part).

The anterior part of the ventral margin is relatively longer in *S. multiradiatus* (77-78% of posterior part) and *S. maculatus* (65-86%), and relatively shorter in *S. plurilineatus* (41-45%) and *S. regalis* (39-50%). Devaraj (1977) reported differences in the shape of the anterior free border of the metapterygoid, as convex, nearly straight, or concave. We have found similar tendencies but it is difficult to place the species of *Scomberomorus* in specific categories.

HYOID ARCH.—The hyoid arch is the chain of bones that connect the lower jaw and the opercular apparatus with the skull. The arch is composed of the hyomandibula, symplectic, quadrate,

hyoid complex (hypohyal, ceratohyal, epihyal, interhyal, and the seven branchiostegal rays), and two median unpaired bones, the glossohyal and urohyal.

Hyomandibula.—The hyomandibula (Fig. 27) is an inverted L-shaped bone that connects the mandibular suspensorium and opercular bones to the neurocranium. There are three prominent condyles on the dorsal end of the hyomandibula. The long dorsal condyle forms the base of the L and fits into the fossa at the junction of the pterotic and sphenotic bones. The anterior condyle articulates with the ventral fossa of the pterotic and the lateral process is attached to the inside of the opercle. Anterolaterally, the hyomandibula is drawn out into a lamellar region that joins the metapterygoid; posterolaterally, it has a long articulation with the preopercle. Ventrally, the hyomandibula has a long symplectic process; at the posterodorsal corner there is a small spine. A strong vertical ridge extends from the ventral margin to a little below the dorsal border, thence it curves anteriorly to confluence with the anterior condyle. The portions lying anterior and posterior to this ridge are grooved for articulation with the metapterygoid and preopercle respectively; in situ only the ridge and a portion of the upper broader surface are visible exteriorly. The upper surface of the symplectic is connected to the ventral border of the hyomandibula by way of a cartilage which is especially well developed in *Acanthocybium*. There are two deep fossae on the inner surface of the hyomandibula of *Acanthocybium* but only one in *Scomberomorus* and *Grammatorcynus*.

The posterodorsal spine is best developed in *Acanthocybium* (Fig. 27b) and *S. commerson*, as pointed out by Devaraj (1977). This spine is also well developed in *S. queenslandicus* and is present but small in the other 16 species of *Scomberomorus* (e.g., *S. semifasciatus*, Fig. 27a). No spine is present in *Grammatorcynus* (Fig. 27c). The total length of the hyomandibula (ventral tip to dorsal margin of dorsal condyle) is greater relative to maximum width (tip of anterior condyle to outer margin of posterior condyle) in *Grammatorcynus* (width 35-36% of length) and *S. multiradiatus* (36-39%). The hyomandibula is shortest relative to width in *S. sinensis* (45-52%). *Acanthocybium* (41-44%) is similar to the majority of species of *Scomberomorus* (39-47%).

Symplectic.—The symplectic is a small bone that fits into a groove on the inner surface of the quadrate (Fig. 27). The symplectic is very narrow in *Scomberomorus*, not filling the groove in the quadrate (Fig. 27a). It is slightly wider in *Grammatorcynus* but the groove is narrower, the symplectic more nearly filling the groove (Fig. 27c). The symplectic is greatly expanded at its dorsal end in *Acanthocybium* (Fig. 27b). In most species of *Scomberomorus*, the symplectic, like the posterior process of the quadrate, extends only a slight distance beyond the dorsal margin of the quadrate. The symplectic is slightly longer than the posterior process in a species with a short process (e.g., *S. multiradiatus*) and in one with a relatively long process (e.g., *S. sinensis*). No bony contact is present between the dorsal end of the symplectic and either the metapterygoid or the hyomandibula in most species of *Scomberomorus*. The metapterygoid is in slight contact with the symplectic in *S. sinensis* and *S. koreanus*. Both *Grammatorcynus* and *Acanthocybium* have much longer symplectics, extending well beyond the dorsal margin of the quadrate and even beyond the dorsal end of the posterior process to make firm contact with the metapterygoids. Devaraj (1977:fig. 11) illustrated the symplectics by themselves for the four Indian species (*koreanus*, *guttatus*, *lineolatus*, and *commerson*) and *Acanthocybium*.

Quadrate.—The lower jaw is suspended from the cranium by means of the articulating facet of the ventral surface of the triangular quadrate. The broad dorsal margin of the quadrate abuts the ventral border of the metapterygoid (Fig. 27). The mesial surface of the quadrate bears a deep groove which accepts the symplectic. There is a strong process on the posterior margin of the quadrate that is attached along the lower anterior arm of the preopercle. The process is relatively short in *Scomberomorus*, extending only a short distance beyond the dorsal margin of the quadrate in most species (e.g., *S. semifasciatus*, Fig. 27a). The process is shortest in *S. multiradiatus*, not reaching the dorsal margin. The process is longest in *S. commerson*, *S. lineolatus*, and *S. sinensis*, but it is still shorter in these three species than in *Acanthocybium* (Fig. 27b) and *Grammatorcynus* (Fig. 27c). An attempt was made to quantify this by measuring from the inside of the articular facet to the tip of the dorsal process and to the tip of the anterior margin of the quadrate. The short process in *S. multiradiatus* is shown by the distance to the anterior

margin being about equal (95-103%) to the distance to the tip of the process. In the other species of *Scomberomorus*, the distance to the anterior margin is less than (76-96%) the distance to the tip of the process. This percent is low in *S. lineolatus* (76%), indicative of a long process, but the figures for *S. commerson* (80-83%) and *S. sinensis* (83-85%) are not much lower than those for many other species with shorter processes. The lowest figures are for *Acanthocybium* (72-80%) and *Grammatorcynus* (65-71%), indicative of the long process in these two genera.

Hyoid complex.—This complex includes the two hypohyals (= basihyal of Mago Leccia 1958), ceratohyal, epihyal, and interhyal bones, and the seven branchiostegal rays (Fig. 29). The hypohyals, ceratohyal, and epihyal are closely associated and form a functional unit.

Hypohyals.—The hypohyals are composed of separate dorsal and ventral elements joined longitudinally. In lateral view, the ventral hypohyal is clearly larger than the dorsal hypohyal in all species of *Scomberomorus* and in *Grammatorcynus* (Fig. 29a, c). The ventral hypohyal is about three times larger than the dorsal in *Acanthocybium* (Fig. 29b). Devaraj (1977:29) stated that the dorsal and ventral hypohyals were of equal size in *S. commerson*, but we find the ventral larger in lateral view, as in the other species of the genus. In mesial view, the dorsal and ventral hypohyals in *S. commerson* and the other 17 species are about equal in size. The ventral hypohyal is perhaps a little larger than the dorsal in mesial view in *S. multiradiatus* and *S. queenslandicus*. Laterally, the suture between the dorsal and ventral hypohals runs almost horizontally in *Acanthocybium* but curves ventrally at various angles in *Scomberomorus* and *Grammatorcynus*. Devaraj (1977) stated that it formed "an upward curve anteriorly in *S. koreanus*, *S. lineolatus*, *S. regalis*, and *S. niphonius* and runs nearly straight in the other species including *A. solandri*." The specimen of *S. commerson* that he illustrated (figure 12D) does show a straight suture, but in our material a downward curve usually is present. Mesially, a pointed lateral process at the anterodorsal end of the dorsal hypohyal forms a symphysis with the glossohyal, urohyal, basibranchial, and the process of the hypohyal from the opposite side in *Scomberomorus* and *Grammatorcynus*. *Acanthocybium* also has a pointed lateral process but it appears to be further posterior due to also having an anterior pointed end to the hypohyals at the junction of the dorsal and ventral hypohyals. In addition, *Acanthocybium* has a prominent anterolateral process on the ventral hypohyal. The groove for the hyoidean artery runs along the outer surface of the epihyal, ceratohyal, and ventral portion of the dorsal hypohyal. The groove extends anteriorly 29-54% of the length of the dorsal hypohyal before becoming a covered tunnel in *Scomberomorus* and *Grammatorcynus* or a foramen in *Acanthocybium* leading to the inner side of the dorsal hypohyal. The opening on the inner side appears as a small to moderate pit usually located in the ventral portion of the dorsal hypohyal in *Scomberomorus* and *Grammatorcynus*. The pit lies astride the junction of the dorsal and ventral hypohyals in *S. brasiliensis* and extends slightly into the ventral hypohyal in *S. maculatus* and *S. sierra*. The pit also is larger in these species.

Ceratohyal.—The ceratohyal is a long flat bone, broadest at the posterior end and with an anteroventral projection that articulates with the posteroventral notch of the ventral hypohyal. It is the largest bone of the hyoid complex. Posteriorly, the middle part of the ceratohyal interlocks with the epihyal by means of odontoid processes issuing from both elements (ceratohyal-epihyal suture of McAllister 1968), while the upper and lower portions are joined by cartilage. Four acinaciform branchiostegal rays are attached to the respective articular surfaces along the concave middle portion of the ventral margin. In *Scomberomorus* (Fig. 29a) the fifth branchiostegal ray usually is attached to the most posterior part of the ceratohyal or on the space between the ceratohyal and epihyal, not on the anterior part of the epihyal as stated by Devaraj (1977) and Mago Leccia (1958:pl. 4). In *Acanthocybium* and *Grammatorcynus*, the fifth ray is on the anterior part of the epihyal (Fig. 29b, c). The hyoidean groove runs the length of the ceratohyal on its lateral surface. The groove is so deep in some specimens of some species that it forms a thin slit through the bone, the ceratohyal window or beryciform foramen. Slits are common in 10 species of *Scomberomorus*: *brasiliensis*, *commerson*, *concolor*, *multiradiatus*, *munroi*, *niphonius*, *queenslandicus*, *semifasciatus*, *sierra*, and *tritor*; rare in four, *cavalla*, *plurilineatus*, *maculatus*, and *sinensis* plus *Acanthocybium* and *Grammatorcynus*; and occasional in the other four species:

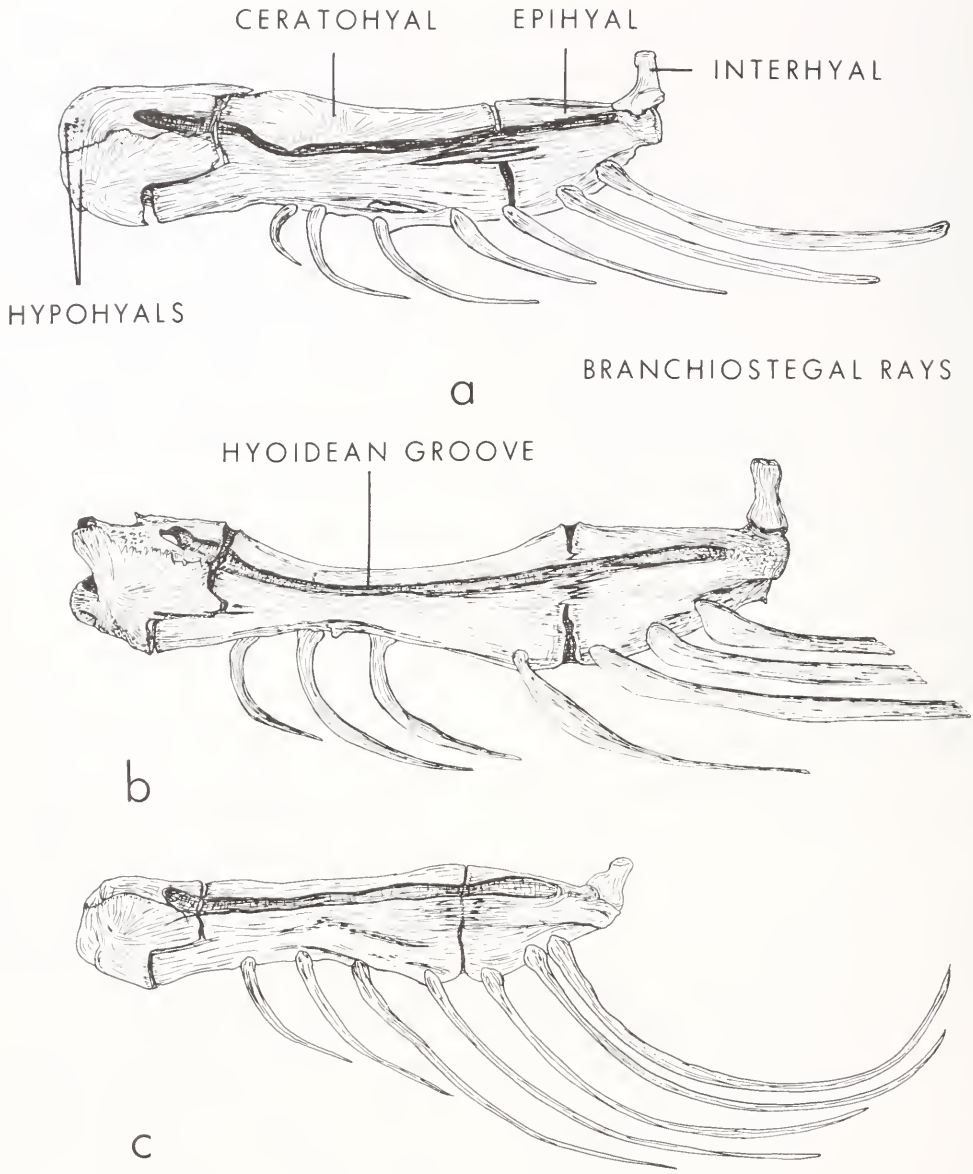


FIGURE 29.—Left hyoid complexes in lateral view. a. *Scomberomorus commerson*, New South Wales, 1,155 mm FL, 1×. b. *Acanthocybium solandri*, Miami, Fla., 1,403 mm FL, 1×. c. *Grammatorcynus bilineatus*, Timor Sea, 453 mm FL, 2×.

guttatus, *koreanus*, *lineolatus*, and *regalis*. Both large (*S. commerson*) and small (*S. multiradiatus*) species have slits. Smaller specimens of a species sometimes have slits (*guttatus*, *plurilineatus*, *queenslandicus*, *regalis*, and *semifasciatus*), while larger specimens lack them; sometimes the situation is reversed (*koreanus*, *lineolatus*, and *tritor*). The dorsal margin of the ceratohyal is deeply concave and very much constricted in *Acanthocybium* such that the dorsal margin of the bone comes closer to the groove for the hyoidean artery. The margin is straight in *Grammatorcynus* and varies in *Scomberomorus*. Devaraj (1977:30-31) stated that the dorsal margin of the ceratohyal is convex in some species (*koreanus* and *lineolatus*), almost straight in others (*gut-*

tatus and *niphonius*), and slightly concave in most (*commerson*, *maculatus*, *regalis*, and *cavalla*). We find similar tendencies, but there is extensive variation even in small samples. Six species tend to have the dorsal margin convex: *guttatus*, *koreanus*, *lineolatus*, *multiradiatus*, *plurilineatus*, and *semifasciatus*; seven species tend to have the dorsal margin concave: *cavalla*, *commerson*, *maculatus*, *munroi*, *queenslandicus*, *regalis*, and *sinensis*; and five usually have the dorsal margin nearly straight: *brasiliensis*, *concolor*, *niphonius*, *sierra*, and *tritor*.

Epihyal.—The epihyal is a triangular bone which interlocks anteriorly with the ceratohyal. It has a posterior process which articulates with the interhyal. In *Scomberomorus*, two branchiostegal rays are seated on the ventral portion of the epihyal, not three as stated by Devaraj (1977) or shown by Mago Leccia (1958). Three branchiostegal rays do articulate with the epihyal in *Acanthocybium* and *Grammatorcynus*. The depth of the epihyal is least in *Acanthocybium*, 58-62% of the length from the smooth anterior margin of the bone to the tip of the posterior process. Two species of *Scomberomorus* (*commerson* and *cavalla*) have relatively low epihyals, 68-71% of length. *Grammatorcynus* also has a relatively low epihyal, 66-77% of length. The deepest epihyals are in four species of *Scomberomorus*: *koreanus* (90-98%), *concolor* (86-94%), *plurilineatus* (87-91%), and *guttatus* (87-90%).

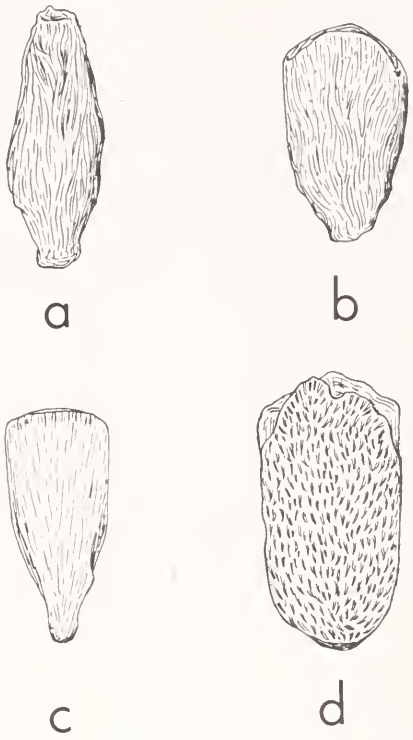


FIGURE 30.—Glossohyals in dorsal view. a. *Scomberomorus plurilineatus*, Natal, 910 mm FL, 4×. b. *Scomberomorus munroi*, New Guinea, 512 mm FL, 5×. c. *Acanthocybium solandri*, Indian Ocean, 1,088 mm FL, 2×. d. *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 4×.

Interhyal.—The interhyal is a small flattened bone that is attached to the epihyal dorsal to the posterior process. The interhyal is directed obliquely upward and links the hyoid complex to the hyomandibula and symplectic. No differences were noted among interhyals.

Glossohyal.—The glossohyal (basihyal) (Fig. 30) is a median bone that supports the tongue and overlies the first basibranchial bone at the anterior end of the branchial arch. In *Scomberomorus*, the glossohyal is roughly rod-shaped or conical in most species. Its width is 35-54% of its length. It generally has a flat or narrowed anterior end and broadens posteriorly, but terminates in a small posterior cone or flattened projection. The glossohyal protrudes ventrally adjacent to the posterior articulation. The glossohyal of *Acanthocybium* is flattened and spatulate with a broad anterior end, a narrow posterior end, and no ventral protrusion (Fig. 30c). *Grammatorcynus* differs in having a quadrangular to oval tooth plate fused to and covering the dorsal surface of the bone (Fig. 30d). Two bonitos, *Cybiosarda* and *Orcynopsis*, have a similar condition but there are two separate oval tooth patches in these genera (Collette and Chao 1975:fig. 43a, b). Another bonito, *Gymnosarda*, has what appears to be a single tooth plate on the glossohyal, but this plate is actually composed of left and right portions that fit over the bone rather than being fused to it (Collette and Chao 1975:fig. 43f). The glossohyal is a little wider in *Grammatorcynus* than in *Acanthocybium* or most species of *Scomberomorus*, 47-55% of length.

The size of the ventral protrusion varies among the species of *Scomberomorus*. It is greatest in *S. sinensis*, *commerson*, and *cavalla*. The glossohyal is narrowest in *S. multiradiatus* and *plurilineatus* (Fig. 30a), 35-36% of width. It is widest in *S. sierra* and *munroi* (Fig. 30b), 52-54%. The anterior end is widest in *S. niphonius* and *sinen-*

sis, narrowest in *brasiliensis*, *cavalla*, and *commerson*.

Urohyal.—The urohyal (Fig. 31) is a compressed, median, unpaired bone. The anterior end of this element lies between, and is connected with, the hypohyals of the left and right sides. The dorsal and ventral margins are thickened. The anterior end has an articulation head and the posterior end is deep. The maximum depth posteriorly is 13-24% of the length of the dorsal margin. The urohyal is not as deep in *Acanthocybium* as in the species of *Scomberomorus*, depth 13-15% of the length of the dorsal margin compared with 16-24%. *Grammatorcynus* also has a low urohyal, depth 15-17% of length. The length of the ventral margin is 68-91% of the length of the dorsal margin. The ventral margin of the urohyal does not extend as far posteriorly in *Grammatorcynus*, only 68-69% of the length of the dorsal margin compared with 80-91% in *Acanthocybium* and *Scomberomorus*. Both Mago Leccia (1958:322) and Devaraj (1977:32) stated that the posterior end of the dorsal margin was pointed but it ends in a distinct fork in all species of *Scomberomorus* and in *Acanthocybium* (Fig. 31c). The major difference in *Grammatorcynus* is that the shape of the posterior end of the dorsal

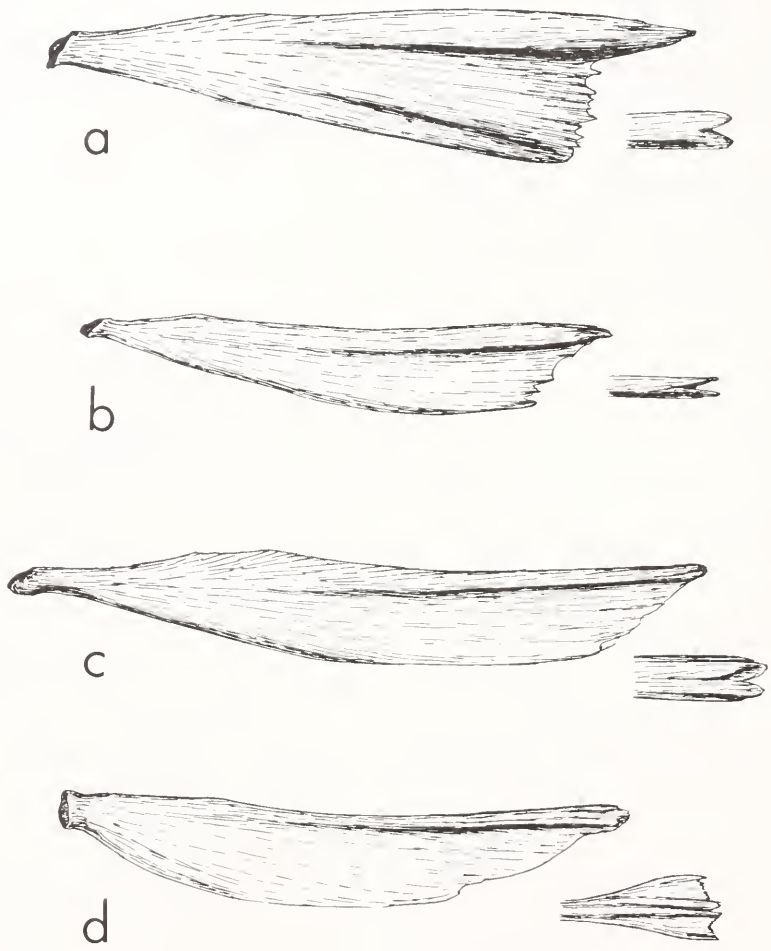


FIGURE 31.—Urohyals in left lateral view. a. *Scomberomorus queenslandicus*, Queensland, 641 mm FL, 2×. b. *Scomberomorus munroi*, New Guinea, 512 mm FL, 2×. c. *Acanthocybium solandri*, Indian Ocean, 1,088 mm FL, 1×. d. *Grammatorcynus bilineatus*, New Guinea, 382 mm FL, 3×. Inset to right is the posterior end of the dorsal margin, in dorsal view.

margin is tripartite (Fig. 31d) instead of forked. Some specimens of *Acanthocybium* differ from the other two genera by having a slight indentation in the anterior end of the urohyal.

OPERCULAR APPARATUS.—Four wide flat bones (opercle, preopercle, subopercle, and interopercle) fit together to form the gill cover which protects the underlying gill arches.

Opercle.—The opercle is broad (Fig. 32), and it is overlapped laterally on its anterior margin by the posterior half of the preopercle. The narrow, elongate, articular facet for the opercular process of the hyomandibula is located on the mesial surface of the anterodorsal corner of the opercle. *Grammatorcynus* (Fig. 32d) and most species of *Scomberomorus* have a weak process at the posterodorsal corner. This process appears to be absent in *Acanthocybium* (Fig. 32c) and *Scomberomorus sinensis*. In several species of *Scomberomorus* (*cavalla*, *regalis*, and *tritor*), there is also a weak anteroventral process. Instead of a distinct process at this point, *Acanthocybium* and the other species of *Scomberomorus* have an angle where the anterior margin meets the anteroventral margin. The posterior margin and/or the posteroventral margin of the opercle are fimbriate in *Acanthocybium* and most species of *Scomberomorus* (*brasiliensis*, *koreanus*, *lineolatus*, *maculatus*, *niphonius*, *queenslandicus*, *semifasciatus* (Fig. 32a), *sinensis*, and *tritor*). *Grammatorcynus* (Fig. 32d) has a much narrower and more elongate opercle than do *Acanthocybium* or the species of *Scomberomorus*. The most elongate opercle among *Scomberomorus* species is in *S. multiradiatus* (Fig. 32b). The broadest is in *Acanthocybium*.

Preopercle.—The preopercle (Fig. 33) is a large crescent-shaped flat bone, broadest at the lower posterior angle. The anterior portion of the bone

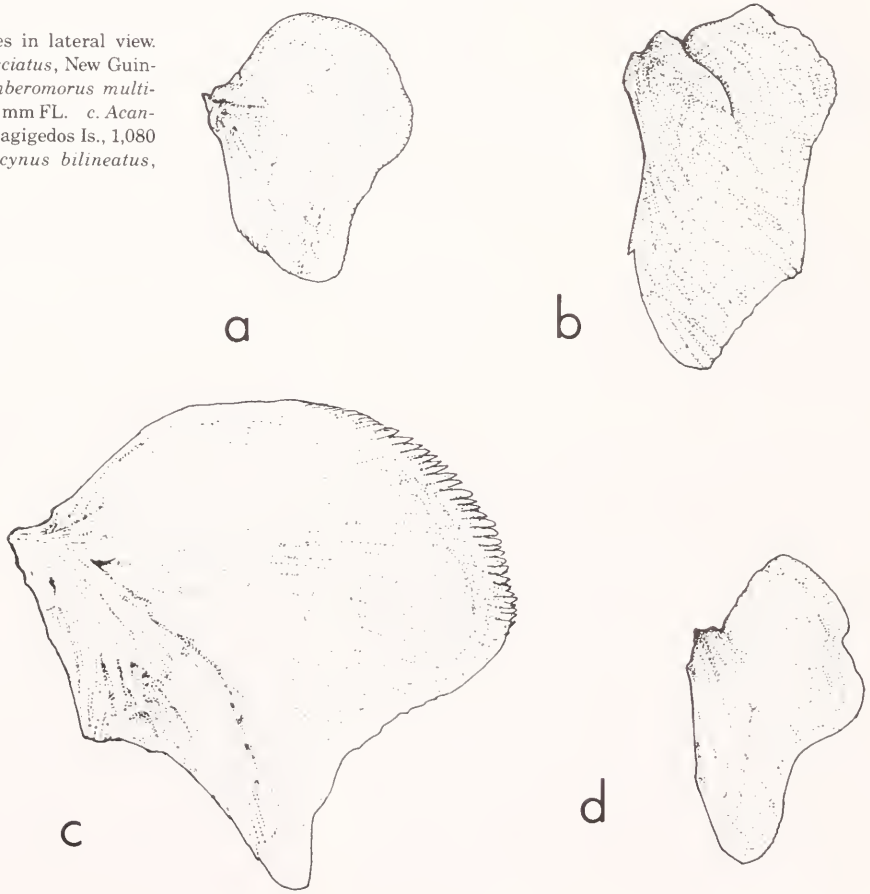


FIGURE 32.—Left opercles in lateral view. a. *Scomberomorus semifasciatus*, New Guinea, 510 mm FL. b. *Scomberomorus multiradiatus*, New Guinea, 294 mm FL. c. *Acanthocybium solandri*, Revillagigedos Is., 1,080 mm FL. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL.

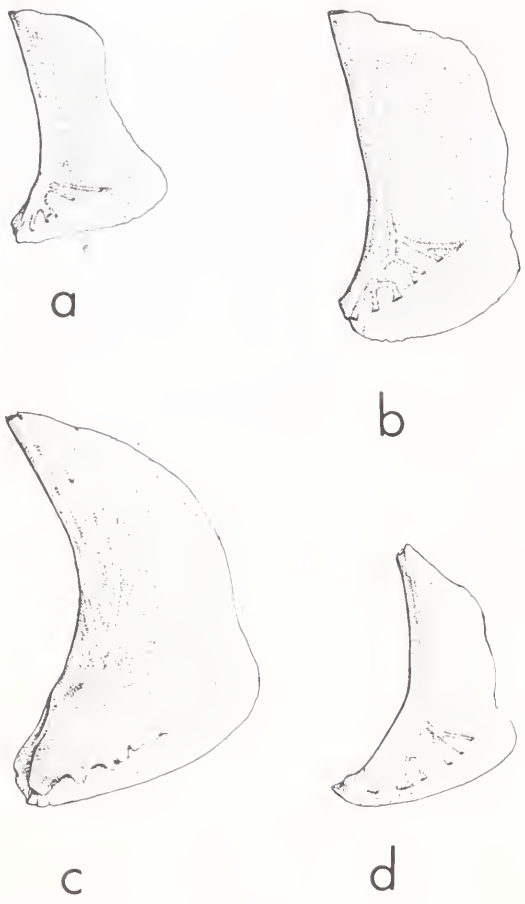


FIGURE 33.—Left preopercles in lateral view. a. *Scomberomorus semifasciatus*, New Guinea, 510 mm FL. b. *Scomberomorus multiradiatus*, New Guinea, 294 mm FL. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL.

is thickened into a bony ridge. A series of 5-7 pores along the lower margin of the ridge represents the preopercular canal of the lateral line system which continues into the dentary. On the mesial side, the ridge possesses a groove for attachment to the hyomandibula and the quadrate. There is a shelf mesial to the anteroventral end of the preopercle in *Acanthocybium* (Fig. 33c) that is not present in *Scomberomorus* (Fig. 33a, b) or *Grammatorcynus* (Fig. 30d). Devaraj (1977:34) referred to this as a groove. The canals leading to the preopercular pores are visible through the bone in *Scomberomorus* and *Grammatorcynus* but cannot be seen in *Acanthocybium* due to the thickness of the bone. The posterior margin of the preopercle is distinctly concave in *Grammatorcynus* and most species of *Scomberomorus*. Devaraj (1977:34) stated that the posterior margin was convex in *S. commerson* and *Acanthocybium*. We find it to be nearly straight in *Acanthocybium* and very slightly concave in *S. commerson*. The concave posterior border makes the upper and lower parts appear as two limbs, the lower of which is longer. As Devaraj (1977:34) noted, the lower portion is longer in *S. guttatus* than in the other species, the distance from the anterior margin of the bony ridge to the posterior end of the lower lobe being 74-80% of the height of the preopercle measured from the ventral margin to the dorsal tip of the bone. Other species with long lower portions include *S. munroi* (73-78%), *S. plurilineatus* (69-79%), *S. niphonius* (73-75%), and *Grammatorcynus* (68-75%). Devaraj (1977:34) stated that the anterior ridge was forked at its upper part in all the Indian species of *Scomberomorus* except *S. commerson* in which the fork is either indistinct or absent, and that the fork was completely absent in *Acanthocybium*. We are unable to confirm this observation and find no differences between *Scomberomorus* and *Acanthocybium*. In these genera, and in *Grammatorcynus*, the anterodorsal margin terminates in a pore similar to the preopercular lateral line canal pore at the anteroventral margin of the bone.

Subopercle.—The subopercle is a flat triangular bone with a prominent anterior projection (Fig. 34). Two ridges converge posteriorly from the anterior projection on the lateral side of the bone. The upper ridge articulates with the lower posterior projection of the opercle and the lower ridge connects to the posterodorsal margin of the interopercle. The dorsal ridge is much stronger than the ventral ridge and extends over the main part of the subopercle as a discrete shelf. The much weaker ventral ridge is difficult to detect in some species. The angle between the anterior projection and the anterior margin of the subopercle varies from approximately a right angle in *Acanthocybium* (Fig. 34c) and most species of *Scomberomorus* to acute in *Grammatorcynus* (Fig. 34d) and *Scomberomorus multiradiatus* (Fig. 34b). The length of the anterior projection varies from 20 to 45% of the length of the anterior margin dorsal to the projection. The projection is longest in *Acanthocybium* (36-45%), *S. sierra* (37-43%), and *S. koreanus* (33-41%). It is shortest in *S. commerson* (20-25%), *S. semifasciatus* (21-23%, Fig. 34a), and *S. queenslandicus* (21-

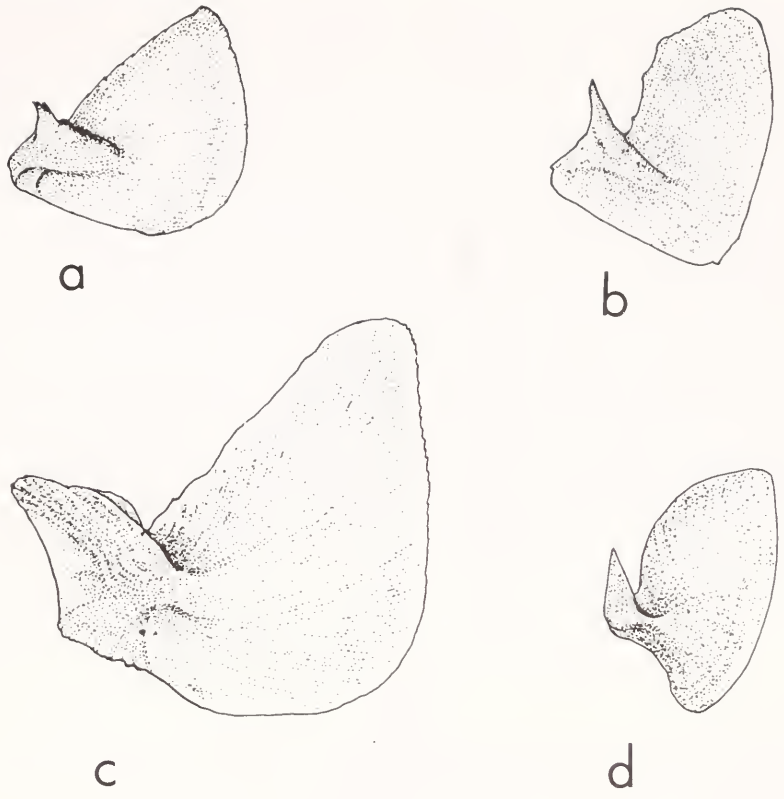


FIGURE 34.—Left subopercles in lateral view. a. *Scomberomorus semifasciatus*, New Guinea, 510 mm FL. b. *Scomberomorus multiradiatus*, New Guinea, 294 mm FL. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL.

27%). It is also short, relative to the long, narrow subopercle, in *Grammatorcynus* (25-26%). Devaraj (1977:33) mentioned differences in the shape of the posteroventral margin and the dorsal edge of the subopercle, but we have not noted any consistent differences between species in these regions.

Interopercle.—The interopercle (Fig. 35) is roughly oval in shape with a crest on the superior margin. There is a well-developed facet on the mesial side to receive the articular process of the interhyal. The depth of the interopercle varies from 37 to 61% of the length of the bone. The deepest interopercles are in *Scomberomorus sinensis* (54-61%, Fig. 35b) and *S. sierra* (57-58%). The interopercles are moderately deep (50-58%) in seven species: *brasiliensis*, *commerson*, *koreanus*, *lineolatus*, *multiradiatus*, *queenslandicus*, and *tritor*. *Grammatorcynus* (37-42%, Fig. 35d) and *Acanthocybium* (40-49%, Fig. 35c) have lower interopercles than most species of *Scomberomorus* (Fig. 35a, b). The shallowest interopercles in this genus are in *S. plurilineatus* (45-47%), *S. munroi* (47-49%), *S. niphonius* (47-49%), and *S. semifasciatus* (47-51%, Fig. 35a). A well-formed notch anterior to the crest on the sloping anterior margin in *Scomberomorus* and *Grammatorcynus* is relatively poorly developed in *Acanthocybium*, rendering the superior margin nearly straight. The posterior margin is rounded in *Scomberomorus* and *Grammatorcynus* but divided into two by a notch in *Acanthocybium*.

BRANCHIAL APPARATUS.—The branchial apparatus is composed of the five pairs of gill arches, gill filaments, gill rakers, pharyngeal tooth patches, and supporting bones. The general arrangement in the Scomberomorini (Fig. 36) is similar to that found in other scombrids such as

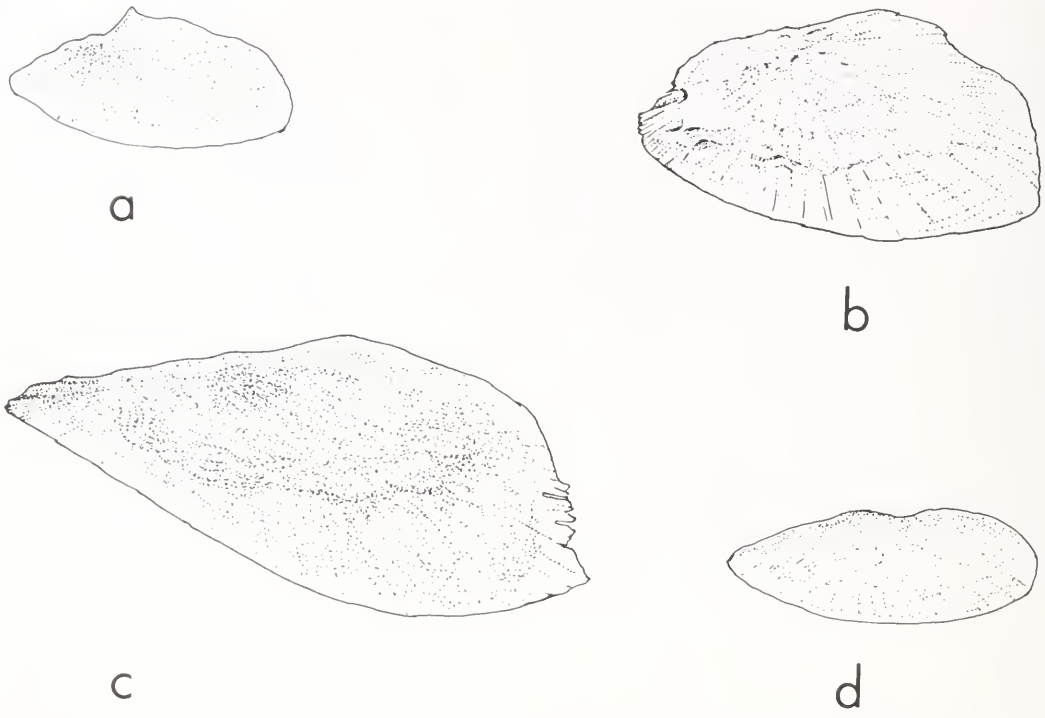


FIGURE 35.—Left interopercles in lateral view. a. *Scomberomorus semifasciatus*, New Guinea, 510 mm FL. b. *Scomberomorus sinensis*, Hong Kong, 677 mm FL. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL.

the Sardini (Collette and Chao 1975), *Thunnus* (Iwai and Nakamura 1964b:22, fig. 1; de Sylva 1955:21, fig. 40), *Scomberomorus* (Mago Leccia 1958:327, pl. 12), and *Rastrelliger* (Gnanamuttu 1971:14, fig. 6). Within the Scomberomorini, the most useful differences are in the number of gill rakers. Most of the branchial bones bear patches of tiny teeth.

Basibranchials.—The three basibranchials form an anteroposterior chain. The first and second are about the same size and considerably shorter than the third. The first is covered dorsally by the glossohyal.

In lateral view the first basibranchial is narrowest in the middle. In *Scomberomorus*, it is short with a wide base where it joins with the second basibranchial but it is much more elongate in *Acanthocybium* and *Grammatorcynus*. The second basibranchial has a prominent notch in the ventral margin and a distinct groove laterally which extends from the anteroventral margin to the middorsal region of the bone. This groove accepts the anterior end of the first hypobranchial. The third basibranchial has an expanded anterior end at its junction with the second basibranchial and then tapers posteriorly. A prominent groove is present anteriorly which accepts the medial anterior end of the second hypobranchial. A section of cartilage extends posteriorly to articulate with the fourth and fifth ceratobranchials.

Hypobranchials.—Three hypobranchials are present. The first is interposed between the second basibranchial and the first ceratobranchial. The second hypobranchial is about the same size as the first, fits into a groove on the third basibranchial, and extends to the second ceratobranchial. The third hypobranchial is smaller than the first or second, fits snugly against the posterolateral margin of the third basibranchial and its posterior end articulates with the third ceratobranchial.

Ceratobranchials.—The five ceratobranchials are the longest bones in the branchial arches. They have a deep groove ventrally for the bran-

chial arteries and veins. The ceratobranchials support most of the gill filaments and gill rakers. The first three are morphologically similar and articulate with the posterior ends of their respective hypobranchials. The fourth is more irregular and attaches to a cartilage posterior to the third basibranchial. The fifth ceratobranchial is also attached to the cartilage, has a dermal tooth plate fused to its dorsal surface, and the complex is termed the lower pharyngeal bone. It is covered with small conical teeth that are directed slightly posteriad.

Epibranchials.—The posterolateral end of each of the four epibranchials is attached to the ends of the first four ceratobranchials. Each epibranchial bears a groove posterodorsally for the branchial arteries and veins. The first epibranchial is the longest and bears two processes mesially. The anterior process articulates with the first pharyngobranchial, and the posterior process attaches with the interarcual cartilage. The second epibranchial is similar to the first, but slightly shorter. The anterior end is divided into two processes: the anterior process attaches to the second pharyngobranchial and the posterior process is coupled with the third pharyngobranchial by way of an elongate cartilage. This process is much more elongate in *Grammatorcynus* than in *Acanthocybium* or *Scomberomorus*. The third epibranchial is the shortest in the series. Laterally, it is attached with the third ceratobranchial; mesially, it is attached with the third pharyngobranchial. An elongate posterodorsal process is present. This process joins with the fourth epibranchial. The fourth epibranchial is larger than

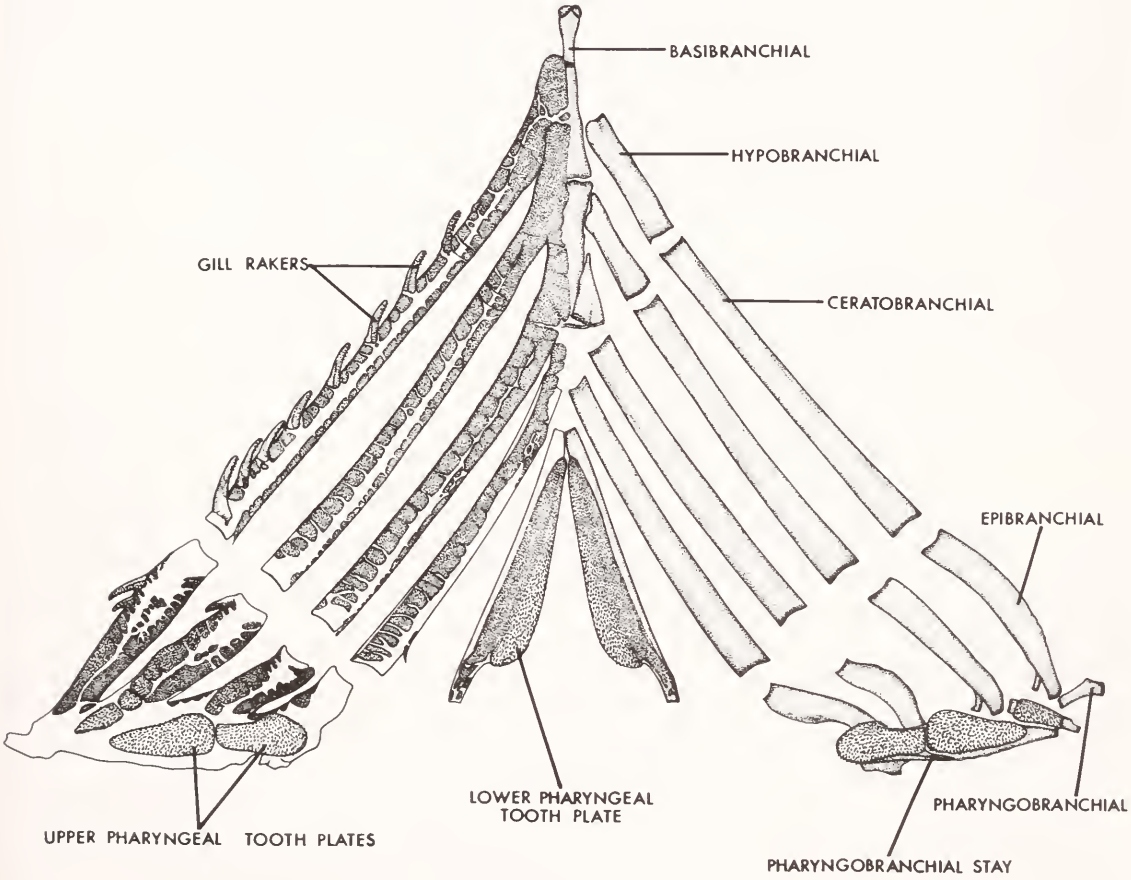


FIGURE 36.—Branchial apparatus of *Scomberomorus semifasciatus*, New Guinea, 510 mm FL. Dorsal view of the gill arches with the dorsal region folded back to show their ventral aspect. Epidermis removed from right hand side to reveal underlying bones.

the third and is interposed between the fourth ceratobranchial and pharyngobranchial. It may be described as a curved bone with the angle formed by the lateral and medial arms being much more acute in *Grammatorcynus* than in *Acanthocybium* or *Scomberomorus*. A dorsal process arises from the middle of the bone and attaches to the third epibranchial.

Pharyngobranchials.—There are four pharyngobranchials attached basally to the epibranchial of their respective gill arch. The first is long and slender, articulates dorsally with the prootic, and is frequently called the suspensory pharyngeal (Iwai and Nakamura 1964b). The elongate second pharyngobranchial bears a patch of teeth. The third is the largest element in the series; it has a broad patch of teeth on its ventral surface, a broad posterior end, and tapers to a narrow anterior end. The third pharyngobranchial of *Scomberomorus* is much more elongate than those of *Acanthocybium* and *Grammatorcynus*. The fourth pharyngobranchial also bears a ventral tooth plate, has a rounded posterior end, and has an elongate strut (pharyngobranchial stay) mesially which overlaps the third pharyngobranchial. This stay is much more elongate in *Scomberomorus* than in *Acanthocybium* and *Grammatorcynus*.

Gill Rakers.—The hypobranchial, ceratobranchial, and epibranchial of the first gill arch support a series of slender, rigid gill rakers. The longest gill raker is at or near the junction of the upper and lower arches, between the ceratobranchial and epibranchial. There is a correlation between numbers of gill rakers, gap between gill rakers, and size of food items, as Magnuson and Heitz (1971) have clearly shown for a number of species of Scombridae. The number of gill rakers is easily countable and is a useful taxonomic character in Spanish mackerels as well as among other groups of the Scombridae.

Acanthocybium differs from *Grammatorcynus*, *Scomberomorus*, and the other genera of Scombridae by completely lacking gill rakers. Three species of *Scomberomorus* have greatly reduced numbers of gill rakers (Table 5): *multiradiatus* (1-4, sometimes only a single gill raker present, at the junction of the upper and lower arches), *commerson* (1-8), and *queenslandicus* (3-9). One species, *concolor*, stands out from the rest of the genus in having many gill rakers, 21-27. *Grammatorcynus* has more gill rakers (19-24) than 17 species of *Scomberomorus* but fewer than *S. concolor*. There is a correlation between number of gill rakers and number of jaw teeth (Tables 3, 4) in *Scomberomorus*. The species with the fewest gill rakers, *S. multiradiatus*, also has the fewest jaw teeth ($\bar{x}$ 8.0 on the upper jaw, 7.8 on the lower jaw) and the species with the most gill rakers, *S. concolor*, has the most teeth ($\bar{x}$ 22.2, 19.7).

AXIAL SKELETON

This section is divided into four parts: vertebral number, vertebral column, ribs and intermuscular bones, and caudal complex.

Vertebral Number

Vertebrae may be divided into precaudal (ab-

TABLE 5.—Total number of gill rakers on the first arch in *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	*N*	$\bar{x}$
S. brasiliensis												1	9	49	37	22	11												129	13.8
S. cavalla								3	8	30	22	1	1	1															66	9.3
S. commerson		1	0	37	28	27	12	3	2																				110	4.3
S. concolor																						1	2	10	10	9	4	3	39	24.2
S. guttatus									3	7	24	53	25	9	2														123	11.1
S. koreanus												5	4	3	11	4													27	13.2
S. lineolatus								1	0	3	9	12	3	1															29	10.5
S. maculatus											1	4	16	27	13	5	1												67	13.0
S. multiradiatus		2	12	10	3																								27	2.5
S. munroi											3	4	1																8	10.8
S. niphonius												3	18	14	2	1													38	12.5
S. plurilineatus													10	15	8	1													34	13.0
S. queenslandicus				2	3	3	11	13	1	1																			34	6.2
S. regalis													1	2	4	19	13	6	1										46	15.4
S. semifasciatus							1	1	1	11	9	5	3	1															32	9.8
S. sierra													1	5	15	33	22	6											82	15.1
S. sinensis												1	7	6	1	1													16	12.6
S. tritor													7	18	11	5													41	13.3
Acanthocybium	30																												30	0
Grammatorcynus																				3	9	17	8	5	1				43	21.1

dominal) and caudal (Tables 6-8). The first caudal vertebra is defined as the first vertebra that bears a notably elongate haemal spine and lacks pleural ribs. Vertebral counts include the urostyle which bears the hypural plate. Of the three genera, *Acanthocybium* has the most vertebrae (62-64), *Grammatorcynus* the least (31), with the species of *Scomberomorus* falling between (41-56). The same situation exists with precaudal vertebrae (*Acanthocybium* 30-32, *Scomberomorus* 16-23, *Grammatorcynus* 12) and caudal vertebrae (*Acanthocybium* 31-33, *Scomberomorus* 20-36, *Grammatorcynus* 19). The presence of only 31 vertebrae in *Grammatorcynus* is a primitive condition agreeing with *Scomber* and *Rastrelliger*, the most primitive members of the Scombrinae. The increased number of vertebrae in *Acanthocybium* is clearly a specialization.

Within *Scomberomorus*, *S. multiradiatus* has the most vertebrae (54-56), followed by *S. maculatus* (51-53), *S. munroi* (50-52), and *S. guttatus* (47-52). The fewest vertebrae are found in *S. cavalla* (41-43) and *S. sinensis* (41-42). Vertebral counts are useful in distinguishing species that had previously been confused (Collette and Russo 1979); *S. koreanus* (46) from *S. guttatus* (usually 48-51) as shown by Devaraj (1976); *S. brasiliensis* (47-49) from *S. maculatus* (51-53) as shown by Collette et al. (1978); and *S. munroi* (50-52) from *S. niphonius* (48-50) as shown by Collette and Russo (1980). In general, low vertebral number is considered primitive in the genus, high vertebral number advanced.

Species with similar total numbers of vertebrae may differ in numbers of precaudal and caudal vertebrae. Both *S. cavalla* and *S. sinensis* have

TABLE 6.—Number of precaudal vertebrae in *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	12	16	17	18	19	20	21	22	23	30	31	32	*N*	$\bar{x}$
S. brasiliensis					4	78	1						83	20.0
S. cavalla		1	28										29	17.0
S. commerson					41	69							110	19.6
S. concolor				1	14	5							20	19.2
S. guttatus					1	14	43	2					60	20.8
S. koreanus						24							24	20.0
S. lineolatus				2	13	1							16	18.9
S. maculatus							30	3					33	21.1
S. multiradiatus						9	16						25	20.6
S. munroi							2	10					12	21.8
S. niphonius							4	23	1				28	21.9
S. plurilineatus					1	12							13	19.9
S. queenslandicus					1	13							14	19.9
S. regalis					1	9							10	19.9
S. semifasciatus				1	21								22	19.0
S. sierra					3	45	3						51	20.0
S. sinensis					9	3							12	19.3
S. tritor				2	24								26	18.9
Acanthocybium										2	4	2	8	31.0
Grammatorcynus	14												14	12.0

TABLE 7.—Number of caudal vertebrae in *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	*N*	$\bar{x}$
S. brasiliensis									7	72	4								83	28.0
S. cavalla						1	27	1											29	25.0
S. commerson					11	33	49	7	9										109	24.7
S. concolor									2	13	5								20	28.2
S. guttatus										12	17	28	3						60	29.4
S. koreanus								22	2										24	26.1
S. lineolatus							1	3	11	1									16	26.8
S. maculatus												15	18						33	30.5
S. multiradiatus																10	13	2	25	34.7
S. munroi										2	8	2							12	29.0
S. niphonius									23	5									28	27.2
S. plurilineatus							2	10	1										13	25.9
S. queenslandicus										10	4								14	28.3
S. regalis										10									10	28.0
S. semifasciatus							1	17	4										22	26.1
S. sierra								1	9	36	5								51	27.9
S. sinensis			2	9															11	21.8
S. tritor									23	3									26	27.1
Acanthocybium													1	4	2				7	32.1
Grammatorcynus	14																		14	19.0

TABLE 8.—Total number of vertebrae in *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	31	//	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	//	62	63	64	*N*	$\bar{x}$
S. brasiliensis									11	67	5												83	47.9
S. cavalla			2	28	1																		31	42.0
S. commerson				7	16	34	39	15															111	44.4
S. concolor								1	11	8													20	47.4
S. guttatus									1	8	5	16	28	2									60	50.1
S. koreanus								23	2														25	46.1
S. lineolatus						1	3	13															17	45.7
S. maculatus													13	19	2								34	51.7
S. multiradiatus																1	15	9					25	55.3
S. munroi												3	9	1									13	50.8
S. niphonius										3	20	6											29	49.1
S. plurilineatus							2	12															14	45.9
S. queenslandicus										12	3												15	48.2
S. regalis									1	9													10	47.9
S. semifasciatus						1	23	3															27	45.1
S. sierra								1	8	38	4												51	47.9
S. sinensis			10	1																			11	41.1
S. tritor								25	1														26	46.0
Acanthocybium																				2	3	2	7	63.0
Grammatorcynus	16																						16	31.0

41-43 vertebrae, but *S. cavalla* has 16-17 precaudal and 24-26 caudal, while *S. sinensis* has 19 or 20 precaudal and 21-22 caudal vertebrae (compare Tables 6 and 7).

Vertebral Column

The neural arches and spines are stout and compressed on the first to the fifth or sixth vertebrae in most species of *Scomberomorus*. Compressed neural spines extend to the seventh vertebra in *S. commerson* and *Acanthocybium* but only to the fourth vertebra in *Grammatorcynus*. Posteriorly, toward the caudal peduncular vertebrae and caudal complex, the neural spines bend abruptly backward and cover most of the neural groove; caudally they merge into the caudal complex as in *Thunnus* (Kishinouye 1923; Gibbs and Collette 1967) and the bonitos (Collette and Chao 1975). Neuropophyses are present on all centra except the last one or two. The neural prezygapophyses on the first vertebra are modified to articulate with the exoccipital where the vertebral axis is firmly articulated with the skull. They are stronger at the anterior portion of the vertebrae and are spurlike spines on the peduncular vertebrae and in the caudal complex. Neural postzygapophyses arise posterodorsally from the centrum and overlap prezygapophyses posteriorly. The postzygapophyses progressively merge into the neural spine in the peduncular region to disappear by the last 6-8 vertebrae. The basic structure and elements of the neural arches and neurapophyses are similar to those of other scombrids (Kishinouye 1923; Conrad 1938; Mago Leccia 1958; Nakamura 1965; Gibbs and Collette 1967; Collette and Chao 1975; Potthoff 1975).

Variable characters are found on the haemal arches and haemapophyses. Laterally directed parapophyses, arising from the middle of the centrum, appear on the fourth to sixth vertebrae, where the intermuscular bones and pleural ribs are encountered (see section on Ribs and Intermuscular Bones). The parapophyses become broader and longer posteriorly and gradually shift to the anteroventral portion of the centra. In lateral view, the first ventrally visible parapophyses are found on the 7th-9th vertebra in *Scomberomorus*, usually the 8th, on the 6th-7th in *Grammatorcynus*, and on the 14th-15th in *Acanthocybium*.

Posteriorly, the distal ends of the paired parapophyses meet, forming the first closed haemal arch. The first closed haemal arch is on the 8th vertebra in *Grammatorcynus* (Fig. 37d), 10th-16th in *Scomberomorus* (Fig. 37a, b), and 25th-28th in *Acanthocybium* (Fig. 37c). This location is correlated with the total number of vertebrae (Table 8). Among the species of *Scomberomorus*, the first closed haemal arch is most anterior in *S. cavalla* (10th-11th vertebra, Fig. 37a) and *S. sinensis* (12th), the two species with the fewest vertebrae (40-43). The most posterior first haemal arch is on the 15th-16th vertebra in *S. munroi* and *S. niphonius* (Fig. 37b) and on the 14th-15th in *S. multiradiatus*, species with many vertebrae (48-56). The other 13 species, including *S. guttatus* and *S. maculatus* with high vertebral counts (47-53), have the first haemal arch located at an intermediate position, on the 13th-14th vertebra. The haemal spines become elongate and point posteriorly until they abruptly become more elongate on the first caudal vertebra. The paired pleural ribs (see section on Ribs and Inter-

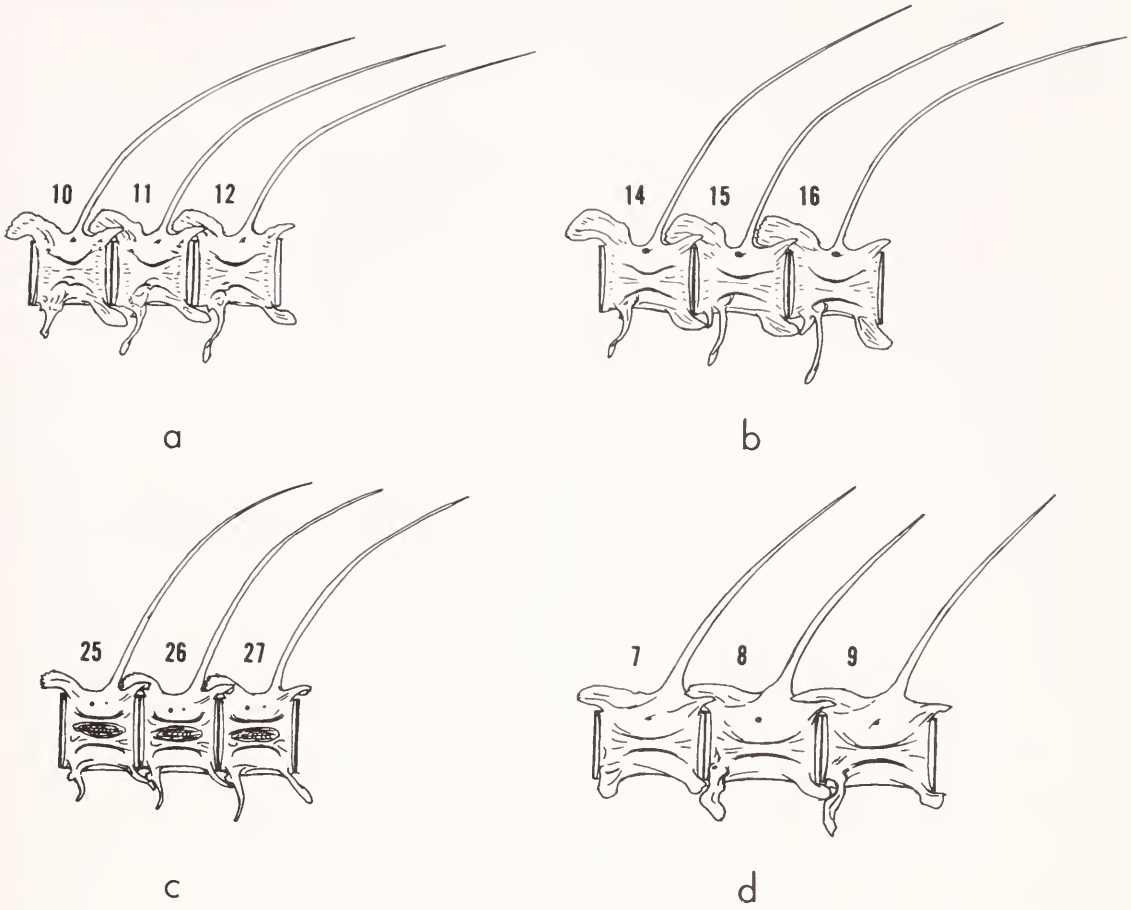


FIGURE 37.—Vertebra bearing first closed haemal arch in left lateral view (middle vertebra of each set of three). Vertebrae numbered from anterior. a. *Scomberomorus cavalla*, Chesapeake Bay, 672 mm FL, 1.5×. b. *Scomberomorus niphonius*, Japan, 683 mm FL, 1.5×. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL, 1×. d. *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 1.5×.

muscular Bones) attach to the distal ends of the parapophyses and arches and extend posteriorly to the last precaudal vertebra. Symmetrically with the neural arches and spines on the caudal vertebrae, the haemal arches and spines bend posteriorly at the caudal peduncle and then merge into the caudal complex.

Haemapophyses include pre- and postzygapophyses but their relative positions are different from those of the neurapophyses, and they do not overlap. The first haemal postzygapophyses arise posteroventrally from the 6th-7th centrum in *Grammatorcynus*, the 6th-8th in *Scomberomorus*, and the 9th-10th in *Acanthocybium*, and they reach their maximum length at about the junction of the precaudal and caudal vertebrae (Fig. 38). The haemal postzygapophyses fuse with the haemal spine or disappear in the caudal peduncle region.

The haemal prezygapophyses arise from the anterior base of the haemal arches on the 8th-11th vertebra in *Grammatorcynus*, the 10th-22d in *Scomberomorus*, and the 23d-25th in *Acanthocybium*. The most anteriorly located prezygapophyses in *Scomberomorus* are in *S. cavalla*, on the 10th-12th vertebra. The most posteriorly located are in *S. sinensis* (22d), *S. queenslandicus* (18th-20th), *S. multiradiatus* (18th-19th), and *S. maculatus* (17th-20th). The other 15 species have the first haemal prezygapophyses on the 13th-19th vertebra. The data from Devaraj (1977) for the four Indian species fall in the interme-

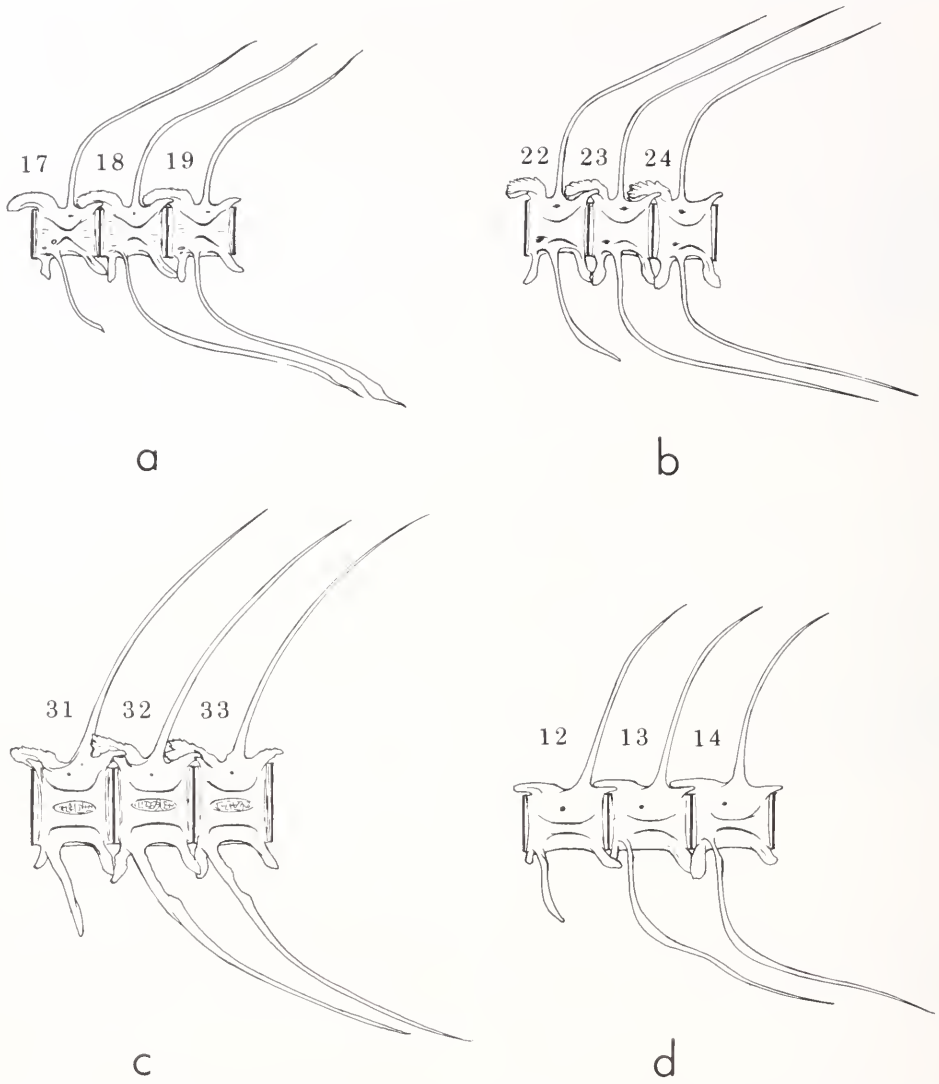


FIGURE 38.—Junction of precaudal and caudal vertebrae in left lateral view (middle vertebra of each set of three is first caudal vertebra). Vertebrae numbered from anterior. a. *Scomberomorus cavalla*, Florida, 688 mm FL, 1×. b. *Scomberomorus munroi*, Cairns, Queensland, 800 mm FL, 1×. c. *Acanthocybium solandri*, Miami, Fla., 1,242 mm FL, 1×. d. *Grammatorcynus bilineatus*, Timor Sea, 453 mm FL, 1.5×.

diate group, but we found more variation, usually a range of three or four vertebrae, than Devaraj did. As do their counterpart neural prezygapophyses, the haemal prezygapophyses persist symmetrically into the caudal complex.

Struts between the haemal arch and the centrum form the inferior foramina. Foramina are present from the 18th-19th to the 27th-28th vertebra in *Grammatorcynus*, the 21st-33d to the 35th-52d in *Scomberomorus*, and the 49th-51st to the 56th-57th in *Acanthocybium*. Devaraj (1977) found only one inferior foramen in *Acanthocybium*, on the 49th vertebra, but we found them on 7-9 vertebrae in 10 specimens from the Atlantic, Indian, and Pacific Oceans. In *Scomberomorus*, inferior foramina begin furthest anteriorly and extend furthest posteriorly in *S. multiradiatus*, from the 21st-23d to the 51st-52d vertebra. They begin furthest posteriorly in *S. maculatus* (29th-33d), *S. niphonius* (27th-33d),

and *S. concolor* (26th-38th). They extend posteriorly only to the 35th-36th vertebra in *S. cavalla*.

Ribs and Intermuscular Bones

Pleural ribs are present from the 2d or 3d vertebra posterior to the 12th-31st vertebra, depending on the species. Intermuscular bones start on the back of the skull or the first vertebra and extend to the 10th-30th vertebra.

Correlated with its high number of vertebrae, *Acanthocybium* has the most pleural ribs (30 pairs) of the three genera. Similarly, *Grammatorcynus* has the fewest pleural ribs (10 pairs) in agreement with its low number of vertebrae. Species of *Scomberomorus* are intermediate in number of vertebrae and pleural ribs (15-21 pairs). The first pleural rib articulates with the centrum of the third vertebra in *Grammatorcynus* and most specimens of *Scomberomorus*. The first rib articulates with the centrum of the second vertebra in *Acanthocybium*, as noted by Devaraj (1977:44), and in one or two specimens of at least three species of *Scomberomorus*: *commerson* (1 of 5), *maculatus* (2 of 10), and *sinensis* (our only specimen). Pleural ribs extend posteriorly usually to about the last precaudal vertebra. They extend to the 31st vertebra in *Acanthocybium*, to the 17th-23d in *Scomberomorus*, and only to the 12th in *Grammatorcynus*. Of the species of *Scomberomorus*, the most ribs are found in *S. munroi* (20-21 pairs), *S. guttatus* (20), *S. brasiliensis* (18-20), and *S. maculatus* (18-20). The fewest are in *S. cavalla* (15 pairs), *S. semifasciatus* (15-17), and *S. concolor* (16-18). Ribs extend back furthest in the same four species with the most pleural ribs, *S. munroi* (to the 22d-23d), *S. guttatus* (20th-22d), *S. brasiliensis* (20th-22d), and *S. maculatus* (17th-22d). They extend back the shortest distance in *S. cavalla* (to the 17th) and *S. semifasciatus* (17th-19th). As Devaraj (1977:44) noted, the anterior ribs in *Acanthocybium* are very broad compared with those in *Scomberomorus*.

Intermuscular bones start on the first vertebra in *Acanthocybium*, *Grammatorcynus*, and some species of *Scomberomorus*. In some specimens of at least 13 species of *Scomberomorus*, the first intermuscular bone is attached to the exoccipital on the skull. This appears to be the usual condition in three species, *S. concolor*, *S. koreanus* (also noted by Devaraj 1977), and *S. sierra*. At least three other species usually appear to have the first intermuscular bone attached to the first vertebra: *S. guttatus*, *S. munroi*, and *S. niphonius*. The condition in the remaining 12 species either varies or is based on only a single specimen. The greatest number of intermuscular bones are found in *S. guttatus*, 26-30 pairs. Counts as high as 27 are found in *S. koreanus*, *S. maculatus*, and *S. multiradiatus*. Except for *S. koreanus*, the other three species with high numbers of intermuscular bones also have high vertebral counts. The fewest intermuscular bones in *Scomberomorus* are found in *S. cavalla* and *S. sinensis*, 20 pairs, and *S. lineolatus*, *S. niphonius*, and *S. semifasciatus*, 20-23 pairs each. *Grammatorcynus* has relatively few intermuscular bones (19-21 pairs) and *Acanthocybium*, unexpectedly, has the fewest (10 pairs) among the genera under discussion. This seems odd in view of its high number of vertebrae and pleural ribs. Intermuscular bones extend back furthest in the four species with the highest number, *S. guttatus* (to the 25th-29th), *S. koreanus* (24th-29th), *S. maculatus* (22d-27th), and *S. multiradiatus* (26th). They extend back the shortest distance in *S. cavalla* (to the 19th), the species with the fewest intermuscular bones. Correlated with their low number in *Grammatorcynus* and *Acanthocybium*, the bones extend back to the 19th-21st and to the 10th vertebra respectively.

Caudal Complex

The supporting bones of the caudal fin (Fig. 39) consist of four or five preural centra in *Scomberomorus*. Having four preural centra supporting the caudal fin is not a diagnostic character of the family as stated by Potthoff (1975). Only three preural centra support the caudal fin in *Grammatorcynus*, *Scomber*, and *Rastrelliger*. Five centra support the caudal fin in *Acanthocybium*. In *Scomberomorus* and *Acanthocybium*, preural centra 4 and 3 bear stout haemal and neural spines. Preural centrum 2 has an epural. Preural centra 2 and 3 each have autogenous haemal spines. The urostyle represents a fusion of preural centrum 1 and the ural centrum (Potthoff 1975). The urostyle is fused with the triangular hypural plate posteriorly and articulates with the uroneural dorsally. Dorsally, the urostyle bears an autogenous epural and ventrally, the autogenous parhypural. Preural centra 2-4 are compressed in *Scomberomorus* and *Acanthocybium* but not so much as in the bonitos and tunas (Collette and Chao 1975; Gibbs and Collette 1967). Preural centrum 4 is not at all shortened in *Grammator-*

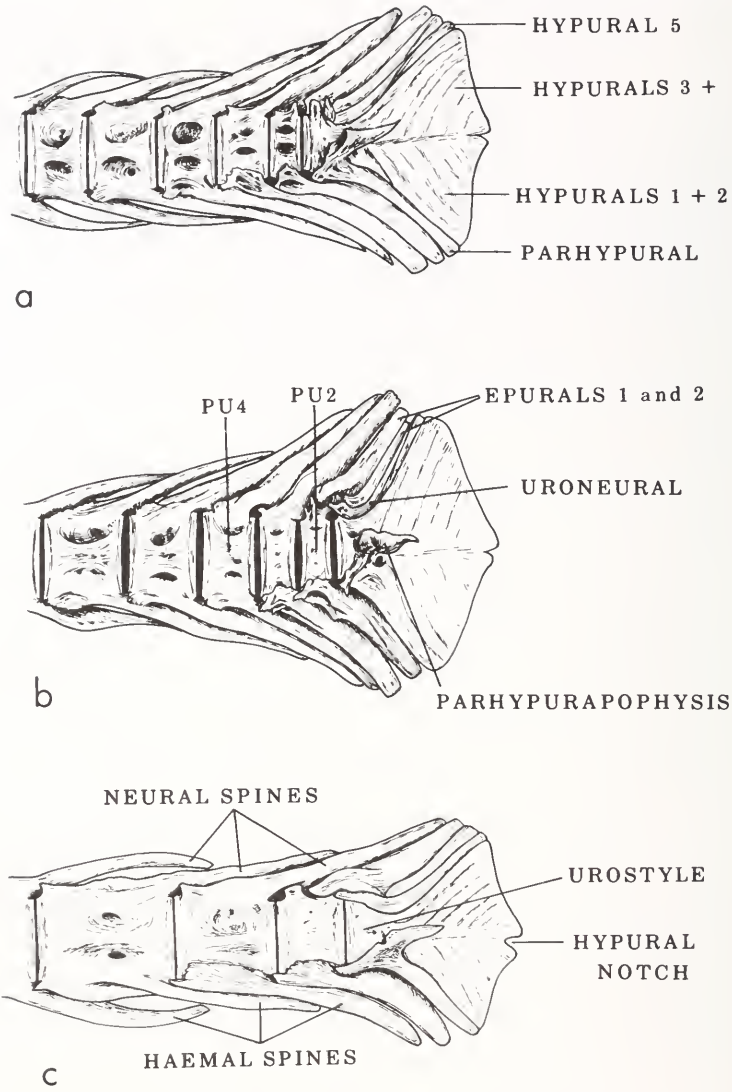


FIGURE 39.—Caudal complex in left lateral view. a. *Scomberomorus semifasciatus*, New Guinea, 510 mm FL, 3×. b. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL, 2×. c. *Grammatorcynus bilineatus*, New Guinea, 382 mm FL, 4×.

cynus and preural centrum 3 is only slightly shortened (Fig. 39c). In *Scomberomorus* and *Acanthocybium*, the posterior three neural and three haemal spines bend abruptly away from the vertebral axis and parallel the dorsal and ventral edges of the hypural plate. Only one neural and one haemal spine do so in *Grammatorcynus*.

The triangular hypural plate is composed of 4-5 fused hypural bones (Potthoff 1975). The dorsalmost (hypural 5) is not fused with the dorsal part of the hypural plate (hypurals 3 and 4). The primitive hypural notch is present on the middle of the posterior margin of the hypural plate (Fig. 39). This notch is a remnant of the fusion of the dorsal part of the hypural plate with the ventral part (1 and 2). The notch is absent in the more advanced bonitos and tunas (Collette and Chao 1975). In two larger specimens of *Grammatorcynus* (453 and 521 mm FL), the fifth hypural is partially fused to the dorsal hypural plate instead of being separate as in three smaller specimens (382-410 mm FL, Fig. 39c). One of the diagnostic characters of the Scombridae is that the bases of the caudal rays completely cover the hypural plate instead of only extending part way over the plate as is true of the Gempylidae and Trichiuridae with caudal fins.

The parhypural is separate from the ventral hypural plate in *Scomberomorus* and *Grammatorcynus* but is fused with it in *Acanthocybium*

(Fig. 39b). This fusion was also noted by Conrad (1938), Fierstine and Walters (1968), and Devaraj (1977). The parhypural appears to be partially fused with the hypural plate in *Scomberomorus niphonius* (see Kishinouye 1923:figure 41) and *S. plurilineatus*. The two haemal arches preceding the parhypural are autogenous in the three genera although Devaraj (1977) stated that the two haemal arches were fused with their centra in *Acanthocybium*.

The parhypural has a strongly hooked process, the parhypurapophysis (or hypurapophysis), at its proximal end. The parhypurapophysis slopes upwards in a similar manner in *Scomberomorus* and *Grammatorcynus* but has a right angle and then a level projection in *Acanthocybium*. Devaraj (1977:44) claimed that "the hypurapophysis is reduced to a small process" in *Acanthocybium*, and his figure seems to show that. This conclusion must be based on a damaged specimen because the parhypurapophysis is well developed in our specimens (Fig. 39b). The concentrations of tendons and muscular bands between the parhypurapophysis and caudal rays in scombroids were described by Fierstine and Walters (1968), but no specific study of this aspect was made during our work.

There are two epurals as in other scombrids (Potthoff 1975). In shape and size, the anterior epural (epural 1) resembles the neural spine of adjacent preural centrum 3. The posterior epural (epural 2) is a free splint located between the anterior epural and the uroneural and fifth hypural which are joined together.

Illustrations of the caudal complex of *Acanthocybium* and 11 species of *Scomberomorus* have been provided by several authors: *S. sinensis* and *S. niphonius* (Kishinouye 1923:pl. 23, fig. 40, pl. 24, fig. 41); *S. cavalla*, *S. maculatus*, and *S. regalis* (Mago Leccia 1958:pl. 15, figs. 1-3); *S. tritor* (Monod 1968:fig. 736); *S. koreanus*, *S. guttatus*, *S. lineolatus*, and *S. commerson* (Devaraj 1977:fig. 15); *S. semifasciatus* (Collette and Russo 1979:fig. 4B); and *Acanthocybium* (Kishinouye 1923:pl. 23, fig. 39; Conrad 1938:fig. 8; and Monod 1968:fig. 737). There are problems with nomenclature and labelling of various elements in these papers, as discussed by Potthoff (1975).

DORSAL AND ANAL FINS

Scombrids have two dorsal fins. The first dorsal fin is composed of stiff spines and is separated from the second dorsal by a short distance, except in *Rastrelliger*, *Scomber*, and *Auxis* which have a greater distance between the fins. The second dorsal fin is composed of soft rays and is followed by a series of free finlets, 6-11 in *Scomberomorus*. The anal fin is located approximately opposite the dorsal fin and is composed largely of soft rays followed by a series of anal finlets similar to the dorsal finlets, 5-12 in *Scomberomorus*. Some scombrids have a free or partially free spine preceding the anal fin, but in *Scomberomorus* it is difficult to tell if the anterior elements are spiny or soft rays; therefore, all are included as "anal rays". Numbers of fin rays are useful characters in distinguishing groups of species in *Scomberomorus*.

The range in number of spines in the first dorsal fin is 11-27 among *Scomberomorus*, *Acanthocybium*, and *Grammatorcynus* (Table 9). The

TABLE 9.—Number of spines in the first dorsal fin of *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	*N*	$\bar{x}$
S. brasiliensis							61	67	2									130	17.5
S. cavalla		1	3	6	42	2	3	1										58	14.9
S. commerson					3	50	107	5										165	16.7
S. concolor					1	3	20	7										31	17.1
S. guttatus					6	30	59	7										102	16.7
S. koreanus				2	20	5	1											28	15.2
S. lineolatus					2	10	15	1										28	16.5
S. maculatus							10	40	7									57	17.9
S. multiradiatus						1	8	14	4									27	17.8
S. munroi										6	8	1						15	20.7
S. niphonius									4	29	5							38	20.0
S. plurilineatus					12	17	2											31	15.7
S. queenslandicus						8	24	2										34	16.8
S. regalis						9	31	6										46	16.9
S. semifasciatus			1	11	17													29	14.6
S. sierra					1	3	36	39										79	17.4
S. sinensis					1	7	6											14	16.4
S. tritor					3	7	19	11										40	17.0
Acanthocybium													2	2	7	19	4	34	25.6
Grammatorcynus	2	42	1															45	12.0

usual variation for a species is 3 or 4 spines. *Acanthocybium* has the most dorsal spines, 23-27. Of the species of *Scomberomorus*, *munroi* (20-22) and *niphonius* (19-21) both usually have 20 or 21 dorsal spines, more than the other 16 species in the genus, and this is one reason that *S. munroi* was not described until recently (Collette and Russo 1980). Four species of *Scomberomorus* have low counts: *cavalla* 12-18, usually 15; *semifasciatus* 13-15; *koreanus* 14-17, usually 15; and *plurilineatus* 15-17. *Grammatorcynus* has even fewer dorsal spines, 11-13, usually 12. Dorsal spine counts are roughly correlated with vertebral number (Table 8). *Acanthocybium* has the highest counts of precaudal and total vertebrae; *S. munroi* and *S. niphonius* have the highest precaudal vertebral counts, but not highest total vertebral number; *S. cavalla* has the lowest precaudal and total counts in the genus; and *Grammatorcynus* has the fewest precaudal, caudal, and total vertebrae.

The range in number of second dorsal fin rays is 10-25 in the three genera (Table 10). The usual variation for a species is 4 or 5 rays. Five species of *Scomberomorus* have high counts: *multiradiatus* 21-25, usually 23 or 24; *koreanus* 20-24, usually 22 or 23; *guttatus* 18-24, usually 20-22; *semifasciatus* 19-22, usually 20; and *plurilineatus* 19-21, usually 20. The lowest counts in *Scomberomorus* are in *sinensis*, 15-17 rays. *Acanthocybium* (12-16) and *Grammatorcynus* (10-12, usually 11) have even fewer second dorsal fin rays. Vertebral counts (caudal and total) are highest in *S. multiradiatus* and lowest in *S. sinensis*. *Grammatorcynus* has the fewest vertebrae.

Dorsal finlets number 6-11 in the three genera (Table 10). The usual variation for a species is 3 or 4 finlets. The highest counts are in *S. commerson* and *S. queenslandicus*, both usually 9 or 10 finlets. The lowest counts, 6 or 7, are in *S. sinensis* and *Grammatorcynus*. The next fewest dorsal finlets, 7 or 8, rarely 9, are found in *S. multiradiatus*. The low number of finlets and high number of second dorsal fin rays in this species may indicate an extension of the fin at the expense of the number of finlets.

Anal fin rays (Table 11) show a similar trend to that of dorsal fin rays. The range in the three genera is 11-29; the usual variation for a species is 4-6 rays. Four of the five species of *Scomberomorus* with high counts of second dorsal fin rays also have high counts of anal fin rays: *multiradiatus* 25-29; *koreanus* 20-24, usually 22 or 23; *guttatus* 19-23, usually 20-22; and *semifasciatus* 19-22, usually 21 or 22. No species of *Scomberomorus* stands out with very low counts but six species usually have 17-19 anal fin rays, lower than the other species of the genus: *brasiliensis*, *cavalla*, *commerson*, *munroi*, *niphonius*, and *sinensis*. *Acanthocybium* (11-14) and *Grammatorcynus* (11-13, usually 12) again have the fewest rays in this fin.

Anal finlets range 5-12 in the three genera (Table 11) with the usual variation for a species being 4 finlets. The most finlets are found in *S. queenslandicus* (9-11, usually 10) followed by *commerson* and *lineolatus* usually having 9 or 10 finlets, similar to the situation with dorsal finlets. The lowest counts, usually 6 finlets, are found in *S. multiradiatus*, *S. sinensis*, and *Grammatorcynus*, just as with dorsal finlets. Again the anal fin of *S. multiradiatus* appears to have

TABLE 10.—Number of second dorsal fin rays and dorsal finlets in *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	Dorsal rays																N	x̄	Finlets						N	x̄
	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25			6	7	8	9	10	11		
S. brasiliensis						1	11	52	48	13							125	17.5			29	89	12		130	8.9
S. cavalla						4	12	25	19								60	17.0		1	15	35	6		57	8.8
S. commerson						1	21	61	67	11	1						162	17.4			12	76	72	4	164	9.4
S. concolor							1	2	10	16	2						31	18.5	1	7	21	1			30	7.7
S. guttatus									3	5	24	40	24	7	1		104	21.0		6	52	43	4		105	8.4
S. koreanus											1	4	8	13	1		27	22.3		7	17	4			28	7.9
S. lineolatus						1	4	9	11	2	0	1	1				29	17.6		2	7	18	2		29	8.7
S. maculatus								5	19	25	7						56	18.6		2	29	25			56	8.4
S. multiradiatus												3	4	10	8	2	27	23.1		15	10	2			27	7.5
S. munroi								3	8	3	1						15	18.1				11	4		15	9.3
S. niphonius						1	12	12	12	1							38	17.0		9	22	7			38	7.9
S. plurilineatus										6	22	8					36	20.1			12	20	3		35	8.7
S. queenslandicus								10	11	10							31	18.0				12	17	2	31	9.7
S. regalis							2	12	28	5							47	17.8		2	39	6			47	8.1
S. semifasciatus										6	18	5	3				32	20.2			9	19	3		31	8.8
S. sierra							2	29	41	6							78	17.7		2	43	33	1		79	8.4
S. sinensis						4	9	1									14	15.8	8	6					14	6.4
S. tritor							6	25	9	1							41	17.1		1	33	7			41	8.1
Acanthocybium		1	3	21	7	1	2										35	13.3		6	16	11	3		36	8.3
Grammatorcynus	5	37	1														43	10.9	40	5					45	6.1

TABLE 11.—Number of anal fin rays and anal finlets in *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	Anal rays																			N	$\bar{x}$	Finlets								N	$\bar{x}$
	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29			5	6	7	8	9	10	11	12		
S. brasiliensis						6	35	30	44	9										124	18.1			1	41	84	2			128	8.7
S. cavalla						1	9	27	21	1										59	18.2			4	33	19	4			60	8.4
S. commerson						8	29	72	43	12	1									165	18.2			1	17	84	57	4	2	165	9.3
S. concolor									1	17	9	2	1							30	20.5		1	15	15				31	7.5
S. guttatus									2	23	49	26	3							103	21.0			20	63	17	4		104	8.0
S. koreanus										1	3	13	11	1						29	22.3			17	11	1			29	7.4
S. lineolatus							2	0	7	17	2	1								29	19.7			2	2	14	11		29	9.2
S. maculatus							4	11	24	18										57	19.0			1	33	21	1		56	8.4
S. multiradiatus															3	7	8	8	1	27	26.9		18	8	1				27	6.4
S. munroi							8	5	2											15	17.6				2	10	3		15	9.1
S. niphonius						1	12	20	3	1										37	17.8		1	7	20	10			38	8.0
S. plurilineatus									4	16	13	1								34	20.3			1	15	17	2		35	8.6
S. queenslandicus						2	1	6	14	8										31	18.8					8	21	2	31	9.8
S. regalis					1	1	4	15	24	1										46	18.4			3	34	8	1		46	8.2
S. semifasciatus									1	4	17	11								33	21.2			1	11	19	2		33	8.7
S. sierra						3	6	19	33	17	1									79	18.7			6	48	23	1		78	8.2
S. sinensis						1	3	9	1											14	17.7	2	9	3					14	6.1
S. tritor							5	20	14	2										41	18.3			6	27	8			41	8.0
Acanthocybium	1	11	14	8																34	12.9			13	12	7	2		34	7.9
Grammatorcynus	5	22	17																	44	12.3	1	39	4					44	6.1

extended posteriorly to reduce the number of anal finlets.

PECTORAL GIRDLE

The pectoral girdle consists of the girdle itself (cleithrum, coracoid, and scapula), the radials to which the pectoral fin rays attach, and a chain of bones that connect the girdle to the rear of the skull (posttemporal, supracleithrum, supratemporal, and two postcleithra).

Posttemporal

The posttemporal (Fig. 40) is a flat elliptical bone with two sturdy anterior processes that attach the pectoral girdle to the neurocranium. The median (dorsal) process is concave at its dorsal surface and articulates with the dorsal surface of the epiotic. The lateral (ventral) process is shorter, round in cross section, and its hollow anterior end articulates with the dorsal protuberance of the intercalar. There is a thin shelf between the median and lateral processes in

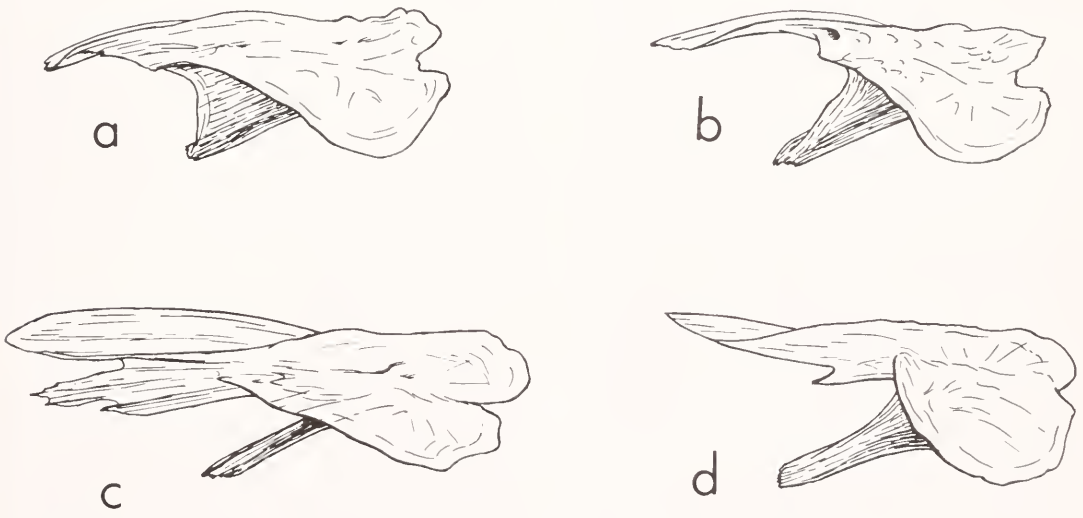


FIGURE 40.—Left posttemporals in lateral view. a. *Scomberomorus cavalla*, Chesapeake Bay, 672 mm FL, 1.5×. b. *Scomberomorus plurilineatus*, South Africa, 910 mm FL, 1×. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL, 1×. d. *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 1.5×.

Scomberomorus (Fig. 40a, b) but this shelf is absent in *Acanthocybium* (Fig. 40c) and *Grammatorcynus* (Fig. 40d). A variably sized notch is present at the middle of the posterior edge of the flat body of the bone. *Grammatorcynus* has a prominent, anteriorly directed spine on the ventral margin of the median process about one-third of the distance from the body of the bone to the anterior tip of the process. In *Acanthocybium*, there is a separate process extending anteriorly from the ventral wall of the median process. This auxiliary process (Kishinouye 1923) is as long or almost as long as the median process itself. It ends in a series of several pointed processes. (Both Conrad 1938 and Devaraj 1977 referred to the auxiliary process as the median process.)

The lengths of the median and lateral processes vary among the species under discussion. To compare the species quantitatively, we made two sets of measurements and divided them by the total length of the posttemporal, from the anterior tip of the median process to the posterior margin of the bone. We measured to the tips of the median and lateral processes from the most posterior point on the shelf between the two processes. Largely because of the lack of a shelf between the processes in *Acanthocybium* and *Grammatorcynus*, both processes appear to comprise a larger proportion of total posttemporal length than they do in the species of *Scomberomorus*, 53-65% vs. 36-51% for the median process and 27-40% vs. 15-36% for the lateral process. The median process is longer in *Acanthocybium* than in *Grammatorcynus*, 56-65% vs. 53-60%, but the lateral process is slightly longer in *Grammatorcynus* than in *Acanthocybium*, 35-40% vs. 27-37%. Among the species of *Scomberomorus*, the longest median processes (48-51% total length) are found in *S. commerson*, *plurilineatus*, and *sierra*; the shortest (36-40%) in *cavalla*, *semifasciatus*, and *sinensis*. The longest lateral processes are in *koreanus* (36%) and *plurilineatus* (30-31%); the shortest (15-19%) in *cavalla*, *munroi*, *niphonius*, *queenslandicus*, and *tritor*.

To eliminate the confounding factor of the shelf between the median and lateral processes, measurements also were made on the inner surface of the bone, from the point where the two processes diverge to the tips of the processes. Measured this way, the longest median processes (74-79% of total length of the posttemporal) are in *Acanthocybium* and six species of *Scomberomorus*. The shortest median processes (63-68%) are in three species of *Scomberomorus*: *multiradiatus*, *niphonius*, and *semifasciatus*. *Grammatorcynus* also has a short median process (66-71%). Measured this way, the longest lateral processes are in *koreanus* (53-55%), *sierra* (52%), *plurilineatus* and *regalis* (50-51%), *guttatus* (49-55%), and *Grammatorcynus* (48-52%). The shortest lateral processes are in *munroi* (37-40%), *tritor* (41-42%), and *cavalla* and *niphonius* (41-44%). *Acanthocybium* also has a relatively short lateral process (42-51%).

Still another way of comparing relative lengths of the processes among species is to divide the length of the lateral process by the length of the median process, both measured on the inner surface of the posttemporal. By this technique, relatively greater proportional measurements of the lateral processes are found in *S. koreanus* (75-77% of median process), *S. semifasciatus* (76%), *Grammatorcynus* (71-74%), *S. multiradiatus* (70-73%), and *S. guttatus* (69-71%). Relatively shorter proportional measurements of these lateral processes (55-63%) are found in *Acanthocybium* and five species of *Scomberomorus*: *cavalla*, *munroi*, *niphonius*, *queenslandicus*, and *tritor*.

Another difference lies in the presence and, if present, in the shape of a spine or process at the base of the lateral process on the inner surface of the posttemporal. It appears to be absent in seven species of *Scomberomorus*: *cavalla*, *guttatus*, *maculatus*, *queenslandicus*, *regalis*, *semifasciatus*, and *tritor*. It is small and inconspicuous in six species: *brasiliensis*, *concolor*, *koreanus*, *lineolatus*, *multiradiatus*, and *sierra*. It is broader, usually shaped more like a shelf with a point in the remaining five species of the genus: *commerson*, *munroi*, *niphonius*, *plurilineatus*, and sometimes in *sinensis*. The process has the form of a wide flap in *Grammatorcynus* and of a long blunt process in *Acanthocybium*. Devaraj's (1977) data for Indian species correspond well with ours.

Supracleithrum

The supracleithrum (Fig. 41) is an ovate bone, overlapped dorsolaterally by the posttemporal and overlapping the anterior part of the dorsal winglike extension of the cleithrum. The anterior border of the bone on the mesial side is thickened into a ridge. Dorsally there is a small handle-shaped process which curves into the posterior margin to end in a notch at the posterodorsal aspect. A branch of the lateralis system extends

from the posterior notch of the posttemporal onto the supracleithrum. This short canal lies ventral to the dorsal process of the supracleithrum and extends to the posterior edge of the bone.

The maximum width of the supracleithrum varies from 42 to 75% of the total length of the bone in the three genera. The supracleithrum is widest in *Grammatorcynus* (72-75% of length), *Scomberomorus niphonius* (55-62%), and *S. lineolatus* (53-57%). It is narrowest in *S. multiradiatus* (43-53%), *sinensis* (45-46%), *semifasciatus* (46-51%), and *sierra* (45-49%). Specimen size is a factor because the smallest species of *Scomberomorus* (*S. multiradiatus*) and small specimens of large species tend to have narrower supracleithra than large species and large specimens. For example, the percentages for a series of five *S. commerson* are as follows: 354-364 mm FL, 38-43%; 493 mm, 42%; 1,052 mm, 39-44%; 1,155 mm, 47%.

The dorsal process is prominent in *Acanthocybium* (Fig. 41c), *Grammatorcynus* (Fig. 41d), *S. cavalla*, *commerson*, and *lineolatus* (Fig. 41a). It is small but distinct in *S. multiradiatus* (Fig. 41b). In most of the other species of *Scomberomorus*, it tends to be less sharply set off from the main body of the supracleithrum.

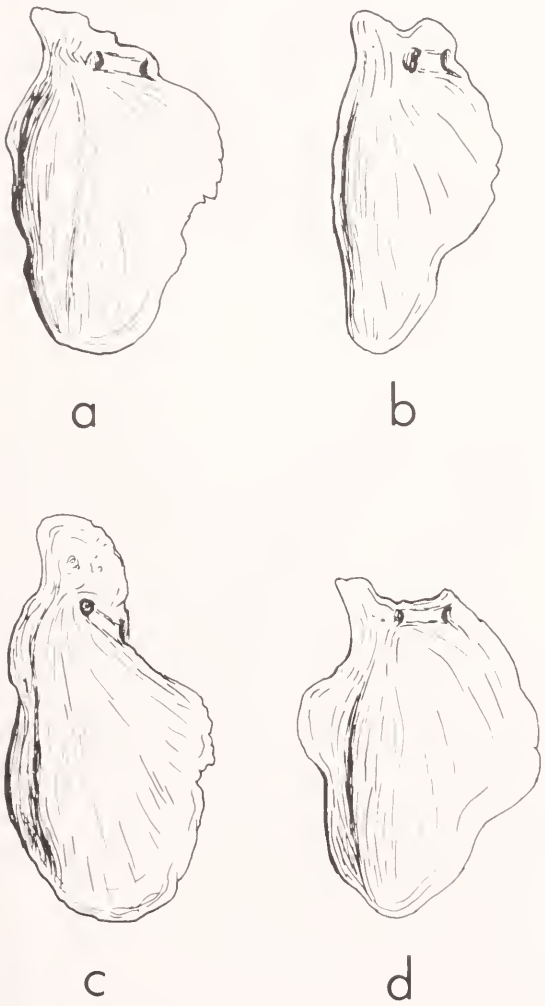


FIGURE 41.—Left supracleithra in lateral view. a. *Scomberomorus lineolatus*, Cochin, India, 786 mm FL, 1.5×. b. *Scomberomorus multiradiatus*, New Guinea, 294 mm FL, 3×. c. *Acanthocybium solandri*, Caribbean Sea, 1,240 mm FL, 1×. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL, 2×.

Supratemporal

The supratemporal (Fig. 42) is a thin flat triangular bone lying just underneath the skin where its lateral process articulates with a dorsal articular surface on the pterotic. Mago Leccia (1958:324) failed to find the supratemporal in his specimens. The anterior margin is concave and the convex posterior margin slightly overlaps the dorsal arm of the posttemporal. The supratemporal is deeper (from the tip of the median anterior arm to the base) than wide (tip of lateral anterior arm to tip of posterior arm), width 49-84% of depth in *Scomberomorus* and *Acanthocybium*. However, the supratemporal is wider than deep in *Grammatorcynus* (Fig. 42d), width 101-113% of length. *Acanthocybium* (Fig. 42c) has a wider supratemporal (84-93% of depth) than do the species of *Scomberomorus* (49-79%). The widest supratemporals in *Scomberomorus* are in *niphonius* (73%), *guttatus* (67-79%), *sierra* (69-74%), and *semifasciatus* (63-72%). The narrowest supratemporals are in *multiradiatus* (49-50%), *koreanus* (54%), *brasiliensis* (53-59%), *queenslandicus* (55-60%), and *sinensis* (54-62%).

The supratemporal bears a prominent lateral line canal that extends out almost to the tips of all three arms. Devaraj (1977:45) did not specifically mention the presence of this canal. In *Scomberomorus*, the canal along the anterior margin of the bone is the longest and best developed, and the canal along the lateral side the next longest. In most species of the genus, the first canal has three or four posteriorly directed branches. Specimens of *S. niphonius* and *S. semifasciatus* (Fig. 42a) had five or six branches. Two specimens of *S. multiradiatus* had only a single posterior branch. A specimen of *S. munroi* had no posterior

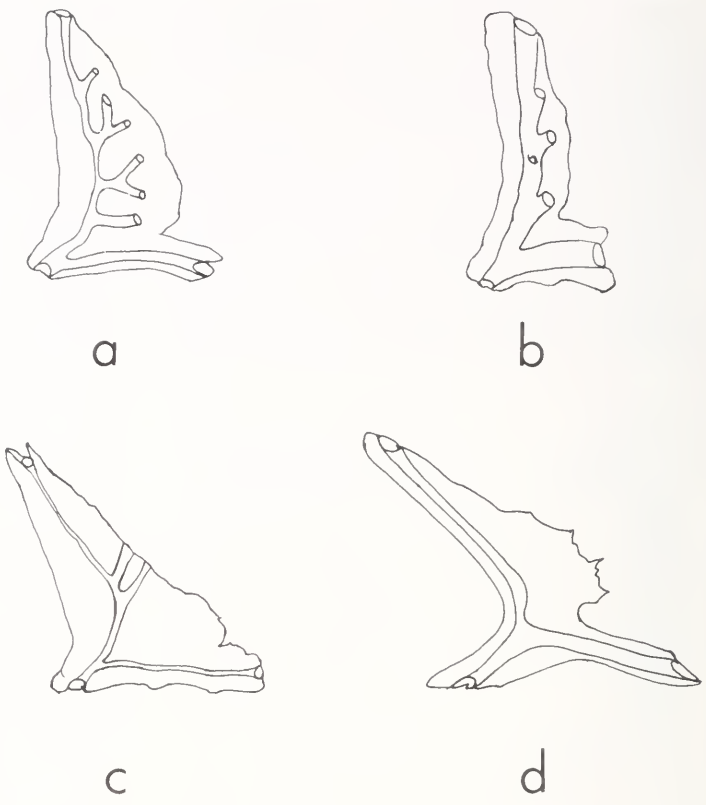


FIGURE 42.—Left supratemporals in lateral view. a. *Scomberomorus semifasciatus*, New Guinea?, 740 mm FL, 1.5×. b. *Scomberomorus multiradiatus*, New Guinea, 224 mm FL, 5×. c. *Acanthocybium solandri*, Caribbean Sea, 1,240 mm FL, 1×. d. *Grammatorcynus bilineatus*, New Guinea, 382 mm FL, 3×.

branches, but it did have four pores along the main part of the canal. *Acanthocybium* has a single short posterior branch that opens into a very large pore (Fig. 42c). *Grammatorcynus* (Fig. 42d) lacks a distinct posterior branch but has a relatively longer canal on the lateral side of the bone.

Cleithrum

The main body of the cleithrum is crescent-shaped with an anterodorsal spine and a posteriorly projecting plate at the upper end, as in other scombrids (Fig. 43). The angle between the spine and the plate is wider in *Acanthocybium* (Fig. 43c) than in *Grammatorcynus* (Fig. 43d) and the species of *Scomberomorus*. The bonitos have wider angles (Collette and Chao 1975:fig. 61), except for *Gymnosarda*. The spine extends about as far dorsally as the plate does in *Acanthocybium* and all the species of *Scomberomorus*, except *S. sinensis* in which the spine extends well past the dorsal margin of the plate. In *Grammatorcynus*, the spine does not extend all the way to the margin of the plate (Fig. 43d). The plate becomes narrower posteriorly in most species of *Scomberomorus* and in *Grammatorcynus*. The posterior plate is longer and of uniform width in *Acanthocybium* (Fig. 43c).

The lower part of the cleithrum is large and folded back upon itself as two walls: one lateral and the other mesial, which meet at their anterior margins and run parallel to each other. The mesial wall of the cleithrum forms a large triangular slit with the coracoid. As Devaraj (1977: 46) pointed out, this slit is hidden in lateral view in the species of *Scomberomorus* by the great width of the lateral wall of the cleithrum. This portion of the cleithrum is narrower in *Acanthocybium* and *Grammatorcynus*, and consequently the upper part of the slit is visible in lateral view.

Coracoid

The coracoid is elongate and more or less triangular in shape (Fig. 43). It connects with the scapula along its dorsal edge and with the mesial shelf of the cleithrum anterodorsally and anteroventrally. There is a prominent elongate slit between the cleithrum and the coracoid that is

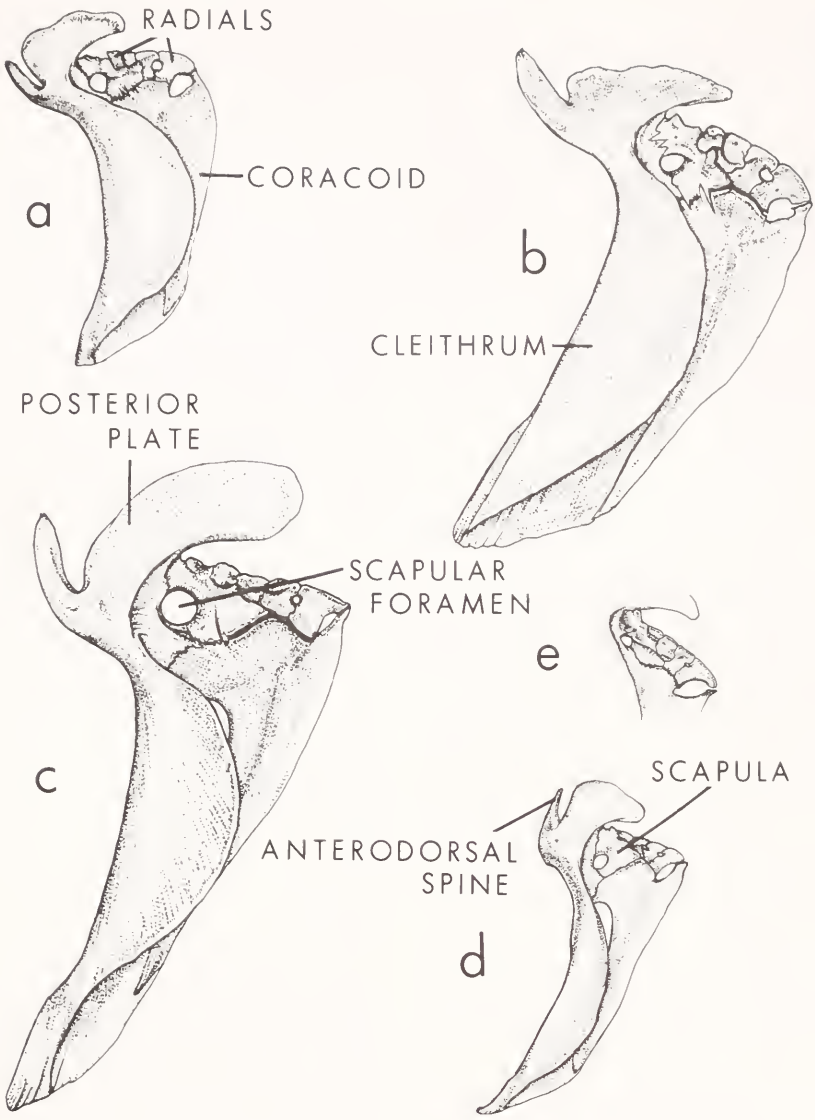


FIGURE 43.—Left pectoral girdles in lateral view. a. *Scomberomorus semifasciatus*, New Guinea, 510 mm FL. b. *Scomberomorus sinensis*, Hong Kong, 677 mm FL. c. *Acanthocybium solandri*, Revillagigedos Is., 1,086 mm FL. d. *Grammatorcynus bilineatus*, Marshall Is., 424 mm FL. e. *Scomberomorus koreanus*, Indonesia, 480 mm FL, inset of scapular and interradial foramina.

visible laterally in *Acanthocybium* and *Grammatorcynus* but is concealed by the lateral shelf of the cleithrum in *Scomberomorus*. The coracoid is relatively narrower in *Acanthocybium* than in *Grammatorcynus* and the species of *Scomberomorus*. We did not find the coracoid to be significantly narrower in *S. commerson*, as reported by Devaraj (1977:47).

Scapula

The anterior margin of the scapula connects to the mesial shelf of the cleithrum (Fig. 43). This attachment extends to the posterior projecting plate anterodorsally. The scapula is attached to the coracoid posteriorly and with the first two and part of the third upper radials posterodorsal-

ly. The posterodorsal margin of the scapula is drawn out into a facet which accepts the most anterior ray of the pectoral fin. The scapula is pierced by a large, usually round foramen near the lateral margin with the inner shelf of the cleithrum. A prominent suture leads from the scapular foramen to the ventral margin of the scapula. The foramen is largest in *Acanthocybium* (Fig. 43c), *Scomberomorus brasiliensis*, and *S. regalis*. It is smallest in *S. guttatus* and *S. niphonius*. We did not find it very large in *S. koreanus* (Fig. 43e), as stated by Devaraj (1977: 47). It is intermediate in size in *Grammatorcynus* (Fig. 43d) and the other species of *Scomberomorus* (e.g., *S. semifasciatus* and *S. sinensis*, Fig. 43a, b).

Pectoral Fin Rays

The first (uppermost and largest) pectoral fin ray articulates directly with a posterior process of the scapula. The other rays attach to the radials. The number of pectoral rays ranges from 19 to 26 in the three genera (Table 12). Most species of *Scomberomorus* usually have 22 or 23 rays. Five species average fewer, with a mode of 21 rays: *concolor*, *guttatus*, *maculatus*, *sierra*, and *tritor*. The two species in the genus with the most pectoral rays are *S. plurilineatus* (21-26, $\bar{x}$ 23.1) and *S. semifasciatus* (22-25, $\bar{x}$ 23.3). *Acanthocybium* and *Grammatorcynus* have slightly higher counts than do the species of *Scomberomorus*, 22-26, mostly 24 or 25.

Within the Scombridae, the number of pectoral fin rays increases from the more primitive members of the family to the more advanced: Scombrini 18-21, Scomberomorini 19-26, Sardini 21-28, Thunnini (except for *Thunnus*) 22-29, *Thunnus* 30-36.

TABLE 12.—Number of pectoral fin rays in *Acanthocybium*, *Grammatorcynus*, and the species of *Scomberomorus*.

Species	19	20	21	22	23	24	25	26	*N*	$\bar{x}$
S. brasiliensis			9	38	21	1			69	22.2
S. cavalla			6	27	18				51	22.2
S. commerson			18	52	32	8			110	22.3
S. concolor	1	8	21	4					34	20.8
S. guttatus		20	57	11	1				89	20.9
S. koreanus		1	4	13	7	3			28	22.3
S. lineolatus		4	2	6	10	3			25	22.2
S. maculatus		8	33	14	1				56	21.1
S. multiradiatus		1	10	10	6				27	21.8
S. munroi			4	4	1				9	21.7
S. niphonius			9	22	5				36	21.9
S. plurilineatus			1	9	14	5	3	1	33	23.1
S. queenslandicus			5	19	5	0	1		30	22.1
S. regalis		1	17	21	4	1			44	21.7
S. semifasciatus				4	15	13	1		33	23.3
S. sierra		16	38	17	1	1			73	21.1
S. sinensis			2	8	3				13	22.1
S. tritor		3	22	13					38	21.3
Acanthocybium				3	4	17	12	1	37	24.1
Grammatorcynus				1	8	13	17	3	42	24.3

Radials

The four radials differ in size and shape and are attached directly to the thickened posterior edges of the scapula and coracoid (Fig. 43). The size of the radials increases posteroventrally. Small foramina are located between the second and third, and the third and fourth radials counting posteriorly. In *Scomberomorus* and *Acanthocybium* (Fig. 43a-c), the first two radials and the upper third of the third radial attach to the scapula; the ventral third of the third plus the fourth radial attach to the coracoid. In *Grammatorcynus* the first two radials attach to the scapula, the second two to the coracoid (Fig. 43d). A much larger foramen is present between the largest (fourth) radial and the coracoid. Posteriorly, this foramen is framed by a posterior process of the upper part of the fourth radial meeting an anterior process from the posterior margin of the coracoid. The process on the fourth radial is only slightly developed in *Grammatorcynus* (Fig. 43d). The foramen is considerably larger than the scapular foramen in five species of *Scomberomorus*: *guttatus*, *koreanus* (Fig. 43e), *lineolatus*, *niphonius*, and *plurilineatus*. It is slightly larger than the scapular foramen in seven species: *commerson*, *concolor*, *maculatus*, *multiradiatus*, *munroi*, *queenslandicus*, and *tritor*. The two foramina are about equal in size in six species of *Scomberomorus* (*brasiliensis*, *cavalla*, *regalis*, *semifasciatus* (Fig. 43a), *sierra*, and *sinensis* (Fig. 43b)) and *Grammatorcynus* (Fig. 43d). The scapular foramen is much larger than the foramen following the fourth radial in *Acanthocybium* (Fig. 43c).

Postcleithra

The posterior projecting plate of the cleithrum has its posterior end attached to the first postcleithrum which connects ventrally to the second postcleithrum. The lamellar first postcleithrum (Fig. 44) is kidney-shaped with a narrow upper end, rounded lower margin, concave anterior border and convex posterior margin. In *Grammatorcynus* (Fig. 44d), the first postcleithrum is very wide and short with a notch in the dorsal margin instead of a pointed end, width/maximum length = 55-62%. It is wider (47-48%) in *Acanthocybium*

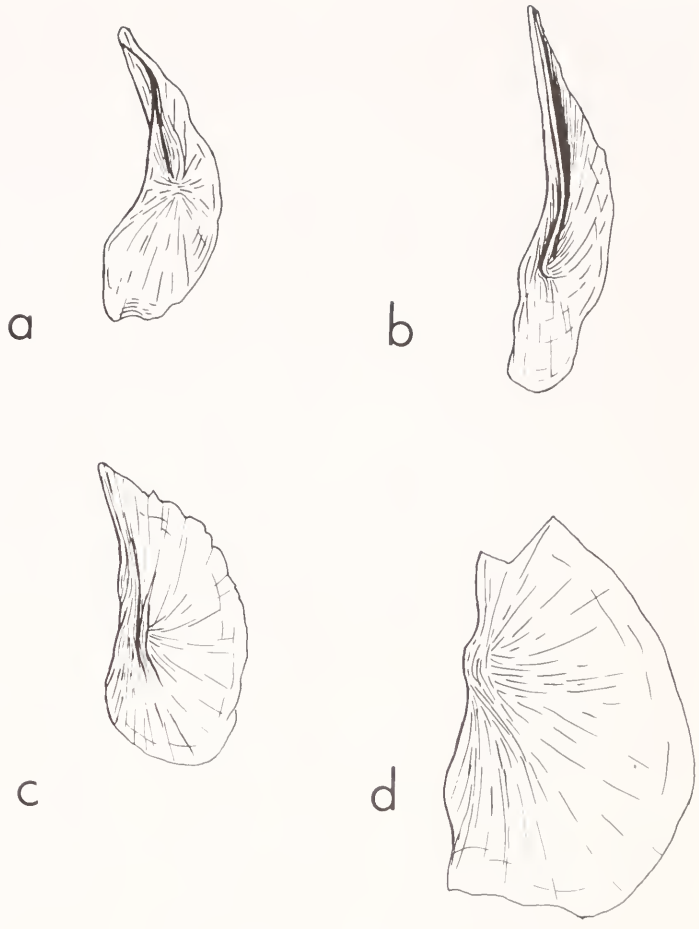


FIGURE 44.—Left first postcleithra in lateral view. a. *Scomberomorus sinensis*, Hong Kong, 677 mm FL, 1×. b. *Scomberomorus koreanus*, Indonesia, 480 mm FL, 2×. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL, 1×. d. *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 2×.

(Fig. 44c) than in the species of *Scomberomorus* (24-41%). Three species of *Scomberomorus* have wide first postcleithra (37-41%): *commerson*, *sinensis* (Fig. 44a), and *tritor*. Three species have narrow first postcleithra: *koreanus* (24-26%, Fig. 44b), *lineolatus* (28-29%), and *guttatus* (28-31%). The other 12 species have moderately wide first postcleithra, 30-39%. Devaraj (1977:48) reported long, narrow first postcleithra in the same three species (plus *S. maculatus* and *S. regalis* from Mago Leccia's 1958 work) and wider ones in *S. commerson* and *S. cavalla*.

The second postcleithrum (Fig. 45) is broad and lamellar at the upper part with a short pointed ascending process and a long styliform descending process. *Grammatorcynus* (Fig. 45d) differs strikingly from *Acanthocybium* and *Scomberomorus* in having a sharp process extending anteriorly from the broad lamellar portion of the bone. Inclusion of this process in measurements of the width of the bone makes the second postcleithrum appear much wider in *Grammatorcynus*, 37-42% of total length compared with 16-27% in the other two genera. The widest second postcleithra in *Scomberomorus*, 22-27% of total length, are in *lineolatus*, *maculatus*, *plurilineatus*, and *queenslandicus* (Fig. 45a). The narrowest ones are in *guttatus* and *koreanus* (15-20%, Fig. 45b), and *cavalla*, *sierra*, and *sinensis* (19-20%). *Acanthocybium* (Fig. 45c) and the other nine species of *Scomberomorus* are intermediate, 20-24%. The ascending process appears longer in 6 species of *Scomberomorus* (*brasiliensis*, *cavalla*, *maculatus*, *queenslandicus*, *regalis*, and *tritor*) than in *Acanthocybium*, *Grammatorcynus*, and the other 12 species of *Scomberomorus*.

PELVIC GIRDLE

The pelvic fin rays (I, 5) attach directly to the

paired basipterygia which make up the pelvic girdle. The bones are united along the midline and are imbedded in the ventral abdominal wall free from contact with any other bones. Each basipterygium is composed of three main parts (Fig. 46): a wide anterodorsal plate; a thin, flat anterior process (anterior xiphoid process of de Sylva 1955, anteromesial process of Devaraj 1977); and a strong posterior process (posterior xiphoid process of de Sylva 1955). There are three wings to the anterodorsal plate (Kishinouye 1923): lateral (external), mesial (internal), and ventral (vertical). Anteriorly, the lateral wing turns into the same vertical plane and merges into the ventral wing. The mesial wing and the lateral wing meet in one plane posteriorly along a ridge.

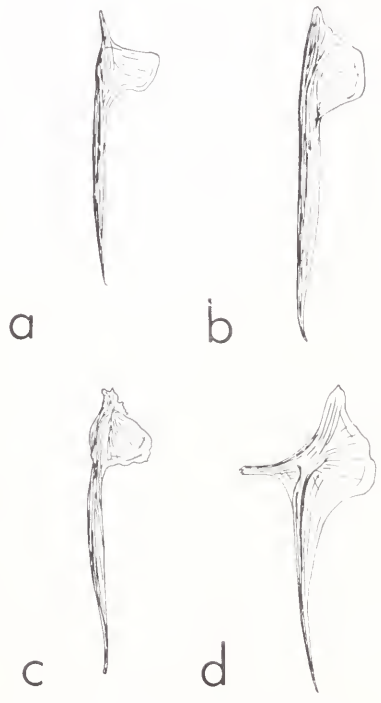


FIGURE 45.—Left second postcleithra in lateral view. a. *Scomberomorus queenslandicus*, Great Barrier Reef, 641 mm FL, 1×. b. *Scomberomorus koreanus*, Indonesia, 480 mm FL, 1.5×. c. *Acanthocybium solandri*, Revillagigedos Is., 1,068 mm FL, 1×. d. *Grammatorcynus bilineatus*, New Guinea, 382 mm FL, 2×.

To compare the pelvic girdles, the lengths of all three parts were measured from their bases to their tips. The anterior process comprised 15-52% of the length of the anterodorsal plate. The longest anterior processes were in *Grammatorcynus* (46-51%, Fig. 46d), *Acanthocybium* (35-47%, Fig. 46c), and seven species of *Scomberomorus*: *sierra* (38-52%), *concolor* (36-44%), *regalis* (31-44%, Fig. 46a), *semifasciatus* (35-36%), *sinensis* (35%), *tritor* (32-36%), and *maculatus* (28-36%). The shortest anterior processes were in three species of *Scomberomorus*: *koreanus* (15-30%), *multiradiatus* (21-26%), and *lineolatus* (23-33%, Fig. 46b), but there is a large range of variation within species. The posterior process comprised 20-85% of the length of the anterodorsal plate. The longest posterior processes were in four American species of *Scomberomorus*: *regalis* (78-90%), *brasiliensis* (81%), *sierra* (62-85%), and *concolor* (67-68%). The other two species that belong to this group have shorter posterior processes: *maculatus* (38-48%) and *tritor* (36-50%). The shortest posterior processes were in five

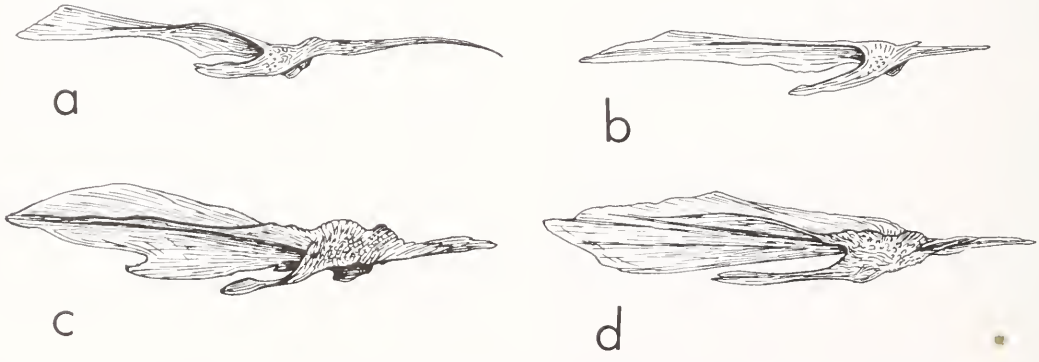


FIGURE 46.—Right basipterygia of the pelvic girdle in mesial view. a. *Scomberomorus regalis*, Miami, Fla., 469 mm FL, 1.5×. b. *Scomberomorus lineolatus*, Palk Strait, India, 428 mm FL, 2×. c. *Acanthocybium solandri*, Miami, Fla., 1,403 mm FL, 1×. d. *Grammatorcynus bilineatus*, Queensland, 521 mm FL, 1.5×.

species of *Scomberomorus*: *guttatus* (20-41%), *koreanus* (25-29%), *lineolatus* (29-35%), *multiradiatus* (27-33%), and *munroi* (28-44%), plus *Grammatorcynus* (29-33%) and *Acanthocybium* (30-39%).

Grammatorcynus and some individuals of *Acanthocybium* and at least seven species of *Scomberomorus* have longer anterior processes than posterior processes. The lengths of the anterior process as a percentage of the posterior process are *Grammatorcynus* (154-158%), *Acanthocybium* (91-156%), and the seven species of *Scomberomorus*: *sinensis* (121%), *semifasciatus* (111-116%), *munroi* (84-120%), *guttatus* (80-116%), *plurilineatus* (89-113%), *koreanus* (57-105%), and *tritor* (66-100%). The shortest anterior processes were in *brasiliensis* (42%), *concolor* (52-65%), and *sierra* (56-62%).

Devaraj (1977:48) alluded to differences in the relative depth of the anterior end of the anterodorsal plate, but we have found this very difficult to assess owing to different sizes and conditions of our material. Devaraj appears to be correct in stating that the anterior end is particularly narrow in *S. lineolatus*. The broadest anterior end is certainly in *Grammatorcynus* (Fig. 43d), which Devaraj did not study.

As Devaraj (1977:48) pointed out, a notch is present on the ventral wing of the anterolateral plate before it joins the other wings in *Acanthocybium* (Fig. 46c) but is absent in *Scomberomorus* (and also in *Grammatorcynus*).

Except for *Grammatorcynus*, no differences were found among the three genera in the fleshy bifid interpelvic process that is ventral to the paired posterior processes of the basipterygia. *Grammatorcynus* differs from *Scomberomorus* and *Acanthocybium* in having a single interpelvic process. *Auxis* and *Gymnosarda* also have a single interpelvic process, the former very large, the latter of moderate size. However, there is a posterior process from each basipterygium regardless of whether the fleshy interpelvic process is single or bifid.

SPECIES ACCOUNTS

Scomberomorus Lacepède

Scomberomorus Lacepède 1801:292 (type-species: *Scomberomorus plumierii* Lacepède 1801 by monotypy, = *Scomberomorus regalis* (Bloch 1793)).

Polipturus Rafinesque 1815:84 (replacement name for *Scomberomorus* Lacepède, therefore, takes the same type-species, *Scomberomorus plumierii* Lacepède 1801).

Cybium Cuvier 1829:199 (type-species: *Scomber commerson* Lacepède 1800 by subsequent designation of Gill 1862:126).

Apolectus Bennett 1831:146 (type-species: *Apolectus immunis* Bennett 1831 by monotypy, = *Scomberomorus tritor* (Cuvier *in* Cuvier and Valenciennes 1831)).

Apodontis Bennett 1832:169 (replacement name for *Apolectus* Bennett, preoccupied by *Apolectus* Cuvier *in* Cuvier and Valenciennes 1831, Pisces).

Chriomitra Lockington 1879a:133 (type-species: *Chriomitra concolor* Lockington 1879a by monotypy).

Sierra Fowler 1905:766 (type-species: *Cybium cavalla* Cuvier 1829 by original designation and monotypy).

Sawara Jordan and Hubbs 1925:214 (type-species: *Cybium niphonium* Cuvier *in* Cuvier and Valenciennes 1831 by original designation and monotypy).

Pseudosawara Munro 1943:68 (type-species: *Cybium kuhlii* Valenciennes 1831 by original designation, = *Scomberomorus guttatus* (Bloch and Schneider 1801)).

Indocybium Munro 1943:68-69 (type-species: *Cybium semifasciatum* Macleay 1884a by original designation).

Diagnosis.—*Scomberomorus* differs from all other scombrids in possessing a spatulate vomer that projects anteriorly well beyond the anterior margin of the neurocranium.

Scomberomorus differs from both *Acanthocybium* and *Grammatorcynus* in a series of 12 osteological characters: 1) posterior horizontal edge of metapterygoid longer than anterior oblique edge (anterior oblique edge longer in *Grammatorcynus* and *Acanthocybium*); 2) dorsal arm of ectopterygoid shorter than ventral arm (dorsal arm longer or equal); 3) lateral wall of cleithrum wide, space between cleithrum and coracoid not visible in lateral view (narrow, space visible in lateral view); 4) epiotic crests originate on anterior part of frontal bones (originate behind midfrontal region); 5) many (more than 11) vertebrae with inferior foramina (few, less than 11); 6) first basibranchial short (long); 7) strut on fourth pharyngobranchial elongate (not elongate); 8) symplectic short, not in contact with

metapterygoid (long, in contact); 9) ventral hypohyal at least three times larger than dorsal hypohyal (less than three times larger); 10) fifth branchiostegal ray on suture between epihyal and ceratohyal (on epihyal); 11) no shelf present between dorsal and ventral arms of posttemporal (shelf present); and 12) epihyal much longer than deep, depth 58-62% of length (depth 66-98% of length).

In three additional characters, *Scomberomorus* differs from *Acanthocybium* and *Grammatorcynus* but is closer to the former than the latter: ventral branch of palatine equal to or longer than (87-107%) dorsal branch (slightly shorter, 112-121%, in *Acanthocybium*; much shorter, 120-123%, in *Grammatorcynus*); supratemporal much deeper than wide, 49-79% (deeper, 84-93%; wider than deep, 101-113%); and first postcleithrum very narrow, 24-41% of length (narrow, 47-48%; wide, 55-62%). *Scomberomorus* has a deep urohyal; it is moderately deep in *Grammatorcynus* and shallow in *Acanthocybium*. *Scomberomorus* has a moderate to high number of vertebrae (40-56) compared with other members of the family, more than *Grammatorcynus* (31), but less than *Acanthocybium* (62-64).

Scomberomorus and *Acanthocybium* agree with each other but differ from *Grammatorcynus* in a series of 16 osteological characters: 1) supracleithrum narrow, 42-62% of length (wide, 72-75% in *Grammatorcynus*); 2) pores present on dorsal arm of supratemporal (absent); 3) nasals do not protrude far beyond ethmoid region (protrude far beyond); 4) posterior end of dorsal margin of urohyal forked (tripartite); 5) glossohyal without teeth fused to bone (large tooth patch fused to bone); 6) hyomandibula wide, 36-52% of length (narrow, 35-36%); 7) angle of lateral and medial arms of fourth epibranchial less acute (more acute); 8) anterior process of second epibranchial not elongate (elongate); 9) four or five vertebrae supporting caudal fin rays (three); 10) no anterior process on second postcleithrum (prominent spinelike process present); 11) anterior end of first postcleithrum pointed (notched); 12) base of third pectoral radial on suture between coracoid and scapula (completely on coracoid); 13) jaw teeth compressed and triangular (conical); 14) ventral surface of parasphenoid convex (concave); 15) upper margin of dentary longer than lower margin (lower longer); and 16) posterior edge of ectopterygoid short, 41-63% of ventral distance (long, 64-68%).

Scomberomorus brasiliensis Collette, Russo, and Zavalla-Camin
Serra Spanish Mackerel

Figure 47

Scomberomorus maculatus. Not of Mitchill 1815. Ribeiro 1915:134-135 (Brazil). Lowe 1962:679-686 (British Guiana continental shelf). Cervigón 1966:720-721 (description, fishery; Venezuela), fig. 303. Bastos 1966: 113-117 (counts and measurements). Nomura 1967:29-39 (biology; Ceará, Brazil). Mota Alves and Tomé 1968a:25-30 (sexual development). Mota Alves and Tomé 1968b:139-140 (sperm). Fonteles Filho 1968:133-137 (fishery; Ceará, Brazil). Nomura and Costa 1968:95-99 (length-weight relationship). Costa and Paiva 1969:89-95 (maximum size 125 cm FL; Ceará, Brazil). Mota Alves 1969:167-171 (digestive tract). *Menezes 1970:171-176 (food). Dahl 1971:278-279 (Colombia), photograph. Alcan-

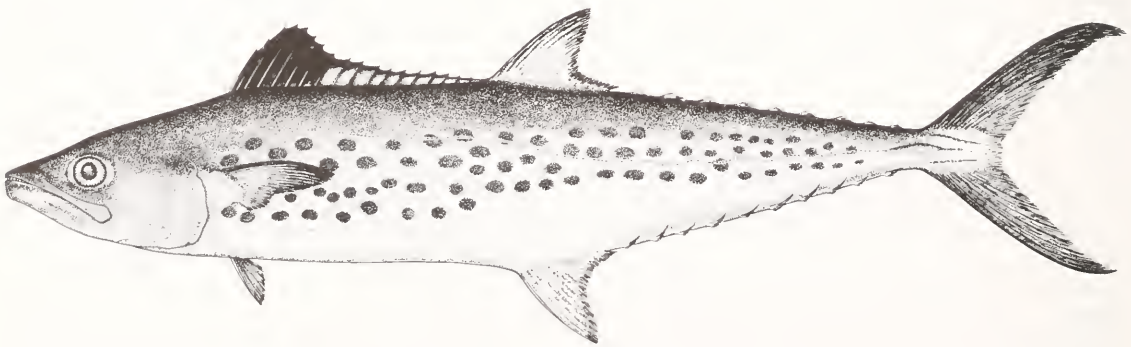


FIGURE 47.—*Scomberomorus brasiliensis*. Belém market, Brazil, 502 mm FL, USNM 217550, holotype.

tara Filho 1972a (gill net fishery; Ceará, Brazil). *Gesteira 1972:117-122 (reproduction and fecundity). Menezes 1972:86-88 (number of gill rakers). Bastos et al. 1973 (canning, Brazil). Costa and Almeida 1974:115-122 (length frequencies). Menezes 1976:45-48 (size, sex-ratio; NE Brazil). Fonteles-Filho and Alcantara-Filho 1977 (gill net mesh selectivity curve; Ceará, Brazil). *Sturm 1978:155-172 (biology, Trinidad). Ximenes 1983 (age and growth; Ceará, Brazil).

Scomberomorus brasiliensis Collette, Russo, and Zavalla-Camin 1978:273-279 (original description; Brazil). Manooch et al. 1978 (annotated bibliography). Collette 1979:29 (characters). Collette and Russo 1979:8-11 (diagnostic characters, range). Cressey et al. 1983:264 (host-parasite list, 4 copepod species). Collette and Nauen 1983:60-61 (description, range, fig.).

Types.—Holotype: USNM 217550 (502 mm FL); Belém market; 22 May 1975; B. B. Collette 1642. D XVIII+17+X; A 19+IX; P_1 22; RGR_1 3+1+10=14; vertebrae 19+28=47. Paratypes: 103 specimens (110-630 mm FL) from 54 Brazilian collections (see Collette et al. 1978:276-278).

Diagnosis.—This species possesses nasal denticles as do the other five species of the *regalis* group (*concolor*, *maculatus*, *regalis*, *sierra*, and *tritor*), has the artery that branches from the fourth left epibranchial artery as do all the species in the group except *S. tritor*, and shares a specialization of the fourth right epibranchial artery (Fig. 7f) with *S. sierra* and *S. regalis*. In these three species an artery connects the fourth right epibranchial with a branch of the coeliacomesenteric artery. *Scomberomorus brasiliensis* has shorter pelvic fins than do the other members of the *regalis* group (Fig. 48), 3.6-5.9% FL compared with 4.7-6.4 in *S. sierra* and 4.4-6.3 in *S. regalis*. Together with three other species of the *regalis* group (*concolor*, *regalis*, and *sierra*), *S. brasiliensis* has a long posterior process on the pelvic girdle, 62-90% of the length of the anterior plate. Differs from *S. sierra* by essentially lacking pterotic spines. Intercalar spine absent as in the other five species of the *regalis* group and *S. niphonius*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3a). Spines in first

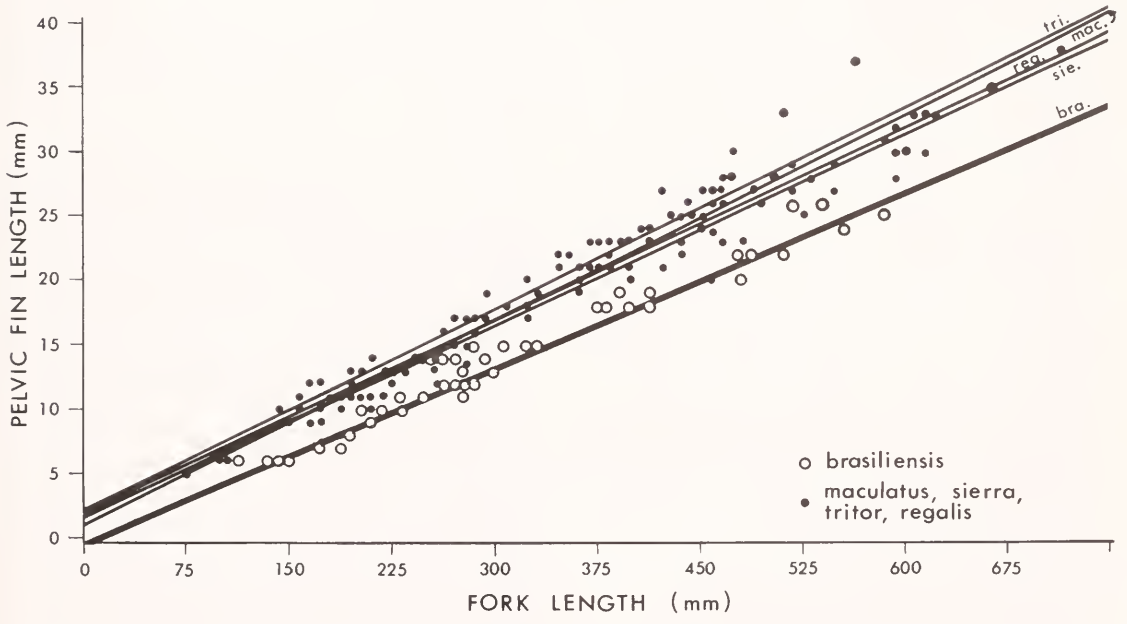


FIGURE 48.—Regression of pelvic fin length on fork length in five species of *Scomberomorus*. The regression line for *S. brasiliensis* is significantly different from those for *S. maculatus*, *S. sierra*, *S. tritor*, and *S. regalis*. The regression lines for the latter four species do not differ significantly from each other. Therefore, the same symbol is used for plotting specimens of these four species. (From Collette et al. 1978:fig. 1.)

dorsal fin 17 or 18, rarely 19 (Table 9); second dorsal fin rays 15-19, usually 17 or 18 (Table 10); finlets 8-10, usually 9 (Table 10); anal fin rays 16-20, usually 17-19 (Table 11); finlets 7-10, usually 9 (Table 11); pectoral fin rays 21-24, usually 22 or 23 (Table 12). For a sample of 90 Brazilian *S. brasiliensis*, Bastos (1966) found the following numbers of fin rays to be most common: dorsal spines 18 (86.6%), rays 18 (76.6%), finlets 9 (75.3%); anal rays 18 (100%), finlets 9 (79.8%), pectoral rays 22 (98.9%). Precaudal vertebrae 19-21, usually 20 (Table 6); caudal vertebrae 27-29, usually 28 (Table 7); total vertebrae 47-49, usually 48 (Table 8). The counts of 46 or 47 reported by Bastos (1966) presumably exclude the hypural plate which we include in our counts. Gill rakers on first arch (1-3)+(9-13)=11-16, usually 2+(11-12)=13-15 (Table 5). For a large sample from Brazil (225 males, 275 females), Menezes (1972) found a similar range, 11-17, and a "typical" count of 3+1+11=15. Morphometric characters are given in Table 13.

Size.—Maximum size 125 cm FL (Costa and Paiva 1969, Ceará, Brazil). Of 16,170 fish measured in Ceará from 1962 to 1966, 9 exceeded 95.0 cm FL, more than 60% each year from 1962 to 1968 were in the size range 40-65 cm (Brazilian records summarized by Collette et al. 1978). Sexual maturity is reached at age III or IV, 46 cm FL in Ceará (Gesteira 1972). The shortest mature male in Trinidad was 38 cm, the shortest ripe female 45 cm (Sturm 1978). The length-weight relationship for the Brazilian population was given by Nomura (1967). Males and females grew at roughly equal rates up to 4 yr of age but then females grew faster on to age XIV (Ximenes 1983).

TABLE 13.—Summary of morphometric data of *Scomberomorus brasiliensis*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			69	111	710	317	136
Snout-A	%	FL	68	508	692	538	24
Snout-2D	‰	FL	68	483	672	511	23
Snout-1D	%	FL	68	196	337	242	20
Snout-P_2	%	FL	69	217	359	253	22
Snout-P_1	%	FL	69	191	317	220	20
P_1-P_2	‰	FL	68	83	159	108	11
Head length	‰	FL	69	121	309	213	22
Max. body depth	%	FL	69	164	263	197	15
Max. body width	‰	FL	67	54	114	81	11
P_1 length	‰	FL	68	97	143	123	9
P_2 length	‰	FL	66	29	59	45	5
P_2 insertion-vent	%	FL	66	234	349	272	18
P_2 tip-vent	%	FL	62	193	298	226	17
Base 1D	‰	FL	68	232	360	263	18
Height 2D	‰	FL	62	92	139	118	11
Base 2D	‰	FL	69	93	153	118	10
Height anal	‰	FL	61	83	149	115	12
Base anal	‰	FL	68	97	142	113	10
Snout (fleshy)	%	FL	69	69	120	82	8
Snout (bony)	%	FL	65	59	102	73	7
Maxilla length	‰	FL	68	104	188	124	13
Postorbital	‰	FL	69	84	127	95	6
Orbital (fleshy)	‰	FL	69	27	57	37	6
Orbital (bony)	%	FL	69	33	77	53	8
Interorbital	‰	FL	69	48	107	57	7
2D-caudal	‰	FL	67	427	594	490	31
Head length			69	33	140	66	25
Snout (fleshy)	‰	HL	69	354	596	386	29
Snout (bony)	‰	HL	65	300	546	344	31
Maxilla length	‰	HL	68	541	937	581	47
Postorbital	‰	HL	69	387	758	446	43
Orbit (fleshy)	‰	HL	69	136	286	175	24
Orbit (bony)	‰	HL	69	172	408	249	31
Interorbital	‰	HL	69	240	564	269	44

Color pattern.—Sides with several rows of round yellowish-bronze (in life) spots (Fig. 47) similar to *S. maculatus* and *S. sierra* but without any lines or streaks such as are present in *S. regalis*. Number of yellowish-bronze spots on sides of body increases with size of fish; young specimens (200 mm) have about 30 spots; adults more, 45 spots (422 mm), 47(455), 46(470), 45(516), and 58(530) (Collette et al. 1978). Spots arranged in three or four rows (sometimes in two rows). The rows are not very well defined but it is possible to recognize them. First dorsal fin black in the anterior half (first seven membranes), posterior half white with upper edge black. Pectoral fin dusky; pelvic and anal fins white.

There is a black and white photograph of a specimen from Colombia in Dahl (1971:278) and a drawing of a Venezuelan specimen in Cervigón (1966:fig. 303).

Biology.—No extensive migrations are known for *S. brasiliensis*, and it is available to the fishery in northeastern Brazil all year round. There does appear to be some seasonal movement around Trinidad (Sturm 1978). There is a spawning peak in the Gulf of Paria, Venezuela, in October-April followed by a postspawning feeding migration away from Venezuela with a period of maximum abundance in Trinidad waters May-September. Some spawning takes place in the Gulf of Paria throughout the year with a peak in October-April (Sturm 1978). Ripe fish are taken on the Guyana continental shelf in September (Lowe 1962). Spawning takes place all year round off northeastern Brazil with a peak in the third trimester, July-September (Gesteira 1972). Spawning probably takes place mostly offshore beyond the main fishing areas. There appear to be no references to eggs or larvae of *S. brasiliensis*. As with other species in the genus,

food consists largely of fishes with smaller quantities of penaeoid shrimps and loliginid cephalopods. The most important component of the food of 1,020 individuals (17.5-87.5 cm FL) from northeastern Brazil was the thread herring, *Opisthonema oglinum*, (more than 25%) followed by Engraulidae, Carangidae, Hemiramphidae, and Pomadasyidae (Menezes 1970).

Interest to fisheries.—This is an important food fish throughout its range—Colombia (Dahl 1971), Venezuela (Cervigón 1966), Trinidad (Sturm 1978), the Guianas (Gines and Cervigón 1968), and especially in northeastern Brazil. The fishery is concentrated in June-August in Trinidad (Sturm 1978) but is conducted year round in northeastern Brazil (Alcantara Filho 1972a). The fishing grounds are 5-16 mi offshore in Brazil (Fonteles Filho 1968; Alcantara Filho 1972a). Most of the catch previously reported as *S. maculatus* from Fishing Area 31 (Western Central Atlantic) for Colombia, Trinidad and Tobago, and Venezuela is *S. brasiliensis* as is also a large proportion of the Brazilian catch of *Scomberomorus* spp. In Trinidad, it is taken by drift gill nets that are fished overnight and with beach seines (Sturm 1978). There are two major fisheries in Brazil. One employs gill nets (rede-de-pesca) from wooden boats not over 10 m long powered by gasoline engines (Fonteles Filho 1968; Alcantara Filho 1972a). The other method is trolling from rafts (Fonteles Filho 1968; Costa and Almeida 1974). Most of the catch is consumed fresh, but in Brazil some has been salted (Paiva and Costa 1966) and some has been canned (Bastos et al. 1973).

Distribution.—Caribbean and Atlantic coasts of Central and South America from Belize at least as far south as Lagoa Tramandai, Rio Grande do Sul, Brazil (Fig. 49). Previously confused with, but not known to overlap the range of, *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*.

FIGURE 49.—Ranges of the *regalis*-group of *Scomberomorus*: *S. tritor*, *S. maculatus*, *S. regalis*, *S. brasiliensis*, *S. sierra*, and *S. concolor*. (Range of *S. regalis* more extensive, see text.)

Geographic variation.—Morphometric data from two populations of *S. brasiliensis* were compared by ANCOVA: Central America (n = 9-11) and Brazil (n = 39-44). Null hypotheses that the 2 sets of regressions are coincident were accepted for 24 of 26 regressions. The two populations were different in Sn-P_2 and 2D-C. Comparison of meristic characters for central and northern South America versus Brazil did not reveal any differences (Collette et al. 1978:tables 1-3).

Material examined.—Total 146 (89-710 mm FL).

meas.: 69 (111-710): Belize (2); Honduras (1); Costa Rica (3); Panama (5); Colombia (1); Venezuela (3); Trinidad (2); Guyana (2); Surinam (4); French Guiana (2); Brazil (44, **S. brasiliensis*).
counts: 146.
diss.: 6 (363-639): French Guiana (2); Belem, Brazil (4).

Scomberomorus cavalla (Cuvier)
King Mackerel

Figure 50

Guarapucu. Marcgrave 1648:178 (Brazil).

Cybium cavalla Cuvier 1829:200 (original description after Marcgrave's Guarapucu; Brazil).

Cybium caballa. Cuvier *in* Cuvier and Valenciennes 1831:187-190 (description; Brazil, West Indies). Günther 1860:373 (synonymy, description; West Indies). Poey 1865:322 (Brazil, Puerto Rico; *C. caballa* is the juvenile of *C. acervum*). Poey 1875:147 (description; Cuba). Poey 1878:3-4 (synonymy, characters).

Cybium immaculatum Cuvier *in* Cuvier and Valenciennes 1831:191 (original description, no locality). Günther 1860:370. Poey 1878:5 (after Cuvier).

Cybium acervum Cuvier *in* Cuvier and Valenciennes 1831:186 (original description, Martinique, Santo Domingo, Cuba). Poey 1865: 322 (Cuba; color pattern of juveniles). Poey 1868:362 (description; Cuba). Poey 1875:147 (after Cuvier *in* Cuvier and Valenciennes 1831). Poey 1878:4 (unable to find this species in Cuba).

?*Cybium clupeoidum* Cuvier *in* Cuvier and Valenciennes 1831:178 (original description, "Île de Norfolk, Nouvelle Hollande").

Scomberomorus caballa. Jordan and Gilbert 1882:427 (synonymy, range). Goode 1884:316 (range, size), pl. 94.

Scomberomorus cavalla. Meek and Newland 1884:233, 235 (description, synonymy, range). Dresslar and Fesler 1889:442 (in key), 444-445 (synonymy, range), pl. 11 (specimen from Woods Hole). Jordan and Evermann 1896b: 875-876 (description, synonymy). Evermann and Marsh 1902:124 (description, synonymy; Puerto Rico). Jordan and Evermann 1902: 287-288 (description, range), photograph. Bean 1903:400-401 (synonymy, description, range). Fowler 1905:766-767 (placed in new subgenus *Sierra*; description, Santo Domingo and St. Martins). Smith 1907:193-194 (diagnosis, range; few or no records from North Carolina). Sumner et al. 1913:750 (references, occurrence; Menemsha Bight and Quisset Harbor, Mass.). Ribeiro 1915:135-136 (description; range S to Angra dos Reis, Brazil). Meek and Hildebrand 1923:322-323 (description, synonymy). Schroeder 1924:7 (maximum weight 75 lb; Fla. Keys), fig. 5. Nichols and Breder 1927: 124 (description, range), fig. 172. Nichols 1929:230-231 (range, description), fig. 84. Beebe and Hollister 1935:213 (Union I., Grenadines). Baughman 1941:16-17 (Texas records). Munro 1943:69, 71-72 (placed in subgenus *Sierra*). La Monte 1945:26 (description, range),

FIGURE 50.—*Scomberomorus cavalla.* Woods Hole, Mass., 1,000 mm FL, USNM 19418. (From Goode 1884:pl. 94.)

color pl. 11. Breder 1948:127 (range), fig. Erdman 1949:301 (West Indies). Fraser-Brunner 1950:160-161 (range), fig. 33. Baughman 1950: 243-244 (previous Texas records). Knapp 1950:141-142 (food in Texas, shrimps, squids, fishes). Rivas 1951:224-225 (synonymy, diagnosis, range). Taylor 1951:270 (popular anglers' fish taken by trolling; North Carolina). La Monte 1952:50 (description, range). Bigelow and Schroeder 1953:349 (description, range; Gulf of Maine record, N Truro, Cape Cod), fig. 184. Pew 1954:26 (description, range, habits), fig. 22. Mather 1954:292 (13 specimens, about 70 cm FL, in trap; Quisset, Mass.). Mather and Gibbs 1957:243 (9 specimens, 600-700 mm FL; Buzzards Bay, Mass.). Briggs 1958:287 (range). *Mago Leccia 1958 (osteology, comparisons with *S. maculatus* and *S. regalis*), figs. Butz and Mansueti 1962:130-135 (description; N Chesapeake Bay; comparison with specimens from Mass. and Fla.), fig. 2 (head). Moe 1963:108-109 (most sought fish in Fla. charter boat fishery). Collette 1966:365-367 (types of *C. acervum* and *C. immaculatum*; both names synonyms of *S. cavalla*). Nomura and Costa 1966:11-13 (length-weight of 666 specimens; Ceará, Brazil). Cervigón 1966:718-719 (description; Venezuela). Randall 1967:753-754 (food of 22 West Indian specimens, 92.3% fishes). Nomura and Rodriguez 1967:79-85 (age and growth, condition factor, 1,504 specimens, 30-120 cm FL; Ceará, Brazil), fig. 1 (sagitta). Mota Alves and Tomé 1967a:103-108 (anatomy and histology of the digestive tract), figs. 1, 2 (arrangement of viscera), figs. 3-7 (histology of gut). Mota Alves and Tomé 1967b:1-9 (histology of gonads), figs. 1-11 (photomicrographs). Mota Alves and Tomé 1967c: 173-175 (anatomy and histology of the liver and gall bladder). Mota Alves and Tomé 1968c: 31-32 (sperm). Fonteles Filho 1968 (fishery; NE Brazil). Nomura and Costa 1968:95-99 (length-weight relationship, 104 males and 90 females; Ceará, Brazil). Randall 1968:119 (description, range, habits), fig. 136. Lyles 1969: 16-21 (summary of U.S. landings, 1880-1967). Menezes 1969a:15-20 (food of 798 specimens; Ceará, Brazil; fishes compose main diet). Menezes 1969b:175-178 (meristic characters, osteology; NE Brazil). Mota Alves and Tomé 1970:181-184 (histology and enzymes of pyloric caeca). Beardsley and Richards 1970:5 (length-weight of 197 specimens, 585-1,500 mm FL, 1.47-32.09 kg; Florida). Wollam 1970 (development, pigmentation, counts, and measurements; 49 larvae and juveniles (3.3-31.0 mm SL), figs. 4, 5, 6B (larvae and juveniles, 3.3-23 mm SL)). Dahl 1971:277 (uncommon in Colombia), fig. Ivo 1972:27-29 (gonadal stages of 4,346 females; Ceará, Brazil). Moe 1972:16-17 (migrations; Florida). Alcantara Filho 1972b (gill net and trolling fisheries; NE Brazil). Richards and Klawe 1972:13 (range), 89 (reference to Wollam 1970). Miyake and Hayasi 1972:III:3 (in key), IV:11 (common names). Dwinell and Futch 1973 (139 larvae and juveniles, 2.8-13.5 mm SL, all months; NE Gulf of Mexico). Bastos et al. 1973 (canning; NE Brazil). *Beaumariage 1973 (age, growth, food, reproduction; Florida). Ivo 1974 (fecundity; Ceará, Brazil). Berrien and Finan 1977a (species synopsis). Erdmann 1977:150 (in spawning condition mainly in July and Aug.; NE Caribbean). Klawe 1977:2 (common name, range). DeVane 1978 (stomach contents; North Carolina). Fritzsche 1978:121-125 (description, larval development), figs. 66-69 (larvae). Collette 1978: Scombm 4 (description, range), figs. Manooch et al. 1978 (annotated bibliography). Lima and Oliveira 1978:6, 23 (common name "cavalla" in Brazil). Collette 1979:29 (characters, range). Collette and Russo 1979:9 (diagnostic characters, range). Manooch 1979 (commercial U.S. catches averaged 2,541 t/yr over last 17 yr, recreational catch statistics are inadequate). Meaburn 1979 (heavy metal contamination). McEachran et al. 1980 (larvae off Texas coast). Fischer 1980:1-21 (size, length-weight, sex ratio; Louisiana). Sutherland and Fable 1980 (annual migration from S Florida N to NE Gulf of Mexico and W to S Texas in the spring). MacGregor et al. 1981 (significant correlation found between gonadosomatic indices and serum estrogens in females and with serum androgens in males). Fable et al. 1981 (temperature effects on catches; NW Florida). Lubbock and Edwards 1981:150 (Saint Paul's Rocks). Richardson and McEachran 1981 (larvae 2.0-2.9 mm SL, pigment characters, measurements; Gulf of Mexico), fig. 2A (2.3 mm larva). Naughton and Saloman 1981 (stomach contents of 139 juveniles, 103-309 mm FL; Cape Canaveral, Fla.; diet mainly clupeoids). Sacchi et al. 1981:3 (French Antilles). Trent et al. 1981 (size composition and sex ratio; SE U.S.). Ximenes et al. 1981 (age and growth; NE Brazil). Morgan and King 1983 (tooth replace-

ment). Johnson et al. 1983 (age, growth, and mortality; SE U.S.). Cressey et al. 1983:264 (host-parasite list, 4 copepod species). Collette and Nauen 1983:61-62 (description, range), fig. Saloman and Naughton 1983a (food in SE U.S.).

Types of nominal species.—*Cybium cavalla* Cuvier, 1829 is based on Marcgrave's description and figure (1648:179) of the "Guarapucu"; there are no extant types for this name.

Cybium acervum Cuvier *in* Cuvier and Valenciennes, 1831. Lectotype: MNHN A.5781; Santo Domingo; Ricord; 130 mm FL; selected by Collette (1966:365); D XV+17+VIII; A 18+VIII; RGR_1 1+1+7=9; vertebrae 17+25=42; upper jaw teeth 8-11; lower jaw teeth 7-8. Paralectotypes: MNHN B.2508, out of A.5781; Santo Domingo; Ricord; 2(133-138 mm FL). A photograph of one of the syntypes was published by Blanc and Bauchot (1964: pl. 1, fig. 1, upper fig.).

Cybium immaculatum Cuvier *in* Cuvier and Valenciennes, 1831. Lectotype: MNHN A.5720; Martinique; Plée; 157 mm FL; selected by Collette (1966:366); D XV+17+IX; A 17+IX; P_1 23; RGR_1 1+1+7=9; vertebrae 17+25=42; upper jaw teeth 9-11; lower jaw teeth 9-12. Paralectotypes: MNHN B.2509; out of A.5720; Martinique; Plée; 147 mm FL; and MNHN A.5780; Martinique; Plée; 164 mm FL. Photographs of two of the syntypes were published by Blanc and Bauchot (1964:pl. 2, fig. 12).

Cybium clupeoidum Cuvier *in* Cuvier and Valenciennes, 1831. Holotype: MNHN A.5784; "Île de Norfolk, à l'oeust de la Nouvelle-Hollande"; Broussonet collection; 302 mm FL; D XV+17+IX; A 18+VIII; RGR_1 1+1+7=9; vertebrae 17+25=42; upper jaw teeth 13-13; lower jaw teeth 11-12. A photograph of the type was published by Blanc and Bauchot (1964:pl. 1, fig. 3). The high gill raker count and low vertebral number show the type to be a specimen of the western Atlantic *S. cavalla* as supposed by Bauchot and Blanc (1961) and Blanc and Bauchot (1964) rather than *S. commerson* as presumed by Collette (1966) based on geography. The locality has been supported by Bauchot (1969), but the data or the specimen must have been mixed with the western Atlantic species sometime in the past.

Diagnosis.—This species shares with *S. commerson* an abrupt downward curve in the lateral line under the second dorsal fin (Fig. 50). *Scomberomorus sinensis* also has an abrupt downward curve in the lateral line under the first dorsal fin but the lateral line gradually descends in the other 15 species. *Scomberomorus cavalla* differs from *S. commerson* in having fewer vertebrae (41-43, usually 42 or fewer compared with 42-46, usually 43 or more) and more gill rakers (7-13, usually 8 or more compared with 1-8, usually 7 or fewer). Ventral process of angular moderate, 87-93% of dorsal process as in *S. sinensis*. Ascending process of premaxilla short as in *S. guttatus*. Anterior ends of pterosphenoid close together as in *S. commerson*. Intercalar spine well developed as in *S. commerson* and *S. queenslandicus*.

Description.—Intestine with two folds and three limbs (Fig. 3b). Spines in first dorsal fin 12-18, usually 15 (Table 9); second dorsal fin rays 15-18, usually 17 or 18 (Table 10); dorsal finlets 7-10, usually 9 (Table 10); anal fin rays 16-20, usually 18 or 19 (Table 11); anal finlets 7-10, usually 8 (Table 11); pectoral fin rays 21-23, usually 22 or 23 (Table 12). Precaudal vertebrae 16 or 17, usually 17 (Table 6); caudal vertebrae 24-26, usually 25 (Table 7); total vertebrae 41-43, usually 42 (Table 8). Gill rakers on first arch (1-2)+(6-11)=7-13, usually 1+(8-9)=9-10 (Table 5). Counts for a large Brazilian sample (353 individuals, Menezes 1969b), were (0-2)+1+(5-9)=6-11, usually 1+1+7=9. Morphometric characters are given in Table 14.

Size.—Maximum size 172.5 cm FL (female, 37.2 kg; Beaumariage 1973); common to 70 cm. The all-tackle angling record is a 40.8 kg fish taken off Key West, Fla., in 1976. In Florida, females usually mature in their fourth summer at a mean length of 83.7 cm, males in the third summer at 73 cm (Beaumariage 1973). In Brazil, females mature at age V-VI, about 77 cm according to Ivo (1972), at age IV and 63 cm according to Gesteira and Mesquita (1976). Males and females grow at roughly equal rates up to age V but then females grow faster (Ximenes et al. 1981). They reach an age of at least XIV (Ximenes et al. 1981; Johnson et al. 1983). Length-weight relationships have been published for Brazil (Nomura and Costa 1968; Ximenes et al. 1981), Florida (Beaumariage 1973), and Louisiana (Fischer 1980).

Color pattern.—Adults have plain silvery sides without bars or spots, juveniles have bronze spots smaller than the pupil of the eye in five or six irregular rows (Randall 1968:119). Adults have no

TABLE 14.—Summary of morphometric data of *Scomberomorus cavalla*. FL = fork length, HL = head length.

Character			United States					West Indies					South America					Total				
			N	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD
Fork length			10	560	1,160	769	179	20	126	710	323	209	23	147	860	326	183	54	126	1,160	405	257
Snout-A	‰	FL	10	510	562	535	15	20	519	582	547	23	23	463	568	533	21	54	463	582	539	21
Snout-2D	‰	FL	10	474	521	499	14	20	486	534	512	12	23	430	524	504	18	54	430	534	505	16
Snout-1D	‰	FL	10	225	266	241	11	20	247	297	268	13	23	210	273	256	15	54	210	297	258	16
Snout-P_2	‰	FL	8	223	260	236	11	20	239	290	266	14	23	205	293	256	21	52	205	293	257	20
Snout-P_1	‰	FL	10	199	241	212	12	20	212	260	243	14	23	194	252	231	14	54	194	260	232	17
P_1-P_2	‰	FL	5	86	103	93	7	13	91	136	107	15	22	73	135	107	15	41	73	136	105	15
Head length	‰	FL	10	192	229	203	10	20	206	250	231	13	23	177	246	224	17	54	177	250	223	17
Max. body depth	‰	FL	7	149	173	159	10	10	153	258	198	37	22	147	237	197	25	40	147	258	190	30
Max. body width	‰	FL	8	95	109	102	5	11	78	101	89	9	21	70	126	85	13	41	70	126	89	12
P_1 length	‰	FL	10	114	138	124	7	15	108	143	129	12	23	111	142	130	7	49	108	143	129	9
P_2 length	‰	FL	10	53	62	58	3	12	54	95	68	10	21	36	85	66	12	44	36	95	64	11
P_2 insertion-vent	‰	FL	8	264	294	281	9	15	245	309	277	17	22	211	298	266	18	46	211	309	272	18
P_2 tip-vent	‰	FL	8	205	237	222	11	12	187	236	214	14	21	162	289	208	26	42	162	289	212	21
Base 1D	‰	FL	9	221	255	242	11	19	224	267	246	11	23	207	269	247	14	52	207	269	245	13
Height 2D	‰	FL	9	85	108	95	7	14	76	127	108	13	20	79	128	114	12	44	76	128	108	13
Base 2D	‰	FL	10	78	103	93	7	14	82	124	105	12	23	81	135	112	15	48	78	135	106	14
Height anal	‰	FL	8	89	102	95	5	11	81	122	107	12	17	89	127	110	9	37	81	127	105	11
Base anal	‰	FL	10	87	111	98	9	17	92	123	107	10	23	83	129	112	12	51	83	129	108	12
Snout (fleshy)	‰	FL	10	74	103	84	8	17	83	98	89	4	23	72	92	86	5	51	72	103	87	6
Snout (bony)	‰	FL	10	68	96	78	8	17	73	86	81	4	22	68	85	78	4	50	68	96	79	5
Maxilla length	‰	FL	10	108	137	117	8	20	120	152	138	9	23	103	147	132	11	54	103	152	132	12
Postorbital	‰	FL	7	86	99	92	4	17	89	112	99	6	23	81	104	98	6	48	81	112	98	6
Orbital (fleshy)	‰	FL	10	24	43	30	5	17	33	58	41	8	23	27	54	39	6	51	24	58	38	7
Orbital (bony)	‰	FL	10	28	48	41	6	17	42	73	55	10	23	38	65	52	6	51	28	73	51	9
Interorbital	‰	FL	10	52	68	55	4	20	56	66	62	3	23	48	66	60	5	54	48	68	60	4
2D-caudal	‰	FL	7	485	527	506	13	13	452	500	473	14	23	445	516	472	18	44	445	527	477	20
Head length			10	112	266	158	45	20	32	151	72	44	24	36	152	73	35	55	32	266	88	51
Snout (fleshy)	%	HL	10	362	451	415	25	17	350	424	391	25	24	354	422	384	17	52	350	451	392	24
Snout (bony)	%	HL	10	355	417	384	20	17	305	388	353	27	23	318	388	351	19	51	305	417	358	26
Maxilla length	%	HL	10	546	604	576	18	20	577	613	598	10	24	570	609	590	10	55	546	613	591	14
Postorbital	%	HL	7	428	485	453	22	17	408	463	434	16	24	395	463	437	16	49	395	485	439	18
Orbit (fleshy)	%	HL	10	123	210	147	24	17	152	233	176	24	24	147	220	171	18	52	123	233	168	24
Orbit (bony)	%	HL	10	138	238	204	28	17	191	305	237	31	24	201	265	231	15	52	138	305	229	27
Interorbital	%	HL	10	256	295	272	11	20	248	284	267	10	24	254	281	269	7	55	248	295	269	9

black area in the anterior part of the first dorsal fin as do many species of *Scomberomorus*.

Black and white photographs are given by Jordan and Evermann (1902) and Randall (1968: fig. 136). The drawing published by Goode (1884: pl. 94) is included here as Figure 50.

Biology.—A summary of biological information has been presented by Berrien and Finan (1977a) and there is also a useful annotated bibliography by Manooch et al. (1978). King mackerel appear to be present all year in Louisiana (Fischer 1980) and in the state of Ceará in northeastern Brazil. Some populations appear to be resident in south Florida waters as they are available to the recreational fishery throughout the year. However, the large schools that are found in south Florida waters during January and February move north along both coasts in the spring (Moe 1972). Schools that occur offshore of Palm Beach and Martin Counties on the east coast of Florida in winter and early spring move north. They appear off North Carolina in April and remain until fall (DeVane 1978). On the west coast of Florida, king mackerel move north to the Naples-Ft. Myers or St. Petersburg-Tampa areas by April and Cape San Blas in May (Sutherland and Fable 1980). The main run usually arrives in Panama City, Fla., in late May or early June. The westward migration along the northern Gulf of Mexico ends off west Texas in June-July (Sutherland and Fable 1980). Return migration in the fall from summer feeding grounds in the northwest Gulf to winter feeding grounds off southern Florida has been confirmed by recaptured tagged fish (Sutherland and Fable 1980). Based on gonad development and larval distribution, spawning takes place in the northeastern Gulf of Mexico and in the Atlantic offshore of Cape Kennedy, Fla., and northward in late summer (Moe 1972). According to Beaumariage (1973), spawning in Florida may be protracted as indicated by successive increase in vitellogenic oocyte size during the summer. Spawning takes place in May-September in the western Gulf of Mexico, especially in September in waters 35-183 m deep over the middle and outer continental shelf (McEachran et al. 1980). In the northeastern Caribbean, spawning peaked in July and August (Erdman 1977). Spawning is year round offshore of Ceará, northeastern Brazil (Ivo 1972). Larvae and juveniles (139 specimens, 2.8-28.8 mm SL) were taken off the northwest

coast of Florida from June to October with larvae <3.1 mm taken in June, August, and September (Dwinell and Futch 1973). Most of these larvae and juveniles were taken in surface plankton tows at surface temperatures of 26.3°-31.0°C and salinities of 26.92-35.0‰. Larvae were taken in increasing numbers from May to September (35% or more of larvae in September of each year) in the western Gulf of Mexico, particularly over the middle and outer continental shelf (McEachran et al. 1980). Larvae and juveniles have been described and illustrated by Wollam (1970; 3 figures, 3.3-23 mm SL), Fritzsche (1978; 12 figures, 2.98-17 mm), and Richardson and McEachran (1981, 2.3 mm SL). As with other members of the genus, food consists primarily of fishes with smaller quantities of penaeoid shrimps and squids (Knapp 1950, Texas; Randall 1967, Caribbean; Menezes 1969a, northeastern Brazil; Beaumariage 1973, Florida; DeVane 1978, North Carolina; Saloman and Naughton 1983a, United States). Clupeids such as *Opisthonema*, *Harengula*, *Sardinella*, and *Brevoortia* are particularly important (Randall 1967; Menezes 1969a; Beaumariage 1973; DeVane 1978; Saloman and Naughton 1983a), even in juveniles 103-309 mm FL (Naughton and Saloman 1981). Other fishes commonly consumed include Carangidae (particularly *Decapterus*), Lutjanidae, Pomadasyidae, and Hemiramphidae (Randall 1967; Menezes 1969a; Beaumariage 1973; Saloman and Naughton 1983a).

Interest to fisheries.—The king mackerel is an important species for recreational, commercial, or artisanal fisheries throughout its range from southeastern United States to northeastern Brazil. North of southern Florida, the fishery is concentrated in the summer months. In North Carolina, sport fishing is carried out from April to December (DeVane 1978) but is concentrated in spring and fall (Taylor 1951). In the Panama City area of the Florida panhandle, fish are taken from April to November and are most often caught in August and September (Fable et al. 1981). From December to March the fishery along the east coast of Florida is concentrated from Jupiter Inlet to Palm Beach Inlet, the rest of the year the fishery is further north from Ft. Pierce to Sebastian Inlet (Beaumariage 1973). There is a winter commercial fishery in the Florida Keys (Beaumariage 1973). King mackerel are taken all year in Louisiana with a maximum in November-January (Fischer 1980). King mackerel is the main species of commercial interest along the coast of northeastern Brazil where they are taken all year (Nomura and Rodrigues 1967). The main fishing grounds in northeastern Brazil are 6-16 nmi from the coastline (Fonteles Filho 1968). An historical summary of the fishery in the United States has been presented by Lyles (1969). Commercial catches in the United States have averaged 2,541 t a year with a value of $1.3 million over 17 yr with a peak in 1974 of 4,764 t (Manooch 1979). The bulk of these landings were made in Florida by hook and line and gill net fisheries (Manooch 1979). Data on the large recreational catch are inadequate. The catch reported from Fishing Area 31 (Western Central Atlantic) totalled 7,122 t in 1982 (FAO 1984) but is higher than this because much of the catch of 1,105 tons of unclassified *Scomberomorus* species is *S. cavalla* (or *S. regalis*). It is fished for with hook and line in all the southeastern United States (Trent et al. 1981). In addition, there is a commercial fishery using snapper hooks and line in Mississippi, a commercial gill net fishery in southern Florida, and commercial hook and line fisheries in North Carolina and southern Florida (Trent et al. 1981). The gill net fishery has employed power block retrieval since 1963 and aerial spotting is sometimes used (Beaumariage 1973). The king mackerel is the staple of the charter boat industry in Florida and is the most sought fish by private boats (Moe 1963). In Florida it is most often fished at the surface with trolled lure or small bait fish (Moe 1963). It is less commonly caught than is *S. brasiliensis* across the northern coast of South America (Dahl 1971; Cervigón 1966; Gines and Cervigón 1968). Both gill nets and trolling are used in northeastern Brazil, the former catching 87.6% II-IV yr fish and the latter 78.2% IV-VI yr fishes (Alcantara Filho 1972b). The Brazilian fishery is also carried out from rafts with hooks baited with thread herring (Fonteles Filho 1968). Most of the catch is processed into steaks or sold fresh (Lyles 1969), but it has been canned (Bastos et al. 1973) and salted (Paiva and Costa 1966) in northeastern Brazil.

Distribution.—Western Atlantic Ocean from Massachusetts to Rio de Janeiro, Brazil (Fig. 51). There are several summer records from the southern side of Cape Cod (Dresslar and Fesler 1889; Sumner et al. 1913; Mather 1954; Mather and Gibbs 1957) but only one stray is known to have moved around to the north side of Cape Cod, to North Truro in the Gulf of Maine (Bigelow and

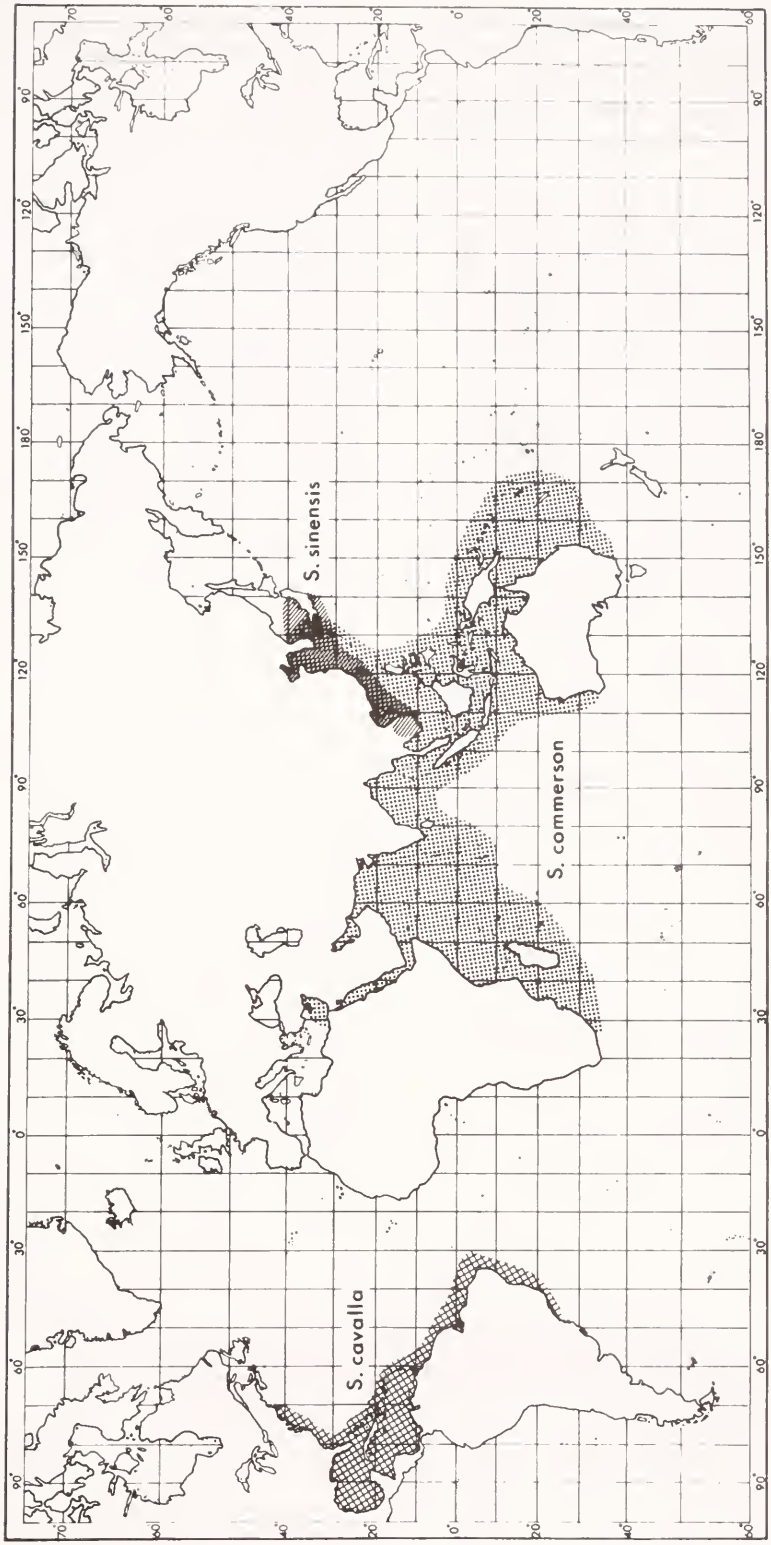


FIGURE 51.—Ranges of *Scomberomorus cavalla*, *S. commerson*, and *S. sinensis*.

Schroeder 1953:349; MCZ 37041, 560 mm FL). Abundant in the West Indies. The range extends south to at least Rio de Janeiro (Angra dos Reis, Ribeiro 1915; Rio de Janeiro, MCZ 17269, BMNH 1903.6.9.79).

Geographic variation.—Samples were adequate to compare the morphometric data of three populations of *S. cavalla* by ANCOVA (Table 14): United States (n = 7-10), West Indies (n = 11-20), and South America (n = 17-23). Null hypotheses that the 3 sets of regressions are coincident were accepted for only 10 of 26 regressions, rejected for the other 16. For 12 regressions (Sn-A, Sn-2D, Sn-1D, Sn-P_2, Sn-P_1, P_1-P_2, Hd L, Sn (fleshy and bony), maxilla L, postorbital, and interorbital), all three populations were significantly different from each other by the Newman-Keuls Multiple Range Test. For these 12 regressions, there is a cline from the United States to the West Indies to South America, a decreasing cline in slopes. The United States and West Indies populations differed in one additional regression (2D-C) and the South America and the West Indies populations differed in two additional regressions (maximum depth and Ht 2D). No meristic differences were found between the three populations, all usually had 15 spines in the first dorsal fin, 9 or 10 gill rakers on the first arch, and 42 vertebrae.

Material examined.—Total 76 (126-1,160 mm FL).

meas.: 54 (126-1,160): E United States (3); Fla. (7); Veracruz (1); West Indies (20) (**C. acervum* Cuvier, **C. immaculatum* Cuvier), Trinidad (3); Guyana (10); Suriname (3); Brazil (7).
counts: 76.
diss.: 7 (557-909): Chesapeake Bay (1); Miami (4); Panama City, Fla. (2).

Scomberomorus commerson (Lacepède) Narrow-Barred King Mackerel

Figure 52

Scomber commerson Lacepède 1800:598, 600-603 (original description after a figure from Commerson's manuscripts), pl. 20, fig. 1.

Scomber Konam Russell 1803:27-28 (description; Vizigapatam, Coromandel coast of India), pl. 135.

Scomber Commersonii. Shaw 1803:589 (description after Lacepède), pl. 85 (bottom fig.).

Scomber Maculosus Shaw 1803:592 (original description based on the Konam of Russell 1803, pl. 135).

Cybium Commerson(*i*)(*ii*). Cuvier 1829:200 (listed in footnote after *Sc. Commersonii* Lacepède). Cuvier *in* Cuvier and Valenciennes 1831:165-170 (description, earlier references; Pondichery and Malabar, India; Mauritius). Richardson 1846:268 (range, references). Bleeker 1853:42 (Malabar and Pondichery, India; Mauritius, Red Sea, China). Günther 1860:370 (synonymy, description; Malayan Peninsula and Cape Seas). Playfair and Günther 1866:67 (Zanzibar and E coast of Africa). Klunzinger 1871:494-495 (description, range). Bleeker 1873:131 (China, listed). Bleeker 1874:100 (Mauritius, listed). Day 1878:255-256 (synonymy, description, range), pl. 56, fig. 5. Bleeker 1879:18 (Mauritius, listed). Castelnau 1879:352 (Port Jackson, Australia; listed). Kent 1893:229 (Great Barrier Reef, Australia), pl. 46, fig. 1. Kishinouye 1923:416-418 (synonymy, *C. multifasciatum* Kishinouye a synonym of *C. commerson*; description, anatomy; Japan, Taiwan, and S China), pl. 22, fig. 36 (adult). Reeves 1927:8 (NE China and Korea; listed). Umali 1936:98-99 (food fish; Philippine Is.), fig. 59. Umali 1938:182 (fishery;

FIGURE 52.—*Scomberomorus commerson.* Queensland, 968 mm FL. (From Munro 1943:pl. 6B.)

Ragay Gulf, Luzon, Philippine Is.). Domantay 1940:379 (important species; Margosatubig, Zamboanga, Philippine Is.). Chevey and Durand 1945:27 (description, food fish; Indochina), fig. Chacko 1949:89 (stomach contents of 12 specimens, 21-43 cm FL; Gulf of Mannar, India; mostly clupeoids such as *Stolephorus* and *Dussumiera*). Chacko 1950:171 (characters of eggs and larvae; Krusadai I., Gulf of Mannar, India). Mori 1952:136 (Fusan, Korea; listed). La Monte 1952:51 (description, range), color pl. 19. Gopalan Nayar 1958:49-51 (fishery; Vizhingam, S India). Munro 1958b:262-263 (many records; New Guinea region). Fourmanoir and Crosnier 1964:386-387 (found along the entire coast of Madagascar; one of most important food fishes; occasional in lagoon at Mayotte, Comores Is.). Chacko et al. 1967:1007-1008 (drift net fishery; Madras State).

Cybium Konam Bleeker 1851a:357 (original description, Batavia). Bleeker 1852:39-40 (description; Batavia). Bleeker 1853:42 (Coromandel, India; East Indies). Kner 1865:144 (description; Manila).

Scomberomorus commerson(*i*)(*ii*). Jordan and Seale 1906:228 (New Guinea, East Indies; listed). Jordan and Seale 1907:13 (description; Cavite, Luzon, Philippine Is.). Jordan and Dickerson 1908:610 (Suva market; Fiji). Fowler 1918:63 (Philippine Is.; listed). Whitley 1927:5 (Fiji; listed). Herre 1931:33 (Philippine localities). Whitley 1932:289 (Snapper I., Great Barrier Reef). Herre 1933:7 (Dumaguete, Philippine Is.; listed). Hardenberg 1936: 252 (mouth of Kapuas R., W Borneo). *Munro 1942:33-48 (spawning, eggs, early larvae; N Queensland), pls. 2-4, figs. 1-17 (eggs and early larvae). *Munro 1943:67, 71-72 (placed in subgenus *Cybium*), 74-82 (description, anatomy, synonymy, occurrence in Australia); pl. 6, fig. B (968 mm Fl specimen; Queensland); fig. 2.4 (viscera); pl. 8, fig. 3 (368 mm FL immature specimen; N Queensland). Chapman 1946:169 (off New Caledonia). Herre and Umali 1948 (common names in several languages and dialects; Philippine Is.). Barnard 1948:380 (49-in, 24-lb specimen; False Bay, South Africa). Norman and Fraser 1949:153-154 (range). Fraser-Brunner 1950:161 (synonymy, range), fig. 34. Umali 1950:9 (found throughout the Philippines in open sea, bays, and gulfs). Warfel and Manacop 1950:42 (in otter-trawl catches; Philippine Is.). Warfel 1950:2 (regularly found in fresh fish market, Philippine Is.). Herre 1953:245-246 (synonymy; Philippine records). Ommanney 1953:66 (off Marie Louise I., S Amirante Is.). Devanesen and Chidambaram 1953:32-36 (names, description, fishery, economic importance), fig. 34. Tham 1953:49 (Singapore Straits). Fowler 1959:167 (description, synonymy, locality records; Suva, Fiji), 583 (additional references). Jones et al. 1960: 136 (Andaman-Nicobar Is. waters). Jones 1962:113-117 (larvae and juveniles; S Kerala, India), figs. 9-14 (postlarvae and juveniles 14.4-278 mm). Bauchot and Blanc 1961:370 (description of "neosyntypes"). Kaikini 1961:357 (largest species in the seerfish fishery at Malwan, India, reaching 17.24 kg). Venkataraman 1961:292 (teleosts in stomachs of 2 specimens; Calicut, India). Kumaran 1964:586-587 (stomach contents 283 specimens, 17-225 mm FL; Vizhingam, W coast of India; 79% small fishes, 43% *Anchoviella*). Baissac 1964:186 (now scarce in Mascarene waters). Boeseman 1964:467 (types of *C. konam* = *S. commersonii*), pl. 4, fig. 16 (lectotype of *S. konam*). Blanc and Bauchot 1964:444-445 ("neosyntypes" of *C. commersonii*), pl. 1-2, figs. 4-7. Gorbunova 1965a:53 (spawning season). George and Athanassiou 1965:1-4 (St. George Bay, Lebanon; first Mediterranean records; description), fig. 1 (49.0 and 60.3 cm TL specimens). Collette 1966:369 (Bauchot and Blanc's "neosyntypes" invalid). Kamohara 1967:44 (description; Japan), color pl. 22, fig. 4. George and Athanassiou 1967:238 (listed among species entering the Mediterranean through the Suez Canal). Anonymous 1967:46 (off NW coast of Borneo). Maugé 1967:120 (listed from Smith's Fishes of South Africa). Arnoult and Fourmanoir 1967:134, 139 (juveniles in mangrove swamp; Nossi-Bé, Madagascar). Ben-Tuvia 1968:35 (commercially important fish; several caught trolling in Dahlak Archipelago; many from coast of Ethiopia, common in Eilat). Ben-Yami 1968:37 (caught by trolling and purse seine; Ethiopia). Wongratana 1968 (trawl survey; Thailand). Silas 1967:1096 (leaping out of the water; Gulf of Mannar), 1,113-1,115 (length-weight). Merçeron 1970:72-81 (length-weight, maturity, food mostly anchovies, movements; Cambodia). *Tongyai 1970 (distribution, peak fishing months, migrations, food, fishery; Thailand). Collette 1970:3, 5 (Mediterranean coast of Israel). *Prado 1970:91-116 (synonymy; description; biology, length-frequency, food, sex ratio,

reproduction; Madagascar). Ben-Tuvia 1971: 20-21 (3 specimens from Mediterranean coast of Israel). Tongyai 1971a:9-13 (description), pl. II (photograph), pl. III (viscera). Tongyai 1971b:3 (economically important; Thailand), pl. 7, 8, 10, 13 (photographs). Dhawan et al. 1972: 183 (trolling line operations; Goa; feed on sardines). Nagabhushanam and Chandrasekhara Rao 1972:303 (Minimoy Atoll, Laccadive Archipelago). Shiino 1972:71 (common name). Richards and Klawe 1972:13 (range), 90-91 (references to eggs, larvae, and juveniles). Magnuson 1973:350 (short pectoral fin). Orsi 1974: 175 (Vietnam; listed). Ronquillo 1974 (caught by light fishing; Philippine Is.). Lewis et al. 1974:82-85 (93 specimens, 53.7-144.5 cm FL; ova diameters, maturity of ovaries; Bismark Archipelago, Papua New Guinea). Van der Elst 1976:25 (important predator on *Pomatomus saltatrix*; Natal, South Africa). Baissac 1976:216 (Mauritius). *Devaraj 1977 (osteology). Klawe 1977:2 (common names, range). Randall et al. 1978:166 (Persian Gulf: photograph), 212 (color photograph 56). Uchida 1978:13, 17, 20 (fishery resource; Cook Is., New Caledonia; Wallis and Futuna Is.). Collette 1979:29 (characters, range). Collette and Russo 1979:9, 13 (diagnostic characters, range). Golani and Kredo 1981:41 (fishery; Mediterranean coast of Israel). Hutchins 1979:83 (Rottnest I., off Perth, W. Australia). Joubert 1981: 5 (minor component of shore angler's catch; Natal, South Africa). McPherson 1981 (biology, migrations; Queensland). Van der Elst 1981:274 (photograph, description, natural history, range). Kyushin et al. 1982:227 (description, photograph). *Devaraj 1982 (age and growth). Sivasubramaniam and Mohamed 1982:65 (Qatar, Persian Gulf). Lewis and Endean 1983 (presence of a ciguatoxin-like substance in Queensland specimens caught between lat. 24°S and 26°S). Lewis et al. 1983: 14-21 (biology; Fiji). Cressey et al. 1983:264 (host-parasite list, 10 copepod species). Lee and Yang 1983:229-230 (Taiwan), fig. 19 (580 mm FL). Collette and Nauen 1983:63-64 (description, range), fig. Jenkins et al. 1984:348-351 (62 larvae, 3.5-9.3 mm SL; off Townsville, Qld.), fig. 3 (6 larvae, 3.7-9.1 mm SL).

Cybium multifasciatum Kishinouye 1915:9 (original description; Yamaguchi Prefecture, Japan), pl. 1, fig. 3.

Scomberomorus konam. Herre 1953:246 (synonymy).

Types of nominal species.—*Scomber commerson* Lacepède, 1800 is based on a figure from Commerson's manuscript; no types of this name are extant.

Scomber Maculosus Shaw 1803 is based on the "konam" of Russell (1803:pl. 135); no types of this name are extant.

Cybium konam Bleeker 1851b. Lectotype: RMNH 6051; Batavia; P. Bleeker; 444 mm FL; selected by Boeseman (1964:467); D XVII+18+ VIII; A 18+IX; P_1 22-22; RGR_1 0+1+2=3; upper jaw teeth 15-16; lower jaw teeth 15-12. A photograph of the lectotype was published by Boeseman (1964:pl. 4, fig. 16). Paralectotypes: RMNH 24087; 12 specimens; in part. The original description was based on 12 specimens 90 to 490 lines (= mm) long from Batavia. Boeseman (1964) found more than 12 specimens in RMNH 6051, selected the largest specimen as lectotype, removed 2 specimens that were below the minimum size of the type-series, and recatalogued the remainder of the material as RMNH 24087.

Cybium multifasciatum Kishinouye 1915. The original description was based on a specimen from Yamaguchi Prefecture, Japan in 1914 and is probably no longer extant. Data from the original description show this name to be a junior synonym of *S. commerson*: D XVII+15+IX; A 14+ IX; GR 1+2=3; vertebrae 20+24=44; and lateral line forming a deep bend. The author himself (Kishinouye 1923:416) subsequently placed *multifasciatum* in synonymy.

Diagnosis.—This species shares with *S. cavalla* an abrupt downward curve in the lateral line under the second dorsal fin (Fig. 52). One species, *S. sinensis*, has an abrupt downward curve in the lateral line under the first dorsal fin but the lateral line descends gradually in the other 15 species. It differs from *S. cavalla* in having more vertebrae (42-46, usually 43 or more compared with 41-43, usually 42 or fewer) and fewer gill rakers (1-8, usually 7 or fewer compared with 7-13, usually 8 or more). Posterodorsal spine of hyomandibula large as in *S. queenslandicus* and *Acanthocybium*. Palatine tooth patch very narrow (Fig. 23b) as in *S. sinensis* and *Acanthocybium*. Ventral process of angular long, 117-126% of dorsal process, as in *S. queenslandicus* and *Acanthocybium*. Anterior ends of pterosphenoid close together (Fig. 17a) as in *S. cavalla*. Intercalar spine well developed (Fig. 11a) as in *S. cavalla* and *S. queenslandicus*.

Description.—Intestine with two folds and three limbs (Fig. 3c). Spines in first dorsal fin 15-18, usually 17 (Table 9); second dorsal fin rays 15-20, usually 17 or 18 (Table 10); dorsal finlets 8-11, usually 9 or 10 (Table 10); anal fin rays 16-21, usually 18 or 19 (Table 11); anal finlets 7-12, usually 9 or 10 (Table 11); pectoral fin rays 21-24, usually 22 or 23 (Table 12). Precaudal vertebrae 19 or 20, usually 20 (Table 6); caudal vertebrae 23-27, usually 24 or 25 (Table 7); total vertebrae 42-46, usually 44 or 45 (Table 8). Gill rakers on first arch (0-2)+(1-8)=1-8, usually (0-1)+(3-4)=3-5 (Table 5). Morphometric characters given in Table 15.

Size.—Maximum size 230 cm FL and 59 kg; commonly 60-120 cm (Lewis 1981). The all-tackle angling record is a 44.9 kg fish taken at Scottburgh, Natal, South Africa, in 1982. Sexual maturity is attained at a length of 70-80 cm FL in Madagascar (Prado 1970), Papua New Guinea (Lewis et al. 1974), and Fiji (Lewis et al. 1983), but not until 90-100 cm in South Africa (van der Elst 1981). Females attain larger sizes than males (Prado 1970; Lewis et al. 1974, 1983).

Color pattern.—Munro (1943:75) presented a good description of Australian specimens. Sides pale silver gray marked with transverse vertical bars of a darker gray. Bars narrow and slightly wavy, sometimes breaking up into spots ventrally. Bars number 40-50 in adults but are usually fewer than 20 in juveniles up to 450 mm FL. Munro reported the cranial regions and upper regions of the back to be mottled with iridescent blue and green. Cheeks, lower jaw, and belly silvery white. First dorsal fin bright blue rapidly fading to blackish blue. Pectoral fin light grey turning to blackish blue. Caudal fin lobes, second dorsal, anal, and dorsal and anal finlets pale grayish white turning to dark gray. Juveniles have the anterior membranes of the first dorsal jet black contrasting with pure white posteriorly (Munro 1943:pl. 8, fig. 3).

There is an excellent illustration of an adult *S. commerson* from Japan in Kishinouye (1923:pl. 22), of an adult (968 mm FL, here reproduced as Figure 52), and a juvenile (368 mm) from Australia in Munro (1943), and of an adult from India in Jones and Silas (1962:fig. 2). There are color paintings in La Monte (1952:pl. 19) and Grant (1982:627) and color photographs of a specimen

TABLE 15.—Summary of morphometric data of *Scomberomorus commerson*. FL = fork length, HL = head length.

Character			Red Sea					Indian Ocean					East Indies					Total				
			N	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD
Fork length			12	266	854	346	162	34	180	1,085	443	275	22	94	628	234	132	119	94	1,155	403	247
Snout-A	‰	FL	12	530	559	549	8	33	426	575	535	26	22	521	635	563	26	117	426	635	543	23
Snout-2D	‰	FL	12	491	525	506	8	34	405	538	501	22	22	500	545	522	13	118	405	625	509	20
Snout-1D	‰	FL	12	233	255	245	8	34	188	261	237	17	22	231	273	258	12	118	188	273	243	16
Snout-P_2	‰	FL	12	247	269	259	6	33	201	321	256	21	22	229	299	269	18	117	201	321	257	18
Snout-P_1	‰	FL	12	228	258	243	8	34	185	260	233	18	22	226	274	254	13	118	185	274	238	17
P_1-P_2	‰	FL	12	89	103	96	4	31	70	105	90	8	22	83	119	99	10	112	70	123	96	9
Head length	‰	FL	12	218	239	230	6	34	177	251	226	18	22	215	261	240	12	119	177	261	229	15
Max. body depth	‰	FL	12	174	202	188	9	32	141	215	177	15	22	165	234	193	19	115	141	235	187	18
Max. body width	‰	FL	12	76	99	87	6	31	74	118	95	10	22	64	142	85	17	109	64	142	93	12
P_1 length	‰	FL	11	118	148	124	8	33	103	137	124	7	22	86	135	108	11	114	86	153	122	12
P_2 length	‰	FL	12	47	67	57	5	33	46	71	56	6	22	38	127	61	16	115	38	127	56	10
P_2 insertion-vent	‰	FL	12	264	285	275	7	33	207	386	270	27	22	269	320	288	14	117	207	386	273	19
P_2 tip-vent	‰	FL	12	203	233	220	10	33	170	238	210	15	22	209	278	231	17	115	170	278	217	16
Base 1D	‰	FL	12	248	276	261	7	33	210	286	257	14	22	243	285	265	11	117	210	286	261	13
Height 2D	‰	FL	12	98	125	108	7	31	91	119	104	8	21	76	108	91	9	102	76	135	103	11
Base 2D	‰	FL	12	87	123	104	14	33	81	130	99	11	22	78	171	106	18	117	78	171	104	14
Height anal	‰	FL	11	90	117	100	7	32	89	120	102	8	21	70	114	91	12	103	70	128	100	10
Base anal	‰	FL	12	89	108	98	6	33	81	113	97	8	22	80	119	98	10	116	80	164	100	11
Snout (fleshy)	‰	FL	12	80	91	88	3	33	66	99	88	7	22	84	100	93	5	117	66	100	89	6
Snout (bony)	‰	FL	12	72	82	77	3	33	61	136	82	12	22	77	91	84	4	117	61	136	81	7
Maxilla length	‰	FL	12	119	137	130	5	32	101	147	129	13	22	115	163	142	13	117	101	163	131	13
Postorbital	‰	FL	12	100	111	104	3	33	81	119	104	9	21	98	109	104	3	114	81	119	104	6
Orbital (fleshy)	‰	FL	12	28	38	34	3	32	21	47	33	6	22	28	50	40	6	115	21	50	34	6
Orbital (bony)	‰	FL	12	35	53	48	5	33	31	81	48	10	22	38	64	54	7	116	31	81	49	8
Interorbital	‰	FL	12	59	66	63	2	33	47	66	60	5	22	58	69	64	3	115	47	71	62	4
2D-caudal	‰	FL	12	458	520	474	20	33	380	540	491	31	21	420	489	454	18	109	380	540	480	27
Head length			12	61	186	79	34	34	41	214	96	50	22	24	135	55	28	119	24	242	89	48
Snout (fleshy)	‰	HL	12	351	402	381	14	33	326	408	388	15	22	356	412	389	12	117	326	424	390	15
Snout (bony)	‰	HL	12	324	372	338	14	33	333	571	362	39	22	329	371	349	10	117	316	571	354	25
Maxilla length	‰	HL	12	548	596	566	13	32	518	610	569	20	22	533	651	593	29	117	518	651	570	23
Postorbital	‰	HL	12	436	483	455	15	33	418	496	461	18	21	397	497	436	22	114	397	504	455	21
Orbit (fleshy)	‰	HL	12	128	167	147	10	32	111	189	144	17	22	129	200	166	18	115	101	224	147	21
Orbit (bony)	‰	HL	12	161	232	209	18	33	155	352	210	35	22	179	256	223	22	116	147	352	211	28
Interorbital	‰	HL	12	256	303	275	12	33	245	286	265	8	22	246	289	266	11	115	245	316	270	12

from Kuwait in Kuronuma and Abe (1972:pl. 17), a Japanese specimen in Masuda et al. (1975:79), a Persian Gulf specimen in Randall et al. (1978: 212), a South African specimen in van der Elst (1981:274), a Queensland specimen in Grant (1982:pl. 325), and a 344 mm specimen from the South China Sea in Kyushin et al. (1982:248).

Biology.—Adults frequently undertake lengthy seasonal longshore migrations (Lewis 1981). Migrations occur along the entire eastern coast of Queensland (McPherson 1981). Tongyai (1970:fig. 4) has mapped the migration route in the Gulf of Thailand; from the Cambodian border in October to the northernmost part of the Gulf of Thailand in December to February, then south along the west coast of the gulf in April. At least some individuals are present year round in some areas, e.g., Cambodia (Merçeron 1970) and East Africa (Williams 1964). Spawning apparently occurs over a long period in some regions, e.g., October to July in East Africa (Williams 1964), July to December in Papua New Guinea (Lewis et al. 1974). Spawning times have been reported as spring in Taiwan (Kishinouye 1923), October-December on the Great Barrier Reef (Munro 1942), October to February, peaking in December and January in Fiji (Lewis et al. 1983), May to July in the coastal waters of Madras State (Chacko et al. 1967), and December-February in Madagascar (Fourmanoir and Crosnier 1964). Munro (1942) described and illustrated the development of artificially fertilized eggs and early larvae from the Great Barrier Reef. Jones (1962) described and illustrated five postlarvae and juveniles (14.4-54.4 mm) from Vizhingam along the coast of southern Kerala taken in shore seines from February to June. The most complete larval description is by Jenkins et al. (1984) of 62 larvae (3.5-9.3 mm SL) from the shelf waters of the Barrier Reef. Tongyai (1970) reported that juveniles 100-450 mm were taken in waters of high turbidity and salinity in the Gulf of Thailand. Juveniles were caught with dip nets in Papua New Guinea waters in July, October, November, and December (Lewis et al. 1974). Like other species of the genus, *S. commerson* feeds primarily on small fishes particularly anchovies such as *Anchoviella* and *Stolephorus* and clupeids such as *Sardinella* (South Africa—van der Elst 1981; Madagascar—Prado 1970; Madras—Chacko et al. 1967; Waltair, east coast of India—Rao 1964; Vizhingam, southern India—Kumaran 1964; Gulf of Manaar—Chacko 1949; and Cambodia—Merçeron 1970). Other food items mentioned by these authors include small carangids, *Leiognathus*, squids such as *Loligo*, and penaeoid shrimps. Feeding apparently takes place day and night (Tongyai 1970).

Interest to fisheries.—This species is taken throughout its range by commercial, artisanal, and recreational fisheries. Although it may be present the year round, e.g., in the coastal water of Madras State (Chacko et al. 1967), fisheries are usually concentrated in some seasons, particularly those with the best weather conditions for fishing. Peak fishing seasons in some areas are as follows: Taiwan—spring (Kishinouye 1923); Great Barrier Reef—August to September (Grant 1978); Cambodia—the dry season, October to April (Merçeron 1970); Gulf of Thailand—October to May (Tongyai 1970); Waltair, northeastern India—March-April, June-July, and December (Venkata Subba Rao et al. 1981); Vizhingam, southeastern India—September to April (Gopalan Nayar 1958); and Malwan, south of Bombay—February to March and October to December (Kaikini 1961). There are important fisheries in Fishing Areas 51, 57, and 71. The total catch fluctuated between 63,290 and 79,047 t/yr in 1979-82 (FAO 1984). The five countries with the largest reported catch in this period were Indonesia, Philippines, Sri Lanka, Yemen, and Pakistan. The landings in Queensland were around 1,000 tons/yr during the mid-1970's but have dropped to 730-770 tons in 1978-80 (McPherson 1981). The 1982 catch in Fiji probably exceeded 300 tons (Lewis et al. 1983). There is also an important drift net fishery in India, but the catch is not identified to species in the statistics. Drift nets (gill nets) that are usually fished over night appear to be the most important gear used for *S. commerson* in Thailand, Malaysia, and India (Tongyai 1970; Pathansali 1968; Kaikini 1961; Chacko et al. 1967, respectively); other gear includes shore seines in Taiwan and India (Kishinouye 1923; Gopalan Nayar 1958), trolling lines in Taiwan, Malaysia, India, and East Africa (Kishinouye 1923; Pathansali 1968; Dhawan et al. 1972; Williams 1964, respectively). Hand lines (bett-tok) baited with mackerel (*Rastrelliger*) or squid (*Loligo*) and trotlines (bett-laak) with spoons are also employed in the Gulf of Thailand (Tongyai 1970). It is taken fairly commonly in the inshore fishery along the Mediterranean coast of Israel with trammel nets and occasionally with purse seines (A. Ben-Tuvia[3]). The yearly catch

will be about 20 t out of the 2,000 t taken in the inshore fisheries according to A. Ben-Tuvia and D. Golani.[4] It is a highly regarded species that commands a good price in the Philippine Islands, Thailand, India, Madagascar, and East Africa (Warfel 1950; Tongyai 1971b; Devanesen and Chidambaram 1953; Fourmanoir and Crosnier 1964; Williams 1964, respectively). It is a prime target of the Natal ski-boat fishermen and is pursued by sport and commercial anglers in South Africa, using lures, feathers, clupeids, and anchovies as bait (van der Elst 1981). It is marketed fresh, on ice, or salted and dried (Gopalan Nayar 1958; Fourmanoir and Crosnier 1964; Williams 1964; Tongyai 1971b; McPherson 1981). A lipid-soluble toxin similar to ciguatoxin has been found in the flesh of *S. commerson* between lat. 24°S and 26°S along the east coast of Queensland (Lewis and Endean 1983). From 1976 to 1980, at least 38 toxic *S. commerson*, resulting in 217 poisonings, came from this area.

Distribution.—Widespread throughout the Indo-West Pacific from South Africa and the Red Sea east through the Indo-Australian Archipelago to Australia and Fiji and north to Hong Kong, Formosa, and Japan (Fig. 51). The northernmost record is from the northern coast of Yamaguchi Prefecture, southern Honshu, on the Sea of Japan (Kishinouye 1923:417). Its range extends farther out into the Pacific islands than any of the other species of *Scomberomorus*, throughout the Philippine Islands, to New Caledonia (Chapman 1946; Fourmanoir and Laboute 1976; Uchida 1978) and Fiji (Jordan and Dickerson 1908; Whitley 1927; Fowler 1959). Records from Wallis and Futuna Islands and Cook Islands (Uchida 1978) are doubtful and need to be verified. In Australia the range extends south to Sydney (Castelnau 1879; AMS I.9693) and, rarely, even to Victoria and Tasmania (Munro 1958a; Whitley 1964a) on the east coast and to Rottnest Island off Perth, Western Australia (Hutchins 1979). From Australia and the East Indies, the range extends along the coast of the Indian Ocean including the Persian Gulf and Red Sea to False Bay, Cape Town, South Africa (Barnard 1948). The range includes many major offshore island groups in the Indian Ocean: Andamans and Nicobars (Jones et al. 1960), Laccadives (Nagabhushanam and Chandrasekhara Rao 1972), Amirantes (Ommanney 1953), Comores and Madagascar (Fourmanoir and Crosnier 1964), and Mauritius (Bleeker 1874; Baissac 1976). It has strayed into the South Atlantic because we have examined the head of a specimen (BMNH 1965.12.1.104) collected by Arthur Loveridge from Egg Island, St. Helena. It has even traversed the Suez Canal and entered the eastern Mediterranean Sea where it is now known from Lebanon (George and Athanassiou 1965) and Israel (Collette 1970; USNM 226334; Golani and Kredo 1981).

Geographic variation.—Samples were adequate to compare the morphometric data of three populations of *S. commerson* by ANCOVA (Table 15): Red Sea (n = 12), Indian Ocean (n = 31-34), and East Indies (n = 21-22). Null hypotheses that the three sets of regressions are coincident were accepted for 11 of 26 regressions, rejected for the other 15. For one set, interorbital width, the regressions for all three populations differed significantly in slope. The Red Sea population differs significantly from the Indian Ocean population in six regressions: Sn-1D, Sn-P_1, Ht 2D, Base 2D, Ht A, and interorbital width. The Indian Ocean population differs from the East Indies population in eight regressions: P_1-P_2, Hd L, P_2 tip-vent, Ht 2D, Sn (fleshy), Sn (bony), maxilla L, and interorbital width.

There are also geographic differences in meristic characters. Populations in the Red Sea and Persian Gulf tend to have fewer vertebrae (23-24 caudal, 43 total) and fewer rays in the second dorsal and anal fins (usually 16-17 second dorsal and 17-18 anal) than other populations (24-27 caudal, 44-46 total vertebrae; 17-18 second dorsal, 18-19 anal rays). Populations in the East Indies and Gulf of Thailand tend to have more vertebrae (25-27 caudal, 45-46 total) and anal finlets (mode 10 rather than 9). Gill rakers tend to be fewer in the East Indies, Gulf of Thailand, and South China Sea (2-6, usually 3 or 4) compared with other populations (3-8, usually 4-6).

Material examined.—Total 262 (94.2-1,155).

meas.: 120 (94.2-115): Israel (2); Red Sea (12); Gulf of Aden (2); St. Helena (1); W Indian Ocean (14); Arabian Sea (14); Bay of Bengal (5); Andaman Sea (7); Gulf of Thailand (14); East Indies (22, **C. ko-*

[3]A. Ben-Tuvia, Professor of Zoology, Zoology Department, The Hebrew University, 91904 Jerusalem, Israel, pers. commun. October 1982.

[4]A. Ben-Tuvia, Professor of Zoology, and D. Golani, Zoology Department, The Hebrew University, 91904 Jerusalem, Israel, pers. commun. October 1982.

nam Bleeker), New Guinea (2); Australia (5); Philippine Is. (6); South China Sea (8); Fiji (5).

counts: 262.

diss.: 14 (260-1,155): Israel (1); W Indian Ocean (2); Pakistan (1); New Guinea (2); New South Wales, Australia (2); Philippine Islands (2); Hong Kong (4).

Scomberomorus concolor (Lockington) Monterey Spanish Mackerel

Figure 53

Chriomitra concolor Lockington 1879a:134-136 (original description; Monterey Bay, Calif.). Lockington 1879b:34 (uncommon; San Francisco market).

Scomberomorus concolor. Jordan and Gilbert 1881a:456 (Monterey Bay; *Chriomitra* placed in synonymy of *Scomberomorus*). Jordan and Jouy 1881:13 (specimens from Soquel, Calif.; USNM 27205; distributed as duplicates). Jordan and Gilbert 1881b:45 (Monterey Bay). Jordan and Gilbert 1882:425-426 (description). Meek and Newland 1884:232-233 (synonymy, description). Goode 1884:316 (Soquel, Monterey Bay; occurrence, price). Dresslar and Fesler 1889:442-443 (synonymy, description). Jordan and Evermann 1896a:341 (listed). Jordan and Evermann 1896b:873-874 (description, synonymy). Jordan and Evermann 1902:284 (description). Starks 1918:121 (not reported from Monterey Bay in 40 yr). Meek and Hildebrand 1923:325-326 (description; Soquel, Calif.). Jordan et al. 1930:257 (listed). Phillips 1932:99 (Monterey Bay; first record in more than 40 yr). Breder 1936:12 (2 specimens, 491-520 mm SL; from Gulf of California; measurements). Croker 1937:245-246 (Long Beach). Walford 1937:25-26 (description, occurrence). Roedel 1939:341 (Long Beach; fifth record of recent years). Munro 1943:69, 71-72 (placed in subgenus *Chriomitra*). Fowler 1944:498 (listed; Mexico; Panama Bay record probably *S. sierra*). Fitch 1948:134 (Santa Monica Bay; sixth specimen since 1880's). *Fitch and Flechsig 1949:275-280 (history of previous captures; description), fig. 75. Fraser-Brunner 1950:157-158 (description), fig. 26. Clothier 1950:53 (47-48 vertebrae). Fitch 1950:70 (Newport Harbor; seventh California record since 1880's; comparison with *S. sierra*). Roedel 1951:510 (Long Beach; 8th to 10th specimens since 1880's; may have spots). Fitch 1952:560 (Los Angeles Harbor). Roedel 1953:85 (occasional in S California). Radovich 1961:21, 30 (years of California captures). Collette et al. 1963:54 (compared with *S. sierra*; previous California records of *S. sierra* = *S. concolor*). Clemens and Nowell 1963:260 (Gulf of California). Fitch and Craig 1964:202, fig. 5 (otolith). Klawe 1966:445 (compared with *S. sierra*; more gill rakers on upper and lower arches). Fitch 1969:65 (jaw fragments and teeth; Chumash Indian village archaeological site; Ventura, Calif.). Castro-Aguirre et al. 1970:156-157 (abundant in Gulf of California). Fitch and Lavenberg 1971:131, 168 (listed). Miller and Lea 1972:192 (description; range Gulf of California to Soquel, Calif.), fig. Buen 1972:291 (Mexico). Bullis et al. 1972:75 (bionumeric code number). Richards and Klawe 1972:13 (range), 91 (references to juveniles). Magnuson 1973:350 (short pectoral fin). Sharp 1973: 384, fig. 3 (hemoglobin electrophoretic patterns

FIGURE 53.—*Scomberomorus concolor.* Gulf of California, 440 mm FL, USNM 233681.

of *S. sierra*, *S. concolor*, and *Acanthocybium* identical or very similar). Johnson 1975:20 (procurrent spur not present). Shiino 1976: 231 (common name). Thomson and McKibbin 1976:46 (description; Gulf of California). Klawe 1977:2 (common name, range). Fitch and Schultz 1978:85, fig. 4G (otolith). Horn and Allen 1978:39 (range lat. 36°N to 32°N along California coast). Collette 1979:29 (characters, range). Collette and Russo 1979: 13 (diagnostic characters, range). Cressey et al. 1983:264 (host-parasite list, 3 copepod species). Collette and Nauen 1983:64-65 (description, range), fig.

Types.—*Chriomitra concolor* Lockington 1879a. Description based on a 21-in FL (533 mm FL) specimen obtained in the San Francisco market and probably originating in Monterey Bay. Lockington stated that the specimen was "in the possession of the Cal. Acad. of Sciences", but it is not now present in the CAS collection. Data from the original description are "D XV+17+VII; A 18+VIII. Body color dark steel blue above, becoming silvery below; no streaks".

Diagnosis.—The species of *Scomberomorus* with the most gill rakers, a total of 21-27 on the first arch, compared with 1-18 in the other 17 species. It possesses nasal denticles as do the other five species of the *regalis* group (*brasiliensis*, *maculatus*, *regalis*, *sierra*, and *tritor*). Like *S. maculatus*, *S. concolor* lacks the artery that goes from the fourth right epibranchial artery to the coeliaco-mesenteric artery (Fig. 7d), but it has the artery that comes off the fourth left epibranchial artery as do all the species in the group except *S. tritor*. Together with three other species of the *regalis* group (*brasiliensis*, *regalis*, and *sierra*), *S. concolor* has a long posterior process on the pelvic girdle, 62-90% of the length of the anterior plate. Intercalar spine absent as in the other five species of the *regalis* group and *S. niphonius*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3d). Spines in first dorsal fin 15-18, usually 17 (Table 9); second dorsal fin rays 16-20, usually 18 or 19 (Table 10); dorsal finlets 6-9, usually 8 (Table 10); anal fin rays 19-23, usually 20 (Table 11); anal finlets 6-8, usually 7 or 8 (Table 11); pectoral fin rays 19-22, usually 21 (Table 12). Precaudal vertebrae 18-20, usually 19 (Table 6); caudal vertebrae 27-29, usually 28 (Table 7); total vertebrae 46-48, usually 47 or 48 (Table 8). Gill rakers on first arch (4-8)+(15-21)=21-27, usually (6-7)+(17-18)=23-25 (Table 5). Morphometric characters given in Table 16.

TABLE 16.—Summary of morphometric data of *Scomberomorus concolor*. FL = fork length, HL = head length.

Character		*N*	Min.	Max.	Mean	SD
Fork length		34	134	685	401	139
Snout-A	FL	34	504	547	524	10
Snout-2D	FL	34	488	534	506	12
Snout-1D	FL	34	220	258	236	10
Snout-P_2	FL	34	192	287	242	18
Snout-P_1	FL	34	124	263	209	21
P_1-P_2	FL	30	89	116	100	6
Head length	FL	34	185	230	202	10
Max. body depth	FL	29	164	220	187	16
Max. body width	FL	32	70	111	89	10
P_1 length	FL	34	116	137	125	6
P_2 length	FL	31	41	61	50	4
P_2 insertion-vent	FL	32	222	294	261	16
P_2 tip-vent	FL	29	173	248	212	18
Base 1D	FL	34	210	292	254	15
Height 2D	FL	26	98	129	111	9
Base 2D	FL	33	108	153	128	10
Height anal	FL	25	26	137	108	20
Base anal	FL	33	107	171	135	14
Snout (fleshy)	FL	33	53	83	72	5
Snout (bony)	FL	33	57	76	64	3
Maxilla length	FL	33	103	128	113	6
Postorbital	FL	29	85	101	96	4
Orbital (fleshy)	FL	33	25	47	32	7
Orbital (bony)	FL	30	34	63	46	8
Interorbital	FL	34	44	55	49	3
2D-caudal	FL	30	413	524	484	24
Head length		34	31	134	80	27
Snout (fleshy)	HL	33	276	389	353	19
Snout (bony)	HL	33	273	355	314	16
Maxilla length	HL	33	532	575	555	11
Postorbital	HL	29	419	524	475	22
Orbit (fleshy)	HL	33	125	212	158	26
Orbit (bony)	HL	30	175	285	226	32
Interorbital	HL	34	220	274	242	12

Size.—Maximum size 76.2 cm FL, 2.3-3.6 kg (Goode 1884).

Color pattern.—According to Walford (1937), males are steel blue on the back, silvery on the sides and below, and are without streaks or spots. Females are darker, with two alternate series of brown spots on sides. The spots on the sides of the females are gold in life (Fitch and Flechsig 1949).

A black and white photograph of *S. concolor* is included in Fitch and Flechsig (1949:fig. 75).

Biology.—Little is known about the biology of *S. concolor*. In the 1880's, they appeared in Monterey Bay in September and disappeared in November (Goode 1884). There are no references to eggs, larvae, or juveniles (Richards and Klawe 1972).

Interest to fisheries.—Some accounts indicate

that *S. concolor* was of considerable commercial importance in Monterey Bay in the 1870's and 1880's, in great demand and at a high price, 30-50 cents a pound according to Goode (1884). According to other authors, such as Lockington (1879a, b), it was not abundant even then. No longer of any commercial significance.

Distribution.—An eastern Pacific endemic originally described from Monterey Bay, Calif. (Lockington 1897a). This apparently was the northern limit of the range, and there have been only about 10 recent records from the California coast (Long Beach, Santa Monica Bay, Newport Harbor; Fitch and Flechsig 1949; Radovich 1961). Its present range is concentrated in the Gulf of California (Castro-Aguirre et al. 1970; Miller and Lea 1972; Collette and Russo 1979:13, fig. 8).

Material examined.—Total 34 (134-685 mm FL).

meas.:	34 (134-685): Soquel, Calif. (6); Gulf of California (27).
counts:	30.
diss.:	6 (420-495): Gulf of Calif.

Scomberomorus guttatus (Bloch and Schneider) Indo-Pacific King Mackerel

Figure 54

Scomber guttatus Bloch and Schneider 1801:23-24 (original description; Tranquebar, India), pl. 5.

Scomber wingeram Russell 1803:26-27 (description; Coromandel coast of India), pl. 134.

Scomber leopardus Shaw 1803:591-592 (original description based on the wingeram of Russell 1803:pl. 134).

Cybium guttatum. Cuvier 1829:200 (listed in footnote from *Sc. guttatus* Bloch and Schneider). Cuvier *in* Cuvier and Valenciennes 1831:173-176 (description). Richardson 1846: 268 (synonymy, range). Cantor 1849:1093-1095 (synonymy, description, range; Pinang). Bleeker 1852:38, 39 (synonymy, description; East Indies). Bleeker 1853:42 (India). Bleeker 1860:13 (Borneo). Günther 1860:371 (synonymy, description). Bleeker 1861a:52 (Singapore; listed). Bleeker 1861b:74 (Pinang; listed). Kner 1865:143-144 (description). Day 1873: 225 (description, range). Bleeker 1873:131 (China; listed). Day 1878:255 (synonymy, description, range), pl. 55, fig. 1 (young), pl. 56, fig. 4 (adult). Tirant 1885:46 (Cambodia; listed). Kishinouye 1923:419-420 (description, anatomy), pl. 34, fig. 61 (adult). Chabanaud 1926:22 (Côte d'Annam, Tonkin; listed). Hardenberg 1931:141 (Sumatra). Delsman 1931: 402 (vertebrae 20+25=45), figs. 1-9 (eggs and larvae). Morice 1953:37 (villiform tongue teeth present). Gopalan Nayar 1958:49-51 (fishery; Vizhingam, S India).

Cybium interruptum Cuvier *in* Cuvier and Valenciennes 1831:172-173 (original description; Pondichery, India). Günther 1860:371 (description after Cuvier). Day 1873:225 (description, range). Day 1878:254-255 (synonymy, description), pl. 56, fig. 3.

Cybium Kuhlii Cuvier *in* Cuvier and Valenciennes 1831:178-179 (original description; Bombay). Hardenberg 1931:140 (often found in river mouths; Sumatra). Delsman 1931:402 (vertebrae 20+25=45), 407 (commonest species of *Cybium* at Bagan Si Api Api).

FIGURE 54.—*Scomberomorus guttatus.* Gulf of Thailand, 459 mm FL, CAS GVF Reg. 1512.

Cybium Croockewitii Bleeker 1851b:161 (original description; Banka). Bleeker 1852:37-38 (description). Günther 1860:372 (description after Bleeker).

Scomberomorus guttatus. Fowler 1905:766 (Sumatra; ANSP 27490-91). Jordan and Richardson 1909:177 (Formosa; FMNH 59284). Reeves 1927:8 (Swatow, China). Fowler 1928:109 (Bombay). Chevey 1934:45-46 (Tirant's *C. guttatum* = *S. guttatus*). Delsman and Hardenberg 1934:341-342 (description; East Indies), fig. 247 (adult), fig. 248 (larva, with myomeres 15 + 35 = 50). Hardenberg 1934: 311 (Sumatra; listed). Hardenberg 1936:252 (mouth of Kapuas R., Borneo). Hardenberg 1937:12 (mouth of Kumai R., Borneo). Herre and Myers 1937:21 (Singapore). Munro 1943: 68, 71 (placed in subgenus *Indocybium*). Quraishi 1945:28 (pyloric caeca arranged in dendritic pattern). Norman and Fraser 1949: 153 (Indo-Pacific species). Fraser-Brunner 1950:160 (synonymy in part, range), fig. 31. Tham 1950:21 (feeds largely on *Stolephorus*). de Beaufort 1951:232-234 (synonymy, description, range). Tham 1953:49 (Singapore Straits), 50 (correlation of catch with physical factors and presence of food fishes such as *Stolephorus*). Vijayaraghavan 1955:360-372 (commonest species of genus in Madras; eggs, larval development). Krishnamoorthi 1957:236 (second in importance among fishes landed at Rameswaram I., Palk Bay), 239-242 (catch), 251 (value of catch). Krishnamoorthi 1958:270-281 (spawning season and fisheries; Rameswaram I., SE India). Venkataraman 1961: 287, fig. 4C (food of 133 specimens; Calicut, India; mostly teleosts). Kaikini 1961:361 (seerfish fishery; Malwan, India). Jones and Silas 1962:195-197 (synonymy, description, range), fig. 3 (533 mm adult), fig. 5D (head, not 5C as labelled), fig. 6C (gill arch), fig. 7C (caudal peduncle keels). Jones 1962:107-113 (development, 14.8-239 mm), figs. 2-6 (specimens 14.8, 22.9, 41.2, 66.8, and 239 mm long). Misra 1962:295-296 (description, distribution), fig. 181 (size given as "1828 mm"). Jones and Kumaran 1964:344-346 (larval development), figs. 1-3 (from Jones 1962). Kumaran 1964: 587-589 (postlarval and juvenile fishes form most of diet of juveniles; W coast of India). Blanc and Bauchot 1964:449 (specimens examined by Cuvier). Boeseman 1964:468 (syntypes of *C. kuhlii*), pl. V, fig. 18 (photograph of syntype). Rao 1964:592-597 (teleosts predominate in food of juveniles and adults; Waltair coast, India). Gorbunova 1965a:52-53 (spawning). Gorbunova 1965b:174-175 (spawning; Gulf of Tonkin), fig. 6 (4.3 and 5.8 mm larvae). Menon 1966:396 (Tranquebar, India). Thiemmedh 1966:129, 140 (Thai names). Tongyai 1966a:7-13 (synonymy, occurrence in Thailand, biology), pl. 2C. Tongyai 1966b:3-17 (length frequency; Andaman Sea). Collette 1966:368-369 (*Cybium kuhlii* a junior synonym of *S. guttatus*, lectotype of *C. kuhlii* selected). Jones 1968:998 (seerfish fishery; India). Pathansali 1968:1001-1002 (fishery on east and west coasts of Malaya). Tongyai 1970:559 (distribution; Thai waters), 561 (spawning), 561-562 (food). Merçeron 1970:75-81 (length-weight; Cambodia). Tongyai 1971a:13-16 (description), pl. I (viscera), pl. IV (photograph). Tongyai 1971b: 3 (undetermined economic potential; Thailand), pl. 8, 13 (photographs). Latiff 1971:92 (description; Penang waters; photograph). Banerjee and Chakrubarty 1972 (drift gill netting; Lower Sundarbans, W Bengal). Fernando 1972:524, 530 (incidental catches in trawls; Wadge Bank, Ceylon). Kuronuma and Abe 1972:105 (description; Kuwait), color pl. 17. Richards and Klawe 1972:13-14 (range), 91-92 (references to eggs, larvae, and juveniles). Magnuson 1973: 350 (small pectoral fin). Banerji 1973:129-130 (seerfish fishery; India). Orsi 1974:175 (listed; Vietnam). Roy and Roy 1974:44, 51, 53 (a principal species in gill net fishery; Balashore, India). Shenoy and James 1974 (ice storage). Devaraj 1976:80-85 (distinguished from *S. koreanus*), fig. 4 (vertebrae), 5 (preopercle and liver). Rao 1976:63-78 (biometric comparison of 5 Indian populations). Shiino 1976: 231 (common names). *Devaraj 1977 (osteology). Rao and Ganapati 1977:107-111 (comparison with postlarvae and juveniles of *S. lineolatus* and *S. commerson*). Klawe 1977:2 (common name, range). Randall et al. 1978: 167 (Persian Gulf; photograph). Collette 1979: 29 (characters, range). Collette and Russo 1979:13 (diagnostic characters, range). Zhang and Zhang 1981:104 (range in part). Nakamura and Nakamura 1982:446 (3 specimens, description; Sea of Japan), fig. 1B. *Devaraj 1982 (age and growth). Sivasubramaniam and Mohamed 1982:64 (Qatar, Persian Gulf). Cressey et al. 1983:264 (host-parasite list, 4 copepod species). Lee and Yang 1983:230-231 (Taiwan), fig. 21 (353 mm FL). Collette and Nauen 1983:65-66 (description, range), fig.

Scomberomorus guttatum. Malpas 1926:72-74 (87 specimens; length, weight, gonads, stomach contents; Ceylon). Scott 1959:113 (description; Malaya), photograph.

Scomberomorus kuhlii. Chevey 1934:20 (Tirant's *C. kuhlii* = *S. kuhlii*). Hardenberg 1934:311 (listed; Sumatra). Hardenberg 1936: 252 (mouth of Kapuas R., Borneo). Hardenberg 1937:12 (mouth of Kumai R., Borneo). Munro 1943:68, 71 (placed in subgenus *Pseudosawara*). Herre and Herald 1951:339 (Sandakan market; N Borneo). Bauchot and Blanc 1961:372 (types of *C. kuhlii*; recognized as valid species). Blanc and Bauchot 1964:447 (types of *C. kuhlii*), pl. III, fig. 14 (photograph of type-specimens). Orsi 1974:175 (listed; Vietnam).

Scomberomorus croockewiti. de Beaufort 1951: 234-235 (description), fig. 40 (drawing made for Bleeker). Boeseman 1964:467 (holotype), pl. V, fig. 17 (photograph of holotype).

Indocybium guttatum. Munro 1955:221 (description; Ceylon), fig. 652. Chacko et al. 1967: 1006 (fishery; Madras).

Scomberomorus lineolatus. Not of Cuvier, 1831. Bauchot and Blanc 1961:371 (type of *C. interruptum*). Blanc and Bauchot 1964:446-447 (type of *C. interruptum*), pl. III, fig. 13 (photograph of holotype of *C. interruptum*).

Scomberomorus guttatus guttatus. Jones and Silas 1964:62-63 (synonymy, description, range), pl. VII, fig. B. Silas 1964:325-329 (synonymy, description, range; *C. koreanum* considered a subspecies of *S. guttatus*).

Types of nominal species. —*Scomber guttatus* Bloch and Schneider 1801. The original description was based on a specimen from Tranquebar, India. No types are known to be extant. The figure in the original description leaves little doubt as to the identity of the name.

Scomber leopardus Shaw 1803 was based on the "wingeram" of Russell (1803:pl. 134); no types are extant.

Cybium interruptum Cuvier *in* Cuvier and Valenciennes 1831. Holotype: MNHN A.5522; Pondichery, India; Leschenault; 375 mm FL; D ?+?+IX; A ?+VII; lateral line branched anteriorly; dried, dorsal fin badly damaged. A photograph of the type was published by Blanc and Bauchot (1964:pl. 3, fig. 13).

Cybium kuhlii Cuvier *in* Cuvier and Valenciennes 1831. Lectotype: MNHN A.5771; Java; Kuhl and van Hasselt; 108 mm FL; selected by Collette (1966:368); D XVII+21+VIII; A 21+VIII; P_1 22; RGR_1 2+1+9=12; vertebrae 21+30 = 51. A photograph of the lectotype was published by Blanc and Bauchot (1964:pl. 3, fig. 14, upper fish). Paralectotypes: RMNH 1239 (1, 190 mm FL) and 1241 (1, 108 mm FL); Java; Kuhl and van Hasselt; and MNHN A.5715 (1, 115 mm FL); Bombay; Dussumier. Photographs of RMNH 1239 and MNHN A.5715 have been published by Boeseman (1964:pl. 5, fig. 19) and Blanc and Bauchot (1964:pl. 3, fig. 14, lower fish), respectively.

Cybium Croockewitii Bleeker 1851. Holotype: RMNH 6054; Banka, Strait near Muntok, East Indies (= Indonesia); J. H. Croockewit; D XV+24 +VII; A 23+VII; P_1 21-21; RGR_1 2+1+9=12; lateral line with fine branches anteriorly. A photograph of the type was published by Boeseman (1964:pl. 5, fig. 18).

Diagnosis. —This species shares with *S. koreanus* the presence of numerous fine auxiliary branches from the anterior part of the lateral line (Fig. 54). It differs from *S. koreanus* in having the usual two loops and three limbs to the intestine instead of four loops and five limbs. Anterior end of premaxilla forms a blunt rather than intermediate or acute angle. Ascending process of premaxilla short as in *S. cavalla*. Scapular foramen small as in *S. koreanus* and *S. niphonius*. Supraoccipital crest high as in *S. koreanus* and *S. multiradiatus*.

Description. —Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 2e). Spines in first dorsal fin 15-18, usually 16 or 17 (Table 9); second dorsal fin rays 18-24, usually 20-22 (Table 10); dorsal finlets 7-10, usually 8 or 9 (Table 10); anal fin rays 19-23, usually 20-22 (Table 11); anal finlets 7-10, usually 8 (Table 11); pectoral fin rays 20-23, usually 21 (Table 12). Precaudal vertebrae 19-22, usually 21 (Table 6); caudal vertebrae 28-31, usually 29 or 30 (Table 7); total vertebrae 47-52, usually 50 or 51 (Table 8). Gill rakers on first arch (1-2)+(7-12)=8-14, usually 2+(9-10)=11-12 (Table 5). Morphometric characters given in Table 17.

Size. —Maximum size 76 cm FL. Size at first maturity 48-52 cm TL in southern India (Krishnamoorthi 1958), 41-45 cm TL in Thailand (Tongyai 1966b).

Color pattern. —Nakamura and Nakamura (1982)

TABLE 17.—Summary of morphometric data of *Scomberomorus guttatus*. FL = fork length, HL = head length.

Character		Indian Ocean					East Indies					Gulf of Thailand					China					Total				
		N	Min.	Max	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD
Fork length		22	109	545	309	144	24	107	515	242	100	17	173	459	331	84	31	63	760	291	167	143	63	760	317	128
Snout-A	FL	20	495	568	519	19	24	503	559	524	14	17	494	518	505	7	28	468	568	517	20	138	468	568	516	17
Snout-2D	FL	22	452	509	483	14	24	454	504	481	12	17	459	494	479	9	28	463	510	481	10	140	451	512	481	11
Snout-1D	FL	22	224	273	242	12	22	225	260	241	10	17	219	248	232	9	29	220	275	238	13	123	219	275	238	11
Snout-P_2	FL	19	228	285	253	17	22	231	278	255	12	17	225	358	248	31	26	225	296	248	20	116	224	358	250	19
Snout-P_1	FL	22	193	241	213	13	23	191	235	212	12	17	190	225	201	8	29	186	245	207	19	124	185	245	208	14
P_1-P_2	FL	19	94	126	109	8	22	93	119	107	7	17	92	120	104	7	25	95	129	106	9	114	89	129	106	8
Head length	FL	22	188	234	211	13	24	188	221	208	9	17	190	218	199	8	31	185	259	207	19	143	185	259	205	13
Max. body depth	FL	19	171	326	218	30	19	190	229	208	10	16	99	226	202	29	30	191	236	209	9	129	99	326	209	18
Max. body width	FL	15	69	125	92	16	15	69	106	88	10	16	85	104	93	6	22	71	106	91	8	92	69	146	93	12
P_1 length	FL	17	92	130	113	9	20	89	130	107	11	11	93	122	107	7	23	89	133	108	9	99	89	133	109	9
P_2 length	FL	13	47	70	63	6	16	47	69	59	5	13	47	62	57	4	20	48	74	59	5	88	41	74	59	6
P_2 insertion-vent	FL	14	224	270	250	16	22	240	279	257	11	15	231	268	245	12	23	218	269	248	13	101	218	288	251	13
P_2 tip-vent	FL	10	158	208	187	17	14	178	223	196	13	12	174	209	187	12	22	167	211	189	13	81	158	229	191	15
Base 1D	FL	22	203	253	232	13	21	210	258	234	13	17	208	256	240	12	29	216	246	232	8	122	203	270	234	12
Height 2D	FL	18	113	153	138	11	20	103	167	124	16	10	114	169	132	15	22	117	155	132	10	113	103	254	131	17
Base 2D	FL	22	125	161	146	11	23	121	156	136	10	17	113	157	136	13	29	100	170	144	13	124	100	170	141	12
Height anal	FL	15	109	165	135	13	16	93	166	122	18	13	107	170	127	15	24	109	153	125	11	106	93	170	127	14
Base anal	FL	22	115	165	138	13	23	83	154	127	13	17	111	147	130	10	29	116	146	134	7	124	83	171	133	12
Snout (fleshy)	FL	22	60	81	72	5	24	64	80	72	3	17	61	75	69	4	29	61	170	75	19	125	60	170	72	10
Snout (bony)	FL	22	56	73	64	4	24	57	69	64	3	17	54	68	61	4	29	48	161	66	19	125	47	161	63	10
Maxilla length	FL	22	92	130	110	9	24	86	121	111	9	17	90	118	102	9	28	95	132	108	11	124	86	132	108	9
Postorbital	FL	22	85	112	97	7	24	87	100	95	4	17	79	105	93	5	29	88	112	95	6	123	79	112	95	5
Orbital (fleshy)	FL	22	25	50	36	7	24	28	56	40	6	17	29	41	34	3	29	23	52	35	8	125	23	56	36	7
Orbital (bony)	FL	22	37	70	53	10	24	47	69	57	6	17	41	60	48	5	29	38	71	52	8	124	37	71	52	8
Interorbital	FL	22	55	66	60	3	24	55	62	59	2	17	52	62	57	3	29	53	63	58	3	124	52	66	58	3
2D-caudal	FL	22	481	552	519	23	23	491	558	534	14	17	480	553	507	23	28	465	579	528	34	138	465	579	527	26
Head length		22	25	125	64	29	24	24	98	50	18	17	38	88	65	15	31	16	145	58	30	143	16	145	64	24
Snout (fleshy)	HL	22	296	383	344	21	24	319	368	344	12	17	319	365	345	12	29	310	734	364	72	125	296	734	351	38
Snout (bony)	HL	22	265	328	303	15	24	281	334	306	12	17	282	320	304	12	29	245	694	320	74	125	232	694	309	38
Maxilla length	HL	22	455	564	523	23	24	451	564	530	26	17	463	550	512	30	28	497	565	531	17	124	451	565	525	23
Postorbital	HL	22	412	499	463	20	24	410	496	457	20	17	413	502	469	25	29	393	563	470	34	123	382	563	465	26
Orbit (fleshy)	HL	22	118	217	173	30	24	148	253	193	24	17	151	198	168	13	29	121	220	169	26	125	118	253	174	27
Orbit (bony)	HL	22	158	306	253	41	24	240	314	275	19	17	214	275	242	18	29	197	304	252	26	124	158	314	252	30
Interorbital	HL	22	244	325	284	16	24	258	298	284	8	17	272	296	284	8	29	254	301	284	13	124	244	325	285	12

described fresh specimens taken in Wakasa Bay in the Sea of Japan. Body greyish blue dorsally, silvery white laterally and ventrally. Several longitudinal rows of small brownish spots scattered rather densely along lateral median line. First dorsal fin membrane black. Pectoral, second dorsal, and caudal fins dark brown. Pelvic and anal fins silvery white.

There are good illustrations of a specimen from the North Pacific in Kishinouye (1923:fig. 61) and of one from India in Jones and Silas (1962:fig. 3). There are photographs of specimens of *S. guttatus* from India in Jones and Silas (1964:pl. 7) and Silas (1964:pl. 2), and there is a good photograph of a specimen from the Sea of Japan in Nakamura and Nakamura (1982:fig. 1B). A good color photograph of a specimen from the Persian Gulf is included in Kuronuma and Abe (1972: pl. 17).

Biology.—Little is reported in the literature about movements and migration of *S. guttatus* but it appears to be less migratory than *S. commerson*. Possible movements in the Gulf of Thailand might be deduced from seasonal changes in peak fishing months along the coast of Thailand. These peaks are November-December in eastern Thailand, late December-January in the northern part of the Gulf, and January-March in the western part of the Gulf (Tongyai 1970). Based on occurrence of ripe females and size of maturing eggs, spawning probably occurs from April to July around Rameswaram Island between India and Sri Lanka (Krishnamoorthi 1958). Ripe females 32.5-46.5 cm FL were taken in Thai waters in May. Larvae and juveniles have been reported from Indonesian and Indian waters but apparently the only certain accounts are those of Jones (1962) and Jones and Kumaran (1964) who illustrated four postlarvae (14.8, 22.9, 41.2, and 66.8 mm). As with other species of *Scomberomorus*, the food is primarily fishes. Juveniles in India feed mainly on teleosts, particularly clupeoids such as *Anchoviella* (Venkataraman 1961; Kumaran 1964; Rao 1964). Adults also feed mainly on teleosts with small quantities of crustaceans and squids (Thailand—Tongyai 1970, India—Rao 1964). Anchovies are particu-

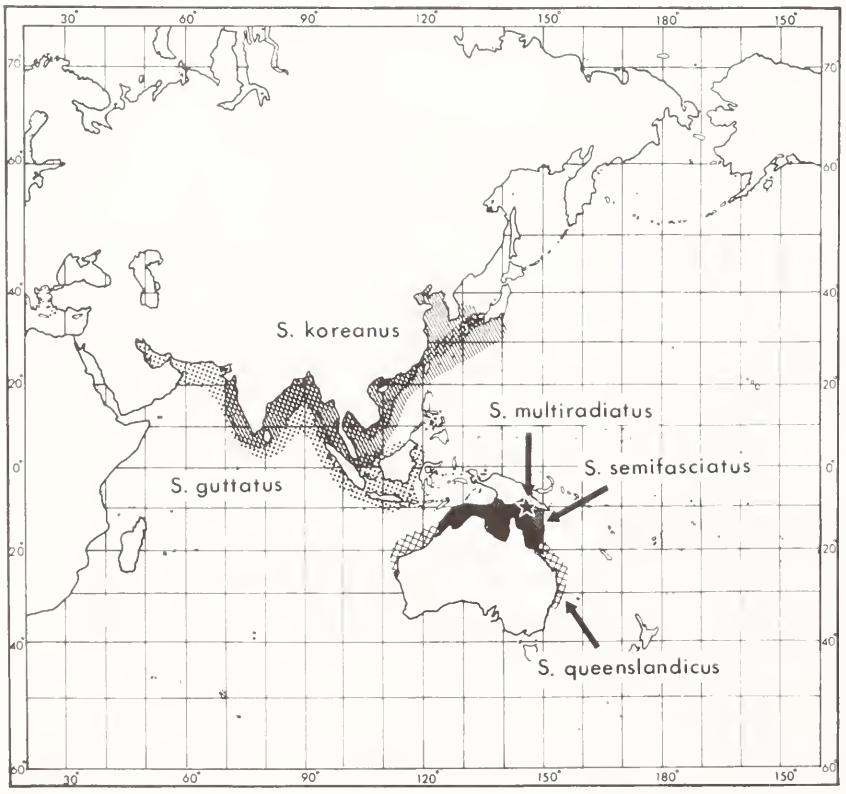


FIGURE 55.—Ranges of five Indo-West Pacific species of *Scomberomorus*: *S. guttatus*, *S. koreanus*, *S. semifasciatus*, *S. queenslandicus*, and *S. multiradiatus*.

larly important: *Stolephorus* in Singapore Straits (Tham 1950, 1953) and *Anchoviella* in Waltair, India (Rao 1964).

Interest to fisheries.—There are commercial or artisanal fisheries for *S. guttatus* in Cambodia (Merçeron 1970), Thailand (Tongyai 1971b), Malaysia (Pathansali 1968), and India, particularly in the lower Sundarbans, West Bengal (Banerjee and Chakrubarty 1972), the Balashore coast (Roy and Roy 1974), around Madras (Vijayaraghavan 1955), the Gulf of Mannar-Palk Bay area (Krishnamoorthi 1957), and Malwan, south of Bombay (Kaikini 1961). It is caught all year round in some areas (Cambodia—Merçeron 1970; Ramaswaram I., India—Krishnamoorthi 1957) but there are peaks of abundance that differ from region to region. It is taken in the non-monsoon months (September-May) along the Balashore coast south of Calcutta with the catch increasing from October to February (Roy and Roy 1974). Catches peak in September-October, December-February, and May in Waltair near Vishakhapatnam further south along the west coast of the Bay of Bengal (Venkata Subba Rao et al. 1981). The season extends from September-October to March-April in Vizhingam, southern India, (Gopalan Nayar 1958) with the peak catches usually in September or October. It is one of the principal species in the drift net seerfish fishery in India, but the catch is not identified to species in the statistics. Indonesia reported the only catch identified as *S. guttatus* (4,254-5,249 t/yr) in 1979-82 (FAO 1984). The primary gear in most areas appears to be the drift gill net which is set overnight, but it is also taken in bamboo stake traps and with hand lines in Thailand (Tongyai 1970) and by trolling or with hook and line in India and Malaysia (Rao 1964; Jones 1968; Pathansali 1968). It is utilized fresh or salted in most areas (India—Jones 1967; Cambodia—Merçeron 1970; Thailand—Tongyai 1971b). It can be stored on ice for 10-13 d (Shenoy and James 1974). Although less abundant than the Indian mackerels (*Rastrelliger* spp.), it is highly esteemed for food and commands a higher price in Thailand and India (Tongyai 1966a; Pathansali 1968).

Distribution.—Indo-West Pacific from Taiwan to the Gulf of Thailand, Java, and Sumatra west around the Bay of Bengal and Arabian Sea into the Persian Gulf (Fig. 55). The northernmost records are from Wakasa Bay, Japan (Nakamura and Nakamura 1982), Taiwan (FMNH 59284), Amoy (BMNH 1860.7.20.110), and Swatow, China (Reeves 1927). There are many records and specimens from Indochina, the Gulf of Thailand, and the East Indies. There are records and specimens of *S. guttatus* from Borneo (Bleeker 1860; Hardenberg 1936; Herre and Herald 1951; ANSP 72282) and Makassar, Celebes (RMNH 24096). The range extends further out in the East Indies than that of either *S. lineolatus* or *S. koreanus*, at least to Bali. The report of *S. guttatus* from Western Australia (McKay 1970) is based on a specimen (HUMZ F-423) of *S. queenslandicus*. Earlier reports of *S. guttatus* from Australia (Macleay 1881; Stead 1906, 1908; Rendahl 1923) are also based on *S. queenslandicus* (Munro 1943: 86). Early reports from New Zealand are based on "a damaged specimen of a *Cybium*, probably *C. guttatum*, was obtained at the Chatham Islands..." (Hutton 1895). This report has led to subsequent records (Hutton 1904; Phillipps 1927; Whitley 1968). We concur with Whitley's conclusion that this record is "very doubtful". The range extends west into the Persian Gulf (Kuronuma and Abe 1972; ZMK 3-4).

Geographic variation.—Morphometric data for five populations of *S. guttatus* were compared with ANCOVA (Table 17): Arabian Sea (n = 7-13), Bay of Bengal (n = 5-9), East Indies (n = 14-24), Gulf of Thailand (n = 10-17), and China (n = 22-31). Null hypotheses that the 5 sets of regression lines are coincident were accepted for 18 sets, rejected for 8 sets: Sn-1D, Sn-P_1, Head L, maximum depth, maxilla L, orbit (fleshy), interorbit, and 2D-C. The five populations were arranged geographically from west to east as listed above. No significant differences were found between populations in the Arabian Sea and Bay of Bengal, but there were significant differences between all other adjacent populations: Bay of Bengal vs. East Indies (Sn-P_1), East Indies vs. Gulf of Thailand (Interorbital), Gulf of Thailand vs. China (Sn-1D, interorbital, and 2D-C). The Arabian Sea and Bay of Bengal populations were combined, the regressions rerun, and compared with the other three populations with ANCOVA. Null hypotheses that the 4 sets of regression lines are coincident were accepted for 15 sets, rejected for 11 sets: Sn-1D, Sn-P_1, Head L, maximum body depth, Base 1D, Base 2D, Base A, maxilla L, orbit (fleshy), interorbital, and 2D-C. The Newman-Keuls Multiple Range Test was able to distinguish populations that differed significantly for 7 sets of regressions but could not do so for 4:

maximum body depth, Base 1D, Base 2D, and Base A. Significant differences were found between the Indian Ocean population and that in the East Indies and Gulf of Thailand population in one (interorbital); and between the Gulf of Thailand and China populations in two (Sn-1D and maxilla L).

One meristic difference was found between populations of *S. guttatus*. The Indian Ocean population has a mode of 50 vertebrae while populations in the East Indies, Gulf of Thailand, and China have modes of 51. Gill rakers were usually 11 and second dorsal rays 21 in all four populations.

Material examined.—Total 149 (63.3-760).

meas.: 144 (80.0-760): Persian Gulf (2); N Arabian Sea (6); Malabar coast of India (25); Gulf of Mannar (7); Coromandel Coast of India (6, **C. interruptum* Cuvier); "India" (4); Burma (2); Andaman Sea (3); East Indies (31, **C. crookewitii* Bleeker); Gulf of Thailand (17); China (33).

counts: 143.

diss.: 14 (367-548): Karachi, Pakistan (6); Cochin, India (1); Gulf of Mannar (4); Hong Kong (2).

Scomberomorus koreanus (Kishinouye) Korean Seerfish

Figure 56

Cybium kuhlii. Not of Cuvier, 1831. Day 1878: 254 (description, synonymy), pl. 46, fig. 2. Delsman 1931:402, 407 (vertebrae 20 + 25 = 45). Hardenberg 1931:140 (common, often found in river mouths; Bagan Si Api Api, Sumatra).

Cybium koreanum Kishinouye 1915:11 (original description; Korea), pl. 1, fig. 6. Kishinouye 1923:420-421 (description), pl. 21, fig. 35. Mori 1928:5 (Fusan, Korea; listed). Morice 1953:37 (villiform teeth on tongue).

Sawara koreanum. Soldatov and Lindberg 1930:112 (description after Kishinouye).

Cybium guttatum. Not of Bloch and Schneider 1801. Delsman 1931:402, 407 (vertebrae 20 + 25 = 45). Hardenberg 1931:141 (Bagan Si Api Api, Sumatra).

Scomberomorus guttatus. Not of Bloch and Schneider 1801. Hardenberg 1934:311 (Sumatra). Delsman and Hardenberg 1934:340-343 (in part, description, fishery), fig. 248 (in part, myomeres 13 + 33 = 46).

Scomberomorus koreanus. Munro 1943:68, 71 (placed in subgenus *Pseudosawara* Munro). Okada 1955:150 (description), fig. 137 (after Kishinouye). Kamohara 1967:43-44 (description, range), color pl. 22, fig. 3. Shiino 1972:71 (common name). Magnuson 1973:350 (short pectoral fin). *Devaraj 1976:79-87 (description, validation of species, comparison with *S. guttatus* and *S. semifasciatus*, synonymy), fig. 2 (745 mm adult; Palk Bay, India), fig. 3 (second dorsal and anal fins), fig. 4 (vertebral column), fig. 5 (preopercle and liver). Shiino 1976:231 (common name). Klawe 1977:2 (common name, range). *Devaraj 1977 (osteology). Collette 1979:24 (characters, range). Collette and Russo 1979:13 (diagnostic characters,

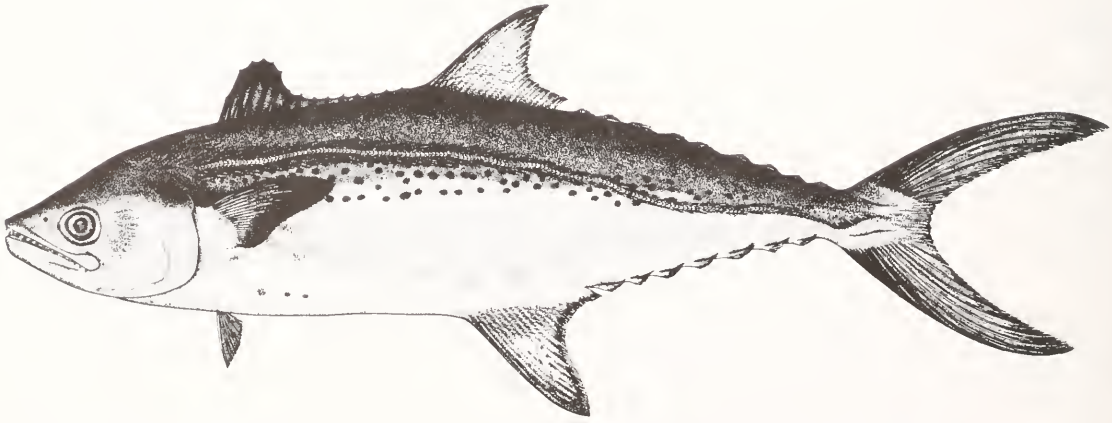


FIGURE 56.—*Scomberomorus koreanus*. Ning Po, China, 525 mm FL, NHMV uncat.

range). Nakamura and Nakamura 1982:445-446 (3 specimens; Wakasa Bay, Sea of Japan; description), figs. 1A, 2A. Kyushin et al. 1982: 249 (description, photograph). Cressey et al. 1983:264 (host-parasite list, 3 copepod species). Lee and Yang 1983:231 (Taiwan), fig. 22 (550 mm FL). Collette and Nauen 1983:66-67 (description, range), fig.

Scomberomorus semifasciatus. Not of Macleay 1884. Fraser-Brunner 1950:159 (*C. koreanus* placed in synonymy of *S. semifasciatus*).

Sawara koreana. Mori 1952:136 (listed; Fusan and Chinnampo, Korea).

Scomberomorus guttatus koreanus. Silas 1964: 313-314, 325-326, 328-329 (description and range in part).

Types.—*Cybium koreanum* Kishinouye 1915 was based on a specimen collected by Yojiro Wakiya on the west coast of Korea in 1913. There is no evidence to indicate that the specimen is still extant. Data from the original description: D XIV + 18-21 + IX; A 18-21 + VIII; GR 3 + 10 = 13; vertebrae 20 + 26 = 46.

Diagnosis.—The only species of *Scomberomorus* with four loops and five limbs to the intestine (Fig. 3f). Other species have two loops and three limbs or a straight intestine. It shares with *S. guttatus* the presence of numerous fine auxiliary branches that branch from the anterior part of the lateral line on the body (Fig. 56). Scapular foramen small (Fig. 43e) as in *S. guttatus* and *S. niphonius*. Supraoccipital crest high (Fig. 15a) as in *S. guttatus* and *S. multiradiatus*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Spines in first dorsal fin 14-17, usually 15 (Table 9); second dorsal fin rays 20-24, usually 22 or 23 (Table 10); dorsal finlets 7-9, usually 8 (Table 10); anal fin rays 20-24, usually 22 or 23 (Table 11); anal finlets 7-9, usually 7 or 8 (Table 11); pectoral fin rays 20-24, usually 22 or 23 (Table 12). Precaudal vertebrae 20 (Table 6); caudal vertebrae 26 or 27, usually 26 (Table 7); total vertebrae 46 or 47, usually 46 (Table 8). Gill rakers on first arch (1-2) + (9-12) = 11-15, usually 2 + (11-12) = 13-14 (Table 5). Morphometric characters given in Table 18.

Size.—Maximum size 150 cm FL and 15 kg in weight; matures at 75 cm and 2.25 kg (Kishinouye 1923); common to 60 cm.

Color pattern.—Nakamura and Nakamura (1982) described fresh specimens taken in Wakasa Bay in the Sea of Japan. Body greyish blue dorsally, silvery white laterally and ventrally. Several longitudinal rows of small brownish spots rather sparsely scattered along lateral median line. First dorsal fin membrane black. Pectoral, second dorsal, and caudal fins dark brown. Pelvic and anal fins silvery white.

There are good drawings of *S. koreanus* from Japan in Kishinouye (1923:pl. 21) and from India in Devaraj (1976:fig. 2), and there is a good photograph of a specimen from the Sea of Japan in Nakamura and Nakamura (1982:fig. 1A). There is a good color illustration of *S. koreanus* in Kamohara (1967:pl. 22) and a color photograph of a 411 mm specimen from the South China Sea in Kyushin et al. (1982:249).

Biology.—Little is known of the migrations or movements of *S. koreanus*. Kishinouye (1923) reported that it spawns at the mouth of Daidoko, near Chinnanpo, Korea, in July. Feeds on sardines, anchovies, and shrimps (Kishinouye 1923).

TABLE 18.—Summary of morphometric data of *Scomberomorus koreanus*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			30	160	812	386	201
Snout-A	‰	FL	30	443	547	493	20
Snout-2D	‰	FL	30	427	512	467	15
Snout-1D	‰	FL	30	215	254	241	9
Snout-P_2	‰	FL	29	224	267	247	11
Snout-P_1	‰	FL	29	189	223	209	9
P_1-P_2	‰	FL	28	99	127	114	7
Head length	‰	FL	30	187	224	207	11
Max. body depth	‰	FL	30	185	263	236	16
Max. body width	‰	FL	26	83	115	101	9
P_1 length	‰	FL	30	112	157	134	11
P_2 length	‰	FL	26	44	67	60	7
P_2 insertion-vent	‰	FL	29	192	265	227	19
P_2 tip-vent	‰	FL	26	135	197	165	19
Base 1D	‰	FL	29	198	270	217	14
Height 2D	‰	FL	26	112	190	165	21
Base 2D	‰	FL	30	120	189	161	14
Height anal	‰	FL	26	96	184	160	19
Base anal	‰	FL	30	100	171	154	15
Snout (fleshy)	‰	FL	30	63	77	70	3
Snout (bony)	‰	FL	30	56	68	62	3
Maxilla length	‰	FL	30	93	120	110	8
Postorbital	‰	FL	29	94	114	101	5
Orbital (fleshy)	‰	FL	30	21	42	33	7
Orbital (bony)	‰	FL	30	32	61	50	9
Interorbital	‰	FL	30	52	69	61	4
2D-caudal	‰	FL	29	508	586	550	21
Head length			30	35	152	78	37
Snout (fleshy)	‰	HL	30	310	367	340	13
Snout (bony)	‰	HL	30	271	335	300	12
Maxilla length	‰	HL	30	484	565	531	17
Postorbital	‰	HL	29	459	536	488	18
Orbit (fleshy)	‰	HL	30	110	197	157	27
Orbit (bony)	‰	HL	30	170	286	238	33
Interorbital	‰	HL	30	259	350	293	22

Interest to fisheries.—The fishery for this species was begun in Daidoko, Korea, by Japanese fishermen in 1917; it is caught in summer and autumn with drift nets and pound nets (Kishinouye 1923). It is usually not distinguished from other species of seerfishes but comprises an important part of the drift net fishery in Palk Bay and the Gulf of Mannar between southeastern India and Sri Lanka (Devaraj 1976).

Distribution.—Continental Indo-West Pacific from Japan, Korea, and China south to Singapore and Sumatra and west to Bombay, India (Fig. 55). The northern limit of the range is Wakasa Bay in the Sea of Japan (Nakamura and Nakamura 1982). This species usually does not occur north of the west and south coasts of Korea (Kishinouye 1923). Specimens obtained in the Tokyo markets apparently are usually imported from Korea (Okada 1955). There are museum specimens from Ningpo (MNHN 5513), Swatow, and Hong Kong (BMNH 1939.1.17.48) along the coast of China. There appear to be few specimens or records from the coast of Indochina or the Gulf of Thailand, but we have examined specimens from "Cochinchine" (MNHN A.6827). There are several reports and specimens from Sumatra (Bagan Api Api, Hardenberg 1931 as *Cybium kuhlii*; Delsman and Hardenberg 1934 as *S. guttatus*; ZMA 114.593), but the range apparently does not extend out further into the East Indies. Dependable Indian records are from Pondicherry (USNM 216698), Palk Bay, and the Gulf of Mannar (Devaraj 1976) on the east coast, and Bombay (ANSP 88360) on the west coast.

Geographic variation.—Morphometric data were compared by ANCOVA for three small samples of *S. koreanus*: India (n = 5), East Indies (n = 9), and Japan and China (n = 8-12). Null hypotheses that the 3 sets of regression lines are coincident were accepted for 25 sets, rejected only for body width. The Newman-Keuls Multiple Range Test showed that the population from Japan and China differed significantly in slope from that in the East Indies. The population in the East Indies did not differ significantly from that in India so these two populations were combined and retested. The only significant difference was again maximum body width and the combined India-East Indies population differed significantly from the Japan-China population (slopes 0.090, 0.123, Q = 5.987**). No meristic differences were found between populations.

Material examined.—Total 30 (160-812 mm FL).

meas.:	30 (160-812) Tokyo market (4); Hong Kong (4); Swatow and Ning-Po (4), China; Indochina (1); Sumatra (8); Indonesia (1); India (5).
counts:	30.
diss.:	6 (420-812): Tokyo market, probably Korean fish (4); Indonesia (1); Hong Kong? (1).

Scomberomorus lineolatus (Cuvier)
Streaked Seerfish

Figure 57

Cybium lineolatum Cuvier *in* Cuvier and Valenciennes 1831:170-172 (original description; Malabar, India). Cantor 1849:1092-1093 (description, range; Pinang). Bleeker 1852:40-41 (description, synonymy; East Indies). Bleeker

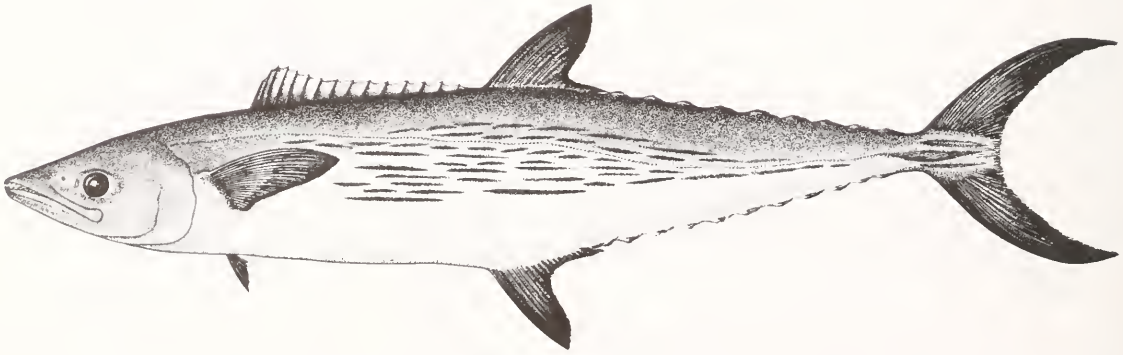


FIGURE 57.—*Scomberomorus lineolatus.* Cochin, India, 588 mm FL, USNM 223538.

1853:42 (India). Günther 1860:370 (description; Malaya). Bleeker 1861a:52 (Singapore; listed). Bleeker 1861b:74 (Pinang, Malaya; listed). Day 1873:225 (description, range). Day 1878:256 (description).

Scomberomorus lineolatum. Malpas 1926:74 (3 males, 54.5-82.5 cm TL, 1.1-3.4 kg, Ceylon). Frost 1928:329 (otolith similar to that of *S. regalis*).

Scomberomorus lineolatus. Munro 1943:68, 70 (placed in subgenus *Indocybium*; vertebral count of 21 + 29 = 50 pertains to another species of *Scomberomorus*, such as *S. guttatus*). De Beaufort 1951:235-236 (synonymy, description, range). Tham 1953:49 (Singapore Straits), 50 (correlation of catch with physical factors and presence of food fishes such as *Stolephorus* and *Clupea*). Scott 1959:114 (description; Malaya), photograph. Bauchot and Blanc 1961:372 (types of *Cybium lineolatum*). Jones 1962:117-119 (eggs, larvae, and juveniles). Jones and Silas 1961:197-198 (description, range), fig. 4 (680 mm adult), fig. 5C (not 5D as legend reads, lateral view of head), fig. 6D (gill arch), fig. 7E (caudal peduncle keels). Jones and Silas 1964: 58-61 (synonymy, description, range), pl. 7, fig. A (photograph of 740 mm specimen). Silas 1964:317, 323-324 (specimens from India only). Jones and Kumaran 1964:347 (larvae as yet undescribed). Blanc and Bauchot 1964:447 (types of *Cybium lineolatum*), pl. III, figs. 15, 16 (photographs of type-specimens). Rao 1964: 592-594 (teleosts constitute 97% of diet of juveniles, Waltair coast of India). Thiemmedh 1966:140 (common names). Collette 1966:367-368 (type of *Cybium lineolatum*). Tongyai 1966a:7-10 (synonymy, occurrence, Thailand), pl. 2D. Tongyai 1966b:3-15 (5 specimens, 46.5-76.5 cm FL; Terutao Is., Andaman Sea). Pathansali 1968:1002-1003 (fishery; Malaya). Silas 1968:1114 (fishery; Gulf of Mannar), pl. 3A (photograph of adult). Rajan et al. 1969:90 (outer channel; Chilka Lake, India). Tongyai 1970:559-561 (found in areas of low turbidity and high salinity offshore; Thailand). Merçeron 1970:72 (specimens from near Sihanoukville, Cambodia). Tongyai 1971a:16-18 (Thailand). Fernando 1972:524, 530 (incidental catches in trawls; Wadge Bank, Ceylon). Richards and Klawe 1972:14 (range), 92 (references to larvae and juveniles). Banerji 1973:129-130 (seerfish fishery; India). Magnuson 1973:350 (short pectoral fin). Orsi 1974:175 (listed; Vietnam). Tham 1974 (possible predator of *Stolephorus*). Shiino 1976:231 (common name). *Rao and Ganapati 1977:101-111 (postlarvae and juveniles; India). Klawe 1977:2 (common name, range). *Devaraj 1977 (osteology). Collette 1979:29 (characters). Collette and Russo 1979:13 (diagnostic characters, range). *Devaraj 1982 (age and growth). Cressey et al. 1983:264 (host-parasite list, 3 copepod species). Collette and Nauen 1983:68 (description, range), fig.

Scomberomorus guttatus. Not of Bloch and Schneider 1801. Fraser-Brunner 1950:160 (*Cybium lineolatum* placed in synonymy of *Scomberomorus guttatus*).

Indocybium lineolatum. Munro 1955:221 (description; Ceylon); fig. 651. Chacko et al. 1968: 1006 (fishery; Madras).

Types.—Holotype: MNHN A.6866; Malabar coast of India; Dussumier; 707 mm FL; D about XVII + 17 + IX; A 19 + X; P_1 21; RGR_1 2 + 1 + 8 = 11; pattern of three rows of elongate streaks still visible on type in 1975. Photograph of type published by Blanc and Bauchot (1964:pl. 3, fig. 15). Paratype: MNHN 6357; Mahé (Malabar Coast), Belenger; only head and tail of a fish about 710 mm FL (judging from head length of 145 mm). Photograph of paratype published by Blanc and Bauchot (1964:pl. 3, fig. 16).

Diagnosis.—The only species of *Scomberomorus* that has a pattern of short lines on its sides (Fig. 57). Other species have some spots, blotches, or bars, or are plain. Posterior end of maxilla greatly expanded as in *S. plurilineatus* and *S. semifasciatus*. Anterior end of premaxilla forms an acute angle (Fig. 22b). Ascending process of premaxilla very long as in *S. sinensis* and *Acanthocybium*. Supracleithrum wide (Fig. 41a), 53-57% of length, as in *S. niphonius*. Foramen between last pectoral radial and coracoid larger than in any other species of *Scomberomorus*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3g). Spines in first dorsal fin 15-18, usually 16 or 17 (Table 9); second dorsal fin rays 15-22, usually 17 or 18 (Table 10); dorsal finlets 7-10, usually 9 (Table 10); anal fin rays 17-22, usually 20 (Table 11); anal finlets 7-10, usually 9 or 10 (Table 11); pectoral fin rays 20-24, usually 23 (Table 12). Precaudal vertebrae 18-20, usually 19 (Table 6); caudal vertebrae 25-28, usually 27 (Table 7); total vertebrae 44-46, usually

46 (Table 8). Gill rakers on first arch (1-2) + (6-11) = 7-13, usually 2 + (8-9) = 10-11 (Table 5). Morphometric characters given in Table 19.

TABLE 19.—Summary of morphometric data of *Scomberomorus lineolatus*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			31	144	786	434	191
Snout-A	‰	FL	30	464	540	507	16
Snout-2D	‰	FL	29	453	525	502	17
Snout-1D	‰	FL	30	214	284	253	17
Snout-P_2	‰	FL	27	209	268	245	13
Snout-P_1	‰	FL	30	175	237	213	14
P_1-P_2	‰	FL	27	81	104	93	6
Head length	‰	FL	31	174	231	207	13
Max. body depth	‰	FL	27	153	211	181	11
Max. body width	‰	FL	25	65	117	96	13
P_1 length	‰	FL	28	117	156	140	11
P_2 length	‰	FL	20	45	70	56	7
P_2 insertion-vent	‰	FL	24	216	276	240	14
P_2 tip-vent	‰	FL	20	156	223	184	15
Base 1D	‰	FL	24	198	270	231	15
Height 2D	‰	FL	23	87	168	124	19
Base 2D	‰	FL	29	89	155	113	15
Height anal	‰	FL	22	80	148	118	15
Base anal	‰	FL	28	100	150	123	14
Snout (fleshy)	‰	FL	30	64	88	82	6
Snout (bony)	‰	FL	30	55	83	74	6
Maxilla length	‰	FL	30	93	136	113	11
Postorbital	‰	FL	30	75	108	92	8
Orbital (fleshy)	‰	FL	30	23	43	33	6
Orbital (bony)	‰	FL	29	34	64	48	9
Interorbital	‰	FL	29	47	61	57	3
2D-caudal	‰	FL	29	462	545	500	23
Head length			31	33	147	88	35
Snout (fleshy)	‰	HL	30	325	438	395	24
Snout (bony)	‰	HL	30	276	398	358	28
Maxilla length	‰	HL	30	473	596	547	24
Postorbital	‰	HL	30	404	512	443	24
Orbit (fleshy)	‰	HL	30	131	215	157	24
Orbit (bony)	‰	HL	29	188	284	231	30
Interorbital	‰	HL	29	255	292	275	10

Size.—Maximum size 80 cm FL.

Color pattern.—Body dark bluish dorsally, silvery white ventrally, marked with several rows of elongate lines (Fig. 57). First dorsal fin black anteriorly, white posteriorly.

There is a good drawing of a specimen from India in Jones and Silas (1962:fig. 4). There are also poor photographs in Jones and Silas (1964:pl. 7) and Silas (1968:pl. 3).

Biology.—Little has been reported in the literature on the biology of *S. lineolatus*. A ripe male (82.5 cm TL, 3.4 kg) was taken on Wadge Bank, off southern India on 2 October (Malpas 1926). A running ripe female (76.5 cm, 4.4 kg) was caught in January in the Bay of Bengal off Satun, Thailand, near the border with Malaysia (Tongyai 1966b). Postlarvae and juveniles (18.4-99.5 mm) were described from Waltair on the east coast of India by Rao and Ganapati (1977). Early stages were taken in shore seines in February-April, more advanced stages from boat seine catches in July-September. Juveniles feed on teleosts in India (Venkataraman 1961; Rao 1964).

Interest to fisheries.—There are small fisheries for *S. lineolatus* in the waters around Thailand, Malaysia, and India. It is taken from October to November in Thai waters of the Indian Ocean (Tongyai 1970). It is less abundant than either *S. commerson or S. guttatus* in the Gulf of Thailand and along the Thai coast of the Bay of Bengal being found in areas of lower turbidity and higher salinity than the other two species (Tongyai 1970). Fished for on both coasts of Malaysia, on the west coast from November to February in the north and March to July in the south, and on the east coast from February to March and August to November (Pathansali 1968). Species of *Scomberomorus* are taken on both coasts of Malaysia mainly by gill nets, but hand lines and trolling lines are also important on the east coast (Pathansali 1968). In India, there is an important coastal fishery for the three species of seerfishes of which *S. lineolatus* is the least common (Silas 1968). Small individuals, up to 50 cm, are taken, together with *S. commerson* and *S. guttatus*, during the multiple troll fishery season (May-September) in gill nets 5-12 mi off Tuticorin in the Gulf of Mannar, India (Silas 1968). Gill nets, hook and line, and trolling are the most important gear types in India (Silas 1968). *Scomberomorus* spp., or pla in-see in Thai, are highly esteemed foodfishes in Thailand and are consumed as spicy fish-burgers (tod-mun pla in-see) or high-quality salted fish (Tongyai 1966a). A monthly average of about 100 t, fresh or salted, is consumed in Bangkok alone (Tongyai 1966a). Seerfishes form a much smaller proportion of the catch in India than mackerels (*Rastrelliger* spp.), but are much in demand both fresh and salt-cured (Jones 1968).

Distribution.—Gulf of Thailand and Java west around India at least to Bombay (Fig. 58). There are records and specimens from Cambodia (Merçeron 1970) and Thailand (Tongyai 1966b, 1971a; CAS-GVF 60-286) in the Gulf of Thailand and from both coasts of Malaysia (Cantor 1849; Bleeker 1861b; Scott 1959; CAS SU 14100; BMNH 1860.3.19.215), Singapore Straits (Tham 1953), Java (USNM 72632), and Sumatra (NHMV 1874.I; ZMA 114.595). Central Indian Ocean reports and specimens are from Madras (ZSI 2156-7), Palk Bay (Devaraj 1977; dissections), Sri Lanka (Fernando

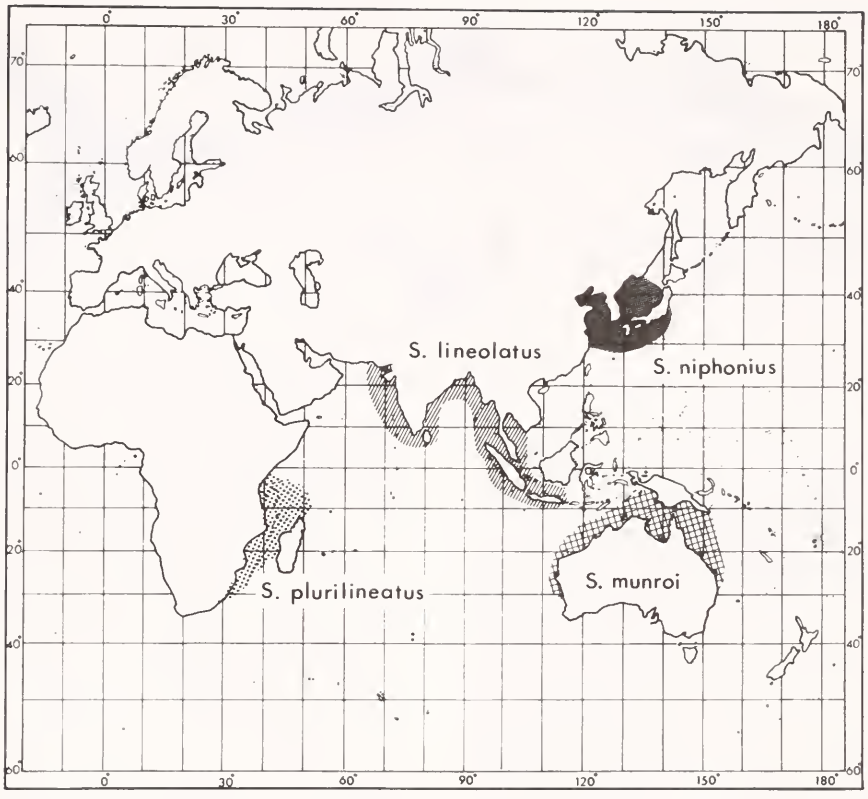


FIGURE 58.—Ranges of four Indo-West Pacific species of *Scomberomorus*: *S. lineolatus*, *S. plurilineatus*, *S. niphonius*, and *S. munroi*.

1972), Wadge Bank south of India (Malpas 1926), the Malabar coast (MNHN A.6866, holotype of *C. lineolatum*), Cochin (5 specimens measured, 1 dissected), and Bombay (MNHN A.5783). Records of *S. lineolatus* from East Africa (Williams 1960) are referrable to *S. plurilineatus*. The report of *S. lineolatus* from Western Australia (McKay 1970) was based on a specimen (HUMZ F-422) of *S. munroi*.

Geographic variation.—Comparisons of morphometric data by ANCOVA were made for four small samples of *S. lineolatus*: Arabian Sea (n = 7-12), Bay of Bengal (n = 4-6), Gulf of Thailand (n = 3-5), and East Indies (n = 4-6). No significant differences were found. No meristic differences were found between populations.

Material examined.—Total 31 (160-786 mm FL).

meas.: 31 (160-786): India, Arabian Sea (8, **C. lineolatum* Cuvier), Bay of Bengal (7); Andaman Sea (4); Gulf of Thailand (5); East Indies (7).

counts: 31.

diss.: 5 (417-786): Palk Strait (4); Cochin (1).

Scomberomorus maculatus (Mitchill) Spanish Mackerel

Figure 59

Scomber maculatus Mitchill 1815:426-427 (original description; New York), pl. 6, fig. 8.

Cybium maculatum. Cuvier 1829:200 (listed in footnote after *Sc. maculatus* Mitchill). Cuvier *in* Cuvier and Valenciennes 1831:181 (description; New York). Storer 1855:146-147 (synonymy, description; exceedingly rare in Massachusetts, 1 from Lynn and 4 from Provincetown), pl. 13, fig. 1. Holbrook 1860:68-72 (synonymy, description, color, anatomy, range in part), pl. 9, fig. 1. Günther 1860:372 (synonymy, description). Poey 1878:4 (synonymy, description).

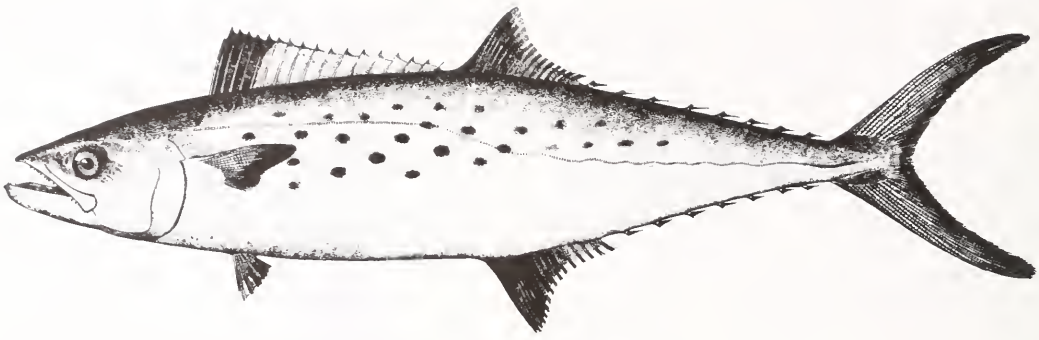


FIGURE 59.—*Scomberomorus maculatus*. New York market, 270 mm FL, USNM 15582. (From Goode 1884:pl. 93.)

Smiley 1881 (distribution, fishery). Ryder 1882 (gonads, embryology, development), pl. 1-4 (eggs, embryos, and larvae). Earll 1883 (name, description, distribution, movements, reproduction, fishery, artificial propagation), pl. 1.

Scomberomorus maculatus. Jordan and Gilbert 1882:426 (synonymy, range in part). Goode 1884:307-315 (range, fishery, reproduction), pl. 93. Meek and Newland 1884:232-234 (description, synonymy, range in part). Dresslar and Fesler 1889:442 (in key), 443 (synonymy and range in part), pl. 9. Jordan and Evermann 1896b:874 (description, synonymy in part). Jordan and Evermann 1900:pl. 134, fig. 368 (specimen from New York market). Jordan and Evermann 1902:285-286 (description, range), fig., photograph. Bean 1903:396-398 (synonymy, description, range in part, occurrence in New York). Smith 1907:190-192 (diagnosis, size, range, catch, price; North Carolina), fig. 77. Sumner et al. 1913:750 (references, occurrence, parasites; Buzzards Bay and Vineyard Sound, Mass.). Schroeder 1924:6-7 (most valuable food fish in the Florida Keys, range in part), fig. 3. Nichols and Breder 1927:123-124 (description, range, biology), fig. 170. Frost 1928 (sagitta similar to that of *S. regalis*). Hildebrand and Schroeder 1928:203-205 (description, range, biology, synonymy; Chesapeake Bay), fig. 115. Nichols 1929:229-230 (synonymy, range, description), fig. 82. Hildebrand and Cable 1938:508-518 (development of larvae and postlarvae; Beaufort, N.C.), figs. 2-10 (larvae and juveniles, 2.75-97 mm). Baughman 1941:17 (migratory off Texas coast). Munro 1943:67, 71-72 (placed in subgenus *Scomberomorus*). Fowler 1945:185-186 (synonymy, description; South Carolina). Gunter 1945:55 (occurrence, Texas), 145 (monthly production, 1937-42; Texas). La Monte 1945:26, 28 (description, range), color pl. 11. Breder 1948:127 (range in part, biology), fig. Erdman 1949:301 (range confined to coastal America and the N coast of Cuba; other West Indian records are misidentifications). Fraser-Brunner 1950: 159 (synonymy and range in part), fig. 29. Baughman 1950:244 (numerous Texas records throughout the year). Knapp 1950:142 (458 stomach contents, Texas). Rivas 1951:225-226 (synonymy in part, diagnosis, range). Taylor 1951:116-118 (biology, occurrence in North Carolina), 271-272 (angling in North Carolina). La Monte 1952:50 (description, range), color pl. 18. Bigelow and Schroeder 1953:347-348 (description, range in part, only a stray in the Gulf of Maine), fig. 182. Pew 1954:26 (description, range, habits), fig. 23. Mather and Day 1954: 185 (comparison of W and E Atlantic specimens; *S. tritor* at best racially distinct from *S. maculatus*). Briggs 1958:286 (range in part). Springer and Pirson 1958:175 (catch in Texas). *Mago Leccia 1958 (osteology, comparisons with *S. regalis* and *S. cavalla*), figs. *Klima 1959 (distribution, biology). Moe 1963: 109 (second most fished for species by private boats in Florida). Jorgensen and Miller 1968: 9, 13 (SL-FL-TL conversions). *Mendoza 1968 (biology; Veracruz). Lyles 1969:1-15 (landings, in part). Wollam 1970 (development, pigmentation, counts, and measurements; 175 larvae and juveniles, 3.1-25 mm SL, from the Gulf of Mexico), figs. 2, 3, 6A (larvae and juveniles, 3.1-25 mm SL). Beardsley and Richards 1970:5 (length-weight of 35 specimens from SE Florida, 330-770 mm FL, 0.45-4.76 kg). Farragut 1972 (use of antioxidants to prevent rancidity during frozen storage). Richards and Klawe 1972:14 (range in part), 92-93 (references to eggs and

larvae). Miyake and Hiyasi 1972:III-3 (in key); IV-11 (common names). Dwinell and Futch 1973 (188 larvae and juveniles, 2.8-42.2 mm SL, caught in June, Aug., and Sept., NE Gulf of Mexico). Márquez 1973 (distribution, biology, fishery). *Powell 1975 (age, growth, reproduction; Florida). *Berrien and Finan 1977b (in part; species synopsis). Klawe 1977:2 (common names, range). Fritzsche 1978:126-132 (description, larval development), figs. 70-74 (eggs, larvae, and juveniles). Collette 1978: Scombm 5 (description, range), figs. Collette et al. 1978:274-275 (comparison with other American species of *Scomberomorus*). Manooch et al. 1978 (annotated bibliography). Pristas and Trent 1978:582-588 (most abundant spring-fall; St. Andrew Bay, Fla.). Collette 1979:29 (characters, range). Collette and Russo 1979:13 (diagnostic characters, range). Trent and Anthony 1979 (commercial and recreational fisheries in U.S.). Doi and Mendizábal 1979 (Mexican catch). Meaburn 1979 (heavy metal contamination). Hale 1979 (preservation technology). Amezcua-Linares and Yáñez-Arancibia 1980:86-90 (Campeche, Mexico). McEachran et al. 1980 (larvae off Texas coast). Sutherland and Fable 1980 (annual migration from wintering grounds off S Florida and Campeche to summer grounds along the N coast of the Gulf of Mexico, return migration in fall). Deardorff and Overstreet 1981 (larvae of 4 forms of the anisakid nematode *Hysterothylacium* found in mesentary of specimens from the Gulf of Mexico). Johnson 1981 (electrophoresis; NW Florida). Skow and Chittenden 1981 (differences between Atlantic coast and Gulf of Mexico populations by hemoglobin electrophoresis). Richardson and McEachran 1981 (larvae 1.8-2.9 mm SL, pigment characters, measurements; Gulf of Mexico), fig. 1B (2.1 mm larva). Naughton and Saloman 1981 (stomach contents of 344 juveniles, 117-432 mm FL; Cape Canaveral, Fla., and Galveston, Tex.; diet mainly clupeoids). Adkins and Bourgeois 1982:12-13, 32-35, 48 (gill net; Louisiana). Cressey et al. 1983:264 (host-parasite list, 4 copepod species). Collette and Nauen 1983:69-70 (description, range), fig. Saloman and Naughton 1983b (food in U.S. waters).

Types.—*Scomber maculatus* Mitchill 1817 was based on a 19-in (482.6 mm) fish from New York. No types known to be extant. The figure (pl. 6, fig. 8) and description (about 20 yellowish spots decorate sides; more than half anterior part of first dorsal fin black, remainder white) leave no doubt as to identity of name.

Diagnosis.—*Scomberomorus maculatus* possesses nasal denticles as do the other five species of the *regalis* group (*brasiliensis*, *concolor*, *regalis*, *sierra*, and *tritor*) and has an artery branching from the fourth left epibranchial artery as do all the species in the group except *S. tritor*. Like *S. concolor*, *S. maculatus* lacks the shunt from the fourth right epibranchial artery to the coeliacomesenteric artery (Fig. 7c). It also has more vertebrae (51-53) than any of the other five species in the group (46-49). Intercalar spine absent as in the other five species of the *regalis* group and *S. niphonius*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3h). Spines in first dorsal fin 17-19, usually 18 (Table 9); second dorsal fin rays 17-20, usually 18 or 19 (Table 10); dorsal finlets 7-9, usually 8 or 9 (Table 10); anal fin rays 17-20, usually 19 or 20 (Table 11); anal finlets 7-10, usually 8 or 9 (Table 11); pectoral fin rays 20-23, usually 21 (Table 12). Precaudal vertebrae 21 or 22, usually 21 (Table 6); caudal vertebrae 30 or 31 (Table 7); total vertebrae 51-53, usually 51 or 52 (Table 8). Gill rakers on first arch (1-4)+(8-13)= 10-16, usually 2+(10-11)=12-14 (Table 5). Morphometric characters given in Table 20.

Size.—Maximum size 77 cm FL, 4.8 kg (Beardsley and Richards 1970). Sexual maturity in Florida is attained by age II, at 25-32 cm FL for females, 28-34 cm for males (Klima 1959). Length-weight equations have been presented for populations in Florida (Powell 1975) and Veracruz (Doi and Mendizábal 1979).

Color pattern.—Dark bluish above, silvery below, sides marked with about three rows of round to elliptical dark spots (Fig. 59), orange in life. First dorsal fin black anteriorly and at distal margin posteriorly, basal part of posterior membranes white.

There is a color painting of an *S. maculatus* in La Monte (1945:pl. 11, 1952:pl. 18), and a black and white photograph of one in Jordan and Evermann (1902). The drawing published by Goode (1884:pl. 93) is included here as Figure 59.

Biology.—Summaries of biological information

have been presented by Mendoza (1968), Márquez (1973), and Berrien and Finan (1977b). There is also a useful annotated bibliography by Manooch et al. (1978). The Spanish mackerel is clearly a migratory species that moves north from Florida along the Atlantic coast of the United States and north and west along the coast of the Gulf of Mexico in the spring and returns in the fall, but the details of the migration are not completely known. There are large concentrations in the winter in Florida and the Florida Keys (Beaumariage 1970) which move north to reach Charleston, S.C., in late March, North Carolina in April, Chesapeake Bay in May, and Sandy Hook, N.J., to Narragansett Bay, R.I., by late July (Earll 1883; Beaumariage 1970). Schools also move north along the Gulf coast of Florida in the spring (Moe 1972), and west across the northern Gulf from Panama City, Fla., to Mobile, Ala. (Sutherland and Fable 1980), and possibly on into Texas reaching Galveston in early March and Port Aransas in late March (Baughman 1941). There is also north-south migration along the Mexican coast, from south to north in March-April, north to south in August-November (Mendoza 1968). Tag returns support the Panama City to Mobile and Port Aransas to Veracruz migrations (Sutherland and Fable 1980). Spawning takes place in New York-New Jersey late August-late September, in Chesapeake Bay mid-June to the end of summer, and in the Carolinas starting in April (Earll 1883). Ripe females were found in Florida from July to September by Klima (1959) and from April to September by Powell (1975). Powell felt that individuals spawned repeatedly in a prolonged spawning season in Florida. Spanish mackerel spawn from May to September in waters <50 m over the inner continental shelf of Texas (McEachran et al. 1980). Spawning in Veracruz takes place in July-September (Mendoza 1968). Early studies on developing eggs and larvae (to 6 d old) were carried out by Ryder (1882) in North Carolina. Larvae have been described from North Carolina (14-20 mm, Hildebrand and Cable 1938; some misidentified, see Wollam 1970), the west coast of Florida (3.1-35.0 mm, June-September, Wollam 1970), the northeastern Gulf of Mexico (2.8-42.2 mm SL, June-September, Dwinell and Futch 1973), and Texas (1.8-11.5 mm SL, May-September, McEachran et al. 1980). Most were taken over the middle and

TABLE 20.—Summary of morphometric data of *Scomberomorus maculatus*. FL = fork length, HL = head length.

Character			Atlantic					Gulf of Mexico					Total				
			N	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD
Fork length			24	163	712	330	137	36	152	593	307	95	60	152	712	316	113
Snout-A	‰	FL	24	515	570	538	14	36	507	565	534	14	60	507	570	536	14
Snout-2D	‰	FL	24	478	540	505	14	36	466	543	502	16	60	466	543	503	15
Snout-1D	‰	FL	24	227	260	240	10	36	226	258	242	7	60	226	260	241	8
Snout-P_2	‰	FL	22	216	279	249	14	32	228	300	263	17	54	216	300	257	17
Snout-P_1	‰	FL	24	199	247	217	14	36	193	261	217	12	60	193	261	217	13
P_1-P_2	‰	FL	21	95	121	108	8	34	97	132	111	9	55	95	132	110	9
Head length	‰	FL	24	195	281	213	18	36	195	227	211	9	60	195	281	212	13
Max. body depth	‰	FL	18	168	232	194	19	33	178	228	198	12	51	168	232	197	15
Max. body width	‰	FL	18	70	110	89	12	36	65	137	92	15	54	65	137	91	14
P_1 length	‰	FL	24	114	146	131	7	35	107	140	129	8	59	107	146	129	8
P_2 length	‰	FL	21	43	66	55	6	33	35	68	50	9	54	35	68	52	8
P_2 insertion-vent	‰	FL	22	241	305	270	16	33	223	299	259	19	55	223	305	263	19
P_2 tip-vent	‰	FL	21	186	246	215	18	31	175	233	208	13	52	175	246	211	15
Base 1D	‰	FL	24	236	288	258	13	36	222	286	254	14	60	222	288	256	13
Height 2D	‰	FL	21	92	153	124	14	28	108	141	125	10	49	92	153	125	12
Base 2D	‰	FL	24	109	150	128	10	35	110	158	128	11	59	109	158	128	11
Height anal	‰	FL	23	97	140	117	13	31	88	133	119	12	54	88	140	118	12
Base anal	‰	FL	24	100	157	122	14	36	101	147	124	10	60	100	157	123	12
Snout (fleshy)	‰	FL	24	73	86	78	3	36	74	90	80	4	60	73	90	80	4
Snout (bony)	‰	FL	24	59	78	69	4	23	63	84	72	5	47	59	84	70	5
Maxilla length	‰	FL	24	108	134	117	7	36	110	136	120	6	60	108	136	119	6
Postorbital	‰	FL	23	87	108	98	5	36	84	101	95	4	59	84	108	96	4
Orbital (fleshy)	‰	FL	24	24	47	34	7	35	26	47	34	4	59	24	47	34	5
Orbital (bony)	‰	FL	24	41	62	50	7	36	40	65	52	6	60	40	65	51	7
Interorbital	‰	FL	24	51	60	56	2	36	52	63	57	3	60	51	63	56	3
2D-caudal	‰	FL	23	462	521	493	19	36	438	524	483	22	59	438	524	487	21
Head length			24	38	147	69	27	36	34	129	65	20	60	34	147	67	23
Snout (fleshy)	‰	HL	24	271	401	369	25	36	346	416	381	16	60	271	416	376	21
Snout (bony)	‰	HL	24	237	360	327	25	23	325	385	343	15	47	237	385	335	22
Maxilla length	‰	HL	24	401	572	552	34	36	546	628	568	15	60	401	628	562	25
Postorbital	‰	HL	23	317	496	461	37	36	407	486	450	16	59	317	496	454	27
Orbit (fleshy)	‰	HL	24	103	204	159	27	35	121	216	160	17	59	103	216	160	21
Orbit (bony)	‰	HL	24	153	284	234	29	36	186	308	246	27	60	153	308	242	28
Interorbital	‰	HL	24	204	296	264	20	36	234	296	268	13	60	204	296	266	16

inner continental shelf, over depths from 12 to 50 m, off Texas at surface water temperatures of 19.6°-29.8° C and salinities of 28.3-37.4‰ (McEachran et al. 1980). Summaries of previous larval work and illustrations of larvae 2.6-13.5 mm and of juveniles 14-97 mm are contained in Fritzsche (1978). As with other members of the genus, food consists chiefly of small fishes with lesser quantities of penaeoid shrimps and cephalopods. Clupeoids such as menhaden (*Brevoortia*), alewives (*Alosa*), thread herring (*Opisthonema*), Spanish sardine (*Sardinella*), and anchovies (*Anchoa*) are particularly important in North Carolina, Florida, Texas, and Veracruz (Earll 1883; Knapp 1950; Miles and Simmons 1951; Klima 1959; Mendoza 1968; Naughton and Saloman 1981; Saloman and Naughton 1983b). Juveniles (100-400 mm FL) ate more anchovies (Naughton and Saloman 1981; Saloman and Naughton 1983b) than adults did. Other fishes commonly consumed include Carangidae, Mugilidae, and Trichiuridae (Klima 1959; Saloman and Naughton 1983b).

Interest to fisheries.—The Spanish mackerel is a valued fish to recreational or commercial fisheries throughout its range. The fishery along the Atlantic coast of the United States north of southern Florida is seasonal (Klima 1959): late July to September from Rhode Island to New Jersey (Earll 1883), May or June to September in Chesapeake Bay (Hildebrand and Schroeder 1928), April to June on the way north, and September-October on the way south through the Carolinas (Smith 1907; Taylor 1951). The fishery in southern Florida is concentrated in the winter months, October-February or March (Klima 1959; Beaumariage 1970). In northwest Florida, the fishery peaks March-April (Beaumariage 1970); in Louisiana in June and October (Adkins and Bourgeois 1982); and in Texas March-April and July-September (Springer and Pirson 1958). As in the Carolinas, there are two major capture seasons in Veracruz: 45% of the annual production is taken March-April during the northward migration and 30% October-December in the southward migration (Doi and Mendizábal 1979). The beginnings of the Spanish mackerel fishery in the United States were discussed by Earll (1883) and a historical summary of the U.S. catch from 1887 to 1967 was provided by Lyles (1969). The commercial fishery began along the middle Atlantic and Chesapeake Bay areas before 1850, and by 1880 about 86% of the total U.S. catch of 1.9 million pounds was landed in the Chesapeake Bay area (Trent and Anthony 1979). Since 1950, over 92% of the total U.S. catch has been landed in Florida (Trent and Anthony 1979). In 1976 about 18 million pounds valued at about $3.2 million were landed by commercial fishermen in the United States; in 1970 an estimated 23 million pounds were landed by recreational fishermen (Trent and Anthony 1979). Spanish mackerel is second in volume among Mexico's Gulf of Mexico fisheries with an average annual production from 1968 to 1976 of 4,900 t (Doi and Mendizábal 1979). Most of this (80%) is produced in the state of Veracruz with lesser amounts from Campeche (15%) and Yucatan (5%). The early fishery in the United States utilized trolling lines, gill nets, and pound nets (Earll 1883). The commercial fishery in Florida utilizes stab or floating gill nets, which capture fish of age II-III, 30-65 cm FL (52% 36-41 cm), and hook and line, which captures smaller fish, age I-II, 21-69 cm FL (38% 33-35 cm) (Klima 1959). Larger vessels now entering the fishery have power-rollers to retrieve the nets which are mostly nylon; airplane spotter pilots locate the fish (Trent and Anthony 1979). Recreational anglers catch Spanish mackerel from boats while trolling or drifting and from boats, piers, jetties, and beaches by casting, livebait fishing, jigging, and drift fishing (Trent and Anthony 1979). Fishermen in Veracruz employ beach seines (chinchorros playeros), gill nets (redes agalleras), trolling spoons (curricanes), and trap nets (almadrabas) (Doi and Mendizábal 1979). Nearly all the catch is consumed fresh, frozen, or smoked (Lyles 1969). A few attempts have been made at canning Spanish mackerel but the product has not been widely accepted (Earll 1883; Lyles 1969). Frozen fish begin to show signs of rancidity after as little as 3 mo time in frozen storage, a problem which has been treated with antioxidants and EDTA (Farragut 1972; Hale 1979).

Distribution.—Western Atlantic Ocean from Massachusetts south along the Atlantic coast of the United States and the coast of the Gulf of Mexico from Florida to Yucatan, Mexico (Fig. 49). There are several summer records from the southern side of Cape Cod, Buzzards Bay, Woods Hole, and Vineyard Sound (Sumner et al. 1913; Bigelow and Schroeder 1953), but only strays are known from further north. Storer (1855) recorded the capture of an individual at Lynn in Massachusetts Bay and stated that individuals had been obtained at Provincetown, at the tip of Cape Cod, and at Monhegan Island in Maine. There do not appear to

be any extant specimens to verify these records; there is one specimen labelled only as "Cape Cod" (MCZ 23929). The known southern limit of the range is Progreso, Yucatan (MCZ 32894); it is replaced by *S. brasiliensis* from Belize to Rio de Janeiro and by *S. regalis* in the Bahamas and West Indies. Reports of *S. maculatus* from the West Indies (except for the north coast of Cuba) are referrable to *S. regalis* (Erdman 1949), those from the eastern Pacific are based on *S. sierra*, and those from the eastern Atlantic on *S. tritor*.

Geographic variation.—Morphometric characters were compared for two populations of *S. maculatus* by ANCOVA (Table 20): Atlantic coast of the United States (n = 18-24) and Gulf of Mexico (n = 28-36). Null hypotheses that the 2 sets of regression lines are coincident were accepted for 20 sets of regressions and rejected for 6: Sn-1D, Sn-P_2, P_1L, Snout (fleshy), Snout (bony), and maxilla length.

There is also a difference in vertebral numbers between the eastern U.S. and Gulf of Mexico populations. The eastern U.S. population usually has 31 caudal and 52 total vertebrae ($\bar{x}$ 30.4, 51.5), the gulf population has 30 or 31 caudal and 51 or 52 total vertebrae ($\bar{x}$ 30.9, 52.1).

The Gulf of Mexico and eastern U.S. populations also differ electrophoretically. Skow and Chittenden (1981) found differences in hemoglobin phenotypes between samples from Port Aransas, Tex., and Beaufort, N.C.

Material examined.—Total 69 (152-712 mm FL).

meas.: 60 (152-712): Atlantic coast of U.S. (24); Gulf of Mexico coast of U.S. (35); Yucatan (1).
counts: 67.
diss.: 16 (281-712): Va.-N.C. (3); Ga.-Fla. (7); St. Andrews Bay, Gulf of Mexico, Fla. (6).

Scomberomorus multiradiatus Munro
Papuan Seerfish

Figure 60

Scomberomorus multiradiatus Munro 1964:168-169 (original description; Gulf of Papua off mouth of Fly R.), fig. 12 (holotype). Munro 1967:200 (description), fig. 339. Magnuson 1973:350 (short pectoral fin). Kailola 1975:235 (4 specimens listed; Orokolo Bay, Tureture, 17 mi W of Fly R.). Klawe 1977:2 (range, common name). Kailola and Wilson 1978:34 (trawled in Gulf of Papua), 60 (number of fin rays). Collette 1979:29 (diagnostic characters). Collette and Russo 1979:13 (diagnostic characters, range). Lewis 1981:16 (photograph, biology). Cressey et al. 1983:264 (host-parasite list, 2 copepod species). Collette and Nauen 1983: 70-71 (description, range), fig.

Types.—Holotype: CSIRO C.3172; off northern mouth of Fly River, Papua New Guinea; MV *Fairwind*; 1948-50; 232 mm FL; D XVII + 23 + VIII; A 28 + VI; P_1 23-23; RGR_1 0 + 1 + 2 = 3; vertebrae 20 + 35 = 55; no spots or vertical bars. Holotype illustrated by Munro (1964:fig. 12, 1967:fig. 339).

Diagnosis.—The species of *Scomberomorus* with the most vertebrae (54-56) and the fewest gill

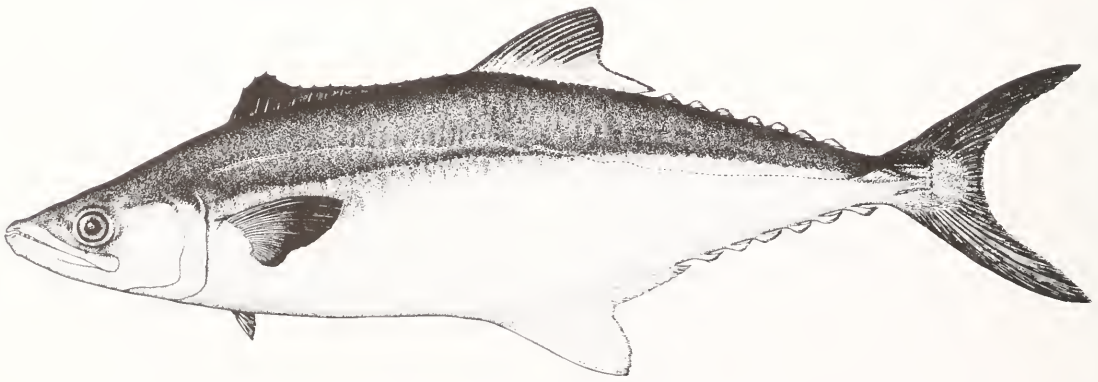


FIGURE 60.—*Scomberomorus multiradiatus*. Gulf of Papua, 312 mm FL, USNM 233696.

rakers (1-4) compared with the other 17 species (vertebrae 41-53, gill rakers 1-27). It has the most rays in the anal fin (25-29, compared with 15-24 in the other 17 species). Posterior end of maxilla only slightly expanded as in *S. sinensis*. Supraoccipital crest high as in *S. guttatus* and *S. koreanus*. Supracleithrum narrow (Fig. 41b), 43-53% of length as in *S. sinensis*, *semifasciatus*, and *sierra*. Foramen between last pectoral radial and coracoid smaller than in any other species of *Scomberomorus*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3i). Spines in first dorsal fin 16-19, usually 17 or 18 (Table 9); second dorsal fin rays 21-25, usually 23 or 24 (Table 10); dorsal finlets 7-9, usually 7 or 8 (Table 10); anal fin rays 25-29, usually 26-28 (Table 11); anal finlets 6-8, usually 6 (Table 11); pectoral fin rays 20-23, usually 21 or 22 (Table 12). Precaudal vertebrae 20 or 21 (Table 6); caudal vertebrae 34-36, usually 34 or 35 (Table 7); total vertebrae 54-56, usually 55 or 56 (Table 8). Gill rakers on first arch 0 + (1-4) = 1-4, usually 0 + (2-3) = 2-3 (Table 5). Morphometric characters given in Table 21.

TABLE 21.—Summary of morphometric data of *Scomberomorus multiradiatus*. FL = fork length, HL = head length.

Character			*N*	Min.	Max.	Mean	SD
Fork length			27	203	350	253	39
Snout-A	‰	FL	27	471	540	505	15
Snout-2D	‰	FL	27	448	508	477	15
Snout-1D	‰	FL	27	230	268	249	9
Snout-P_2	‰	FL	27	228	255	243	7
Snout-P_1	‰	FL	27	201	229	213	7
P_1-P_2	‰	FL	26	93	118	102	6
Head length	‰	FL	27	198	247	208	8
Max. body depth	‰	FL	27	205	265	228	16
Max. body width	‰	FL	27	81	113	95	9
P_1 length	‰	FL	22	121	143	131	5
P_2 length	‰	FL	25	29	56	40	6
P_2 insertion-vent	‰	FL	26	204	299	247	19
P_2 tip-vent	‰	FL	24	160	269	207	24
Base 1D	‰	FL	25	188	243	216	13
Height 2D	‰	FL	17	144	186	167	12
Base 2D	‰	FL	27	154	198	177	13
Height anal	‰	FL	20	151	178	164	8
Base anal	‰	FL	27	176	268	216	18
Snout (fleshy)	%	FL	27	70	84	77	3
Snout (bony)	%	FL	27	59	74	67	4
Maxilla length	%	FL	27	117	134	125	3
Postorbital	%	FL	27	77	96	86	6
Orbital (fleshy)	%	FL	27	30	41	34	3
Orbital (bony)	%	FL	27	43	60	52	4
Interorbital	%	FL	27	51	71	58	5
2D-caudal	%	FL	24	470	522	494	15
Head length			27	42	73	53	9
Snout (fleshy)	%	HL	27	317	407	372	18
Snout (bony)	%	HL	27	278	349	321	19
Maxilla length	%	HL	27	514	630	603	21
Postorbital	%	HL	27	339	469	415	35
Orbit (fleshy)	%	HL	27	121	195	165	16
Orbit (bony)	%	HL	27	190	287	252	23
Interorbital	%	HL	27	257	342	280	22

Size.—Maximum size 35 cm FL, 0.5 kg, the smallest species in the genus, sexually mature at < 30 cm (Lewis 1981).

Color pattern.—Dark bluish black dorsally, silvery white ventrally, with no spots, blotches, or bars (Fig. 60). First dorsal fin black anteriorly and along distal edge posteriorly with some white at base of fin posteriorly. The only previously published figures were of the holotype by Munro (1964:fig. 12, 1967:fig. 339) and a photograph by Lewis (1981:16).

Biology.—Schooling and other behavior unknown (Lewis 1981).

Interest to fisheries.—Trawled in the Gulf of Papua but too small to be of any commercial significance.

Distribution.—Restricted to shallow turbid waters of the Gulf of Papua off the mouth of the Fly River (Fig. 55). The western known limit is Tureture village, 12 mi west of Daru (Kailola 1975; DASF FO 2851), and the eastern limit Freshwater Bay at Kerema (lat. 8°12′S, long. 145°59′E; Kailola 1975; several dissected specimens, USNM).

Material examined.—Total 28 (203-350 mm FL).

meas.: 27 (203-350): off Fly R., Gulf of Papua (**S. multiradiatus*).
counts: 28.
diss.: 4 (224-323).

Scomberomorus munroi Collette and Russo
Australian Spotted Mackerel

Figure 61

Scomberomorus niphonius. Not of Cuvier 1831. Munro 1943:86-90 (first Australian record, description, range) pl. vii, fig. A. Serventy 1950: 19 (throughout N Australia, S to Kimberly). Roughley 1951:110 (description), pl. 45 (fig. after Munro 1943). Taylor 1964:282 (Arnhem Land; listed after Munro 1958a). Marshall 1964:364-365 (description after Munro 1943), pl. 50, fig. 351. Marshall 1966:205 (description), pl. 50, fig. 351. Kailola 1974:72 (description, first record from Papua New Guinea). Kailola 1975: 237 (listed, fish reference collection). Zhang and Zhang 1981:104 (Australia).

Sawara niphonia. Not of Cuvier 1831. Munro

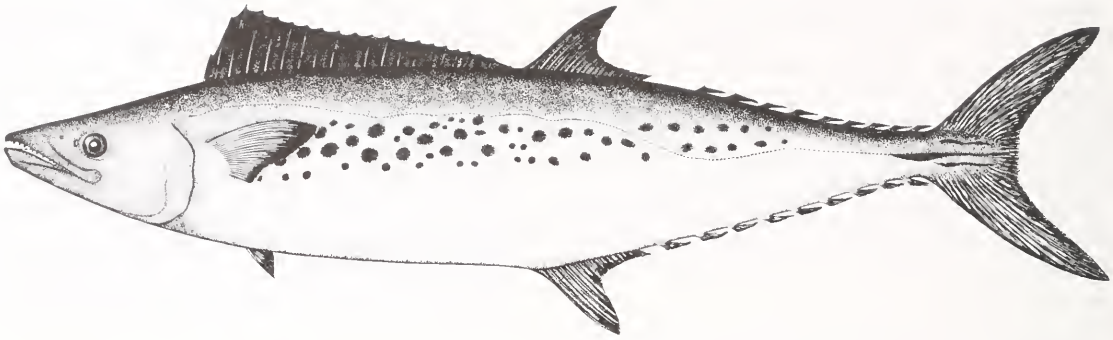


FIGURE 61.—*Scomberomorus munroi*. Deception Bay, Queensland, 740 mm FL, USNM 218387, holotype.

1958a:20 (description; new record for W Australia); fig. Whitley 1964a:240 (fig. 5, range), 252 (range, size). Whitley 1964b:48 (listed). Grant 1965:175 and 1972:104 (description after Munro 1958a), fig. Grant 1975:162 (description), 163 (color pl. 41). Grant 1978:190 (description), 191 (color pl. 73).

Sawara niphonius. Not of Cuvier 1831. Rohde 1976 (no monogenes found on 1 specimen from Coffs Harbour, N.S.W.).

Scomberomorus sp. Collette 1979:29 and Collette and Russo 1979:13 (Australian population referred to *S. niphonius* actually an undescribed species).

Scomberomorus munroi Collette and Russo 1980: 243-248 (original description; Australia, Papua New Guinea), fig. 1 (holotype). Lewis 1981: 18 (photograph, biology). Grant 1982:622 (description), 623 (color pl. 323). Cressey et al. 1983:264 (host-parasite list, 4 copepod species). Collette and Nauen 1983:71-72 (description, range), fig.

Types.—Holotype: AMS I.21029-001; Deception Bay N of Brisbane, Queensland; M. Dredge; 15 May 1975; 705 mm FL; D XXI+18+X; A 18+X; $P_1$22; RGR_1 2+1+7=10; vertebrae 22+30=52. Paratypes: 10 (373-820 mm FL) from Queensland and southern coast of Papua New Guinea (see Collette and Russo 1980:247).

Diagnosis.—This species differs from all other species of *Scomberomorus* in lacking an anterior process on the outer surface of the head of the maxilla (Fig. 23b). It is superficially similar to *S. niphonius* in being spotted and having many spines (20-22) in the first dorsal fin. It differs from *S. niphonius* in having the usual two loops and three limbs to the intestine instead of having a straight intestine, and in having more vertebrae (50-52, usually 51 vs. 48-50, usually 49).

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3j). Spines in first dorsal fin 20-22, usually 20 or 21 (Table 9); second dorsal fin rays 17-20, usually 18 (Table 10); dorsal finlets 9 or 10, usually 9 (Table 10); anal fin rays 17-19, usually 17 or 18 (Table 11); anal finlets 8-10, usually 9 (Table 11); pectoral fin rays 21-23, usually 21 or 22 (Table 12). Precaudal vertebrae 21 or 22, usually 22 (Table 6); caudal vertebrae 28-30, usually 29 (Table 7); total vertebrae 50-52, usually 51 (Table 8). Gill rakers on first arch 2+(8-10)=10-12, usually 8+(8-9)=10-11 (Table 5). Morphometric characters given in Table 22.

Size.—Maximum size 100 cm FL, 8 kg; more commonly 50-80 cm and 4.5 kg in weight (Lewis 1981); size at first maturity 50-55 cm (A. D. Lewis[5]). A 9.1 kg fish was caught near Rockhampton, Queensland, in 1976 (G. McPherson[6]).

Color pattern.—Sides with several poorly defined rows of round spots, larger than pupil but smaller than diameter of eye (Fig. 61). *Scomberomorus niphonius* has more numerous, smaller spots, usually about size of pupil. Munro (1943:87) reported sides of freshly caught specimens light silvery grey, upper part of back and inner surface of pectoral fin dark blue, cheeks and belly silvery

[5]A. D. Lewis, Principal Fisheries Officer, Department of Agriculture & Fisheries, P.O. Box 358, Suva, Fiji, pers. commun. February 1983.

[6]G. McPherson, Fishery Biologist, Northern Fisheries Service, Queensland Fisheries Service, % Post Office, Bungalow, Cairns, Qld. 4870, Australia, pers. commun. February 1983.

white, anal fin light silvery grey, and anal finlets silvery grey. First dorsal fin black (bright steely blue in fresh specimens according to Munro) with blotches of white toward bases of more posterior membranes in some specimens. First dorsal fin membranes entirely black in holotype (Fig. 61). Most other species of *Scomberomorus* with more extensive white areas on posterior half or middle third of dorsal fin.

An excellent black and white illustration of *S. munroi* drawn by Munro has appeared several times in the literature (Munro 1943, 1958a; Roughley 1951; Marshall 1964, 1966) and another drawing by George Coates has been published by Grant (1965 and subsequent editions). We (Collette and Russo 1980) illustrated the holotype with the same figure that is included here. Grant has included a color photograph of a freshly caught specimen in the last three editions of his book (1972:pl. 41, 1978:pl. 73, 1982:pl. 323). A photograph was included by Lewis (1981:18).

Biology.—At the end of summer in the Southern Hemisphere (December to April or May), large schools of *S. munroi* move close inshore along the coast of Queensland from Double Island Point to Southport (Grant 1982). Other biological information is lacking on this species.

Interest to fisheries.—Together with *Grammatorcynus* and three other species of *Scomberomorus*, mackerel fishing is Queensland's second major finfishery with an annual output of about 1,000 tons of whole and filleted fish (Anonymous 1978). The best catches are made by drifting or anchoring over inshore Queensland reefs and fishing with lines baited with small fish on a gang of three or four linked hooks (Grant 1982). Also taken by trawlers in the Gulf of Papua.

Distribution.—Inshore coastal waters of the northern coast of Australia (Fig. 58) from Abrolhos Islands region in Western Australia to Coffs Harbour and Kempsey in northern and central New South Wales (Munro 1943, 1958a; Serventy 1950; Whitley 1964a; Lewis 1981) and Gulf of Papua along southern coast of Papua New Guinea from Kerema to Port Moresby (Kailola 1974, 1975). Previously referred to as *S. niphonius* in Australia (Munro 1943).

Material examined.—Total 19 (296-820 mm FL).

meas.: 19 (296-820): Papua New Guinea (12); Australia: N. Territory (3); Queensland (3, **S. munroi*); W. Australia (1).
counts: 19.
diss.: 4 (373-800): New Guinea (3); Queensland (1).

TABLE 22.—Summary of morphometric data of *Scomberomorus munroi*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			19	296	820	517	177
Snout-A	‰	FL	17	521	572	547	12
Snout-2D	‰	FL	17	507	545	527	10
Snout-1D	‰	FL	17	198	237	222	10
Snout-P_2	‰	FL	17	228	267	249	10
Snout-P_1	‰	FL	17	178	222	202	11
P_1-P_2	‰	FL	18	95	126	105	7
Head length	‰	FL	18	176	213	198	8
Max. body depth	‰	FL	19	169	203	189	9
Max. body width	‰	FL	15	85	122	100	9
P_1 length	‰	FL	14	100	126	108	7
P_2 length	‰	FL	15	48	59	54	4
P_2 insertion-vent	‰	FL	16	261	308	282	14
P_2 tip-vent	‰	FL	13	200	244	225	12
Base 1D	‰	FL	17	281	322	307	12
Height 2D	‰	FL	12	99	125	111	7
Base 2D	‰	FL	17	106	128	116	8
Height anal	‰	FL	12	93	120	108	8
Base anal	‰	FL	18	87	125	105	9
Snout (fleshy)	‰	FL	18	70	85	76	4
Snout (bony)	‰	FL	18	63	77	70	4
Maxilla length	‰	FL	18	91	115	103	5
Postorbital	‰	FL	19	73	100	90	6
Orbital (fleshy)	‰	FL	19	20	36	26	4
Orbital (bony)	‰	FL	19	30	50	39	6
Interorbital	‰	FL	19	52	63	56	3
2D-caudal	‰	FL	19	435	521	468	25
Head length			18	62	151	98	29
Snout (fleshy)	‰	HL	18	354	426	386	19
Snout (bony)	‰	HL	18	314	389	351	19
Maxilla length	‰	HL	18	486	544	521	16
Postorbital	‰	HL	18	390	496	456	29
Orbit (fleshy)	‰	HL	18	113	174	134	18
Orbit (bony)	‰	HL	18	163	242	199	23
Interorbital	‰	HL	18	256	318	282	16

Scomberomorus niphonius (Cuvier)
Japanese Spanish Mackerel

Figure 62

Cybium niphonium Cuvier *in* Cuvier and Valenciennes 1831:180-181 (original description based on a figure of a specimen from Japan). Temminck and Schlegel 1844:101-102 (description), pl. 53, fig. 2 (color painting of adult). Richardson 1846:268 (Sea of Japan). Günther 1860:371 (description after Cuvier and Temminck and Schlegel). Günther 1880:66 (Inland Sea, Japan). Kitahara 1897:3 (description), fig. 11. Kishinouye 1915:10 (description), pl. 1, fig. 4. *Kishinouye 1923:421-424 (description, biology), pl. 15, fig. 6 (soft anatomy in color); pl. 16, fig. 9 (transverse section of vertebrae); pl. 20, fig. 32 (adult); pl. 24, fig. 41 (skull and vertebral

FIGURE 62.—*Scomberomorus niphonius*. Japan, 719 mm FL, USNM 268909.

column). Boeseman 1947:95-96 (specimens in Burger's collection).

Cybium gracile Günther 1873:378-379 (original description; Cheefo, China). Morice 1953:37 (tongue smooth).

Scomberomorus niphonius. Steindachner and Döderlein 1884:180-181 (description; Japan). Jordan et al. 1913:121 (Japanese common names). Kamiya 1922:14-15, 26-32 (eggs and larvae; Japan), pl. IV-V, figs. 1-24 (developmental sequence of eggs and larvae). Kamiya 1924:35 (eggs). Tanaka 1927:154-157 (description from 530 mm specimen from Tokyo market), pl. 42, figs. 163 and 164, pl. 44, fig. 173. Soldatov 1929:5 (listed). Munro 1943:67-68, 71 (subgenus *Sawara*). Fraser-Brunner 1950: 157-158 (description, range; *"Scomber" gracile* a synonym of *S. niphonius*), fig. Okada 1955: 149 (description, range, biology), fig. 136 (after Kishinouye). Mori 1956:23 (Kasumi, Hamada; S. Japan Sea). Mito 1960:79, 93 (eggs compared with those of *S. commerson*). Mito 1961:457 (eggs and larvae). Tominaga 1964:vol. 1, pl. 198 (figure; anatomy), vol. 3:256-257 (description, habits, distribution). Jones and Silas 1964:52-54 (description, synonymy, range; in part, only Chinese and Japanese specimens). Gorbunova 1965a:53 (spawning season). Sha et al. 1966:1-12 (eggs and larvae), figs. Mito 1966:22-23 (fig. 15a, egg), 46-47 (fig. 26, larva). Mito 1967:41 (vertical distribution of larvae). *Hamada and Iwai 1967:1013-1020 (fishing seasons, length-weight, growth; Inland Sea of Japan), pl. 1 (otoliths). Kamohara 1967:43 (description, range in part), color pl. 22, fig. 2. Tokida and Kobayashi 1967:158 (identification of *C. niphonium* from Uchimura's unpublished 1884 manuscript). Kim 1970:37-40 (age determination; Korea). Uyeno 1971:79 (Japan Sea). Richards and Klawe 1972:14 (range), 93 (references to eggs and larvae). Shiino 1972:71 (common name). Magnuson 1973:350 (short pectoral fin). Kusaka 1974:146 (urohyal), fig. 269. Anonymous 1975:184 (description, range), map of fishery, color fig. Masuda et al. 1975:79 (fig. G, color photograph), 256 (range). Uyeno and Fuji 1975:14 (characters of caudal complex). Shiino 1976:231 (common name). Klawe 1977: 2 (common name, range). Collette 1979:24 (characters, range). Collette and Russo 1979: 13 (diagnostic characters, range). Liu 1981: 129-137 (age and growth). Zhang and Zhang 1981:104 (range in part). *Liu et al. 1982:170-178 (age and growth; Yellow Sea). *Wang 1982:51-55 (catch, length-weight, management; Yellow Sea). Cressey et al. 1983:264 (host-parasite list, 4 copepod species). Lee and Yang 1983:230 (Taiwan), fig. 20 (619 mm FL). Collette and Nauen 1983:72-73 (description, range), fig. Ye and Zhu 1984 (bioeconomics).

Sawara niphonia. Jordan and Hubbs 1925:214 (new genus *Sawara*; specimen from Kobe market). Reeves 1927:9 (Ningpo, Peitaiho, China; listed). Mori 1928:5 (Fusan, Korea). Soldatov and Lindberg 1930:112 (synonymy, description, range). Suyehiro 1942:123-124 (intestine straight), fig. 78 (pyloric caeca). Honma 1952: 143 (Echigo Prov. = Niigata Pref., Japan). Mori 1952:136 (Fusan, Masan, Quelpart I., Korea; listed). Nalbant 1970:58 (Kamchatka?).

Scomberomorus gracileus (sic). Reeves 1927:8 (Cheefo, Chinwangtao, China; listed).

Types of nominal species.—*Cybium niphonium* Cuvier *in* Cuvier and Valenciennes 1831 was based on a figure of a specimen from Japan, no type-specimens extant (Blanc and Bauchot 1964:449).

Cybium gracile Günther 1873. Holotype: BMNH 1873.9.23.4; Cheefoo, N China; R. Swinhoe; 547 mm FL; D XX + 16 + IX; A 18 + VIII; P_1 22-23; RGR_1 2 + 1 + 10 = 13; vertebrae 22 + 27 = 49.

Diagnosis.—The only species of *Scomberomorus*

with a straight intestine (Fig. 3k). The other species have two or four loops. Scapular foramen small as in *S. guttatus* and *S. koreanus*. Intercalar spine absent as in the six species of the *regalis* group. Supracleithrum wide, 55-62% of length, as in *S. lineolatus*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Spines in first dorsal fin 19-21, usually 20 (Table 9); second dorsal fin rays 15-19, usually 16-18 (Table 10); dorsal finlets 7-9, usually 8 (Table 10); anal fin rays 16-20, usually 17 or 18 (Table 11); anal finlets 6-9, usually 8 or 9 (Table 11); pectoral fin rays 21-23, usually 22 (Table 12). Precaudal vertebrae 21-23, usually 22 (Table 6); caudal vertebrae 27 or 28, usually 27 (Table 7); total vertebrae 48-50, usually 49 (Table 8). Gill rakers on first arch (2-3)+(9-12)=11-15, usually 2+(10-11)=12-13 (Table 5). Morphometric characters given in Table 23.

Size.—Maximum size 100 cm FL, 4.5 kg in weight (Kishinouye 1923). Age and growth studies have been published by Hamada and Iwai (1967), Kim (1970), and Liu et al. (1982).

Color pattern.—Kishinouye (1923:422) described *S. niphonius* as shining with a metallic lustre. Dorsum light greyish blue washed with green, belly silvery. Seven or more rows of longitudinal spots on the sides. Some spots connected together (Fig. 62). There are more numerous, smaller spots than in *S. munroi*, about pupil size (Collette and Russo 1980). Anterior quarter of first dorsal fin and a narrow distal margin of the rest of the dorsal fin black, most of basal membranes of posterior three-quarters of fin white.

There are color paintings of *S. niphonius* in Kamohara (1967:pl. 22) and Anonymous (1975:pl. 184), a color photograph in Masuda et al. (1975:79), and a good black and white illustration in Kishinouye (1923:fig. 32). We (Collette and Russo 1980: fig. 1b) included the drawing that is presented here in the paper describing *S. munroi*.

Biology.—There are two migrations in the Inland Sea of Japan, a spawning migration in the spring (March to June) and feeding migration in the fall (September to November) according to Hamada and Iwai (1967). The spawning season in Japan is from April to May (Kishinouye 1923). The ripe

TABLE 23.—Summary of morphometric data of *Scomberomorus niphonius*. FL = fork length, HL = head length.

Character		Japan and Korea					China					Total				
		N	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD
Fork length		13	157	788	439	200	16	105	623	280	167	32	105	788	351	197
Snout-A	FL	11	539	574	553	10	16	558	605	573	14	30	484	605	563	22
Snout-2D	FL	12	505	563	535	17	16	523	576	542	13	31	427	576	536	25
Snout-1D	FL	12	202	271	239	21	16	224	278	256	16	31	202	278	248	20
Snout-P_2	FL	12	227	307	255	23	15	232	305	269	20	29	227	307	263	22
Snout-P_1	FL	12	184	252	216	20	16	197	264	232	18	31	184	264	225	20
P_1-P_2	FL	12	89	125	100	11	13	95	129	109	12	26	89	129	105	12
Head length	FL	13	180	249	207	18	16	192	252	223	18	32	180	252	215	19
Max. body depth	FL	11	148	203	167	17	11	152	190	172	13	23	148	211	171	17
Max. body width	FL	10	77	95	88	6	12	71	92	80	7	25	71	103	84	8
P_1 length	FL	12	87	122	105	9	16	104	125	115	6	31	87	125	111	9
P_2 length	FL	11	51	76	62	7	15	56	127	74	16	29	45	127	68	14
P_2 insertion-vent	FL	12	243	318	283	25	13	258	321	290	18	27	232	321	285	23
P_2 tip-vent	FL	11	186	256	221	23	12	188	245	216	17	25	186	256	218	20
Base 1D	FL	12	271	320	293	17	16	259	310	280	14	31	219	320	282	20
Height 2D	FL	12	66	110	92	10	13	95	112	101	5	28	66	124	98	10
Base 2D	FL	12	90	131	104	12	16	94	132	113	11	31	90	189	113	19
Height anal	FL	9	84	108	92	7	15	63	106	97	11	27	63	124	97	11
Base anal	FL	11	92	117	105	9	16	93	135	106	11	30	92	147	107	12
Snout (fleshy)	FL	13	66	88	78	7	16	70	95	84	7	32	66	95	81	8
Snout (bony)	FL	13	59	83	72	7	16	62	89	77	7	32	56	89	75	8
Maxilla length	FL	13	94	136	114	13	16	103	145	125	11	32	93	145	119	14
Postorbital	FL	13	91	104	98	4	16	89	115	104	7	31	89	115	102	7
Orbital (fleshy)	FL	13	19	41	28	6	16	25	51	36	7	32	19	51	33	8
Orbital (bony)	FL	13	29	59	41	9	16	36	65	51	8	32	29	65	47	10
Interorbital	FL	13	51	63	56	4	16	54	61	57	2	32	51	63	57	3
2D-caudal	FL	12	412	490	459	27	15	420	488	468	16	29	412	490	465	21
Head length		13	39	142	88	34	16	27	120	60	30	32	27	142	72	35
Snout (fleshy)	HL	13	351	401	377	16	16	362	393	378	11	32	345	401	376	14
Snout (bony)	HL	13	314	373	346	15	16	325	365	348	12	32	294	373	346	16
Maxilla length	HL	13	504	582	549	23	16	538	582	560	14	32	484	582	553	22
Postorbital	HL	13	417	511	477	26	16	405	518	470	26	31	405	518	473	26
Orbit (fleshy)	HL	13	103	170	136	19	16	122	204	158	21	32	103	204	150	23
Orbit (bony)	HL	13	161	250	194	28	16	188	257	230	23	32	161	257	215	30
Interorbital	HL	13	248	294	271	14	16	226	285	258	18	32	226	303	264	18

eggs are large, about 1.5 mm in diameter and number about 550,000-870,000 (Kishinouye 1923). Immature fish of about 30 mm are found in April and May (Kishinouye 1923). Eggs and larvae up to 35 mm TL are described by Sha et al. (1966) from plankton net samples from Kiaochow Bay, Tsingtao, China. Although it feeds on small fishes (Kishinouye 1923), no detailed food studies seem to have been published.

Interest to fisheries.—In the Inland Sea of Japan, the main fishing seasons are from March to June and from September to November (Hamada and Iwai 1967). Angling and gill nets are important gear in this region. There are also important fisheries in the Huanghai Sea (Yellow Sea) and Bohai Sea (Liu et al. 1982). Ye and Zhu (1984) have developed a bioeconomic model for this fishery, estimating maximum revenue, optimum economic effort, and optimum energy consumption. The annual catch reported by China, Japan, and Korea varied from 60,733 to 77,356 t between 1979 and 1982 (FAO 1984).

Distribution.—Confined to temperate and subtropical waters of the western North Pacific, Japan, Korea, and northern China (Fig. 58). The northernmost locality is Vladivostok, U.S.S.R., in the Sea of Japan (BMNH 1893.1.27.10-12). In Japan, it is found from southern Hokkaido to Honshu, Shikoku, and Kyushu, west to Pusan, Korea (CAS SU 31263), and Ningpo, Peitaiho (Reeves 1927; ZMA 114.597), Cheefo (= Yentai) (Günther 1873; BMNH 1873:9.23.40; UMMZ 167374), and Tsingtao (USNM 130474) on the Shantung Peninsula of northern China. Records of *S. niphonius* from northern Australia and southern Papua New Guinea are referrable to the recently described *S. munroi* (Collette and Russo 1979).

Geographic variation.—Morphometric characters were compared for two populations of *S. niphonius* by ANCOVA (Table 23): Japan and Korea (n = 9-13) and China (n = 11-16). Null hypotheses that the 2 sets of regression lines are coincident were accepted for 21 regressions and rejected for 5 sets: Sn-A, Sn-1D, maximum body width, P_1L, and orbit (bony). No meristic differences were found between the two populations.

Material examined.—Total 38 (86.5-788 mm FL).

meas.:	31 (97.5-705): Japan (8); Korea (5); China (16); unknown locality (2).
counts:	38.
diss.:	2 (683-788): Japan.

Scomberomorus plurilineatus Fourmanoir
Queen Mackerel or Kanadi Kingfish

Figure 63

Cybium lineolatum. Not of Cuvier 1831. Gilchrist and Thompson 1911:41 (description; Durban).

Scomberomorus lineolatum. Not of Cuvier 1831. Gilchrist and Thompson 1917:395 (Natal).

Scomberomorus lineolatus. Not of Cuvier 1831. Barnard 1927:803 (description; Natal). Fowler 1934:441 (Durban). Smith 1935:210-211 (description; Port Alfred, South Africa). *Williams 1960:183-192 (description, synonymy, range), pl. 2. *Williams 1964:151-154 (distribution, fishery biology). Merrett and Thorpe 1966:371-372 (references, range, size, biology).

FIGURE 63.—*Scomberomorus plurilineatus.* Durban, South Africa, 598 mm FL, USNM 264809.

Scomberomorus leopardus. Not of Shaw 1803. Fowler 1929:254 (description; Natal). Smith 1949, 1953, 1961:301 (description, range), fig. 841, pl. 64. Morrow 1954:815 (near Shimoni and Pemba I., East Africa). Talbot 1965:469 (Mafia area, Tanganyika). Maugé 1967:234 (Anakao, Tulear region, Madagascar). Shiino 1976:231 (common name).

Scomberomorus sp. Williams 1956:44 (Kenya).

Scomberomorus guttatus. Not of Bloch and Schneider 1801. Smith 1956:722 (Aldabra). Smith and Smith 1963:43 (Seychelles), pl. 30B. Smith 1964:176-177 (description; Durban and Delagoa Bay), pl. 8, figs. 3-5. Silas 1964: 314-328 (western Indian Ocean population only). Smith and Smith 1966:72 (Natal), color pl. 841.

Cybium leopardus. Not of Shaw 1803. Fourmanoir 1957:227 (description; Mozambique Channel).

Cybium lineolatus. Not of Cuvier 1831. Fourmanoir and Crosnier 1964:387-388 (Madagascar).

Scomberomorus plurilineatus Fourmanoir 1966: 223-226 (original description; Madagascar), fig. 1. Klawe 1977:2 (range, common name). Collette 1979:29 (characters). Collette and Russo 1979:13 (diagnostic characters, range). *Van der Elst 1981:275 (description, natural history, range, photograph). Joubert 1981:5 (minor component of shore angler's catches; Natal, South Africa). Cressey et al. 1983:264 (host-parasite list, 5 copepod species). Collette and Nauen 1983:73-74 (description, range), fig.

Types.—*Scomberomorus plurilineatus* Fourmanoir 1966 was based on a 740 mm specimen collected near Nossi-Bé, Madagascar, in 1965. The type was supposed to be transferred from the O.R.S.T.O.M. collections to the MNHN collection but apparently was inadvertently discarded (M.-L. Bauchot and P. Fourmanoir[7]).

Diagnosis.—The only species of *Scomberomorus* that has a pattern of short wavy lines and spots on its sides (Fig. 63). Other species have straight lines, spots, blotches, or bars on the side or are plain. Posterior end of maxilla greatly expanded as in *S. lineolatus* and *S. semifasciatus*.

[7]M.-L. Bauchot, Curator of Fishes, Laboratoire d'Ichtyologie Générale et Appliquée, Muséum National d'Histoire Naturelle, 43 Rue Cuvier, 75231 Paris Cedex 05, France, and P. Fourmanoir, Office de la Recherche Scientifique et Technique Outre-Mer, Institut Français d'Oceanie, Nouméa, B.P. 4, Nouvelle-Calédonie, pers. commun. December 1974.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 31). Spines in first dorsal fin 15-17, usually 15 or 16 (Table 9); second dorsal fin rays 19-21, usually 20 (Table 10); dorsal finlets 8-10, usually 9 (Table 10); anal fin rays 19-22, usually 20 or 21 (Table 11); anal finlets 7-10, usually 8 or 9 (Table 11); pectoral fin rays 21-26, usually 22 or 23 (Table 12). Precaudal vertebrae 19 or 20, usually 20 (Table 6); caudal vertebrae 25-27, usually 26 (Table 7); total vertebrae 45 or 46, usually 46 (Table 8). Gill rakers on first arch (2-3)+(9-13)=12-15, usually 2+(10-11)=12-13 (Table 5). Morphometric characters given in Table 24.

TABLE 24.—Summary of morphometric data of *Scomberomorus plurilineatus*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			37	144	910	547	211
Snout-A		FL	36	478	614	502	22
Snout-2D		FL	36	446	622	473	28
Snout-1D		FL	36	202	247	221	12
Snout-P_2		FL	36	207	261	232	12
Snout-P_1		FL	37	176	228	192	11
P_1-P_2		FL	26	96	117	103	5
Head length		FL	37	175	222	193	11
Max. body depth		FL	32	184	225	205	11
Max. body width		FL	20	76	123	97	13
P_1 length		FL	31	98	140	123	10
P_2 length		FL	35	44	66	51	6
P_2 insertion-vent		FL	24	223	257	244	9
P_2 tip-vent		FL	23	158	207	187	15
Base 1D		FL	23	219	256	240	11
Height 2D		FL	29	122	166	148	11
Base 2D		FL	27	101	156	128	11
Height anal		FL	27	91	155	135	14
Base anal		FL	27	111	143	126	9
Snout (fleshy)		FL	35	61	75	67	3
Snout (bony)		FL	25	48	67	58	4
Maxilla length		FL	36	83	113	96	7
Postorbital		FL	36	81	107	94	6
Orbital (fleshy)		FL	37	22	139	34	19
Orbital (bony)		FL	27	33	60	45	8
Interorbital		FL	36	46	67	56	4
2D-caudal		FL	25	518	575	549	15
Head length			37	31	159	104	37
Snout (fleshy)		HL	35	309	371	348	13
Snout (bony)		HL	25	256	327	305	15
Maxilla length		HL	36	469	529	496	14
Postorbital		HL	36	413	527	485	23
Orbit (fleshy)		HL	37	121	769	179	104
Orbit (bony)		HL	27	178	276	231	27
Interorbital		HL	36	253	352	290	21

Size.—Maximum size 120 cm FL, South African angling record 10.0 kg, sexual maturity attained at about 80 cm FL (van der Elst 1981).

Color pattern.—Williams (1960) published a good description of fresh specimens from Zanzibar. Head blue-grey above, silvery white below, except for lower jaw tip, preorbital area and maxillary groove dusky to black. Pupil of eye black, rest silvery. Body iridescent blue-grey above lateral

line, silver below becoming whitish ventrally. A series of about six to eight interrupted horizontal black lines on sides of body much narrower than interspaces. Anteriorly, usually only one of these lines above lateral line; replaced posteriorly by a number of short oblique black lines becoming somewhat confused, and only two or three continue through to caudal peduncle. Horizontal black lines on body interrupted to varying degrees, beginning almost intact in places, but broken up into a series of small rectangular "spots" in others. Juveniles have spots but develop adult pattern of interrupted lines by the time they reach a length of 400 mm (Smith 1964:177). Upper areas of caudal peduncle and median keel black, lower areas dusky. First dorsal fin black except lower areas of membrane may be pale posteriorly. Second dorsal fin with leading edge and tips of rays dusky, rest silver to pale; finlets dusky with a silver area at center. Anal fin, leading edges and tips of rays dusky, rest silvery; finlets white with a dusky central area. Pectoral fins black inside, as is axil; dusky outside with edges black; pelvic fins pale whitish with outside of midrays dusky, groove on body a little dusky. Caudal fin basally pale, rest of fin dusky to black.

Black and white photographs of *S. plurilineatus* have been published by Williams (1960:pl. 2, 640 mm Zanzibar specimen) and Fourmanoir (1966: fig. 1, 740 mm holotype from Madagascar). Illustrations of a spotted 300 mm juvenile and two adults over 1 m long were presented by Smith (1964:pl. 8). A colored figure of the juvenile is included in Smith and Smith (1966:fig. 841).

Biology.—Large schools are present in the Zanzibar Channel from March-April until August-September, average weight 3.2-3.5 kg (Williams 1960). Angling statistics point to a peak abundance in Natal, South Africa, during May (van der Elst 1981). Spawning probably takes place in August-September in the Zanzibar Channel (Williams 1964). There do not appear to be any published references to eggs or larvae of *S. plurilineatus*. This species feeds mainly on anchovies (*Anchoviella* sp.), clupeids (*Amblygaster* sp., *Sardinella fimbrata*, *S. perforata*), other small fishes, squids, and mantis shrimps (Williams 1964; Merrett and Thorp 1966; van der Elst 1981).

Interest to fisheries.—In the Malindi area of Kenya, catches of *S. plurilineatus* are mainly made by trolling and hand lines, while in the Zanzibar Channel all methods are used but the gill net prevails (Williams 1964). On the west coast of Zanzibar a trap net called the mensab is used to intercept fish on their projected paths of movements (Williams 1964). More recently, tuna purse seines are used in Zanzibar with catches of several tons reported off the northwest coast (Merrett and Thorp 1966). In Natal, South Africa, it is a popular gamefish with ski-boat fishermen and also with spearfishermen (van der Elst 1981).

Distribution.—Common in coastal waters, especially near rocky and coral reefs. Western Indian Ocean along the coast of East Africa from Kenya (lat. 1°30′S) and Zanzibar (Williams 1964) to Natal, South Africa (Fig. 58). The southernmost records are from Algoa Bay (Smith and Smith 1966). Also found in the Seychelles Islands (Smith and Smith 1963) and along the west coast of Madagascar.

Material examined.—Total 37 (165-910 mm FL).

meas.:	37 (165-910): Natal, South Africa (25); Mozambique (1); Kenya (1); Zanzibar (10, F. Williams' data).
counts:	37.
diss.:	5 (490-910): South Africa (4); Kenya (1).

Scomberomorus queenslandicus Munro
Queensland School Mackerel

Figure 64

Cybium guttatum. Not of Bloch and Schneider 1801. Macleay 1880:559 (description; Port Jackson, Australia). Ogilby 1887:30 (listed; Port Jackson).

Scomberomorus guttatus. Not of Bloch and Schneider 1801. Waite 1904:42 (New South Wales). Stead 1906:165-166 (N.S.W.). Stead 1908:98 (description; N.S.W.). McCulloch 1922:105 (N.S.W.). McCulloch 1929:264-265 (range in part; Queensland, N.S.W.).

Scomberomorus (Cybium) queenslandicus Munro 1943:82-86 (original description; Queensland and west Australia), pl. 7, fig. B, pl. 8, fig. 1. Coates 1950:24 (description), fig. Roughley 1951:110 (description), pl. 45, top fig. (after Munro). Jones and Silas 1962:202 (may turn up in Indian waters), fig. 8 (after Munro). Jones and Silas 1964:61-62 (description, range), fig. 11 (after Munro). Taylor 1964:282 (listed after Whitley 1954). Marshall 1964:363-364 (description; Qld.), pl. 49, fig. 350 A and B (after

FIGURE 64.—*Scomberomorus queenslandicus*. Exmouth Gulf, Western Australia, 635 mm FL, USNM 268910.

Munro). Marshall 1966:205 (Qld.), pl. 49, fig. 350 A and B (after Munro). Richards and Klawe 1972:14 (range), 94 (references to juveniles). Magnuson 1973:350 (short pectoral fin). Kailola 1974:71 (description; Gulf of Papua; range extension). Kailola 1975:237 (specimen in Kanudi Fisheries collection). Shiino 1976:231 (common name). Klawe 1977: 2 (common name; range). Kailola and Wilson 1978:35 (trawled in Gulf of Papua), 60 (number of fin rays). Collette 1979:29 (characters, range). Collette and Russo 1979:13 (diagnostic characters, range). Grant 1982:624 (description, fishery in S Qld.), 625 (color pl. 324). Rainer and Munro 1982:1046 (inshore group, Gulf of Carpentaria), 1050-1051 (avoids low salinity areas in the southern Gulf). Cressey et al. 1983:264 (host-parasite list, 5 copepod species). Collette and Nauen 1983:74-75 (description, range), fig. Jenkins et al. 1984:348-351 (193 larvae, 3.5-9.9 mm SL; off Townsville, Qld.), fig. 4 (6 larvae, 3.6-9.5 mm SL).

Cybium queenslandicum. Whitley 1947:129 (W. Australia). Whitley 1948:24 (W. Australia). Whitley 1954:27 (Parry Shoal, N. Territory). Whitley 1964a:251-252 (description; W. Australia and N. Territory). Whitley 1964b:48 (listed).

Cybium queenslandicus. Munro 1958a:112 (description, range), fig. 750 (after Munro). Grant 1965:174 (description after Munro; Moreton Bay, Queensland), fig. Grant 1972:103, 1975:161, 1978:194 (description after Munro; fishery in S Qld.), fig.

Types.—Holotype: QM I.6588; Cape Cleveland, N Queensland, Australia; G. Coates; 463 mm FL; D XVII + 18 + IX; A 20 + IX; P_1 23; RGR_1 1 + 1 + 4 = 6.

Diagnosis.—This species has relatively few large spots (larger than the diameter of the eye) on its sides (Fig. 64). In having few gill rakers (3-9), it is superficially similar to *S. commerson* but differs in lacking an abrupt downward curve in the lateral line under the second dorsal fin and in having more vertebrae (48 or 49 vs. 42-46). Posterodorsal spine of hyomandibula large as in *S. commerson* and *Acanthocybium*. Ventral process of angular long, 117-126% of dorsal process, as in *S. commerson* and *Acanthocybium*. Intercalar spine well developed as in *S. cavalla* and *S. commerson*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3m). Spines in first dorsal fin 16-18, usually 17 (Table 9); second dorsal fin rays 17-19 (Table 10); dorsal finlets 9-11, usually 9 or 10 (Table 10); anal fin rays 16-20, usually 19 (Table 11); anal finlets 9-11, usually 10 (Table 11); pectoral fin rays 21-23, rarely 25 (Table 12). Precaudal vertebrae 19 or 20, usually 20 (Table 6); caudal vertebrae 28 or 29, usually 28 (Table 7); total vertebrae 48 or 49, usually 48 (Table 8). Gill rakers on first arch (0-2) + (3-8) = 3-9, usually 1 + (5-6) = 6-7 (Table 5). Morphometric characters given in Table 25.

Size.—Maximum size 100 cm FL, 8 kg in weight, commonly 50-80 cm (Lewis 1981).

Color pattern.—In his original description of the species, Munro (1943) provided a good description of freshly caught specimens from Queensland. Cranial regions and upper part of back iridescent bluish green, cheeks and belly silvery white. In adult fish, sides marked with about three indefinite rows of indistinct bronze-grey blotches, each a little larger than orbit. Membrane of first dorsal fin jet black with large contrasting areas of

TABLE 25.—Summary of morphometric data of *Scomberomorus queenslandicus*. FL = fork length, HL = head length.

Character		N	Min.	Max.	Mean	SD
Fork length		28	156	641	392	123
Snout-A	% FL	28	502	558	525	12
Snout-2D	% FL	28	470	518	502	11
Snout-1D	% FL	28	219	254	234	10
Snout-P_2	% FL	27	234	273	252	11
Snout-P_1	% FL	27	211	252	228	10
P_1-P_2	% FL	27	85	118	99	7
Head length	% FL	28	203	245	220	10
Max. body depth	% FL	25	161	207	188	11
Max. body width	% FL	26	81	118	101	11
P_1 length	% FL	24	103	135	119	8
P_2 length	% FL	23	44	62	55	5
P_2 insertion-vent	% FL	24	233	275	254	12
P_2 tip-vent	% FL	22	178	222	198	13
Base 1D	% FL	28	239	283	263	11
Height 2D	% FL	18	89	136	114	12
Base 2D	% FL	28	80	135	113	11
Height anal	% FL	17	94	157	112	15
Base anal	% FL	28	89	141	108	12
Snout (fleshy)	% FL	28	78	97	86	4
Snout (bony)	% FL	27	73	125	80	9
Maxilla length	% FL	27	109	146	125	8
Postorbital	% FL	28	90	110	102	5
Orbital (fleshy)	% FL	28	23	41	31	5
Orbital (bony)	% FL	27	39	66	49	8
Interorbital	% FL	28	56	74	63	5
2D-caudal	% FL	17	440	532	496	22
Head length		28	36	141	85	25
Snout (fleshy)	% HL	28	357	423	390	17
Snout (bony)	% HL	27	331	554	363	41
Maxilla length	% HL	27	526	597	568	17
Postorbital	% HL	28	410	502	463	21
Orbit (fleshy)	% HL	28	112	171	141	16
Orbit (bony)	% HL	27	183	283	222	29
Interorbital	% HL	28	259	330	287	17

intense white between sixth and last spines. Second dorsal fin, finlets, and caudal fin pearly grey with darker margins. Pelvic fins, anal fin, and anal finlets white. Pectoral fins greyish, darkest on inner surface. Munro also noted the absence of characteristic blotches in a 95 mm juvenile.

Munro (1943:pl. 7, 8) provided excellent illustrations of adult (545 mm FL) and juvenile (140 mm FL) specimens from Queensland. There is also a figure drawn by George Coates in Grant (1982 and previous editions). A photograph of two juveniles (about 300 mm FL) was included in Lewis (1981: 15). A color photograph of a 230 mm specimen was added to the fifth edition of Grant (1982:pl. 324).

Biology.—Schools move into bays and estuaries and inshore coastal waters the length of the entire coast of Queensland during midwinter and early spring in the Southern Hemisphere (Grant 1982). A female 450 mm FL with mature ovaries was collected in Moreton Bay, Queensland, in January 1980 (Lewis, footnote 5). Information on eggs (Richards and Klawe 1972) and on spawning and food habits is lacking. Larvae (3.5-9.5 mm SL) were described and illustrated by Jenkins et al. (1984).

Interest to fisheries.—Caught by recreational and commercial line-fishermen trolling with lures and spoons, and using cut baits along the coast of Queensland (Grant 1982). They also form the basis of a substantial net fishery, using set nets by day or night. Considerable quantities of juveniles are trawled in parts of Moreton Bay during autumn (March-May). Together with *Grammatorcynus* and three other species of *Scomberomorus*, mackerel fishery is Queensland's second major finfishery with an annual output of about 1,000 tons of whole and filleted fish (Anonymous 1978). It was known to south Queensland fishermen as school mackerel for over 60 yr prior to its formal description by Munro (1943). Trawled in the Gulf of Papua.

Distribution.—Confined to inshore coastal waters of southern Papua New Guinea and the northern three quarters of Australia (Fig. 55). The westernmost records are from Shark Bay (Munro 1943) and Onslow (AMS IB.1576, WAM P. 8669-8678), Western Australia. The range extends south to Port Jackson (USNM 4795, AMS I.15026) and Botany Bay (USNM 47948) in the Sydney area. A tentative record from Fiji (Collette and Russo 1979) was based on small specimens of *S. commerson* (USNM 227183, 203-242 mm FL) with less dip in the lateral line than is usual in the species. The origin of a specimen of *S. queenslandicus* (USNM 213539, 215 mm FL) that was purchased in the Anbon market in the Moluccas is unknown but joint venture trawlers which fish in the Arafua Sea unload at Anbon (Lewis footnote 5).

Geographic variation.—Comparisons were made of morphometric characters of three small samples of *S. queenslandicus* by ANCOVA: Western Australia (n = 5-9), eastern Australia (n = 9-13), and southern New Guinea (n = 3-5). Null hypotheses that the 3 sets of regression lines are coincident were accepted for 24 sets of regressions and rejected for 2 sets: orbit (fleshy) and orbit (bony). In both cases, the Western Australian population was significantly different by the Newman-Keuls Multiple Range Test from the population in eastern Australia (intercepts 5.140, 2.847, Q = 5.630** for fleshy orbit; intercepts 8.380, 1.951, Q = 4.562** for bony orbit) and the population in eastern Australia was not significantly different from that in New Guinea. No significant meristic

differences were found between populations.

Material examined.—Total 35 (156-641 mm FL).

meas.: 28 (156-641): New South Wales, Australia (5); Queensland (8, **S. queenslandicus*); W. Australia (9); New Guinea (5); Anbon market (1).
counts: 35.
diss.: 6 (354-641): Queensland (4); W. Australia (1); New Guinea (1).

Scomberomorus regalis (Bloch)
Cero

Figure 65

Scomber regalis Bloch 1793:38-43 (original description, after a drawing by Plumier; Martinique), color pl. 333. Bloch 1797:31-34 (French translation of original description), color pl. 333. Bloch and Schneider 1801:22 (description after Bloch). Shaw 1803:583 (after Bloch). Lacepède 1803:711 (Scomberomore plumier is the same as *Scomber regalis*).

Scomberomorus Plumierii Lacepède 1802:292-294 (original description after Plumier's drawing; Martinique).

Cybium regale. Cuvier 1829:200 (listed in footnote from *Sc. regalis* Bloch; *Scomberomorus plumieri* a synonym). Cuvier *in* Cuvier and Valenciennes 1831:184-185 (description; Santo Domingo). Castelnau 1855:23 (Bahia, Brazil). Günther 1860:372-373 (synonymy, description; Jamaica). Poey 1865:322 (description; Santo Domingo). Kner 1865:144 (description; Rio de Janeiro). Poey 1868:362 (description; Cuba). Poey 1875:147 (description; Cuba). Poey 1878: 4 (synonymy, characters).

Scomberomorus regalis. Jordan and Gilbert 1882:426 (description, synonymy). Jordan and Gilbert 1883c:573 (*Scomberomorus plumierii* identical with *Scomber regalis*). Goode 1884: 316 (size; Fla. Keys), pl. 94. Meek and Newland 1884:233-234 (description, synonymy, range). Jordan 1884:120 (description; Key West). Dresslar and Fesler 1889:442 (in key), 444 (synonymy, range Cape Cod to Brazil), pl. 10. Jordan and Evermann 1896b:875 (description, synonymy). Jordan and Evermann 1900:pl. 135, fig. 369 (Key West specimen). Evermann and Marsh 1902:124 (description, synonymy in part; Puerto Rico), fig. 28. Jordan and Evermann 1902:286-287 (description, range), fig. Bean 1903:398-400 (synonymy, description, range). Fowler 1905:766 (description; Santo Domingo). Smith 1907:192 (diagnosis; North Carolina record from Yarrow 1877), fig. 78. Sumner et al. 1913:750 (references, occurrence; Buzzards Bay, Mass.). Ribeiro 1915:135 (description, range S to Angra dos Reis, Brazil). Meek and Hildebrand 1923:323-324 (description, synonymy). Schroeder 1924:7 (Fla. Keys), fig. 4. Nichols and Breder 1927:124 (description, distribution, biology), fig. 171. Frost 1928:329-330 (sagittae), pl. 12, fig. 7 (sagitta). Beebe and Tee-Van 1928:97 (description; Port-au-Prince Bay, Haiti), fig. Hildebrand and Schroeder 1928:205 (description, range in part, biology; Chesapeake Bay), fig. 116. Nichols 1929:230 (range, description; Puerto Rico), fig. 83. Beebe and Hollister 1935:213 (Union I., Grenadines). Hubbs 1936:253 (description of 4 juveniles, 36-50 mm, from Yucatan). Baughman 1941:17-18 (Texas records). Munro 1943: 67, 71-72 (placed in subgenus *Scomberomorus*). Fowler 1945:186 (synonymy, description; Charleston, S.C.), 290 (Florida). La Monte

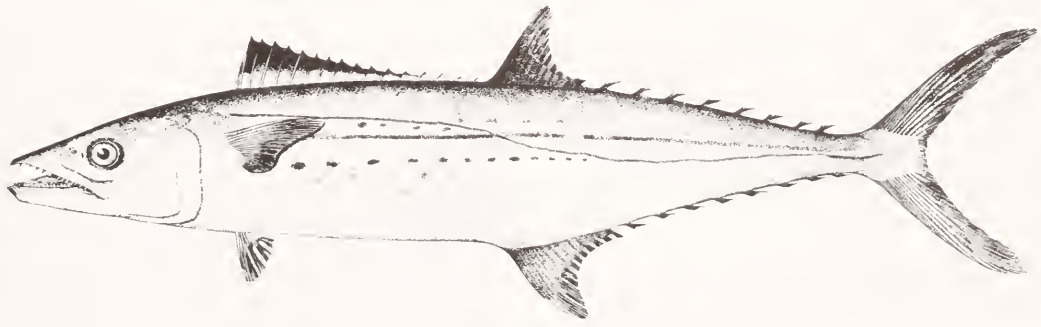


FIGURE 65.—*Scomberomorus regalis.* Key West, Fla., 625 mm FL, USNM 12527. (From Goode 1884:pl. 94.)

1945:28 (description, range). Breder 1948: 127 (range), fig. Erdman 1949:301 (frequently found in the West Indies). Fraser-Brunner 1950:160 (synonymy in part, range), fig. 32. Baughman 1950:244 (previous Texas records). Rivas 1951:225 (synonymy, diagnosis, range). La Monte 1952:50-51 (description, range). Bigelow and Schroeder 1953:348 (description; one record from Gulf of Maine, Monomoy, Cape Cod), fig. 183. Pew 1954:26, 28 (description, range, habits; 3-ft specimen from Port Aransas, Tex.), fig. 24. *Erdman 1956:317 (range, spawning periods; Puerto Rico). Briggs 1958: 286 (range). *Mago Leccia 1958 (osteology, comparisons with *S. maculatus* and *S. cavalla*), figs. Cervigón 1966:720-721 (description; Venezuela). *Randall 1967:754 (food of 116 West Indian specimens, 96.1% fishes). Böhlke and Chaplin 1968:573 (description, range), fig. Randall 1968:117-118 (description, range, habits), fig. 134 (photograph of Virgin Is. specimen). Beardsley and Richards 1970:5 (length-weight of 58 specimens, 213-835 mm FL, 0.13-4.88 kg; Florida). Dahl 1971:278 (common in Colombia), fig. Richards and Klawe 1972:14 (range), 94 (reference to Hubbs 1936). Miyake and Hayasi 1972:III-3 (in key), IV-11 (common names). Klawe 1977:2 (common name, range). Erdman 1977:150 (spawn virtually all year; NE Caribbean). Collette et al. 1978:274-275 (comparison with other American species of *Scomberomorus*). Fritzsche 1978:133-135 (description, larval development), figs. 75-76 (larvae). Collette 1978:Scombm 6 (description, range), figs. Lima and Oliveira 1978:13, 24 (common name "sierra-penincho" in Brazil). Manooch et al. 1978 (annotated bibliography). Collette 1979:29 (characters, range). Collette and Russo 1979:13 (diagnostic characters, range). Sacchi et al. 1981:3 (French Antilles). Köster 1981:55 (Isla Rosario, Colombia). Cooper 1982 (fishery in Jamaica). Cressey et al. 1983:264 (host-parasite list, 7 copepod species). Garzon and Acero 1983:18 (Isla Providencia, Colombia). Collette and Nauen 1983:75-76 (description, range), fig. Finucane and Collins 1984 (reproductive biology, Fla.).

Types of nominal species.—Both *Scomber regalis* Bloch 1793 and *Scomberomorus plumierii* Lacepède 1802 are based on Plumier's drawing of a specimen from Martinique, and there are no known type-specimens extant. The pattern of spots and lines in the color plate published by Bloch (color pl. 333) leaves no doubt as to the identity of the species.

Diagnosis.—The only species of *Scomberomorus* that has a stripe on its sides (which may be broken into several segments) with small dots above and below the stripe (Fig. 65). Other species have lines, spots, blotches, or bars, or are plain. *Scomberomorus regalis* possesses nasal denticles as do the other five species of the *regalis* group (*brasiliensis*, *concolor*, *maculatus*, *sierra*, and *tritor*), has an artery that comes off the fourth left epibranchial artery as do all the species in the group except *S. tritor*, and shares a specialization of the fourth right epibranchial artery (Fig. 7g) with *S. brasiliensis* and *S. sierra*. In these three species an artery connects the fourth right epibranchial with a branch of the coeliaco-mesenteric artery. Together with three other species of the *regalis* group (*brasiliensis*, *concolor*, and *sierra*), *S. brasiliensis* has a long posterior process on the pelvic girdle (Fig. 46a), 62-90% of the length of the anterior plate. Intercalar spine absent as in the other five species of the *regalis* group and *S. niphonius*. Pectoral fin covered with scales.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3n). Spines in first dorsal fin 16-18, usually 17 (Table 9); second dorsal fin rays 16-19, usually 17 or 18 (Table 10); dorsal finlets 7-9, usually 8 (Table 10); anal fin rays 15-20, usually 18 or 19 (Table 11); anal finlets 7-10, usually 8 (Table 11); pectoral fin rays 20-24, usually 21 or 22 (Table 12). Precaudal vertebrae 19 or 20, usually 20 (Table 6); caudal vertebrae 28 (Table 7); total vertebrae 47 or 48, usually 48 (Table 8). Gill rakers on first arch (2-4)+(10-14)=12-18, usually 3+(12-13)=15-16 (Table 5). Morphometric characters given in Table 26.

Size.—Maximum size 83.5 cm FL, 4.9 kg (Beardsley and Richards 1970). Sexual maturity in Florida is attained at about 350 mm FL for males, 380 mm for females (Finucane and Collins 1984).

Color pattern.—Bluish green on back, sides silvery, with a midlateral row of yellow streaks of variable length and small yellow spots above and below this row (Randall 1968). Distal part of anterior lobe of first dorsal fin black, rest of fin white.

Bloch (1793:pl. 333) included a color plate in his original description of *Scomber regalis*. There is a

TABLE 26.—Summary of morphometric data of *Scomberomorus regalis*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			53	77	544	329	121
Snout-A	‰	FL	53	509	583	548	14
Snout-2D	‰	FL	53	489	560	520	14
Snout-1D	‰	FL	53	226	285	254	11
Snout-P_2	‰	FL	49	210	306	264	16
Snout-P_1	‰	FL	53	195	286	233	16
P_1-P_2	‰	FL	50	96	128	109	7
Head length	‰	FL	53	190	258	222	11
Max. body depth	‰	FL	49	113	231	197	18
Max. body width	‰	FL	45	56	176	91	18
P_1 length	‰	FL	51	87	166	125	12
P_2 length	‰	FL	49	40	63	55	5
P_2 insertion-vent	‰	FL	50	238	304	267	16
P_2 tip-vent	‰	FL	48	187	252	210	17
Base 1D	‰	FL	53	227	283	258	12
Height 2D	‰	FL	45	75	145	115	11
Base 2D	‰	FL	53	94	135	116	9
Height anal	‰	FL	44	84	138	112	10
Base anal	‰	FL	53	89	130	111	10
Snout (fleshy)	‰	FL	53	72	98	86	5
Snout (bony)	‰	FL	52	64	88	78	5
Maxilla length	‰	FL	53	105	145	123	7
Postorbital	‰	FL	52	87	128	97	6
Orbital (fleshy)	‰	FL	53	31	63	40	6
Orbital (bony)	‰	FL	53	40	73	55	6
Interorbital	‰	FL	53	49	64	58	3
2D-caudal	‰	FL	51	416	509	480	23
Head length			53	20	119	72	25
Snout (fleshy)	‰	HL	53	357	426	390	16
Snout (bony)	‰	HL	52	316	383	351	17
Maxilla length	‰	HL	53	528	606	556	15
Postorbital	‰	HL	52	376	569	440	26
Orbit (fleshy)	‰	HL	53	150	248	178	20
Orbit (bony)	‰	HL	53	199	292	247	21
Interorbital	‰	HL	53	220	286	262	13

good black and white photograph of a 400 mm specimen from the Virgin Islands in Randall (1968:fig. 134) and a small color photograph in Walls (1975:fig. 410). The drawing published by Goode (1884:pl. 94) is included here as Figure 65.

Biology.—Little is known about migrations or movements of *S. regalis*. Young adults are taken throughout the year in small numbers over the Jamaica shelf (Cooper 1982). Around Puerto Rico, spawning takes place virtually all year (Erdman 1977). Spawning takes place from April to October at California Bank, south of Jamaica (Cooper 1982). The majority of fish appeared to be sexually mature during most of the period between August and October in the coastal waters of southern Florida (Finucane and Collins 1984). Fecundity estimates for 20 females 380-800 mm FL ranged from 161,000-2,234,000 (Finucane and Collins 1984). The only published reference to eggs and larvae is by Fritzsche (1978:133-135) based on C. A. Mayo's Ph.D. thesis. Food in the West Indies is 96% fishes, particularly small schooling clupeoids (*Harengula*, *Jenkinsia*, and *Opisthonema*) and atherinids (*Allanetta*) but also including squids and shrimps (Randall 1967).

Interest to fisheries.—Taken commercially with gill nets and on lines in Florida, the West Indies, and the Bahama Islands. Also a valued sportfish taken by trolling with cut bait. It is taken by trolling and with hooks baited with live bait in Jamaica (Cooper 1982). Only 76-106 t identified as *S. regalis* were reported from Fishing Area 31 (Western Central Atlantic) in 1979-82, all from the Dominican Republic (FAO 1984), but the actual catch is higher because an additional 985-1,108 t of unidentified *Scomberomorus* was also reported from this area and this is *S. cavalla* and *S. regalis*.

Distribution.—Most abundant in clear waters around reefs in southern Florida, the Bahamas, and West Indies (Fig. 49), but there are scattered records from Cape Cod to Brazil. The northernmost records appear to be Monomoy at the southern elbow of Cape Cod (Bigelow and Schroeder 1953:348) and Buzzards Bay on the south shore of Cape Cod (Sumner et al. 1913). There are also records from Chesapeake Bay (Hildebrand and Schroeder 1928) and further south along the Atlantic coast of the United States. Several authors have reported occurrences in Texas (Baughman 1941, 1950; Pew 1954). Reports are scattered from the northern coast of South America-Isla Providencia, Colombia (Garzon and Acero 1983); Colombia (Dahl 1971; USNM 94766), Venezuela (Cervigón 1966; USNM 123081). The southern end of the range is apparently about at Rio de Janeiro (Ribeiro 1915; BMNH 1903.6.9.80).

Material examined.—Total 60 (76.5-544 mm FL).

meas.: 53 (76.5-544): Florida (3); Bahamas (6); Cuba (5); Hispaniola (3); Jamaica (4); Puerto Rico (2); Virgin Is. (13); Antigua (1); St. Eustatius (2); Martinique (1); Barbados (5); Colombia (1); Curacao (1); Venezuela (1); Brazil (3); Mexico (1).

counts: 60.

diss.: 5 (456-544): Florida (2); Bahamas (3).

Scomberomorus semifasciatus (Macleay)
Broad-barred Spanish Mackerel

Figure 66

Cybium semifasciatum Macleay 1884a:205-206 (original description; Burdekin R., Queensland). Macleay 1884b:28 (Burdekin R.). Whitley 1936:40-42 (description in part; AMS IA.1598 and IA.6573 = *S. queenslandicus* (Munro 1943:

FIGURE 66.—*Scomberomorus semifasciatus*. Queensland, 451 mm FL. (From Munro 1943:pl. 6A.)

95); *C. tigris* a synonym of *S. semifasciatum*); fig. 3 (holotype of *C. semifasciatum*), fig. 4 (holotype of *C. tigris*).

Cybium tigris De Vis 1884:545 (original description; Cape York).

Scomberomorus semifasciatum. McCulloch and Whitley 1925:142 (Burdekin R.; after Macleay 1884a, b).

Scomberomorus tigris. McCulloch and Whitley 1925:142 (Cape York; after De Vis 1884). McCulloch 1929:265 (Cape York; after De Vis 1884).

Scomberomorus semifasciatus. McCulloch 1929: 264 (Burdekin R.; after Macleay 1884). *Munro 1943:91-95 (description, range, synonymy), pl. 6A (451 mm FL specimen from Mackay Dist., N Queensland), fig. 4 (45 and 58 mm juvs., Townsville, N Qld.). Coates 1950:23 (description), fig. Fraser-Brunner 1950:159 (description, range and synonymy in part). Roughley 1951, 1953:110-111 (description), pl. 45, fig. C (after Munro). Jones and Silas 1964:57-58 (description, range), fig. 10 (after Munro). Taylor 1964:282 (description, references, specimens from Nightcliffe, N. Territory). Marshall 1964:365-366 (description; Qld.), pl. 50, figs. 350 A & B (after Munro). Marshall 1966:205 (Qld.), pl. 50, figs. 350 A & B (after Munro). Richards and Klawe 1972:14 (range), 95 (references to juveniles). Magnuson 1973:350 (short pectoral fin). Kailola 1975:237 (3 collections from Gulf of Papua in Kanudi Fisheries collection). Shiino 1976:231 (common name). Klawe 1977:2 (common name, range). Collette 1979:29 (characters, range). Collette and Russo 1979:13 (diagnostic characters, range). Grant 1982:630 (description, fishery in Qld.), 631 (color pl. 328). Cressey et al. 1983:264 (host-parasite list, 5 copepod species). Collette and Nauen 1983:76-77 (description, range), fig. Jenkins et al. 1984:345, 348-351 (101 larvae, 3.3-10.5 mm SL; off Townsville, Qld.), fig. 2 (6 larvae, 3.8-10.5 mm SL).

Indocybium semifasciatus. Fraser 1953:6 (abundant along NW coast of Western Australia).

Indocybium semifasciatum. Whitley 1947:129 (Western Australia). Whitley 1948:24 (W. Australia). Whitley 1954:27 (between Darwin and Pt. Charles, Northern Territory). Munro 1958a:112 (description, range), fig. 752. Whitley 1964a:252 (description, range in part; material from Qld., N. Territory, W. Australia). Whitley 1964b:48 (listed). Grant 1965:173 (description after Munro), fig. Grant 1972: 106, 1975:164, 1978:194 (description after Munro; fishery in Qld.), fig.

Types of nominal species.—Cybium semifasciatum Macleay 1884a. Holotype: AMS I.18288; lower Burdekin River, Queensland, Australia; A. Morton; Aug. 1883; 285 mm FL; D ? + 20 + VIII; A 21 + VIII; P_1 24-24; RGR_1 2 + 1 + 6 = 9; vertebrae 19 + 26 = 45.

Cybium tigris De Vis 1884. Holotype: QM I.119; Cape York, Queensland, Australia; K. Broadbent; 286 mm FL; D XIV + 19 + IX; A 21 + IX; P_1 24-24; RGR_1 2 + 1 + 7 = 10.

Diagnosis.—This species has wider lateral keels on the caudal peduncle than other species in the genus, but this is difficult to quantify and so is not a very useful diagnostic character. Superficially similar to *S. commerson* in having prominent vertical bars on the sides (specimens over 700 mm FL lose their bars), but the bars are much wider (Fig. 66) than the many narrow bars of *S. commerson*. Also differs in lacking an abrupt downward curve in the lateral line under the second dorsal fin, in having fewer spines in the first dorsal fin (15 or fewer vs. usually 16 or 17), and in having more gill rakers on the first arch (6-13, usually 9 or more vs. 1-8, usually 6 or less). Palatine tooth

patch wider (Fig. 26a) than in any other species of *Scomberomorus*. Posterior end of maxilla expanded (Fig. 23a) as in *S. lineolatus* and *S. plurilineatus*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3o). Spines in first dorsal fin 13-15, usually 14 or 15 (Table 9); second dorsal fin rays 19-22, usually 20 (Table 10); dorsal finlets 8-10, usually 9 (Table 10); anal fin rays 19-22, usually 21 or 22 (Table 11); anal finlets 7-10, usually 8 or 9 (Table 11); pectoral fin rays 22-25, usually 23 or 24 (Table 12). Precaudal vertebrae 18 or 19, usually 19 (Table 6); caudal vertebrae 25-27, usually 26 (Table 7); total vertebrae 44-46, usually 45 (Table 8). Gill rakers on first arch (1-2)+(5-11)=6-13, usually 2+(7-9)=9-10 (Table 5). Morphometric characters given in Table 27.

Size.—Maximum size 120 cm FL, 10 kg (Lewis 1981).

Color pattern.—Munro (1943) provided good descriptions of the colors of juveniles and adults from Queensland. Juveniles (<100 mm) with cranial regions and upper regions of the back pale green with a bronze sheen and marked with 12-20 broad vertical dark grey bands. Bars confined to region of body above lateral line, number increasing with age. Cheeks and belly silver white. Snout dark slate grey, patch of green above orbit. First dorsal fin jet black with contrasting areas of white in central region. Second dorsal fin cream with yellow anteriorly. Anal fin and finlets transparent white. Caudal flukes creamy white at margins and dusky or blackish near hypural. Pectoral fins dusky.

With increase in size the bronze-green coloration of the back turns greenish blue. The vertical bands on the back are most marked in specimens <500 mm and in larger fish there is a tendency for these markings to become less distinct, break into spots or fade out more or less completely. Above 700 mm, dead fish assume a drab greyish-yellow blotchy appearance with little or no evidence of markings. This uniform grey color apparently accounts for the vernacular "grey mackerel" of Queensland fishermen as applied to older age groups of the species.

Munro included excellent illustrations of a 451 mm specimen and a 140 mm juvenile in his 1943 paper (pl. 6, 8). The illustration of the larger individual has been reproduced in Grant (1982 and previous editions) and herein (Fig. 66). There is a color photograph of a 470 mm specimen in Grant (1982:pl. 328).

TABLE 27.—Summary of morphometric data of *Scomberomorus semifasciatus*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			31	142	840	344	217
Snout-A	‰	FL	31	477	533	505	16
Snout-2D	‰	FL	31	452	495	472	11
Snout-1D	‰	FL	30	212	261	245	12
Snout-P_2	‰	FL	29	195	273	249	18
Snout-P_1	‰	FL	31	183	248	219	15
P_1-P_2	‰	FL	29	85	116	104	7
Head length	‰	FL	31	180	236	212	14
Max. body depth	‰	FL	29	190	231	210	10
Max. body width	‰	FL	29	71	121	94	13
P_1 length	‰	FL	30	132	166	147	10
P_2 length	‰	FL	28	36	59	50	6
P_2 insertion-vent	‰	FL	22	198	271	237	13
P_2 tip-vent	‰	FL	19	168	210	187	10
Base 1D	‰	FL	30	170	236	210	14
Height 2D	‰	FL	25	112	177	160	13
Base 2D	‰	FL	30	119	211	138	18
Height anal	‰	FL	23	135	220	156	17
Base anal	‰	FL	29	124	168	145	11
Snout (fleshy)	‰	FL	30	72	89	81	4
Snout (bony)	‰	FL	30	63	80	72	4
Maxilla length	‰	FL	30	92	134	118	11
Postorbital	‰	FL	29	84	109	95	6
Orbital (fleshy)	‰	FL	30	23	46	35	7
Orbital (bony)	‰	FL	31	34	63	51	8
Interorbital	‰	FL	31	48	80	56	5
2D-caudal	‰	FL	25	470	565	518	34
Head length			31	33	156	70	39
Snout (fleshy)	‰	HL	30	355	409	379	17
Snout (bony)	‰	HL	30	289	409	340	26
Maxilla length	‰	HL	30	496	596	554	21
Postorbital	‰	HL	29	385	486	448	24
Orbit (fleshy)	‰	HL	30	122	202	162	24
Orbit (bony)	‰	HL	31	176	269	237	24
Interorbital	‰	HL	31	242	357	266	20

Biology.—Little is known of the biology of this species other than it forms small schools. Juveniles ranging in size from 45 to 100 mm are common along the beaches in the vicinity of Townsville, Queensland, during November and grow to twice this size by January (Munro 1943). Larvae (3.3-10.5 mm SL) were described and illustrated by Jenkins et al. (1984).

Interest to fisheries.—Fish of 60-90 cm are caught on fishing grounds north of Yeppoon, Queensland, in November while smaller age groups are caught in estuaries along the Queensland coast north of Moreton Bay (Munro 1943). It is taken by setnetting as well as by trolling and is popularly fished by Queensland anglers in small outboard-powered boats trolling with small lures or cut bait (Grant 1982). Together with *Grammatorcynus* and three other species of *Scomberomorus*, mackerel fishing is Queensland's second major finfishery with an annual output of about 1,000 tons of whole and

filleted fish (Anonymous 1978). Also trawled in the Gulf of Papua.

Distribution.—This is the most estuarine of the species of *Scomberomorus* in Australia. It is confined to estuarine and coastal waters of northern Australia from Shark Bay, Western Australia, through the Northern Territory, and Queensland to northern New South Wales (Whitley 1964a:252, fig. 5f; Lewis 1981:17) and southern Papua New Guinea (Fig. 55). Reports of specimens collected by D. G. Stead from Thailand and Malaya (Whitley 1964a:252) are based on misidentifications.

Geographic variation.—Comparisons of morphometric characters for three small samples of *S. semifasciatus* were made with ANCOVA: Queensland (n = 3-4), Northern Territory (n = 3-5), and New Guinea (n = 13-22). Null hypotheses that the 3 sets of regression lines are coincident were accepted for 23 sets, rejected for 3 sets: Base 1D, orbit (fleshy), and orbit (bony). The Newman-Keuls Multiple Range Test showed that the Queensland and New Guinea populations differed significantly from each other in Base 1D (slopes 0.256 and 0.211, Q = 4.392**) and that the New Guinea population differed from the Northern Territory population in fleshy orbit (slopes 0.020 and 0.030, Q = 5.492**) and bony orbit (slopes 0.034 and 0.046, Q = 7.523**).

Material examined.—Total 34 (142-840 mm FL).

meas.: 31 (142-840): Queensland, Australia (4, **C. semifasciatus*, **S. tigris*); N. Territory, Australia (5); New Guinea (22).
counts: 33.
diss.: 6 (406-840): New Guinea.

Scomberomorus sierra Jordan and Starks
Sierra

Figure 67

Scomberomorus maculatus. Not of Mitchill 1815. Jordan and Gilbert 1882:426 (in part; E. Pacific). Jordan and Gilbert 1883a:106 (Mazatlan). Jordan and Gilbert 1883b:110 (Panama). Meek and Newland 1884:234 (synonymy in part; E. Pacific). Dresslar and Fesler 1889:443 (synonymy in part; E. Pacific). Evermann and Jenkins 1891:128 (not previously reported N of Mazatlan), 137 (important food fish; Guaymas, Mexico). Meek and Hildebrand 1923:324-325 (in part; Pacific coast of Panama; *S. sierra* considered a synonym of *S. maculatus*). Herre 1936:105 (description, several specimens; Albemarle I., Galapagos; *S. sierra* considered a synonym of *S. maculatus*). Fowler 1938:30-31 (synonymy in part, description; specimen from Charles I., Galapagos). Hildebrand 1946:376-377 (synonymy in part; 14 specimens, 100-606 mm SL, from Gulf of Guayaquil; comparison of Atlantic and Pacific populations, "...at most different races for the opposite coasts"). Fraser-Brunner 1950:159 (*S. sierra* considered a synonym of *S. maculatus*). Bini and Tortonese 1955:32 (specimens from several localities in Peru). Ricker 1959:13 (Petalco Bay and San Blas I., Mexico). Castro-Aguirre et al. 1970: 156 (Gulf of California). Sánchez T. and Lam C. 1970:58-59 (length-weight; weights of body parts; diagram of vertebral column, 19+28= 47); photograph. León 1973:22 (Puntarenas, Costa Rica). Amezcua-Linares 1977:10 (lagoon system; Sinaloa, Mexico). Kong 1978:6-9 (Antofagasta, Chile). Yañez-Arancibia 1980:111-

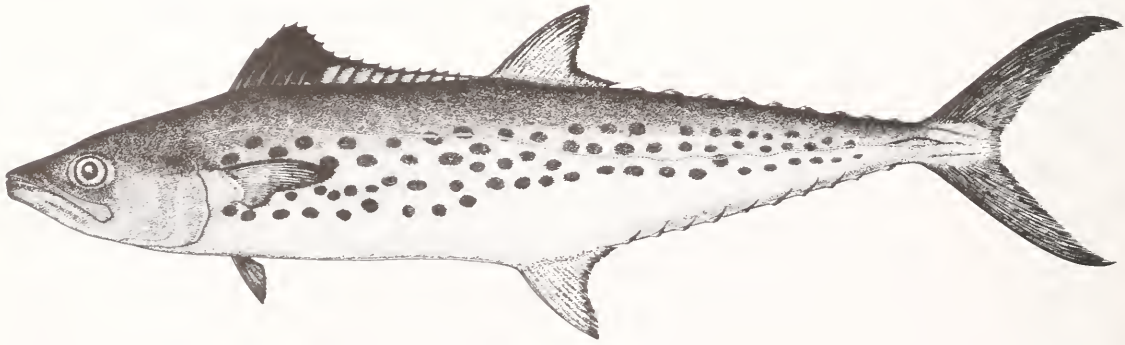


FIGURE 67.—*Scomberomorus sierra*. Gulf of California, 354 mm FL, USNM 217368.

112 (Guerrero, Pacific coast of Mexico), pl. 29, fig. 1.

Scomberomorus sierra Jordan and Starks *in* Jordan 1895:428-429 (original description; Mazatlan, Mexico; also found in Panama). Jordan and Evermann 1896a:341 (listed). Jordan and Evermann 1896b:874-875 (description). Jordan and Evermann 1902:286 (description). Gilbert and Starks 1904:68-69 (description; Panama Bay; comparison with *S. maculatus*). Snodgrass and Heller 1905:360 (Albemarle I., Galapagos). Starks 1910:89-90 (osteology, vertebrae 19+30=49). Kendall and Radcliffe 1912:96 (2 specimens from Panama Bay; description). Osburn and Nichols 1916:158 (Agua Verde Bay; Gulf of California). Evermann and Radcliffe 1917:55-56 (synonymy, description; specimen from Paita, Peru). Starks 1918:120-121 (description, occurrence), fig. 64. Higgins 1920:33-34 (imported to San Diego from Mexico). Craig 1926:167 (used locally; Calexico, Mexico). Ulrey 1929:6 (Gulf of California). Jordan et al. 1930:257 (listed). Croker 1933:14-15 (fishery), fig. 3, fig. 59 (yearly deliveries to San Diego and San Pedro by California boats fishing off Baja California). Breder 1936:11 (specimen taken by second "Pawnee" expedition). Walford 1937:24-25 (description, range, angling notes), color pl. 39. Seale 1940:16-17 (taken along the coast of Mexico and in the Galapagos Is.). Munro 1943:67, 71-72 (placed in subgenus *Scomberomorus*). Fowler 1944: 172-173 (synonymy, description, specimen from Balboa Harbor, Panama). Nichols and Murphy 1944:240 (Bay of Malaga, and Buenaventura, Colombia; more spots than in *S. maculatus*). La Monte 1945:29 (common names, range). Eckles 1949:247-250 (description of 12 juveniles, 21-71 mm FL, 9 from Costa Rica, 3 from the Gulf of California; vertebrae (19-20)+28=(47-48), fig. 2 (21 mm specimen), fig. 3 (71 mm specimen). Fitch and Flechsig 1949:278 (compared with *S. concolor*). Fitch 1950:70 (comparison of 17 *S. sierra* with 30 *S. concolor*). Clothier 1950:52-53 (vertebrae 47-49), pl. X (outline of axial skeleton). Roedel 1951:510 (comparison with *S. concolor*). Mead 1951:121 (2 ripe females, Gulf of California). Roedel 1953:85 (Mexican species; California records of *S. sierra* probably refer to *S. concolor*). Clemens 1956:76, 78 (14 postlarvae, 12-22 mm SL, caught at lat. 08°06'N, long. 79°06'W; 2 survived in shipboard aquaria for 13 d), fig. 2 (postlarvae 16.5 and 54.0 mm SL). Clemens 1957:306 (specimens taken with bait net and night light; Panama, Nicaragua). Collette et al. 1963:53-54 (594 mm FL specimen, La Jolla, first California record, comparison with *S. concolor*), fig. 1. Clemens and Nowell 1963:260 (19 stations, Gulf of California, off Baja California, Mexico, Costa Rica, Gulf of Panama, Gulf of Guayaquil). Fitch and Craig 1964:202 (sagitta similar to that of *S. concolor*). Quiroga and Orbes 1964 (fishery; Esmeraldas Prov., Ecuador). Klawe 1966:445-451 (occurrence of young and spawning; E. Pacific), fig. 2 (11 mm specimens). Fierstine and Walters 1968:4 (localities), 12 (aspect ratio of caudal fin; vertebral counts), fig. 12D (caudal fin complex). Lindsey 1968:1988-1990 (muscle temperature 1.15°C higher than surface water temperature). Matsumoto 1968:309-310 (jaw development compared with that in *Acanthocybium*). Wollam 1970:22 (larval differences between *S. maculatus* and *S. sierra* warrant recognition of *S. sierra*). Erdman 1971:68 (gonads ripe late Aug. to end of Nov., Gulf of Nicoya, Costa Rica; *S. sierra* distinct from *S. maculatus*). *Artunduaga Pastrana 1976 (species synopsis, Colombia). Miller and Lea 1972:192 (description, range), fig. Richards and Klawe 1972:14 (range), 95 (references to larvae and juveniles). Magnuson 1973:350 (short pectoral fin). Sharp 1973:384 (electrophoretic patterns of hemoglobin the same as in *S. concolor*). Shiino 1976: 231 (common name). Thomson and McKibbin 1976:46 (description; Gulf of California), fig. Klawe 1977:2 (common name, range). Collette et al. 1978:274-275 (comparison with *S. brasiliensis* and other American species of *Scomberomorus*). Horn and Allen 1978:41 (California range lat. 33°N to 32°N). Collette 1979:29 (characters, range). Collette and Russo 1979: 13 (diagnostic characters, range). Phillips 1981:54 (El Salvador). Cressey et al. 1983:264 (host-parasite list, 3 copepod species). Collette and Nauen 1983:77-78 (description, range), fig.

Cybium concolor. Not of Lockington, 1889. Boulenger, 1899:3 (Golfe de Panama).

Scomberomorus maculatus sierra. Chirichigno 1969:75 (common names, Ecuador, Peru, and Chile). Chirichigno 1974:325 (in key), fig. 641, 349 (range—S. Calif. to Bahía de Pisco, Peru and Galapagos Is.).

Types.—The original description was based on at least two specimens: "Types, 1720, L. S. Jr. Univ. Mus.; the largest 24 inches long" (Jordan 1895:

429). Böhlke (1953:105) considered SU 1720 to be the holotype of the species but there is a specimen in the British Museum (BMNH 1895.5.24.104) which is also labelled as "type". To clarify the issue, we hereby select CAS SU 1720 as lectotype: Mazatlan, Mexico; D. S. Jordan; 332 mm FL; D XVIII+17+IX; A 19+VIII; P_1 22; RGR_1 4+1 +11=16; 3 rows of faint small spots visible on both sides in 1962, size of spots about equal to half diameter of eye. Paralectotype: BMNH 1895.5.24.104; Mazatlan, Mexico; D. S. Jordan; tin tag with no. 1720 attached to specimen; 550 mm FL; D XVII+17+IX; A 16+IX; P_1 21-22; LGR_1 3+1+10=14; 3 rows of spots on sides.

Diagnosis.—This species possesses nasal denticles (Fig. 1a, b) as do the other five species of the *regalis* group (*brasiliensis*, *concolor*, *maculatus*, *regalis*, and *tritor*), has an artery branching off the fourth left epibranchial artery as do all the species in the group except *S. tritor*, and shares a specialization of the fourth right epibranchial artery (Fig. 7e) with *S. brasiliensis* and *S. regalis*. In these three species, an artery connects the fourth right epibranchial with a branch of the coeliaco-mesenteric artery. *Scomberomorus sierra* has a longer pelvic fin (Fig. 48) than does *S. brasiliensis* (4.7-6.4% FL vs. 3.6-5.9%) and lacks the lateral stripe that is the diagnostic feature of the pigment pattern of *S. regalis*. Together with three other members of the *regalis* group, *S. sierra* has a long posterior process on the pelvic girdle, 62-90% of the length of the anterior plate. Differs from *S. brasiliensis* by having distinct pterotic spines. Intercalar spine absent as in the other five species of the *regalis* group and *S. niphonius*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3p). Spines in first dorsal fin 15-18, usually 17 or 18 (Table 9); second dorsal fin rays 16-19, usually 17 or 18 (Table 10); dorsal finlets 7-10, usually 8 or 9 (Table 10); anal fin rays 16-21, usually 18-20 (Table 11); anal finlets 7-10, usually 8 or 9 (Table 11); pectoral fin rays 20-24, usually 21 (Table 12). Precaudal vertebrae 19-21, usually 20 (Table 6); caudal vertebrae 26-29, usually 28 (Table 7); total vertebrae 46-49, usually 48 (Table 8). Gill rakers on first arch (2-4)+(9-14)=12-17, usually 3+(12-13)=15-16 (Table 5). Morphometric characters given in Table 28.

TABLE 28.—Summary of morphometric data of *Scomberomorus sierra*. FL = fork length, HL = head length.

Character			Mexico					Panama					Colombia					Total				
			N	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD	*N*	Min.	Max.	Mean	SD
Fork length			36	163	615	344	139	21	98	596	349	154	14	180	266	226	22	97	68	621	340	139
Snout-A	‰	FL	35	518	565	539	13	21	519	560	536	12	14	510	562	526	13	95	510	616	537	17
Snout-2D	‰	FL	35	496	534	513	10	21	466	529	507	14	14	489	511	504	6	95	466	586	510	14
Snout-1D	‰	FL	36	222	268	245	13	21	221	266	242	12	14	216	251	237	11	97	213	276	241	14
Snout-P_2	‰	FL	36	224	297	255	18	20	238	286	257	15	14	250	264	257	5	96	198	330	252	22
Snout-P_1	‰	FL	36	195	249	222	14	21	205	245	220	11	14	211	227	219	5	97	181	260	220	15
P_1-P_2	‰	FL	31	93	118	106	8	20	93	123	104	8	14	91	111	105	5	91	89	123	104	8
Head length	‰	FL	36	190	246	216	14	21	197	237	212	9	14	206	219	213	4	97	183	260	212	14
Max. body depth	‰	FL	34	157	205	191	12	19	164	210	184	14	14	190	221	205	9	93	157	221	190	15
Max. body width	‰	FL	32	53	111	84	13	19	63	104	86	11	14	64	86	74	8	90	53	115	84	12
P_1 length	‰	FL	36	110	141	123	7	21	102	140	123	11	14	117	135	127	6	97	78	145	123	9
P_2 length	‰	FL	36	40	64	53	4	19	36	64	53	9	14	50	61	55	3	94	32	64	53	6
P_2 insertion-vent	‰	FL	35	215	318	268	23	20	239	294	271	16	14	235	277	255	11	95	193	339	267	25
P_2 tip-vent	‰	FL	35	162	264	216	20	19	194	262	221	18	14	183	216	200	10	93	162	284	221	22
Base 1D	‰	FL	35	232	286	261	11	20	206	280	253	18	14	238	288	260	12	95	206	306	259	16
Height 2D	‰	FL	35	103	139	120	8	18	109	139	124	8	13	127	141	135	5	88	103	146	123	10
Base 2D	‰	FL	36	69	142	118	13	21	105	140	120	10	14	109	144	125	8	97	69	184	120	14
Height anal	‰	FL	35	103	130	115	7	20	106	135	123	8	14	121	136	128	5	93	91	136	118	9
Base anal	‰	FL	36	97	163	121	12	21	103	157	121	12	14	115	131	122	5	97	88	163	119	12
Snout (fleshy)	‰	FL	36	69	91	81	6	21	73	89	80	4	14	73	78	76	2	97	62	92	79	6
Snout (bony)	‰	FL	33	43	82	72	7	19	65	78	71	4	9	62	69	66	2	85	43	150	70	11
Maxilla length	‰	FL	36	103	146	124	11	21	115	139	122	6	14	114	129	120	4	97	99	150	121	10
Postorbital	‰	FL	31	91	107	100	4	21	90	102	97	3	14	94	101	98	2	92	85	116	98	5
Orbital (fleshy)	‰	FL	36	25	49	34	7	21	23	48	34	7	14	34	43	39	2	97	2	53	34	7
Orbital (bony)	‰	FL	31	39	64	50	8	21	37	64	50	8	14	50	61	54	3	92	16	77	50	9
Interorbital	‰	FL	36	29	62	56	6	21	52	59	54	2	14	51	58	54	2	97	2	65	54	7
2D-caudal	‰	FL	30	430	520	476	25	20	436	509	471	18	14	443	511	467	18	89	234	580	475	38
Head length			36	40	135	73	26	21	23	122	73	31	14	39	57	48	5	97	18	135	71	26
Snout (fleshy)	‰	HL	36	350	405	375	13	21	345	434	379	23	14	344	370	358	7	97	338	434	371	16
Snout (bony)	‰	HL	33	182	375	332	30	19	310	373	336	21	9	299	320	308	8	85	182	576	332	37
Maxilla length	‰	HL	36	540	610	573	18	21	561	610	578	13	14	542	592	566	12	97	531	610	570	17
Postorbital	‰	HL	31	403	502	458	26	21	415	497	460	22	14	446	472	460	8	92	388	509	461	26
Orbit (fleshy)	‰	HL	36	124	200	156	22	21	114	203	158	27	14	160	196	182	11	97	9	232	158	27
Orbit (bony)	‰	HL	31	184	278	226	25	21	173	292	234	33	14	228	280	256	15	92	81	337	235	35
Interorbital	‰	HL	36	143	284	257	22	21	220	288	257	14	14	241	270	254	8	97	11	288	253	33

Size.—Maximum size 96.5 cm FL, 5.44 kg; of 271 sierra caught in the Gulf of Nicoya, Costa Rica, 50 measured more than 63.5 cm and weighed more than 5.4 kg (Erdman 1971). Size at first maturity 26-32 cm FL in Colombia (Artunduaga Pastrana 1976). A length-weight regression curve has been published for 310 Colombian specimens 15-63 cm, 0.03-2.4 kg (Artunduaga Pastrana 1976:fig. 6).

Color pattern.—Bluish above, silvery white ventrally, sides with numerous round brownish (orange in life) spots, three rows below lateral line, one above (Fig. 67). First dorsal fin black distally, white at base. Second dorsal tinged with yellow, margins black. Anal white.

There is a color painting of *S. sierra* by Malmquist in Walford (1937:pl. 39), and there is a good black and white underwater photograph of several specimens in the Gulf of California in Thomson et al. (1979:fig. 115).

Biology.—Spawning probably takes place near the coast over most of its range (Klawe 1966). Spawning occurs off Mexico in July-September (Klawe 1966). Ripe males and females were found from late August to the end of November in the Gulf of Nicoya, Costa Rica (Erdman 1971). The maximum incidence of ripe females extends from November to April in Colombia with a peak in February-April (Artunduaga Pastrana 1976). Larvae and juveniles, 4.5-139 mm FL, of *S. sierra* have been taken from Baja California to Peru during January-April and July-September (Klawe 1966:fig. 1, table 1). The smallest larvae were taken off Baja California July-September: 4.5-9.5 mm FL, 13 September; 4.8 mm, 12 August; 8.4 mm, 9 July (Klawe 1966:table 1). Food of adults consists of small fishes (Walford 1937). In Colombia (Artunduaga Pastrana 1976), the commonest fishes in stomach contents were anchovies (Engraulidae, *Anchoa* and *Cetengraulis*) and clupeids (*Odontognatus* and *Opisthonema*).

Interest to fisheries.—According to Walford (1937), *S. sierra* seems to be the most abundant game fish along the Pacific coasts of Mexico and Central America. It is an excellent food fish frequently taken by anglers and abundant enough to support a commercial fishery (Eckles 1949). Statistics are reported from Fishing Areas 77 and 87; the bulk of the catch is reported for Mexico 4,028-11,999 t/yr and for Peru 320-579 t/yr in 1979-82 (FAO 1984). No specific commercial fishery exists for *S. sierra* in Colombia, but it is taken by the shrimp fleet and by artisanal fishermen for a total catch in 1971 of 127 tons (Artunduaga Pastrana 1976).

Distribution.—Eastern Pacific (Fig. 49) from La Jolla, southern California (Collette et al. 1963) south past Payta, Peru (Collette and Russo 1979: fig. 8) to Antofagasta, Chile (lat. 23°24′S, long. 70°26′W, Kong 1978). Also found around the Galapagos Islands.

Geographic variation.—Comparisons were made of morphometric data for three populations of *S. sierra* by ANCOVA (Table 28): Mexico (n = 31-36), Panama (n = 18-21), Colombia (n = 9-14). Null hypotheses that the 3 sets of regression lines are coincident were accepted for 18 sets, rejected for 8 sets: Sn-1D, Sn-P_2, Head L, maximum body depth, Ht 2D, Ht A, Snout (fleshy), and maxilla L. The Newman-Keuls Multiple Range Test identified populations that were significantly different for 6 sets of regressions. Five of these (Sn-1D, Sn-P_2, Head L, Ht A, and maxilla L) indicated that the populations from Mexico and Panama were significantly different, one (maximum depth) that the Panama and Colombia populations were significantly different. The samples from Panama and Colombia were then combined and the combined regressions were compared with those for Mexico. Null hypotheses were rejected for 7 of the 26 sets of regression lines; the same ones as were rejected in the first test except for maximum body depth. No meristic differences were found between populations.

Material examined.—Total 123 (68-621 mm FL).

meas.:	97 (68-621): California (1); Mexico (39, **S. sierra*); El Salvador (1); Costa Rica (5); Panama (21); Colombia (14); Ecuador (7); Peru (6); Galapagos Is. (3).
counts:	123.
diss.:	13 (368-590): Mexico (2); Panama (5); Ecuador (5).

Scomberomorus sinensis (Lacepède)
Chinese Seerfish

Figure 68

Scomber sinensis Lacepède 1800:599 (original description). Lacepède 1802:23 (description based on a Chinese drawing). Günther 1860: 369 (footnoted as dubious species).

Cybium chinense Cuvier *in* Cuvier and Valenciennes 1831:180 (original description based on

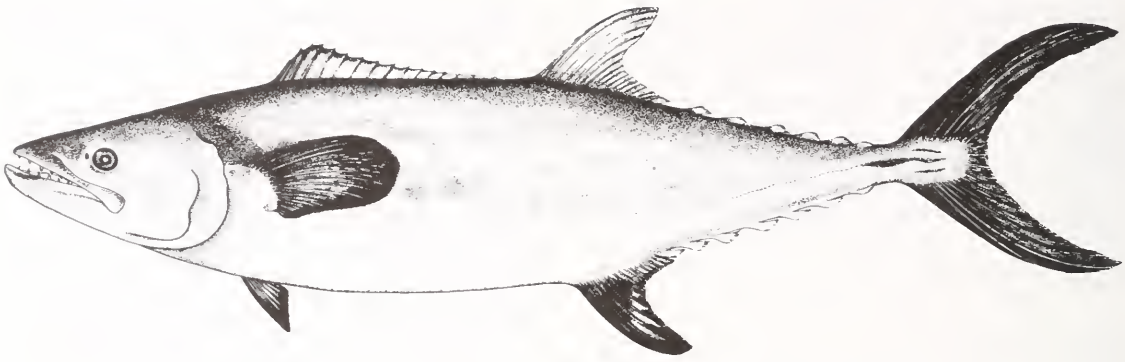


FIGURE 68.—*Scomberomorus sinensis.* Shanghai, China, 714 mm FL, USNM 220856.

same figure used by Lacepède). Temminck and Schlegel 1844:100-101 (description), pl. 53, fig. 1 (color painting of adult). Richardson 1846:268 (synonymy; seas of China and Japan). Günther 1860:369 (footnoted as dubious species). Bleeker 1873:131 (China; listed). Kishinouye 1915:11 (description), pl. 1, fig. 5. *Kishinouye 1923:418-419 (description, range), pl. 21, fig. 34 (adult), pl. 23, fig. 40 (skull, vertebral column). Kishinouye 1924:92 (26 mm juvenile from skipjack stomach). Boeseman 1947:95 (identification of Burger's plate). Morice 1953: 37 (villiform tongue teeth present).

Scomberomorus sinensis. Jordan and Snyder 1900:352 (Tokyo; listed). Jordan and Snyder 1901:64 (Japanese localities). Reeves 1927:8 (Chefoo, China; listed). Mori 1928:5 (Fusan, Korea; listed). Soldatov and Lindberg 1930:111 (synonymy, description, range). Munro 1943: 69, 71 (placed in subgenus *Sierra*; *C. cambodgiense* Durand a junior synonym of *S. sinensis*). Mori 1952:137 (Fusan, Korea; listed). Mori 1956:23 (Kasumi and Hamada, S Japan Sea; listed). Blanc et al. 1965:121-123 (*C. cambodgiense* Durand a junior synonym of *S. sinensis*). *D'Aubenton and Blanc 1965:233-243 (description, range, biology), fig. 1 (191 mm juvenile), fig. 2 (1,170 mm adult). Kamohara 1967:43 (comparison with *S. niphonius*). Tokida and Kobayashi 1967:158 (identification of *C. chinense* of Uchimura's unpublished 1884 manuscript). Sugiura 1970:205 (Bonin Is., listed). Richards and Klawe 1972:15 (range), 95-96 (reference to Blanc et al. 1965 and D'Aubenton and Blanc 1965). Shiino 1972:71 (common name). Magnuson 1973:350 (short pectoral fin). Orsi 1974: 175 (Vietnam; listed). Shiino 1976:231 (common name). Klawe 1977:2 (common name, range). Zama and Fujita 1977:118 (Ogasawara Is., listed after Sugiura 1970). Collette 1979: 29 (characters, range). Collette and Russo 1979:13 (diagnostic characters, range). Ohe et al. 1981:42-43 (comparison with Miocene *Acanthocybium* from Japan). Zhang and Zhang 1981:104 (range). Lee and Yang 1983:229 (Taiwan), fig. 18 (1,056 mm). Cressey et al. 1983: 264 (host-parasite list, 3 copepod species). Collette and Nauen 1983:78 (description, range), fig.

Scomberomorus chinensis. Jordan et al. 1913: 122 (Japanese common names). Norman and Fraser 1949:153 (China and Japan). Devaraj 1977:56-57 (*S. chinensis* intermediate between *Acanthocybium* and other species of *Scomberomorus*).

Cybium cambodgiense Durand 1940:37-38 (original description; Phnom Penh, Cambodia), pl. 6.

Scomberomorus cavalla (not of Cuvier 1829). Fraser-Brunner 1950:160-161 (*Cybium sinensis* placed in synonymy of *S. cavalla* and considered a subspecies of it).

Scomberomorus chinense. Richards and Klawe 1972:13 (range), 90 (reference to Kishinouye 1924).

Scomberomorus sp. Kawamoto et al. 1972:49 (description; Mekong Delta, Vietnam), fig. 96.

Scomberomorus cambodgiense. Orsi 1974:174 (Vietnam; listed).

Types of nominal species.—Both *Scomber sinensis* Lacepède 1800 and *Cybium chinense* Cuvier *in* Cuvier and Valenciennes 1831 are based on a Chinese drawing; no types are extant (Blanc and Bauchot 1964:449).

Cybium cambodgiense Durand 1940. The original description was based on a 215 mm specimen

taken in Phnom Penh, Cambodia, 28 January 1939. Because this specimen is not known to still exist, data are presented from the original description: D XVI + 16 + VII; A 19 + VI; P_1 22; GR 3 + 9 = 12. The figure (pl. 6) accompanying the original description clearly shows the deep dip in the lateral line under the posterior part of the first dorsal fin.

Diagnosis.—The only species of *Scomberomorus* that has a swim bladder and the only species with an abrupt downward curve in the lateral line beneath the first dorsal fin (Fig. 68). Two species, *S. cavalla* and *S. commerson*, also have abrupt downward curves in the lateral line but they are under the second dorsal fin. The lateral line in the other 15 species descends gradually without any prominent dips. The pectoral fins are large and rounded rather than pointed as in the other 17 species. Palatine tooth patch very narrow as in *Scomberomorus commerson* and *Acanthocybium*. Ventral process of angular moderate, 87-93% as long as the dorsal process, as in *S. cavalla*. Posterior end of maxilla only slightly expanded as in *S. multiradiatus*. Ascending process of premaxilla very long as in *S. lineolatus* and *Acanthocybium*.

Description.—Intestine with two folds and three limbs (Fig. 3q). Spines in first dorsal fin 15-17, usually 16 or 17 (Table 9); second dorsal fin rays 15-17, usually 15 or 16 (Table 10); dorsal finlets 6-7 (Table 10); anal fin rays 16-19, usually 17 or 18 (Table 11); anal finlets 5-7, usually 6 (Table 11); pectoral fin rays 21-23, usually 22 (Table 12). Precaudal vertebrae 19 or 20 (Table 6); caudal vertebrae 21 or 22, usually 22 (Table 7); total vertebrae 41 or 42, usually 41 (Table 8). Gill rakers on first arch (1-3) + (10-12) = 11-15, usually 2 + (10-11) = 12-13 (Table 5). Morphometric characters given in Table 29.

Size.—Maximum size 200 cm FL, 80 kg in weight (Kishinouye 1923). A length-weight graph for fish up to 120 cm FL and 18 kg was published by D'Aubenton and Blanc (1965:fig. 4).

Color pattern.—Back greenish blue, belly silvery, fins mostly blackish. Pelvic and anal fins with blackish margins, anal finlets colorless (Kishinouye 1923). Large (larger than the diameter of the eye), round, indistinct spots on sides in two poorly defined rows in adults (Fig. 68). Juveniles with saddlelike blotches extending down to about middle of body (D'Aubenton and Blanc 1965:fig. 2).

There is an excellent figure of *S. sinensis* in Kishinouye (1923:fig. 34) and there are drawings of a juvenile (191 mm FL, fig. 1) and an adult (1,017 mm FL, fig. 2) of *S. sinensis* from the Mekong River in Cambodia in D'Aubenton and Blanc (1965).

Biology.—No information is available on the movements of *S. sinensis*. Although it penetrates great distances up the Mekong River, D'Aubenton and Blanc (1965) reported that they failed to find the slightest trace of sexual activity in Cambodian freshwater specimens and so they concluded that *S. sinensis* must reproduce exclusively in the sea. No information is available on eggs or larvae (Richards and Klawe 1972), but D'Aubenton and Blanc (1965) did report on juveniles as small as 166 mm FL from Tonle Sap, Cambodia.

Interest to fisheries.—No catches were reported as *S. sinensis* by FAO for the period 1979-82 (FAO 1984). However, it is a prized food fish in Japan and probably in China as well. Kishinouye (1923)

TABLE 29.—Summary of morphometric data of *Scomberomorus sinensis*. FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			18	157	714	330	176
Snout-A	‰	FL	14	573	605	584	11
Snout-2D	‰	FL	14	526	571	558	13
Snout-1D	‰	FL	16	268	309	292	9
Snout-P_2	‰	FL	16	270	318	290	12
Snout-P_1	‰	FL	16	234	279	259	11
P_1-P_2	‰	FL	16	101	128	113	7
Head length	‰	FL	18	230	264	255	8
Max. body depth	‰	FL	16	201	231	218	10
Max. body width	‰	FL	16	77	127	102	14
P_1 length	‰	FL	18	133	186	157	14
P_2 length	‰	FL	16	75	89	83	5
P_2 insertion-vent	‰	FL	15	254	295	273	13
P_2 tip-vent	‰	FL	15	161	216	189	17
Base 1D	‰	FL	16	230	282	260	12
Height 2D	‰	FL	15	130	164	145	10
Base 2D	‰	FL	15	99	137	121	11
Height anal	‰	FL	16	129	164	145	10
Base anal	‰	FL	16	99	149	122	12
Snout (fleshy)	‰	FL	16	86	106	97	5
Snout (bony)	‰	FL	16	77	99	90	5
Maxilla length	‰	FL	16	131	159	147	7
Postorbital	‰	FL	16	104	126	117	7
Orbital (fleshy)	‰	FL	16	25	40	35	5
Orbital (bony)	‰	FL	16	40	61	52	7
Interorbital	‰	FL	16	54	72	63	5
2D-caudal	‰	FL	13	394	469	445	27
Head length			18	41	173	83	41
Snout (fleshy)	‰	HL	16	360	414	382	14
Snout (bony)	‰	HL	16	335	387	355	14
Maxilla length	‰	HL	16	561	603	578	12
Postorbital	‰	HL	16	404	482	460	24
Orbit (fleshy)	‰	HL	16	104	155	138	17
Orbit (bony)	‰	HL	16	157	236	202	23
Interorbital	‰	HL	16	208	289	249	23

reported that 2 or 3 dozens of this species were often caught on an autumn day in pound nets on the southern coast of Korea. It is caught in the Mekong River of Cambodia and commanded a high price in the Phnom Penh market in 1964 (D'Aubenton and Blanc 1965:242).

Distribution.—Western Pacific from Japan and China south to Cambodia and Vietnam where it enters the Mekong River (Fig. 51). The northern limit is Akita, Honshu, in the Sea of Japan and the Chiba-Tokyo area on the Pacific coast (Kishinouye 1923:418). There are records or specimens from Pusan, Korea (Mori 1928, 1952), Cheefo (= Yentai) on the Shantung Peninsula (Reeves 1927), the Zhoushan Islands (lat. 30°N, long. 122°E, USNM 220856), Foochow (ZMH 11384), Amoy (USNM 221277), and Hong Kong (CAS GVF HK 127). A record from the Bonin (or Ogasawara) Islands (Sugiura 1970; repeated by Zama and Fujita 1977) has not been verified and seems very far offshore for this species. It has been taken on the coast of Vietnam at Nha Trang (Blanc et al. 1965). *Scomberomorus sinensis* is the only species of the genus and of the family to move any significant distance into freshwater. It was described as a distinct species, *Cybium cambodgiense*, by Durand (1940) from material from Phnom Penh, Cambodia, about 300 km up the Mekong River. Specimens (MNHN 1965-286-9) have come from Tonle Sap (or Grand Lac) which is even further up the Mekong River (Blanc et al. 1965).

Geographic variation.—Morphometric data for two small samples of *S. sinensis* were compared with ANCOVA: China (n = 7-10) and the Mekong River, Cambodia (n = 6). Null hypotheses that the 2 sets of regression lines are coincident were accepted for all but 1 set of the 26 sets, Sn-P_2 (intercepts 7.552 and 8.385 respectively). The Chinese sample had slightly fewer gill rakers on the first gill arch (11-14, mode 12, $\bar{x}$ 12.30) than the Mekong sample (12-15, mode 13, $\bar{x}$ 13.17). No other meristic differences were found.

Material examined.—Total 19 (157-714 mm FL).

meas.:	18 (157-714): China (10); Mekong R., Cambodia (6); Cochinchine (2).
counts:	18.
diss.:	1 (plus 1 head, 431 mm).

Scomberomorus tritor (Cuvier)
West African Spanish Mackerel

Figure 69

Cybium tritor Cuvier *in* Cuvier and Valenciennes 1831:176-177 (original description; Gorée, Sénégal), pl. 218. Günther 1860:372 (description after Cuvier). Rochebrune 1882:96 (very common; Gorée, Dakar). Osorio 1898:197 (Principe). Pellegrin 1908:75 (Dakar). Chabanaud and Monod 1927:278 (Port-Étienne), fig. 30 A. Cadenat 1947:15 (common names; W. Africa). Postel 1954:357-358 (stomach contents of 286 specimens), 362 (gonosomatic index). A. Postel 1955:60-61, fig. 3 (lower jaw teeth 10-21, upper jaw teeth 13-27; 190 specimens), 63, fig. 5 (number of jaw teeth in males and females). *Postel 1955a:4-158 (distribution, size, reproduction), pl. II, bottom figure. Postel 1955b: 31-32 (sex ratio, maximum size, number of eggs). Frade and Postel 1955:35 (histology of

FIGURE 69.—*Scomberomorus tritor.* Liberia, 430 mm FL, USNM 193178.

gonads; mature in June), fig. 7 (oocytes). Postel 1958:107-111 (summary of Postel 1955a). Postel 1959:163 (listed). Postel 1960:257 (Cap Blanc to Senegambie). Marchal 1961:106 (lat. 9°12′N, long. 13°42′W). Franca 1964:table 3 (Angola). Daget and Iltis 1965:280-281 (Ebrie and Abi lagoons, Ivory Coast), fig. 178. Sanches 1966:146 (Angola). Blache et al. 1970:375 (in key), fig. 960 (not fig. 961). Conand 1970:40 (distribution of larvae).

Apolectus immunis Bennett 1831:146 (original description; "Atlantic Coast of North Africa").

Cybium maculatum. Not of Mitchill 1815. Stassano 1890:44 (Spanish Sahara). Vinciguerra 1890:100-103 (synonymy). Osorio 1898:197 (São Thome).

Scomberomorus argyreus Fowler 1905:764-765 (original description, "West Africa"), pl. 51.

Scomberomorus maculatus. Not of Mitchill 1815. Fowler 1936:628-629. Cadenat 1937:482 (Dakar). Scaccini 1941:19 (synonymy in part; Mauritania). Navarro 1943:131 (Cabo Barbas and Blanco, Banco Arguín, Mauritania). Tortonese 1949:65 (accidental in Mediterranean Sea). Sanz Echeverría 1950:1-2 (sagitta compared with other scombrids), pl. 1, figs. 1-4 (photographs of sagittae). Mather and Day 1954:182, 185 (Sierra Leone, Dakar, Canary Is.; *S. tritor* not specifically distinct from *S. maculatus*). Tortonese 1956:7 (accidental in Mediterranean Sea). Poll 1959:104-106 (description; S to Baie des Tigres, Angola), fig. 34. Maurin et al. 1970:19 (Nouakchott, NW Africa). Lozano Cabo 1970:158 (Sahara coast). Fagade and Olaniyan 1973:212, 220, 224 (piscivorous, feeding largely on *Ethmalosa fimbriata* in Lagos). Fagade and Olaniyan 1974:249 (caught in Lagos Lagoon when water was brackish). Tortonese 1975:354-355 (description, Italy), fig. 155.

Scomberomorus tritor. Munro 1943:67-71 (placed in subgenus *Scomberomorus*). Irvine 1947: 186-187 (Accra, Ghana), fig. 108. Fraser-Brunner 1950:158 (synonymy in part), fig. 27. Chaine 1957:504-509 (otoliths), pl. IV (otoliths). Gras 1961:583 (Lagune de Cotonou and Lac Nokoue, Dahomey). Bauchot and Blanc 1961: 372-373 (types). Blanc and Bauchot 1964:448 (types), pl. IV, figs. 19-20 (photographs of types). Gorbunova 1965a:54 (spawning season). Collette 1966:367 (types). Williams 1968:436, table 593 (taken from Gambia to the Congo during the Guinean Trawling Survey). Collette 1970: 4-5 (in key; Mediterranean Sea). Richards and Klawe 1972:15 (range), 96 (references to larvae). Miyake and Hayasi 1972:III-3 (in key), IV-10 (common names). Magnuson 1973:350 (short pectoral fin). Klawe 1977:2 (common name; range). Penrith 1978:187 (Baia dos Tigres, Angola). Collette et al. 1978:274-275 (comparison with W. Atlantic species). Collette 1979: 29 (characters, range). Collette and Russo 1979:13 (diagnostic characters, range). Collette 1981:Scombm 7 (description, range), fig. Seret and Opic 1981:332-333 (description), fig. Cressey et al. 1983:264 (host-parasite list, 4 copepod species). Collette and Nauen 1983:79 (description, range), fig.

Types of nominal species.—Holotype: MNHN A.6871; Gorée, Sénégal; Rang; 658 mm FL; D XV + 17 + VIII; A 17 + VIII; P_1 21; RGR_1 2 + 1 + 10 = 13. Paratype: MNHN A.6868; Gorée; Sénégal; Rang; 505 mm FL. Photographs of the holotype and paratype were published by Blanc and Bauchot (1964:pl. 4, figs. 19, 20).

Scomberomorus argyreus Fowler 1905. Holotype: ANSP 11400; west coast of Africa; Dr. Savage; 148 mm FL; D XVII + 17 + VIII; A 19 + VIII; P_1 22-22; RGR_1 2 + 1 + 11 = 14; vertebrae 18 + 28 = 46.

Diagnosis.—This species possesses nasal denticles as do the other five species of the *regalis* group (*brasiliensis*, *concolor*, *maculatus*, *regalis*, and *sierra*) but lacks the artery branching from the fourth left epibranchial artery that is present in the other species (Fig. 7b). Intercalar spine absent as in the other five species of the *regalis* group and *S. niphonius*.

Description.—Lateral line gradually descending to midline on caudal peduncle. Intestine with two folds and three limbs (Fig. 3r). Spines in first dorsal fin 15-18, usually 17 or 18 (Table 9); second dorsal fin rays 16-19, usually 17 (Table 10); dorsal finlets 7-9, usually 8 (Table 10); anal fin rays 17-20, usually 18 or 19 (Table 11); anal finlets 7-9, usually 8 (Table 11); pectoral fin rays 20-22, usually 21 (Table 12). Precaudal vertebrae 18 or 19, usually 19 (Table 6); caudal vertebrae 27 or 28, usually 27 (Table 7); total vertebrae 46 or 47, usually 46 (Table 8). Gill rakers on first arch (1-3) + (10-13) = 12-15, usually 2 + (11-12) = 13-14 (Table 5). Postel (1955a) reported a range of 10-15 gill rakers for 240 males and 520 females, 94% of both sexes 12-14. Morphometric characters given in Table 30.

Size.—Maximum size of males 83.9 cm FL, fe-

males 97.5 cm FL; commonly 50-70 cm; age at first maturity of both sexes 45 cm (Postel 1955a).

Color pattern. —Upper parts of body bluish, belly silvery, sides marked with several poorly defined rows of elongate spots (Fig. 69). First dorsal fin black anteriorly and along distal margin posteriorly, white at base.

There are drawings of *S. tritor* in Postel (1955a: pl. 2) and Poll (1959:fig. 34), Collette (1981: Scombm 7), and Seret and Opic (1981:333).

Biology. —Sexual maturity in both sexes of *S. tritor* occurs from April to October in Sénégal (Postel 1955a). Postel (1955a) reported 1 million eggs in a 95 cm FL female. Juveniles have been seined along the shore near Dakar in July (Postel 1955a). Seven larvae 3.5-8.1 mm were caught in September, December, February, and March, south of the Ivory Coast at water temperatures of 23.2°-26°C and salinities of 34.38-35.45‰ (Zhudova 1969). Three larvae identified as *S. tritor* were reported from a station track from Dakar to Recife (Zharov and Zhudova 1967), but this distribution seems highly unlikely. In Lagos Lagoon, Nigeria, stomach contents of 24 of 26 specimens of *S. tritor* with food contained the clupeid *Ethmalosa fimbriata* (Fagade and Olaniyan 1973). No sexually mature stages of *S. tritor* were found in the lagoon so Fagade and Olaniyan concluded that the lagoon served as a feeding ground for this and other piscivorous fishes that could tolerate the reduced salinity of the lagoon.

TABLE 30.—Summary of morphometric data of *Scomberomorus tritor.* FL = fork length, HL = head length.

Character			N	Min.	Max.	Mean	SD
Fork length			40	102	658	347	151
Snout-A	%	FL	40	506	567	533	15
Snout-2D	%	FL	39	482	551	513	14
Snout-1D	%	FL	39	190	276	246	13
Snout-P_2	%	FL	40	237	301	266	17
Snout-P_1	%	FL	40	197	247	222	13
P_1-P_2	%	FL	40	95	138	111	11
Head length	%	FL	40	199	242	217	10
Max. body depth	%	FL	38	166	240	206	21
Max. body width	%	FL	36	67	110	90	11
P_1 length	%	FL	39	110	152	134	9
P_2 length	%	FL	38	48	71	60	6
P_2 insertion-vent	%	FL	39	213	304	250	18
P_2 tip-vent	%	FL	38	146	243	190	17
Base 1D	%	FL	38	238	304	262	14
Height 2D	‰	FL	31	97	161	126	14
Base 2D	%	FL	40	101	144	122	10
Height anal	‰	FL	36	92	159	125	13
Base anal	‰	FL	40	93	139	119	10
Snout (fleshy)	‰	FL	40	73	93	81	5
Snout (bony)	‰	FL	40	64	86	72	5
Maxilla length	‰	FL	40	110	143	123	8
Postorbital	%	FL	39	89	107	96	4
Orbital (fleshy)	‰	FL	40	26	52	38	6
Orbital (bony)	%	FL	40	28	68	53	8
Interorbital	‰	FL	40	51	68	59	4
2D-caudal	‰	FL	38	432	534	476	29
Head length			40	23	145	74	31
Snout (fleshy)	‰	HL	40	332	409	376	18
Snout (bony)	‰	HL	40	290	388	333	21
Maxilla length	%	HL	40	541	608	568	14
Postorbital	‰	HL	39	399	474	443	20
Orbit (fleshy)	‰	HL	40	124	233	173	23
Orbit (bony)	%	HL	40	133	307	245	32
Interorbital	‰	HL	40	230	301	272	13

Interest to fisheries. —Taken throughout the Gulf of Guinea, but catches are reported only for Ghana and Angola in the period 1979-82. Most of the catch is reported for Ghana, 1,569 to 4,412 t/yr (FAO 1984).

Distribution. —Eastern Atlantic, concentrated in the Gulf of Guinea from the Canary Islands (Mather and Day 1954; MCZ 26416), West Sahara (Stassano 1890), and Dakar, Sénégal (original description), south to Baia dos Tigres, southern Angola (Fig. 49). Accidental and rare in the Mediterranean Sea (Tortonese 1949, 1956), with several extant specimens from Nice (NHMV 14599, MSUF M.1665), Villefranche, and Palermo (Tortonese 1975).

Material examined. —Total 49 (69-658 mm FL).

meas.: 40 (102-658): N. Mediterranean (2); Canary Is. (1); Spanish Sahara (1); Sénégal (4, **C. tritor*), Guinea (1); Sierra Leone (5); Liberia (5); Ivory Coast (10); Ghana (5); Nigeria (4); Angola (2); "West Africa" (1, **S. argyreus* Fowler).

counts: 49.

diss.: 10 (394-600): Ivory Coast.

RELATIONSHIPS

After comparing the species of *Scomberomorus* with each other and with *Grammatorcynus* and *Acanthocybium* (Comparative Morphology), all the characters that differentiated species or genera were listed. Character polarities were determined by considering the character state present in *Grammatorcynus* to represent the plesiomorphous condition. *Scomberomorus*, *Acanthocybium*, the Sardini, and the Thunnini have 4 or 5 caudal vertebrae supporting the caudal fin and 37 or more total vertebrae. These derived characters indicate that these taxa form a monophyletic group within the Scombridae. *Grammatorcynus* lies between the Scombrini and the higher scombrids and is clearly more primitive than *Scomberomorus* because it has, as in the

Scombrini, only 3 vertebrae supporting the caudal fin and only 31 total vertebrae. Therefore, we have used it as the outgroup for comparison with *Scomberomorus*. Of the 72 characters that differentiated at least 1 taxon from the others, 14 were autapomorphies of *Acanthocybium*. These cannot contribute to an understanding of relationships within *Scomberomorus* and were omitted from the analysis. The remaining 58 characters were employed to generate a cladogram using a computer program (WAGNER 78) written by J. S. Farris (following Farris 1970 and Farris et al. 1970). The order of the taxa was "shuffled" to determine if another equally parsimonious tree would be generated. Another cladogram was produced with the same total length, 112 steps. The first cladogram has a deviation ratio (sum of the homoplasies between all pairwise combinations of terminal taxa divided by the sum of the character changes between all pairwise combinations of terminal taxa) of 0.24, the second 0.21. The difference is due to characters 3 and 17. We feel that the first cladogram (Fig. 70) more reasonably reflects our concepts of evolution within the genus. A summary of the character states with references to the relevant figures is presented as Appendix 1.

We recognize six species groups within *Scomberomorus* (Fig. 70, Table 31): *sinensis* from node 17; *commerson* from node 15; *munroi* from node 11; *semifasciatus* from node 9; *guttatus* from node 8; and *regalis* from node 5.

The *sinensis* group is monotypic. It is defined by the presence of an abrupt downward curve in the lateral line under the first dorsal fin (character 19, state 1). A similar abrupt downward curve is present in two species of the *commerson* group but the curve is under the second dorsal in those two species. *Scomberomorus sinensis* is the only species in the genus with a well-developed swim bladder (character 18, state 0), but this is a plesiomorphous character. This species is restricted to the northwestern Pacific from Cambodia to Japan. There is no genus-group name available for this group.

The *commerson* group contains four species: *niphonius*, *queenslandicus*, *cavalla*, and *commerson*. This group is defined by the presence of an intercalar spine of at least moderate length (character 17, state 1). Three species (*queenslandicus*, *cavalla*, and *commerson*) have a long (state 2) intercalar spine. *Scomberomorus cavalla* and *S. commerson* share two additional specializations: the pterosphenoid bones are close together (character 13, state 1) and there is an abrupt downward curve in the lateral line under the second dorsal fin (character 19). Three of these species are Indo-West Pacific: *niphonius* from China, Korea, and Japan; *queenslandicus* from off northern Austra-

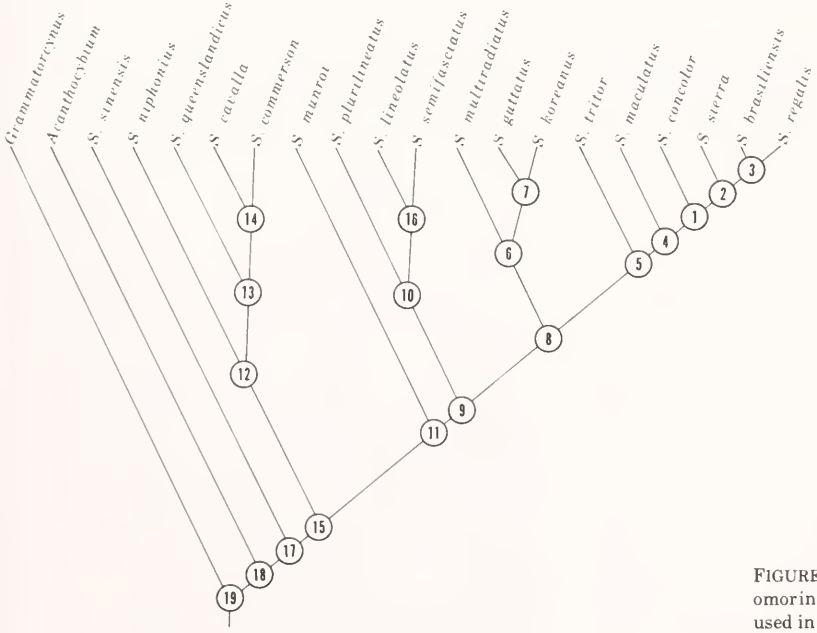


FIGURE 70.—Cladogram of the Scomberomorini, node numbers refer to numbers used in Table 31.

TABLE 31.—Changes in character states based on the most parsimonious cladogram in Figure 70. Numbers under acquisition and reversal columns refer to nodes, three-letter mnemonics refer to species of *Scomberomorus*, and four-letter mnemonics refer to genera, i.e., ACAN = *Acanthocybium*. Two or more components per cell indicate independent acquisition or loss of a character state. Two or more states of the same character acquired at a single node assume that the more primitive state was transitional during the acquisition of the more advanced state.

Character	State	Acquisition	Reversal
1	0	19	
	1	18	
	2	ACAN, 13	CAV
2	0	19	
	1	18	SEM
	2	COM, 18	15
3	0	8, 17	11
	1	19	
	2	ACAN	
4	0	19	
	1	13, 18	15
	2	13, ACAN	CAV
5	0	19	
	1	17	
	2	15	MUL
	3	10	
6	0	8	GUT
	1	17	NIP, 16
	2	19	
	3	ACAN	
7	0	19	
	1	16, 18	CAV, 9
8	0	19	
	1	18	GUT
	2	ACAN, LIN	
9	0	CAV, GUT	
	1	19	
	2	18, LIN	15
10	0	19	
	1	5	BRA
11	0	ACAN	
	1	19	
	2	NIP, 7	
12	0	19	
	1	17	
	2	17	14
13	0	19	
	1	LIN, 14	
14	0	19	
	1	6	
15	0	19	
	1	3, 9	LIN, 4
16	0	19	
	1	1	
17	0	19	
	1	5, 12	
	2	13	
18	0	19	
	1	15	
19	0	19	
	1	14, 18	15
20	0	19	
	1	7	
21	0	19	
	1	5	
22	0	19	
	1	4	
	2	2	
23	0	19	
	1	17	MUL
	2	LIN	
24	0	19	
	1	18	
	2	17	
25	0	19	
	1	18	
	2	17	

Character	State	Acquisition
26	0	19
	1	18
	2	17
27	0	19
	1	18
	2	ACAN
28	0	ACAN
	1	19
	2	17
29	0	19
	1	17
30	0	19
	1	17
31	0	19
	1	17
32	0	19
	1	17
33	0	19
	1	17
34	0	19
	1	17
35	0	19
	1	17
36	0	19
	1	17
37	0	19
	1	17
38	0	19
	1	17
39	0	19
	1	17
40	0	19
	1	17
41	0	19
	1	18
42	0	19
	1	18
43	0	19
	1	18
44	0	19
	1	18
45	0	19
	1	18
46	0	19
	1	18
47	0	19
	1	18
48	0	19
	1	18
49	0	19
	1	18
50	0	19
	1	18
51	0	19
	1	18
52	0	19
	1	18
53	0	19
	1	18
54	0	19
	1	18
55	0	19
	1	18
56	0	19
	1	18
57	0	19
	1	18
58	0	17
	1	19

lia and southern Papua New Guinea; and *commerson* widespread throughout the Indo-West Pacific. The fourth, *cavalla*, is restricted to the western Atlantic. The genus-group name *Cybium* Cuvier (type-species *S. commerson*) is available for this group.

Scomberomorus niphonius is the only species in the genus with a straight gut. This species has very small scapular foramina (character 11, state 2), a character state also found, evidently homoplasiously, in *S. guttatus* and *S. koreanus*. It is restricted to the northwestern Pacific from China, Korea, and Japan. The genus-group name *Sawara* Jordan and Hubbs is available for *S. niphonius*.

The *munroi* group is monotypic. It is defined by the loss of the anterior process on the outer surface of the head of the maxilla. It is restricted to northern Australia and southern Papua New Guinea. There is no genus-group name available for this group.

The *semifasciatus* group contains three species: *plurilineatus*, *lineolatus*, and *semifasciatus*. This group is defined by the presence of a greatly expanded posterior end of the maxilla (character 5, state 3). Two species, *S. lineolatus* and *S. semifasciatus*, share an additional specialization, a wide parasphenoid (character 7, state 1). This character state appears independently in several other lines. All are Indo-West Pacific species, *plurilineatus* along the coast of East Africa plus Madagascar, *lineolatus* along the continental coast from India to Indonesia, and *semifasciatus* in northern Australia and southern Papua New Guinea. The genus-group name *Indocybium* Munro (type-species *S. semifasciatus*) is available for this group.

The *guttatus* group contains three species: *multiradiatus*, *guttatus*, and *koreanus*. This group is defined by a high supraoccipital crest (character 14, state 1). Two species, *guttatus* and *koreanus*, share the presence of auxiliary branches of the lateral line (character 20, state 1). They also have very small scapular foramina (character 11, state 2), a character state shared homoplasiously with *S. niphonius*. All are Indo-West Pacific species, *guttatus* and *koreanus* along the coast of Asia and *multiradiatus* confined to a small section of the Gulf of Papua off the mouth of the Fly River. The genus-group name *Pseudosawara* Munro (type-species *S. guttatus*) is available for this group.

The *regalis* group contains six Atlantic and eastern Pacific species: *tritor*, *maculatus*, *concolor*, *sierra*, *brasiliensis*, and *regalis*. This group is defined by the presence of nasal denticles (char-

acter 21, state 1), a synapomorphy unique to the group. All species also have a moderately long intercalar spine (character 17), but this is also present in *S. niphonius*. All species in the group have a vomerine ridge (character 10, state 1) except for *S. brasiliensis* in which it has been secondarily lost. The five most advanced species (all except *S. tritor*) have an artery arising from the fourth left epibranchial artery (character 22, state 1). The four most advanced species (all except *S. tritor* and *S. maculatus*) have developed a long posterior process on the pelvic girdle (character 16, state 1). The three most advanced species (*sierra*, *brasiliensis*, and *regalis*) have a coeliaco-mesenteric shunt connecting the fourth right epibranchial artery with the coeliaco-mesenteric artery (character 22, state 2). The two most advanced species (*brasiliensis* and *regalis*) have lost the pterotic spine (character 15, state 1) but this spine has also been independently lost in other lines. The genus-group name *Scomberomorus* Lacepède sensu stricto (type-species *S. regalis*) applies to this group.

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APPENDIX 1.

Characters used in analysis of *Scomberomorus* relationships

1) Posterodorsal spine of hyomandibula (Fig. 27). Plesiomorphous condition: absent. Character states: 0(absent), 1(present and small), 2 (large).

2) Palatine tooth patch (Fig. 26). Plesiomorphous condition: wide. Character states: 0(wide), 1(narrow), 2(very narrow).

3) Inner process of palatine bone. Plesiomorphous condition: short. Character states: 0(very short, distance from dorsal hook of palatine to end of inner process 54-72% of length to end of outer process), 1(short, 70-84%), 2(long, 97-99%).

4) Ventral process of angular (Fig. 25). Plesiomorphous condition: short. Character states: 0(short, 42-80% of length of dorsal process), 1 (moderate, 87-93%), 2(long, 117-126%).

5) Posterior expansion of maxilla (Fig. 23). Plesiomorphous condition: no expansion. Character states: 0(no posterior expansion of maxilla), 1 (slight expansion), 2(moderate expansion), 3 (marked expansion).

6) Length of head of maxilla. Plesiomorphous condition: long. Character states: 0(short), 1 (medium), 2(long), 3(very long).

7) Width of parasphenoid. Plesiomorphous condition: narrow. Character states: 0(narrow), 1(wide).

8) Angle of margins of anterior end of premaxilla (Fig. 22). Plesiomorphous condition: blunt. Character states: 0(blunt), 1(intermediate), 2 (acute).

9) Length of ascending process of premaxilla (Fig. 22). Plesiomorphous condition: moderately long. Character states: 0(short), 1(moderately long), 2(very long).

10) Vomerine ridge (Figs. 17-19). Plesiomorphous condition: absent. Character states: 0 (absent), 1(present).

11) Relative size of scapular foramen (Fig. 43). Plesiomorphous condition: medium-sized. Character states: 0(large), 1(medium), 2(small).

12) Pineal foramen (Figs. 11-13). Plesiomorphous condition: present. Character states: 0 (present), 1(reduced), 2(absent).

13) Anterior ends of pterosphenoids (Figs. 17-19). Plesiomorphous condition: far apart. Character states: 0(far apart), 1(close together).

14) Height of supraoccipital crest (Figs. 14-16). Plesiomorphous condition: low. Character states: 0(low), 1(high).

15) Pterotic spine (Figs. 11-13). Plesiomorphous condition: well developed. Character states: 0 (well developed), 1(essentially absent).

16) Pelvic girdle: relative length of posterior process (Fig. 46). Plesiomorphous condition: short to moderate-sized posterior process. Character states: 0(short to moderate posterior process, 20-50% of length of anterior plate), 1(long posterior process, 62-90% of length of anterior plate).

17) Spine on intercalar (Figs. 17-19). Plesiomorphous condition: absent. Character states: 0(absent), 1(moderate length), 2(long).

18) Swim bladder. Plesiomorphous condition: present. Character states: 0(present), 1(absent).

19) Curvature of lateral line (Figs. 50, 52, 68). Plesiomorphous condition: no abrupt curve. Character states: 0(no abrupt curve), 1(abrupt downward curve).

20) Auxiliary branches off lateral line (Figs. 54, 56). Plesiomorphous condition: absent. Character states: 0(absent), 1(present).

21) Nasal denticles (Fig. 1). Plesiomorphous condition: nasal chamber without denticles. Character states: 0(denticles absent), 1(nasal denticles present).

22) Anterior epibranchial artery (Fig. 7). Plesiomorphous condition: unmodified. Character states: 0(unmodified), 1(esophageal artery arises from fourth epibranchial), 2(coeliaco-mesenteric shunt arises from fourth epibranchial).

23) Relative size of foramen between last radial and coracoid (Fig. 43). Plesiomorphous condition: small. Character states: 0(small), 1(large), 2(very large).

24) Length of branches of palatine bone (Fig. 26). Plesiomorphous condition: ventral branch much shorter than dorsal branch. Character states: 0(ventral branch much shorter than dorsal branch, 120-123%), 1(ventral branch slightly shorter, 112-121%), 2(ventral branch equal to or longer than dorsal branch, 87-107%).

25) Width of supratemporal (Fig. 42). Plesiomorphous condition: wider than deep. Character states: 0(wider than deep, 101-113%), 1(deeper than wide, 84-93%), 2(much deeper than wide, 49-79%).

26) Width of first postcleithrum (Fig. 44). Plesiomorphous condition: wide. Character states: 0(wide, 55-62% of length), 1(narrow, 47-48%), 2(very narrow, 24-41%).

27) Total number of vertebrae (Table 8). Plesiomorphous condition: few (31). Character states: 0(few, 31), 1(moderate number, 41-56), 2(many, 62-64).

28) Depth of urohyal (Fig. 31). Plesiomorphous condition: moderately deep. Character states: 0(shallow), 1(moderately deep), 2(deep).

29) Shape of metapterygoid (Fig. 27). Plesiomorphous condition: anterior oblique edge longer than posterior horizontal edge. Character states: 0(anterior oblique edge longer than posterior horizontal edge), 1(posterior horizontal edge longer than anterior oblique edge).

30) Length of arms of ectopterygoid (Fig. 27). Plesiomorphous condition: dorsal arm longer than or equal to ventral arm. Character states: 0(dorsal arm longer than or equal to ventral arm), 1(dorsal arm shorter than ventral arm).

31) Vomer (Figs. 17-19). Plesiomorphous condition: not spatulate. Character states: 0(not spatulate), 1(spatulate, extending beyond anterior margin of ethmoid complex).

32) Width of lateral wall of cleithrum (Fig. 43). Plesiomorphous condition: lateral wall narrow. Character states: 0(lateral wall narrow, space between cleithrum and coracoid visible in lateral view), 1(lateral wall wide, space between cleithrum and coracoid not visible in lateral view).

33) Epiotic crests (Figs. 11-13). Plesiomorphous condition: originate behind midfrontal region. Character states: 0(originate behind midfrontal region), 1(originate on anterior part of frontals).

34) Vertebrae with inferior foramina. Plesiomorphous condition: few. Character states: 0 (few, < 11), 1(many, more than 11).

35) Size of first basibranchial. Plesiomorphous condition: elongate. Character states: 0(elongate), 1(short).

36) Strut on fourth pharyngobranchial. Plesiomorphous condition: not elongate. Character states: 0(not elongate), 1(elongate).

37) Length of symplectic (Fig. 27). Plesiomorphous condition: long. Character states: 0(long, in contact with metapterygoid), 1(short, not in contact with metapterygoid).

38) Size of dorsal and ventral hypohyals (Fig. 29). Plesiomorphous condition: ventral < 3 times larger than dorsal. Character states: 0(ventral hypohyal < 3 times larger than dorsal hypohyal in lateral view), 1(ventral hypohyal > 3 times larger than dorsal).

39) Position of fifth branchiostegal ray (Fig. 29). Plesiomorphous condition: located on epihyal. Character states: 0(completely on epihyal), 1(on suture between epihyal and ceratohyal).

40) Posttemporal shelf (Fig. 40). Plesiomorphous condition: no shelf present. Character states: 0(no shelf present between dorsal and ventral arms of posttemporal), 1(shelf present).

41) Width of supracleithrum (Fig. 41). Plesiomorphous condition: wide. Character states: 0 (wide, 72-75% of length), 1(narrow, 42-62%).

42) Supratemporal pores (Fig. 42). Plesiomor-

phous condition: no pores. Character states: 0(no pores), 1(pores present on dorsal arm).

43) Position of nasals (Figs. 11-13). Plesiomorphous condition: protrude beyond ethmoid region. Character states: 0(protrude far beyond ethmoid region), 1(do not protrude, located adjacent to ethmoid region).

44) Shape of posterior end of dorsal margin of urohyal (Fig. 31). Plesiomorphous condition: tripartite. Character states: 0(tripartite), 1 (forked).

45) Glossohyal teeth (Fig. 30). Plesiomorphous condition: glossohyal teeth present. Character states: 0(patch of teeth fused to dorsal surface of glossohyal), 1(no glossohyal teeth).

46) Width of hyomandibula (Fig. 27). Plesiomorphous condition: narrow. Character states: 0(narrow, width 35-36% of length), 1(wide, width 36-52% of length).

47) Angle of lateral and medial arms of fourth epibranchial. Plesiomorphous condition: more acute. Character states: 0(more acute), 1(less acute).

48) Anterior process of second epibranchial. Plesiomorphous condition: elongate. Character states: 0(elongate), 1(not elongate).

49) Preural centra 2-4 (Fig. 39). Plesiomorphous condition: not shortened and compressed. Character states: 0(not compressed), 1(compressed).

50) Number of vertebrae supporting caudal fin. Plesiomorphous condition: 3 vertebrae support caudal fin. Character states: 0(3 vertebrae support caudal), 1(4 or 5 vertebrae).

51) Anterior process on second postcleithrum (Fig. 45). Plesiomorphous condition: elongate process present on anterior margin of second postcleithrum. Character states: 0(process present), 1(process absent).

52) Anterior end of first postcleithrum (Fig. 44). Plesiomorphous condition: notched. Character states: 0(notched), 1(pointed).

53) Position of third pectoral fin radial (Fig. 43). Plesiomorphous condition: base of third radial completely on coracoid. Character states: 0(completely on coracoid), 1(on suture between coracoid and scapula).

54) Tooth shape. Plesiomorphous condition: conical. Character states: 0(conical), 1(triangular and compressed).

55) Parasphenoid contour. Plesiomorphous condition: concave ventrally. Character states: 0(concave), 1(convex).

56) Relative length of arms of dentary (Fig. 24). Plesiomorphous condition: lower arm longest. Character states: 0(lower arm longer than upper arm), 1(upper arm longer than lower arm).

57) Length of posterior edge of ectopterygoid (Fig. 27). Plesiomorphous condition: posterior edge long. Character states: 0(posterior edge long, 64-68% of ventral distance), 1(posterior edge short, 41-63%).

58) Shape of epihyal (Fig. 29). Plesiomorphous condition: not much longer than deep. Character states: 0(depth 68-98% of length), 1(much longer than deep, 58-62% of length).

GENETIC VARIATION AND POPULATION STRUCTURE IN A SPINY LOBSTER, *PANULIRUS MARGINATUS*, IN THE HAWAIIAN ARCHIPELAGO[1]

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ABSTRACT

Samples of the commercially important spiny lobster, *Panulirus marginatus*, were collected from localities throughout the Hawaiian Archipelago and subjected to starch gel electrophoretic analysis of protein variation. The amount and pattern of genetic variation exhibited by specific enzymes was determined and analyzed to see whether or not there was evidence that the species was composed of multiple stocks or subpopulations throughout its range.

The lobster exhibited polymorphisms at 7 loci (Est-3, Umb, Gpi, Mpi, Pep-1, Pep-2, and Pgm) out of the 46 enzyme-coding loci screened. However, genetic variability in the species was quite low, the average heterozygosity for all loci was 0.021. Observed genotype distributions at the variable loci agreed with Hardy-Weinberg expectations. Allele-frequency distributions for each locus were remarkably similar across localities and statistical tests failed to reveal clear patterns of genetic differentiation within the Archipelago. The results are consistent with the existence of a single panmictic stock of *Panulirus marginatus* throughout the Hawaiian Archipelago.

The rational management of any fisheries resource, whether directed at exploitation, conservation, or some other goal, requires many different types of information about the species in question, and its interaction with environmental and biological factors in its environment. Data on basic biology (taxonomy, distribution and abundance, food habits, behavior, etc.), ecological requirements, reproductive characteristics, and population dynamics are all relevant to management decisions. Although the above types of information are necessary to any meaningful management plan, they are not sufficient. Information concerning the stock or subpopulation structure of the species is also of critical importance to the formulation of any comprehensive, long-term management program (MacLean and Evans 1981).

Subpopulations or stocks are generally considered to be self-sustaining subunits of a species which are more-or-less reproductively isolated from other such groups. It is reasonable to assume that as a result of random processes and local selection pressures, these subpopulations (stocks) will become genetically differentiated from one another. For this reason, the electrophoretic analysis of genetic characteristics provides one of the most direct, and therefore theoretically powerful, approaches to the problem of defining subpopulation structure. However, it should be emphasized that all tests of stock structure, including electrophoretic ones, are really one-sided. It is actually only possible to establish the existence of multiple differentiated stocks by falsifying the null hypothesis of a single, widespread, panmictic stock. It is not possible to prove that only a single panmictic population exists although the data (be they genetic, morphological, behavioral, or whatever) may be consistent with this hypothesis.

In the last decade, a substantial, multispecies, commercial fishery has developed in the Northwestern Hawaiian Islands (NWHI). This fishery is directed almost exclusively at demersal species and is dominated by catches of spiny lobsters (Palinuridae), snappers (Lutjanidae), and groupers (Serranidae). Because of the largely unknown and previously unexploited nature of this fishery, a coordinated, large-scale, multidisciplinary study involving personnel from the National Marine Fisheries Service Honolulu Laboratory, the U.S. Fish and Wildlife Service, the Hawaii Division of Fish and Game, and the University of Hawaii was initiated to describe, analyze, and model the major components of the NWHI ecosystem (Grigg and Pfund 1980). The genetic analysis

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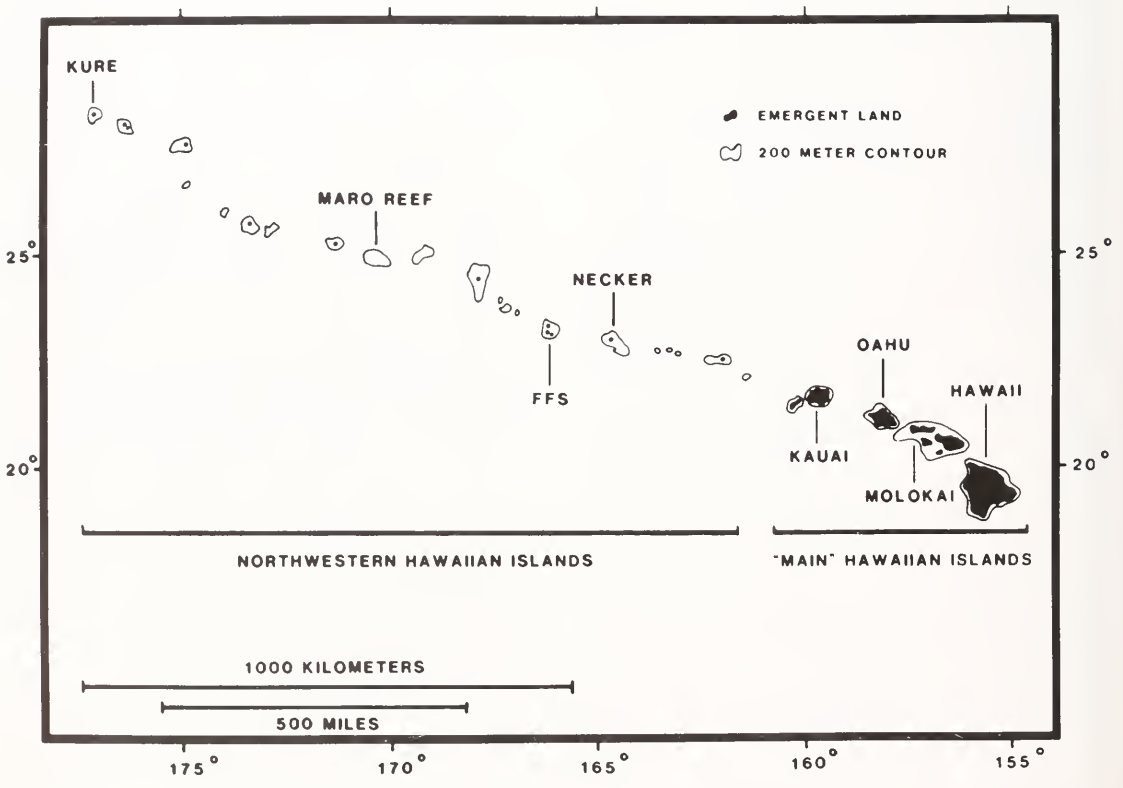
of stock structure of the lobster detailed in this report was one part of this overall program (Shaklee and Samollow 1980).

Two general questions regarding lobster subpopulation structure were asked in the present study. First, was there any detectable stock heterogeneity within the entire Hawaiian Archipelago? Second, and specifically relating to the potential impact of the emerging fishery in the NWHI on the existing fishery in the main islands, was there evidence that populations in the main islands were differentiated, and thus independent, from populations in the NWHI?

The spiny lobster, *Panulirus marginatus*, is endemic to the Hawaiian Archipelago where it occurs in large numbers from Hawaii in the southeast to Kure Atoll in the northwest (Fig. 1). Highest apparent abundances are localized at Necker Island and Maro Reef (Uchida et al. 1980), the two localities where the lobster fishery is presently concentrated. *Panulirus marginatus* is generally found in waters deeper than 10 m. *Panulirus marginatus* has an annual fecundity of from 125,000 to 450,000 eggs per female (Honda 1980). After mating, females carry one or more spermatophores ventrally on the thorax until the eggs are extruded and fertilized. Embryonic development in this species takes about 30 d during which time the embryos remain attached to the pleopods of the female (Morris 1968). Based on studies of related species it appears that, after hatching, the larvae are planktonic for a period of 6-12 mo passing through 8-12 phyllosoma larval stages (Johnson 1956, 1968; Johnson and Knight 1966; Inoue 1978). The larvae metamorphose into puerulus postlarvae. The postlarvae settle from the plankton and assume the benthic lifestyle characteristic of the adults. Based on tag-recapture studies at Kure Atoll and French Frigate Shoals (MacDonald[4]) and similar studies at Oahu (Morris 1968), adults appear to be relatively sedentary, not exhibiting large-scale movements.

[4]C. MacDonald, Zoology Department, University of Hawaii, Honolulu, HI 96822, pers. commun. May 1982.

FIGURE 1.—Map of the Hawaiian Islands showing sampling localities. Note the 200 m depth contours.



MATERIALS AND METHODS

Sample Collection and Processing

A total of 1,869 spiny lobsters from the five localities was collected over a 2½-yr period (Fig. 1). Lobsters from Kure Atoll, Oahu, and Hawaii were collected by hand by divers using scuba. Lobsters from Maro Reef and Necker Island were collected using standard, wire mesh lobster traps. The sampling periods and numbers of lobsters collected for each of the five localities are Kure: October 1978-January 1979 (N = 21), June 1979-September 1979 (N = 136), August 1979-June 1980 (N = 249), and June 1980-January 1981 (N = 176); Maro Reef: October 1978 (N = 60), November 1979 (N = 213), and September 1980 (N = 145); Necker: October 1978 (N = 97), March 1979-June 1979 (N = 421), and December 1980 (N = 148); Oahu: May 1979-January 1980 (N = 53), July 1980-December 1980 (N = 71), and March 1981 (N = 30); and Hawaii: April 1980-March 1981 (N = 49). Because not all individuals were sexed and measured (in some cases one or both types of data were unavailable for entire collections), sex ratios and size compositions could not be accurately calculated. However, all animals included in the data analyses were adults. Some samples were frozen at −20°C in the field (as whole animals, as carcasses minus tails, or as isolated pereiopods—walking legs) and shipped frozen to the laboratory. Other samples were transported live to Honolulu where they were dissected and sampled. In the initial screening for polymorphic loci, samples of pereiopod muscle, abdominal muscle, digestive gland, green gland, eye, heart, and gills were dissected from whole, frozen lobsters. Each of these samples was homogenized at 4°C in an equal volume of 0.1 M Tris-HCl pH 7.0 buffer (containing 1×10^{-3} M EDTA and 5×10^{-5} M $NADP^+$) using a loose fitting, motorized pestle. Homogenates were centrifuged at 4°C for at least 20 min at a minimum of 20,000 × g. Digestive gland supernatants were routinely centrifuged a second time to minimize lipid content. The resulting supernatants were transferred to individually labeled glass vials which were capped and stored at −75°C until the electrophoretic analyses were completed. Since all variable enzymes could be analyzed in pereiopod muscle extracts (and digestive gland extracts for peptidase-1 (PEP-1)) only these tissues were examined in the subsequent analyses.

Electrophoresis

The supernatants were analyzed by a combination of vertical and horizontal starch gel electrophoresis (Selander et al. 1971; Shaklee et al. 1973). Each enzyme system surveyed in the initial screening for genetic variation was electrophoresed on 2-10 different buffer systems, using extracts of several different tissues. Following electrophoresis, isozyme patterns were visualized using standard recipes (modified from Shaw and Prasad 1970; Selander et al. 1971; Siciliano and Shaw 1976). Esterases of the lobster were detected using α-naphthyl acetate (EST) or 4-methylumbelliferyl acetate (Umb = Est-D) as substrates, both variable peptidases were stained using leucylleucylleucine as substrate.

Gel Scoring and Data Analysis

Patterns of enzyme variation that were consistent with the subunit structure of presumably homologous proteins of other species (when known), and with simple genetic models, were scored and recorded as genotypes. Names of enzymes and Enzyme Commission numbers follow the recommendations of the Commission on Biochemical Nomenclature (1973). For multilocus enzyme systems, loci were consecutively numbered beginning with the most anodal isozyme. Alleles at each locus were designated according to the relative electrophoretic mobilities of the homomeric isozymes they encode. The most common allele at a locus was designated "100" and all other alleles at that locus were numbered according to the electrophoretic mobilities of their products relative to that of the product of the 100 allele. Negative numbers were given to alleles encoding isozymes with cathodal migration. In the case of the glucosephosphate isomerase (GPI) system of the spiny lobster, subbanding anodal to the 100 isozyme was often quite pronounced, especially in older samples. Because we could not be confident of scoring allelic variation in this region, no attempt was made to score isozymes having an electrophoretic mobility greater than that of the most common (100) isozyme. Many samples were reelectrophoresed with controls of known mobility to verify the identity of rare alleles for each enzyme system.

Despite that all alleles were initially identified and assigned numerical designations as described above, in many cases data summaries and statistical analyses employed fewer electromorph (allelic)

classes. This pooling was necessary because many of the alleles were extremely rare. The distribution of genotypes at each locus in each sample was examined for internal consistency with the Mendelian inheritance model by chi-square tests of observed genotype ratios with those expected for a single random mating population in the absence of differential selection among alleles. The expected ratios were calculated from observed allele numbers using Levene's (1949) unbiased method for small samples. The heterozygosity at each locus (h) was calculated as $h = 1 - \Sigma X_i$ where X_i is the frequency of the ith allele. Average heterozygosity (H) was calculated as the unweighted arithmetic mean of h (the individual locus heterozygosity) over all loci examined. A locus was considered polymorphic if the frequency of the most common allele was <0.99.

Three levels of analysis were employed to examine genetic differentiation (stock heterogeneity) among the population samples. First, for each polymorphic locus, contingency chi-square tests of all possible pairwise combinations of localities were conducted. Second, contingency tests comparing pooled samples representing the main Hawaiian Islands and the Northwestern Hawaiian Islands were conducted for all loci. Finally, large samples of spiny lobsters collected from three localities allowed the analysis of year-to-year variability within and among these localities.

RESULTS

Forty-six presumed gene loci encoding 28 different enzyme systems were surveyed for genetic variation in *Panulirus marginatus*. Thirty-nine of these were either monomorphic in the first 100 or more animals screened or exhibited only rare variants ($P < 0.01$) These enzymes which were not studied further were aspartate aminotransferase (2 loci), acid phosphatase (2 loci), adenylate kinase, alkaline phosphatase (3 loci), alanine aminotransferase, arginine kinase, esterase (3 loci), glyceraldehyde-3-phosphate dehydrogenase, glycerol-3-phosphate dehydrogenase, glucose-6-phosphate dehydrogenase, hexokinase, isocitrate dehydrogenase (2 loci), lipoamide dehydrogenase (= diaphorase), lactate dehydrogenase (2 loci), malate dehydrogenase (2 loci), malate dehydrogenase-NADP$^+$ (= malic enzyme) (2 loci), monophenolmonooxygenase (= tyrosinase), naphthyl amidase (= leucine aminopeptidase), peptidase (3 loci), peroxidase (2 loci) pyruvate kinase, superoxide dismutase (2 loci), and triosephosphate isomerase (2 loci). The remaining seven loci were polymorphic (frequency of the most common allele <0.99 in at least one population) and the conditions for their analysis are summarized in Table 1. Thus, *P. marginatus* exhibits a $P_{.99} = 0.152$.

TABLE 1.—Polymorphic enzymes in the spiny lobster, *Panulirus marginatus*: Characteristics and conditions for analysis. M = muscle, DG = digestive gland, V = vertical starch gel, H = horizontal starch gel.

Enzyme (EC Number)	Locus	Subunit structure[1]	Tissue	Gel	Buffer
Esterase (3.1.1.-)	Est-3	monomer	M	V	EBT[2]
Glucosephosphate isomerase (5.3.1.9)	Gpi	dimer	M	H	TC-1[3]
Mannosephosphate isomerase (5.3.1.8)	Mpi	monomer	M	V	EBT
Peptidase-1 (3.4.11.-)	Pep-1	monomer	DG	H	LiOH[4]
Peptidase-2 (3.4.11.-)	Pep-2	monomer	M	V	EBT
Phosphoglucomutase (2.7.5.1)	Pgm	monomer	M	H	TC-1
Umbelliferyl esterase	Umb	dimer	M	H	LiOH-2[5]

[1]Presumed structure based on enzyme banding pattern in heterozygotes (see text).
[2]EDTA-boric acid-Tris pH 8.6 buffer of Boyer et al. (1963).
[3]Tris-citric acid pH 7.0 buffer; buffer 1 of Shaw and Prasad (1970).
[4]Discontinuous lithium hydroxide pH 8.1 buffer (slightly modified buffer 2 of Selander et al. 1971).
[5]Continuous lithium hydroxide pH 8.1 buffer (modified buffer 2 of Selander et al. 1971 with stock "B" of gel buffer replaced with water).

Zymogram patterns for 6 of the 7 polymorphic enzymes are shown in Figure 2. The allele frequencies, heterozygosity per locus, and number of alleles successfully scored for each polymorphic locus at each locality are presented in Table 2. Although all seven loci in Table 2 are polymorphic at the 0.99 level in at least one sample, only two loci [Mpi (mannosephosphate isomerase) and Pep-1] exhibit a per locus heterozygosity of >0.1. As a result, the heterozygosity (H) averaged over all loci is only 0.021 for this species.

Several features of the data summarized in Table 2 warrant explanation. First, as mentioned in Materials and Methods, many of the allelic classes summarized in this table are heterogeneous containing two or more rare alleles. For example, the Est-3 (esterase) "fast" (Est-3^f) class contains alleles Est-3^{105} and Est-3^{103}, the "medium" class consists of allele Est-3^{100} only, and the "slow" class contains alleles Est-3^{97}, Est-3^{95}, and Est-3^{90}. Similar groupings were carried out for several other loci as indicated in Table 2. The allelic classes for Mpi, Pep-1, and Pep-2 were not detectably heterogeneous. Examples of phenotypes expressing several of the rare alleles contributing to these pooled allelic classes are shown and identified in Figure 2. Second, because

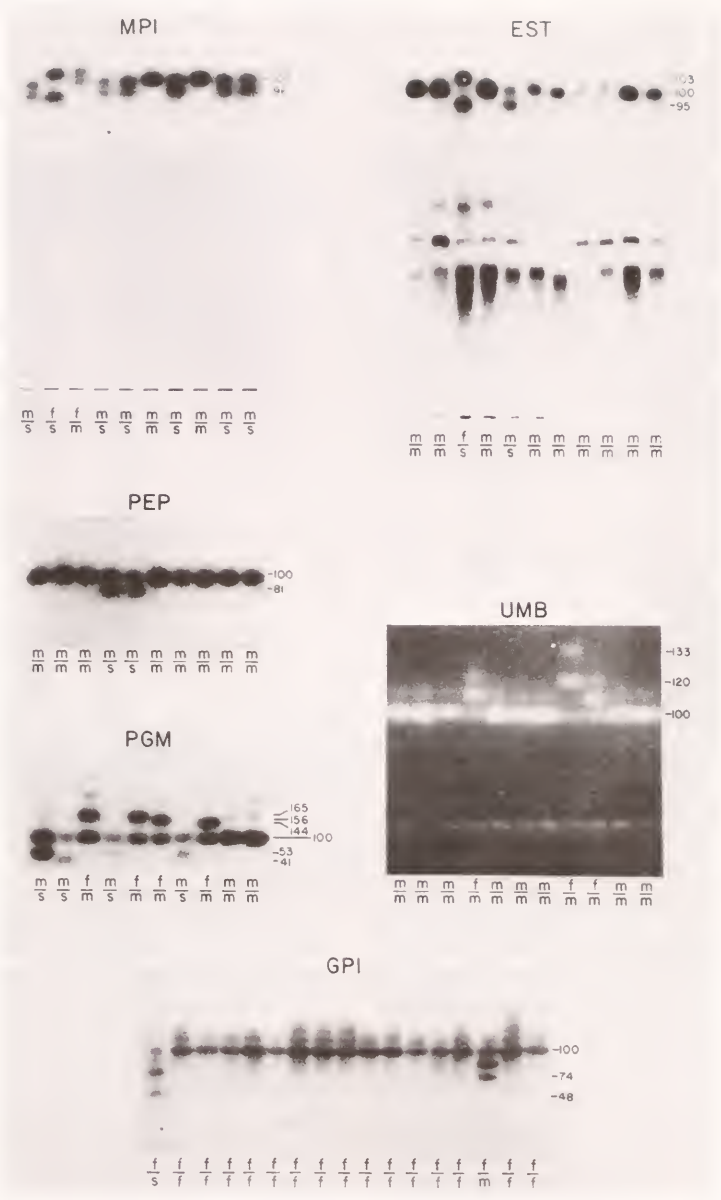


FIGURE 2.—Isozyme patterns of spiny lobster, *Panulirus marginatus*. MPI = mannosephosphate isomerase, EST = esterase-3, PEP = peptidase-2, PGM = phosphoglucomutase, UMB = umbelliferyl esterase (= EST-D), GPI = glucose-phosphate isomerase. Alleles are indicated at the right of each gel. Scoring of individual genotypes (by allelic class) is indicated at the bottom of each gel. Note that the sample origin is at the bottom and the anode is toward the top.

of the rarity of variant alleles, and therefore, of all but the common homozygote at all loci except Pep-1 and Mpi, tests of Hardy-Weinberg equilibrium were not very robust; most genotypic classes had to be pooled to obtain adequate numbers of expected genotypes. In all cases when there were three or more alleles, these were pooled into two groups; a group consisting of only the most common allele and a group including all other alleles. Furthermore, in the case of Mpi the unusual na-

TABLE 2.—Allele frequencies and heterozygosity values at seven polymorphic loci in the spiny lobster, *Panulirus marginatus*. N = number of individuals in total sample; h = per locus heterozygosity; number of genes successfully scored in parentheses; localities as in Figure 1.

		Locality						
Locus	Allelic class[1]	Kure $N = 582$	Maro Reef $N = 418$	Necker $N = 666$	Oahu $N = 154$	Hawaii $N = 49$	NWHI[2] $N = 1,666$	Main[3] $N = 203$
Est-3	f	0.004	0.003	—	0.003	0.010	0.002	0.005
	m	0.975	0.957	0.971	0.980	0.958	0.969	0.975
(h=0.059)	s	0.021	0.040	0.030	0.017	0.031	0.028	0.020
		(1,164)	(772)	(1,332)	(300)	(96)	(3,268)	(396)
Gpi	f	0.958	0.959	0.966	0.944	0.976	0.962	0.951
	m	0.037	0.039	0.033	0.049	0.024	0.036	0.043
(h=0.076)	s	0.005	0.002	0.001	0.007	—	0.003	0.005
		(1,058)	(640)	(1,070)	(288)	(82)	(2,768)	(370)
Mpi	f	0.008	0.011	0.007	0.019	0.010	0.008	0.017
(h=0.374)[4]	m+s	0.992	0.989	0.993	0.981	0.990	0.992	0.983
		(1,156)	(836)	(1,298)	(308)	(98)	(3,290)	(406)
Pep-1	f	0.784	0.725	0.785	0.638		0.763	0.638
(h=0.370)	s	0.216	0.275	0.215	0.362		0.237	0.362
		(190)	(284)	(284)	(58)		(758)	(58)
Pep-2	f	0.002	—	0.001	—	—	0.001	—
	m	0.985	0.988	0.984	1.000	0.969	0.985	0.994
(h=0.026)	s	0.013	0.012	0.015	—	0.031	0.014	0.006
		(600)	(670)	(850)	(266)	(64)	(2,120)	(330)
Pgm	f	0.013	0.007	0.007	0.003	—	0.009	0.003
	m	0.976	0.984	0.976	0.983	1.000	0.978	0.986
(h=0.042)	s	0.012	0.009	0.017	0.014	—	0.013	0.011
		(1,036)	(690)	(1,116)	(292)	(78)	(2,842)	(370)
Umb	f	0.006	0.001	0.011	0.010	—	0.003	0.008
	m	[5]0.983	[5]0.988	[5]0.980	0.983	1.000	0.991	0.986
(h=0.032)	s	.011	0.010	0.008	0.007	—	0.006	0.005
		(1,010)	(680)	(1,066)	(288)	(78)	(2,756)	(366)

[1]Pooled allelic classes as follows: Est-3^{f} includes alleles 105 and 103 while Est-3^{s} includes alleles 97, 95, and 90; Gpi^{m} includes alleles 80, 77, 74, 72, and 68 while Gpi^{s} includes alleles 65, 58, 54, 48, and 33; Pgm^{f} includes alleles 240, 186, 180, 165, 157, and 144 while Pgm^{s} includes alleles 82, 73, 53, 41, 35, and 25; Umb^{f} includes alleles 133, 120, 115, and 111 while Umb^{s} includes alleles 85, 80, and 75.

[2]Consisting of lobsters from Kure Atoll, Maro Reef, and Necker Island.

[3]Consisting of lobsters from Oahu and Hawaii.

[4]Subject to sex-restricted allele distribution (see text).

[5]Significantly different annual samples combined (see text).

ture of the distribution of alleles at this sex-linked locus (Shaklee 1983) effectively precluded Hardy-Weinberg analysis involving the two most common alleles. In spite of these caveats, out of 30 χ^2 tests (6 loci × 5 localities) only 1 significant deviation from Hardy-Weinberg expectation was observed; a heterozygote deficiency for Pep-1 at Necker Island ($\chi^2_1 = 7.63$ $P < 0.01$). Third, the data in Table 2 represent the pooled allele frequencies observed at each locality over the 2½-yr period of the study. In three cases (Umb at Kure Atoll, Maro Reef, and French Frigate Shoals), there was statistically significant year-to-year fluctuation in allele frequencies. The significance of this finding is discussed below. Fourth, because of the unusual relationship between MPI phenotype and sex in this species (Shaklee 1983), the medium and slow alleles had to be pooled into one class to prevent differences in sex ratio in each collection from biasing the allele-frequency analysis.

The first level of analysis, involving χ^2 tests of all pairwise comparisons, failed to reveal convincing evidence of stock heterogeneity in this lobster. Of the 66 comparisons, only three were significant: 1) Est, Kure vs. Maro ($\chi^2_1 = 4.76$ $P < 0.05$); 2) Pep-1, Kure vs. Oahu ($\chi^2_1 = 5.07$ $P < 0.025$); and 3) Pep-1, Necker vs. Oahu ($\chi^2_1 = 5.73$ $P < 0.025$). Given an $\alpha = 0.05$ level of significance, one would expect, on the basis of chance alone, about 3 significant outcomes from 60 tests. Additionally, given the basic linear arrangement of islands within the Hawaiian Archipelago (Fig. 1), population differentiation, if it were based upon isolation by distance (Wright 1943), would be expected to be most pronounced between widely separated localities. In contrast to these expectations, two of the three observed significant outcomes involve adjacent, not distant, localities.

The second statistical test compared the allelic composition of lobsters from the NWHI (Kure Atoll, Maro Reef, and Necker Island samples pooled) with that of lobsters from the main Hawaiian Islands (Oahu and Hawaii samples

pooled). Only one out of these seven contingency χ^2 tests was significant—Pep-1 ($\chi^2_1 = 4.50$ $P < 0.05$). Thus, in spite of the considerably larger sample sizes resulting from pooling, there is still no strong evidence of stock heterogeneity.

The third analysis involved the three cases of year-to-year differences in Umb allele frequency (Table 3). In each of the three cases, the frequency of the two rare alleles (allelic classes) was higher in the 1980 collections than in those from 1979. When the rare alleles were pooled to allow χ^2 tests of the distributions, all three cases exhibited significant year-to-year changes: Kure Atoll A vs. B ($\chi^2_1 = 3.85$ $P < 0.05$), Maro Reef A vs. B ($\chi^2_1 = 4.44$ $P < 0.05$), and Necker Island A vs. B ($\chi^2_1 = 5.81$ $P < 0.025$). However, when allele distributions were compared among localities in either 1979 or 1980 (or in pooled 1979 + 1980) no significant differences between localities were observed. These results suggest annual fluctuations in Umb allele frequency within at least the NWHI. Unfortunately the sample sizes from the main Hawaiian Island localities were not large enough to be subdivided by year to see whether or not this annual fluctuation in Umb allele frequency occurred there also. Given that statistically significant annual fluctuations in Umb allele frequency were occurring at all three localities where this could be tested, it is important that they were parallel and did not lead to any significant differences in allele frequency between localities. This pattern of fluctuating allele frequency, common to the three NWHI localities, argues for the existence of a single panmictic lobster population throughout this region and suggests that a cohort having "unusual" Umb allele frequency was recruited into the fishery throughout the NWHI in 1980.

TABLE 3.—Umbelliferyl esterase allele frequencies in *Panulirus marginatus* at three localities in successive years.

Locality (year)	Number of genes scored	Allelic class f	m	s
Kure Atoll A (June 1979-Sept. 1979)	232	0.000	0.996	0.004
Kure Atoll B (June 1980-Jan. 1981)	350	0.009	0.974	0.017
Maro Reef A (Nov. 1979)	284	0.000	0.996	0.004
Maro Reef B (Sept. 1980)	290	0.003	0.976	0.021
Necker Island A (Mar. 1979-June 1979)	662	0.006	0.986	0.008
Necker Island B (Dec. 1980)	290	0.028	0.962	0.010

DISCUSSION

Electrophoretic studies of genetic variation have been reported for several decapod crustacean species. With the exception of *Panulirus argus* (Menzies 1981), all species that have been examined exhibit relatively little genetic diversity either within or between populations (Tracey et al. 1975; Mulley and Latter 1980; Nelson and Hedgecock 1980; Redfield et al. 1980; Smith et al. 1980; Hanley 1980). Nevertheless, several of the enzymes found to be polymorphic in *P. marginatus* in the present study have been shown to be variable in other decapods. Because of their relevance to the genetic interpretations in the present investigation, published accounts of genetic variation for these enzymes are summarized below.

Esterases (EST). Nearly all species of decapod crustaceans studied to date exhibit multiple esterases which hydrolyze naphthol esters. In many species, one or more esterase loci are reported to be polymorphic and, in virtually all published studies where banding patterns of heterozygotes have been described, the variable esterases appear to be monomeric proteins (Menzies and Kerrigan 1979b). Analysis of the mode of inheritance of variable esterases has only been accomplished for one esterase locus in decapods (Hedgecock et al. 1975). This locus exhibited simple Mendelian segregation of alleles. The genetic interpretation of EST-3 variation in *P. marginatus* (single- and double-banded phenotypes) is consistent with these findings. Since there have been no published reports of UMB (= EST-D) variation in decapod crustaceans, the observed variation in UMB in *P. marginatus* must stand on its own. However, as shown in Figure 2, the staining intensities of the three isozymes in presumed heterozygotes are approximately those expected for a dimeric enzyme (i.e., 1:2:1). Furthermore, as noted above, no deviations from Hardy-Weinberg expectations were observed for this enzyme.

Glucosephosphate Isomerase (GPI). The enzyme glucosephosphate isomerase is frequently variable in decapod crustaceans. Although as many as three loci have been reported in decapods, most investigations have focused on a single locus whose apparently dimeric protein product is predominant in muscle extracts. The inheritance of this enzyme in *Homarus americanus* follows a simple Mendelian pattern (Hedgecock et al. 1975). It would appear that the polymorphic GPI in *P.*

marginatus is homologous to this GPI locus of other decapods.

Mannosephosphate Isomerase (MPI.) Mannosephosphate isomerase is polymorphic in many crustaceans and behaves as a monomeric protein. The observed MPI phenotypes in *P. marginatus* are consistent with this presumed subunit structure (Fig. 2). Further, a more detailed analysis of the MPI variation in *P. marginatus* indicates that the MPI locus in this species is sex-linked and that, although there are three alleles segregating in the species, males always have at least one slow allele while females only very rarely carry this same allele (Shaklee 1983). Because of this restriction on segregation, the slow allele was pooled with the medium (100) allele (Table 2) for the statistical analyses of population structure.

Peptidases (PEP). Like esterases, the peptidases represent a family of enzymes sharing similar catalytic activities. However, unlike the esterases, there are a relatively small number of different peptidases, and they exhibit differential and somewhat characteristic substrate specificities (Frick 1983). Peptidases have been studied in both *P. argus* and *P. cygnus*. Hanley (1980) reported that two peptidases (using leucylglycylglycine and leucyltyrosine as substrates) are monomorphic in *P. cygnus*. Menzies and Kerrigan (1979a) and Menzies (1981) reported two monomorphic and three polymorphic peptidases in *P. argus*. One of these variable peptidases is a prolidase (stained with leucylproline or phenylalanylproline) which appears to be a dimer and exhibits three alleles. The other two variable peptidases (stained with leucylglycine or phenylalanyltyrosine) are apparently monomers. Whether or not the two variable peptidases in *P. marginatus* (which behave as monomers, Fig. 2) are homologous to any of those described in *P. argus* is not clear at this point.

Phosphoglucomutase (PGM). Essentially all species of decapod crustaceans exhibit one PGM in muscle. The enzyme is reported to be monomeric and it exhibits Mendelian inheritance in *H. americanus* (Hedgecock et al. 1975). The PGM of *P. marginatus* appears to be homologous to this PGM of other decapods.

Despite that direct inheritance testing of the presumed genetic variation observed in the Hawaiian *P. marginatus* was not attempted, the general agreement between the observed isozyme patterns and those reported for other decapod crustaceans, the data indicating the genetic basis for variation in EST, GPI, MPI, and PGM in other decapods, and the general agreement in *P. marginatus* between observed genotypic distributions and those expected assuming Hardy-Weinberg equilibrium, strongly support the assumption that the observed variation in the Hawaiian spiny lobster is under direct genetic control.

The present study of *P. marginatus* has revealed electrophoretic variation encoded by 7 gene loci. However, in spite of the fact that over 1,800 lobsters from five localities were analyzed, none of the statistical tests of stock structure provided convincing evidence of subpopulation differentiation within the Hawaiian Archipelago. Indeed, the overall impression is one of remarkable genetic uniformity throughout the range of this species. This outcome is perhaps not too surprising, since levels of detectable genetic variation are quite low in *P. marginatus*: hence, a robust test of stock structure using electrophoresis is difficult at best and requires very large sample sizes. Additionally, assuming that this species has larval life history characteristics similar to those of other species in the family, namely a series of planktonic phyllosoma stages lasting from 6 to 12 mo, dispersal and mixing of larvae throughout the Hawaiian Archipelago might be expected. However, this same current-driven transport and dispersal might also be expected to disperse larvae to other Pacific island groups near Hawaii (e.g., Johnston Atoll, the Line Islands, the Marquesas, the Tuamotus, the Gilbert Islands, the Marshall Islands, etc.). It is, therefore, somewhat of a paradox that, with the exception of one report of a single individual that was collected at Johnston Atoll (Brock 1973), *P. marginatus* is only found in the Hawaiian Islands.

The lack of demonstrable subpopulation differentiation in *P. marginatus* is not unusual for a decapod crustacean. Studies of other decapods have also generally failed to reveal stock heterogeneity (Lester 1979; Smith et al. 1980). Even in those cases where some genetic differences among stocks have been reported, the amount of differentiation is almost always very small (Tracey et al. 1975; Hanley 1980; Mulley and Latter 1981a, b). The only notable exception is the case of *P. argus* which exhibits substantial variation throughout the Caribbean (Menzies and Kerrigan 1979a; Menzies 1981). Hence, the Hawaiian spiny lobster fits the common decapod pattern of low heterozygosity and little subpopulation differentiation. At this point, all indications suggest

that the *P. marginatus* fishery in the Hawaiian Islands should be managed on a unit stock basis.

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GENETIC VARIATION AND POPULATION STRUCTURE IN A DEEPWATER SNAPPER, *PRISTIPOMOIDES FILAMENTOSUS*, IN THE HAWAIIAN ARCHIPELAGO

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ABSTRACT

Pink snapper were collected from six different locations in the Hawaiian Archipelago and subjected to starch gel electrophoretic analysis. Of a total of 44 enzyme-coding loci screened for genetic variation, 5 polymorphic loci were detected (Adh, Gpi-A, Iddh, Ldh-C, and Umb). Each polymorphic locus exhibited two common alleles (range of individual locus heterozygosity = 0.293-0.495). The heterozygosity averaged over all 44 loci was 0.047. Observed genotype distributions at the five polymorphic loci were in general agreement with Hardy-Weinberg equilibrium expectations. However, when the collections were subdivided into two major age groups (fish about 2-5 years old vs. fish 5-14 years old), significant differences in allele frequency between groups were detected for both alcohol dehydrogenase and lactate dehydrogenase-C.

Repetitive samples in 1979 and 1980 from two localities suggested that the allele-frequency distributions were stable during the period of the study. Contingency χ^2 tests of the entire data set failed to reveal significant genetic differences among the five primary localities (Maro Reef, French Frigate Shoals, Necker, Molokai, and Hawaii) or between the two major areas (Northwestern Hawaiian Islands and main Hawaiian Islands) represented by the collections. The mean value of Wright's F_{ST} for the five polymorphic loci was 0.005 indicating little subpopulation differentiation.

The data fail to reveal significant genetic differentiation among localities. Indeed, the results are entirely consistent with the existence of a single, panmictic stock of pink snapper throughout the Hawaiian Archipelago.

The pink snapper, or opakapaka, *Pristipomoides filamentosus*, is a deepwater species found throughout the Indo-West Pacific, including South Africa, Japan, Australia, the Philippines, Samoa, and the Hawaiian Islands (Kami 1973). In the Hawaiian Islands it occurs in significant numbers from Hawaii in the southeast through Maro Reef in the northwest and is found in greatest abundance at depths of 80-150 m (Ralston 1980). For the past 15 or more years, this snapper has been the dominant species in the deep-sea handline fishery in Hawaii (Hawaii Division of Fish and Game 1960-80[3]; Ralston and Polovina 1982). Due largely to the developing fishery in the Northwestern Hawaiian Islands (NWHI) the annual commercial harvest of *P. filamentosus* has increased from about 33 t in 1970 to 105 t in 1980 (Hawaiian Division of Fish and Game footnote 3).

Spawning of pink snapper in Hawaii appears to be concentrated in the fall of the year, and presumed annual fecundity may be as high as 1×10^6 eggs per female (B. S. Kikkawa[4]). Fertilization in opakapaka is external and the eggs are planktonic. After hatching, the larvae remain pelagic for about 1-2 mo during which time they attain a size of 20-25 mm (J. Leis[5]). Adults are essentially demersal but virtually nothing is known about the magnitude of adult movements, either daily or seasonally.

The present genetic investigation of stock structure in *P. filamentosus* was initiated to address two questions relevant to the future management of this fishery. First, was there any detectable stock heterogeneity within the entire Hawaiian Archipelago? Second, and specifically relating to the potential impact of the emerging fishery in the NWHI on the existing fishery in the main Hawaiian Islands, was there evidence that popu-

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lations in the NWHI were differentiated, and thus independent, from populations in the main islands?

MATERIALS AND METHODS

All specimens were obtained using commercial handline gear and were either frozen or iced at sea. Details of the collections are presented in Table 1. One series of samples (from French Frigate Shoals and Maro Reef) was filleted at sea, and the remaining carcasses (containing the tissues of interest) were preserved in an ice cold brine solution. This means of sample handling had the unfortunate effect of inactivating some of the enzymes (especially glucosephosphate isomerase and lactate dehydrogenase) so that these two enzymes could not be reliably scored in these samples. Initial screening for polymorphic loci in the pink snapper was conducted on extracts of white skeletal muscle, red skeletal muscle, heart, eye, brain, and liver. Each of these tissue samples was dissected from fresh or frozen specimens and homogenized in an equal volume of 0.1 M Tris-HCl pH 7.0 buffer (containing 1×10^{-3} M EDTA and 5×10^{-5} M $NADP^{+}$) using a loose fitting, motorized pestle. Homogenates were centrifuged for at least 20 min at a minimum of $20{,}000 \times g$ (liver supernatants were routinely centrifuged a second time to minimize lipid content). The resulting supernatants were transferred to individually labeled glass vials which were capped and stored at −75°C until the electrophoretic analysis was completed.

TABLE 1.—Collection details for total samples and individual collections of *Pristipomoides filamentosus* used in the electrophoretic analysis.

Collection[1]	Number	Dates	Average size[2]
Maro Reef	129	Oct. 1978-Nov. 1980	584 (±130)
a	12	Oct. 1978	
b	59	Oct. 1979	
c	9	Oct. 1979-Nov. 1980	
d	49	Nov. 1980	
French Frigate Shoals	254	Mar. 1979-May 1980	372 (±125)*
a	27	Mar. 1979	
b	67	Oct.-Nov. 1979	
c	46	May 1980	
d	114	Nov. 1980	
Necker	127	Mar. 1979-Nov. 1980	519 (±104)**
a	107	Mar.-May 1979	
b	20	Nov. 1979-Nov. 1980	
Kauai	25	Feb.-Apr. 1981	441 (±90)
a	20	Feb. 1981	
b	5	Apr. 1981	
Molokai	118	Mar. 1979-Apr. 1981	333 (±47)
a	9	Mar. 1979	
b	20	Sept. 1979	
c	5	July 1980	
d	84	Mar.-Apr. 1981	
Hawaii	63	June 1979-Apr. 1981	393 (±55)
a	17	June-July 1979	
b	46	Mar.-Apr. 1981	

[1]See figure 1 of Shaklee and Samollow (1984) for locality information.
[2]Fork length, FL (±1 standard deviation) in mm.
*FL of 38 fish from collections a and b unknown.
**FL of 79 fish from collection a unknown.

Electrophoresis

The supernatants were analyzed by horizontal starch gel electrophoresis (Selander et al. 1971). Each enzyme system surveyed in the initial screening for genetic variation was electrophoresed on from two to eight different buffer systems using extracts of several different tissues. Following electrophoresis, isozyme patterns were visualized using standard recipes (modified from Shaw and Prasad 1970; Selander et al. 1971; Siciliano and Shaw 1976). The umbelliferyl esterase (often called EST-D in the literature) was visualized using 4-methylumbelliferyl acetate as substrate.

Gel Scoring and Data Analysis

Patterns of enzyme variation which were consistent with the subunit structure of the homologous protein in other fishes (when known) and simple genetic models were scored and recorded as genotypes. Names of enzymes and Enzyme Commission numbers follow the recommendations of the Commission on Biochemical Nomenclature (1973). For multilocus enzyme systems, loci were given alphabetic designations to indicate homology with known forms (e.g., Gpi-B and Ldh-C). With the exception of one very rare allele (observed once) for both ADH and UMB, each of the polymorphic enzymes screened exhibited only two detectable alleles. These two alleles are referred to hereafter by their relative electrophoretic mobility from the origin as f (= fast) and s (= slow).

Tests of Hardy-Weinberg equilibrium and calculations of average heterozygosity (H) were accomplished as described in Shaklee and Samollow (1984). A locus was considered polymorphic if the frequency of the most common allele was ≤ 0.95.

Two types of χ^2 tests were used to test for genetic differentiation and, therefore, stock heterogeneity. First, for all polymorphic loci, contingency tests of all possible pairwise combinations of localities were conducted. Second, contingency tests comparing pooled samples representing the main Hawaiian Islands and the NWHI were conducted for all loci. Wright's F_{ST} statistic (Wright 1965, 1978) was calculated using the BIOSYS-1 computer program (Swofford and Selander 1981).

RESULTS

Forty-four presumed gene loci encoding 29 different enzymes were surveyed in a total of 716 pink snapper collected at six localities over a 2½-yr period. Thirty-nine of these loci were monomorphic in the first 100 animals screened (21 from Maro Reef, 44 from FFS, and 35 from Necker). These enzymes, which were not studied further, were aspartate aminotransferase (2 loci), acid phosphatase, adenosine deaminase, adenylate kinase, alkaline phosphatase, alanine aminotransferase (2 loci), catalase, creatine kinase (3 loci), esterase (2 loci), glyceraldehyde-3-phosphate dehydrogenase (2 loci), glutamate dehydrogenase, glucosephosphate isomerase-A, glycerol-3-phosphate dehydrogenase (2 loci), hexosediphosphatase (2 loci), isocitrate dehydrogenase, lipoamide dehydrogenase (= diaphorase), lactate dehydrogenase (A and B), malate dehydrogenase (2 loci), malate dehydrogenase-NADP$^+$ (= malic enzyme), mannosephosphate isomerase, peptidase (4 loci), peroxidase, phosphogluconate dehydrogenase, phosphoglucomutase, pyruvate kinase, superoxide dismutase, and xanthine dehydrogenase. The remaining five loci were polymorphic and the conditions for their analysis are summarized in Table 2. Since only 5 out of 44 loci in pink snapper were found to be polymorphic, $P_{.95}$ is estimated to be 0.114 in this species.

Zymogram patterns showing the commonly observed phenotypes for 4 of the 5 polymorphic enzymes in pink snapper are shown in Figure 1. The

TABLE 2.—Polymorphic enzymes in pink snapper, *Pristipomoides filamentosus*: Characteristics and conditions for analysis.

Enzyme (EC number)	Locus	Subunit structure[1]	Tissue	Buffer
Alcohol dehydrogenase (1.1.1.1)	Adh	dimer	liver	EBT[2]
Glucosephosphate isomerase (5.3.1.9)	Gpi-B	dimer	muscle	CAEA[3]
L-iditol dehydrogenase (1.1.1.14)	Iddh	tetramer	liver	TC-1[4]
Lactate dehydrogenase (1.1.1.27)	Ldh-C	tetramer	eye	TC-5[5]
Umbelliferyl esterase (3.1.1.-)	Umb	dimer	liver	EBT

[1]Presumed structure based on isozyme banding pattern in heterozygotes (see text).
[2]EDTA-boric acid-Tris pH 8.6 buffer of Boyer et al. (1963).
[3]Citric acid-aminopropyldiethanolamine (gel = pH 7.5, electrodes = pH 7.2) buffer of Clayton and Tretiak (1972).
[4]Tris-citric acid pH 7.0 buffer (buffer 1 of Shaw and Prasad 1970).
[5]Tris-citric acid pH 7.0 buffer (same as TC-1 but gel buffer is a 1:6.5 dilution of the electrode buffer).

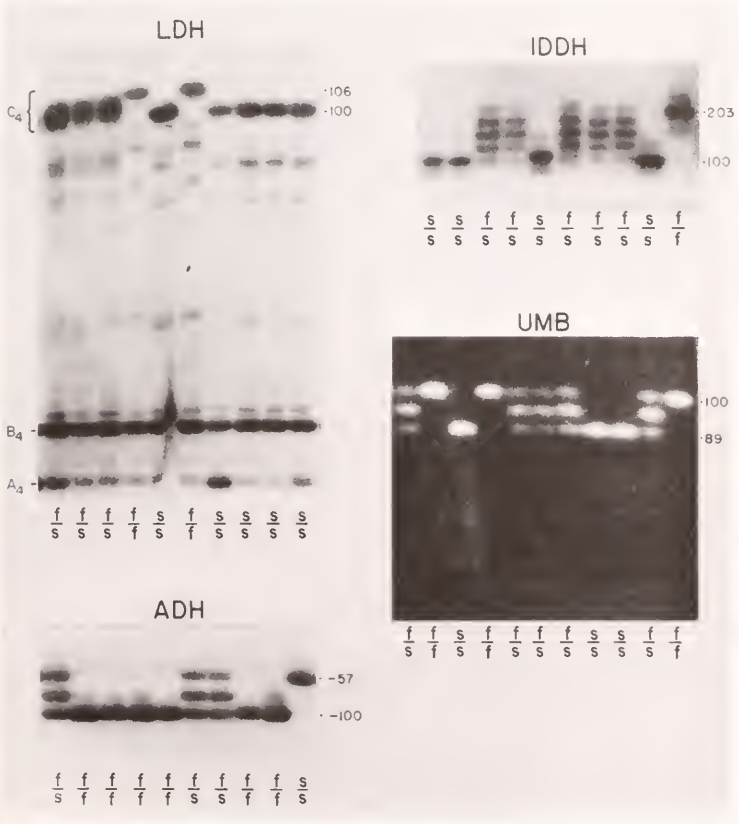

FIGURE 1.—Isozyme patterns of pink snapper, *Pristipomoides filamentosus*. LDH = lactate dehydrogenase, IDDH = L-iditol dehydrogenase (= sorbitol dehydrogenase), ADH = alcohol dehydrogenase, UMB = umbelliferyl esterase. Alleles are indicated at the right of each gel. Scoring of individual genotypes (by allelic class) is indicated at the bottom of each gel. Note that the sample origin is at the bottom and the anode is toward the top except for ADH where the origin is at the top (and the cathode is toward the bottom).

allele frequencies, heterozygosity per locus, F_{ST} per locus, and the number of genes successfully scored for each polymorphic locus at each locality are presented in Table 3. Glucosephosphate isomerase-B (Gpi-B), lactate dehydrogenase-C (Ldh-C), and L-iditol dehydrogenase (Iddh) (= sorbitol dehydrogenase) each exhibited only the two alleles shown in Figure 1 and Table 3. Alcohol dehydrogenase (Adh) exhibited one additional allele ("very slow") in one heterozygote. This rare allele was pooled with the "slow" allele in the analysis. Similarly, umbelliferyl esterase (Umb) exhibited one additional allele ("very slow") in one heterozygote. This rare allele was pooled with the "slow" allele in the analysis. χ^2 tests of goodness of fit to Hardy-Weinberg expectations of genotype distributions revealed two significant deviations (out of a total of 25 tests). These were a heterozygote deficiency for Ldh-C at Necker Island ($\chi^2_1 = 8.17$; $P < 0.005$), and a heterozygote excess for Umb at Hawaii ($\chi^2_1 = 3.95$; $P < 0.05$). Since one significant outcome in 20 tests is expected by chance given an $\alpha = 0.05$, this is not surprising. The per locus heterozygosity ranged from 0.293 for the Gpi-B locus to 0.495 for the Umb locus. The average heterozygosity across all loci (H) was 0.047.

A comparison of the allele frequencies at each locus across the five localities (Table 3) revealed that there was little overall variation among locations. χ^2 contingency tests of all possible pairwise comparisons of localities (10 comparisons × 5 loci = 50 tests) yielded only one significant value, that for Iddh, Necker Island vs. Molokai ($\chi^2_1 = 5.99$; $P < 0.025$). The apparent homogeneity was even more evident in χ^2 tests of the two pooled groups (NWHI vs. main) where no significant outcomes occurred in the five tests. Three other measures of genetic characteristics of these samples also failed to reveal subpopulation differentiation. The number of common alleles per polymorphic locus was two at all localities for all enzymes. The average heterozygosity per locus (H) showed almost no difference (Maro Reef $H = 0.045$, French Frigate Shoals $H = 0.047$, Necker Island $H = 0.048$, Molokai $H = 0.047$, Hawaii $H = 0.046$) among localities. Finally, the values of Wright's F_{ST} were small for all five polymorphic loci and the mean F_{ST} was only 0.005. Overall, none of the measures used indicated subpopulation or stock heterogeneity in this species in the Hawaiian Islands.

It could reasonably be argued that the above analyses of pooled collections consisting of fish of

TABLE 3.—Allele frequencies, heterozygosity values, and F_{ST} values at five polymorphic loci in pink snapper, *Pristipomoides filamentosus*. Localities as in figure 1 of Shaklee and Samollow (1984).

Locus[1] (heterozygosity)	Alleles[2]	Locality						
		Maro Reef	FFS	Necker	Molokai	Hawaii	NWHI[3]	Main[4]
Adh	f	0.673	0.679	0.607	0.638	0.611	0.657	0.632
(h = 0.456)	s	0.327	0.321	0.393	0.362	0.389	0.343	0.368
F_{ST} = 0.004	(n/N)	(220/119)	(346/187)	(224/117)	(232/116)	(126/63)	(790/423)	(408/204)
Gpi-B	f	0.164	0.180	0.154	0.179	0.155	0.171	0.177
(h = 0.287)	s	0.836	0.820	0.846	0.821	0.845	0.829	0.823
F_{ST} = 0.001	(n/N)	(140/70)	(316/160)	(104/52)	(212/107)	(110/55)	(560/282)	(372/187)
Iddh	f	0.314	0.301	0.410	0.262	0.336	0.325	0.299
(h = 0.431)	s	0.686	0.699	0.590	0.738	0.664	0.675	0.701
F_{ST} = 0.006	(n/N)	(210/119)	(186/96)	(78/42)	(214/107)	(110/55)	(474/257)	(374/187)
Ldh-C	f	0.209	0.257	0.232	0.307	0.236	0.243	0.273
(h = 0.379)	s	0.791	0.743	0.768	0.693	0.764	0.757	0.727
F_{ST} = 0.011	(n/N)	(110/58)	(358/185)	(142/78)	(228/116)	(110/55)	(610/321)	(388/196)
Umb	f	0.571	0.502	0.572	0.582	0.563	0.537	0.556
(h = 0.496)	s	0.429	0.498	0.428	0.418	0.437	0.463	0.444
F_{ST} = 0.003	(n/N)	(254/129)	(494/254)	(250/127)	(232/116)	(126/63)	(998/512)	(408/204)

[1]Adh = alcohol dehydrogenase, Gpi = glucosephosphate isomerase, Iddh = L-iditol dehydrogenase (= sorbitol dehydrogenase), Ldh = lactate dehydrogenase, Umb = umbelliferyl esterase, h = per locus heterozygosity, F_{ST} = Wright's (1965) fixation index.

[2]f = fast, s = slow, n = number of genes successfully scored, N = number of individuals analyzed.

[3]Consisting of fish from Maro Reef, French Frigate Shoals (FFS), and Necker Island.

[4]Consisting of fish from Molokai, Hawaii, and 25 specimens from Kauai.

very different sizes (and therefore different ages) taken over a considerable period of time may have obscured important information and possible heterogeneity in the data. This is particularly true since the pink snapper were collected over a 2½-yr period and ranged in size from 230 to 770 mm FL (fork length)—presumably representing a range of ages from 2 to over 16 yr (Ralston and Miyamoto 1983). With this in mind, the data set was partitioned (where fish lengths were known and sample sizes were large enough to allow reasonable statistical tests) to allow analyses of the collection for 1) evidence of variation in allele frequency between age classes, 2) evidence of year-to-year variability in allele frequency at a location, and 3) evidence of allele frequency variation within a homogeneous age class among localities. The samples from Maro Reef and French Frigate Shoals (FFS) allowed partitioning with regard to size classes. The frequency distributions characterizing individual collections making up the samples for Maro Reef and FFS as well as those for the three unpartitioned areas (Necker, Molokai, and Hawaii) are shown in Figure 2. Because the collections from both Maro Reef and FFS contained adequate numbers of specimens throughout the size range, they were subdivided into two groups. One group consisting of small, young fish (300-500 mm FL; about ages 2-5 yr—see Ralston and Miyamoto 1983) and one of large, old fish (501-770 mm FL; about ages 5-16+ yr). The allele-frequency distributions characteristic of these separate groups are shown in Table 4. For Maro Reef and FFS, χ^2 analysis of the data for goodness-of-fit to Hardy-Weinberg expectations revealed no significant deviations (5 loci × 2 locations × 2 size groups = 20 tests), although it should be emphasized that the statistical test is not robust for small sample sizes (Fairbairn and Roff 1980). Heterogeneity χ^2 tests between size classes at both Maro Reef and FFS revealed only one statistically significant difference (for Adh at Maro Reef, $\chi^2_1 = 4.72; P < 0.05$). A third test for changes in allele frequency with size was conducted on a pooled data set including all fish of known fork length from Maro Reef, FFS, and Necker. This pooled NWHI sample had considerably larger sample sizes in each cell making the statistical tests more robust. Genotype proportions at all five loci in both size (age) groups in the combined NWHI samples were in agreement with Hardy-Weinberg expectations. Of the five contingency χ^2 tests between size (age) groups, only that for Ldh-C was significant ($\chi^2_1 = 4.22; P <$ 0.05). This significant outcome was due to an increase in the frequency of the more common (slow) allele with increased size (age). The increase in the frequency of the slow allele with increasing size was characteristic of the individual samples from both Maro Reef and FFS. A similar trend in allele-frequency change, this one involving an increase in the frequency of the rarer (slow) allele of Adh, was observed in the samples. Although the trend for Adh was statistically significant in the Maro Reef sample, it was not in the pooled NWHI

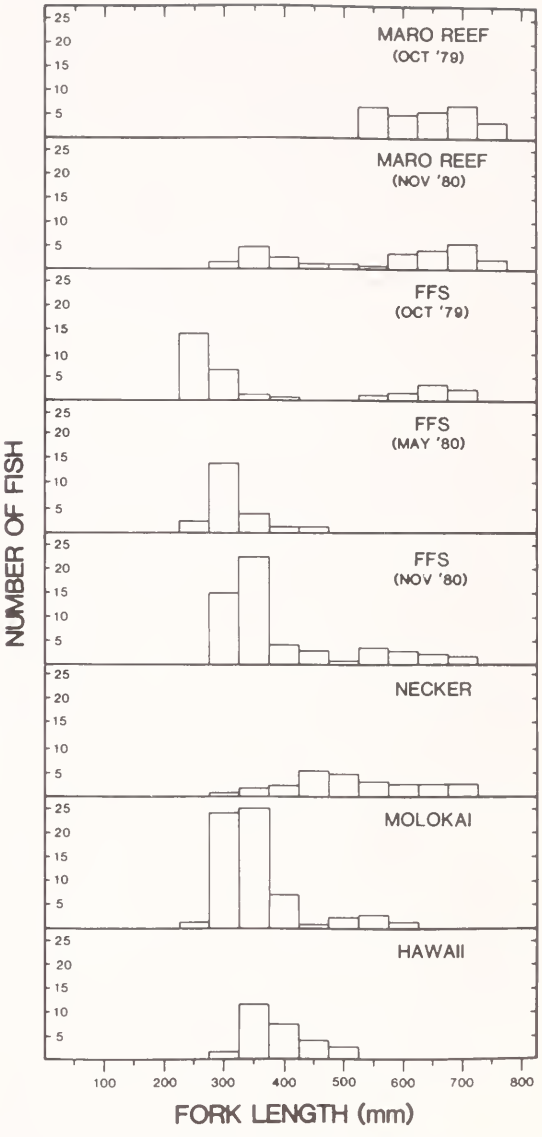

FIGURE 2.—Size-frequency histograms for eight snapper collections.

TABLE 4.—Frequencies of the more abundant allele at each polymorphic locus in pink snapper of different sizes (ages).

Locus[1]	Allele[1]	Maro Reef 300-500 mm	Maro Reef 501-770 mm	FFS 300-500 mm	FFS 501-770 mm	NWHI[2] 300-500 mm	NWHI[2] 501-770 mm
Adh	f	0.800	0.635	0.697	0.639	0.702	0.624
	(*N*)	(25)	(78)	(117)	(18)	(161)	(117)
Gpi-A	s	0.846	0.845	0.833	0.816	0.830	0.847
	(*N*)	(26)	(42)	(120)	(19)	(171)	(85)
Iddh	s	0.708	0.676	0.687	0.833	0.695	0.649
	(*N*)	(24)	(74)	(75)	(3)	(118)	(97)
Ldh-C	s	0.740	0.821	0.731	0.816	0.735	0.833
	(*N*)	(25)	(28)	(117)	(19)	(149)	(54)
Umb	f	0.654	0.564	0.476	0.500	0.514	0.555
	(*N*)	(26)	(94)	(125)	(36)	(176)	(155)

[1]Abbreviations of loci and alleles as in Table 3; *N* = number of fish successfully scored.
[2]Consisting of fish from Maro Reef and French Frigate Shoals (FFS) and fish from Necker with known fork length.

TABLE 5.—Frequencies of the more abundant allele at each polymorphic locus in pink snapper collected at different times. — = no data because tissues had been stored in brine (see Materials and Methods).

Locus[1]	Allele[1]	Maro Reef Oct. 1979	Maro Reef Nov. 1980	French Frigate Shoals Oct. 1979	French Frigate Shoals May 1980	French Frigate Shoals Nov. 1980
Adh	f	0.593	0.750	—	0.656	0.693
	(*N*)	(54)	(50)		(45)	(109)
Gpi-A	s	—	0.827	—	0.807	0.825
	(*N*)		(52)		(44)	(114)
Iddh	s	0.696	0.677	—	0.656	0.740
	(*N*)	(51)	(43)		(45)	(48)
Ldh-C	s	—	0.796	—	0.733	0.752
	(*N*)		(49)		(43)	(113)
Umb	f	0.568	0.590	0.433	0.478	0.540
	(*N*)	(59)	(50)	(67)	(45)	(112)

[1]Abbreviations of loci and alleles as in Table 3; *N* = number of fish successfully scored.

sample. The other three loci exhibited no such clear trends in changing allele frequency with size (age). These analyses indicate that allele frequencies at some loci (Adh and Ldh-C) in the opakapaka may exhibit important changes related to size (age) and caution against an uncritical analysis of pooled data.

It was possible to analyze temporally subdivided samples from Maro Reef and FFS to see whether or not significant changes in allele frequency at a location were occurring through time. The allele frequencies characteristic of these temporal samples are shown in Table 5. Unfortunately, in order to obtain adequate sample sizes it was necessary to include specimens of all sizes (ages) in these samples. Of the 19 sets, only Umb in the May 1980 sample from FFS was significantly out of Hardy-Weinberg equilibrium ($\chi^2_1 = 6.14$; $P < 0.025$), exhibiting an excess of heterozygotes. Of the 10 contingency χ^2 tests between successive samples, only that for Ad at Maro Reef was statistically significant ($\chi^2_1 = 5.80$; $P < 0.025$) and that involved fish of significantly different sizes in the two samples (Fig. 2). Although this temporal analysis is not as complete as one might wish, it does suggest that allele frequencies were reasonably constant over the 2½ yr period of the present study.

Given that allele frequencies remained relatively constant through time but exhibited significant changes (at two loci) associated with fish size (age), a final analysis of the data was conducted. This involved fish from all five locations but only fish of 300-550 mm FL (about 2-6 yr old; see Ralston and Miyamoto 1983). The allele frequencies characteristic of these samples are presented in Table 6. In all cases (5 loci × 5 locations = 25 tests) the data were in agreement with Hardy-Weinberg equilibrium expectations. Even more importantly, the outcomes of all five χ^2 contingency tests (involving all locations) were nonsignificant. The results reinforce the earlier conclusions that no among-locality genetic differentiation exists in pink snapper throughout the

TABLE 6.—Frequencies of the more abundant allele at each polymorphic locus in pink snapper between 300 and 550 mm FL.

Locus[1]	Allele[1]	Maro Reef	FFS	Necker	Molokai[2]	Hawaii	NWHI[3]	Main[4]
Adh	f	0.759	0.696	0.542	0.658	0.630	0.688	0.645
	(*N*)	(29)	(120)	(24)	(101)	(54)	(173)	(155)
Gpi-A	s	0.850	0.837	0.806	0.815	0.852	0.832	0.831
	(*N*)	(30)	(123)	(31)	(100)	(54)	(184)	(154)
Iddh	s	0.722	0.687	0.667	0.723	0.657	0.698	0.697
	(*N*)	(27)	(75)	(24)	(101)	(54)	(126)	(155)
Ldh-C	s	0.750	0.729	0.833	0.715	0.769	0.735	0.740
	(*N*)	(26)	(120)	(9)	(100)	(54)	(155)	(154)
Umb	f	0.667	0.480	0.581	0.569	0.565	0.526	0.568
	(*N*)	(33)	(128)	(31)	(101)	(54)	(192)	(155)

[1]Abbreviations of loci and alleles as in Table 3; *N* = number of fish successfully scored.
[2]Including 25 fish from Kauai.
[3]Consisting of fish from Maro Reef, French Frigate Shoals, and Necker.
[4]Consisting of fish from Kauai, Molokai, and Hawaii.

Hawaiian Islands. Absolutely no evidence of multiple stocks was found.

DISCUSSION

Genetic Inferences

Because it was not possible in the present study to verify the Mendelian nature of the observed variation in enzyme phenotypes in *Pristipomoides filamentosus* by direct genetic tests, such a genetic basis can only be inferred from the results of the χ^2 goodness-of-fit tests (to Hardy-Weinberg expectations) and by comparison of the snapper data with genetic (Purdom et al. 1976; May et al. 1979; Kornfield et al. 1981), molecular (Darnall and Klotz 1975; Mo et al. 1975), and electrophoretic data (Engel et al. 1971) for these same enzymes in other fish species. The genetic and molecular bases of four of the enzymes scored for variation in *P. filamentosus* have been well documented in other fish species. For three of these (ADH, GPI, and IDDH) the banding patterns observed in presumed heterozygote snappers were entirely consistent with expectations from other studies. However, the results for two enzymes require additional comment.

Lactate Dehydrogenase-C

Three distinct Ldh loci characterize diploid bony fishes (Markert et al. 1975). The Ldh-C locus typically encodes the eye-specific LDH isozyme (Whitt 1969, 1970; Shaklee et al. 1973), but in some groups it encodes an isozyme predominant in liver (Sensabaugh and Kaplan 1972; Shaklee et al. 1973). Both the eye-specific and the liver-predominant LDH isozymes have been characterized biochemically (Whitt 1970; Sensabaugh and Kaplan 1972). Electrophoretic variants of the eye-specific LDH encoded at the Ldh-C locus have been shown to be inherited in Mendelian fashion in freshwater sunfish (Whitt et al. 1971) and poeciliids (Leslie and Vrijenhoek 1977; Morizot and Siciliano 1979). The Ldh-C locus has been reported to be variable in numerous species. In essentially all of these cases, the isozyme pattern of the heterozygote has been difficult to resolve into the expected five isozymes, rather it typically appears as a smear of LDH activity extending from the region of the slow allele homozygote to the region of the fast allele homozygote. The pattern of LDH-C variation in *P. filamentosus* shown in Figure 1 is similar to that reported for these other species. Although we were unable to resolve the theoretically predicted five C subunit-containing bands in presumed heterozygotes, their status as heterozygotes seems secure since these individuals exhibited two bands at the position of the B_3C_1 heterotetrameric isozyme (one having the same mobility as the single slow $B_3C_1^3$ heterotetramer in the slow homozygotes and one having the same mobility as the single fast $B_3C_1^f$ heterotetramer in the fast homozygotes), just as expected for such heterozygotes (Fig. 1).

Umbelliferyl Esterase

Although there are numerous published studies of biochemical properties, genetic variation, and inheritance in fish esterases (Koehn 1969; Fujino 1970; Holmes and Whitt 1970; Metcalf et al. 1972; Smith et al. 1978; Leslie and Pontier 1980; Van Beneden et al. 1981), the diversity and heterogeneity of these enzymes makes the assignment of homology difficult. However, since virtually all of the above investigations involved the use of α-naphthyl esters as substrates in the staining reaction and the UMB of *P. filamentosus* (stained using 4-methylumbelliferyl acetate as substrate) does not show detectable activity with α-naphthyl acetate, it seems unlikely that the umbelliferase of the pink snapper is homologus with any of these esterases of other fishes. The only other reports of UMB variation in fish are those of Ward and Beardmore (1977) (= "Est-D") for plaice and of Shaklee et al. (1983) for blue marlin. In both of these species, as in *P. filamentosus*, UMB exhibits single-banded homozygotes and triple-banded heterozygotes (with isozyme staining intensities in an approximate 1:2:1 ratio as expected for a dimeric protein). These observations and the general agreement between observed genotype distributions and those expected, assuming Hardy-Weinberg equilibrium, support our genetic interpretations of the observed variation in UMB in pink snapper.

Stock Structure

Significant differences in allele frequency among fish of differing ages within a single Mendelian population or stock can be due to 1) the differential mortality of certain genotypes (natural selection), 2) genotype-specific differences in catchability (distribution, activity, behavior, etc.), 3) chance fluctuations due to nonrepresentative spawning in different years (genetic

drift) or, 4) some combination of the above. Unfortunately, the short duration of most electrophoretic studies and/or inadequate sample sizes for various age classes often prevent or limit investigations of such age-dependent changes in allele frequency. No year class heterogeneity in transferrin allele frequencies was detected in 27 consecutive year classes of Atlantic cod by Jamieson (1975). Similarly, no year class variation was reported for mackerel EST by Smith et al. (1981). On the other hand, changing patterns of allele-frequency distribution with increasing age (size) have been noted in several fish species, including the blenny, *Anoplarchus purpurescens* (Johnson 1971), the eelpout, *Zoarces viviparous* (Christiansen et al. 1974), the mummichog, *Fundulus heteroclitus* (Mitton and Koehn 1975), the plaice, *Pleuronectes platessa* (Beardmore and Ward 1977), and several New Zealand commercial fishes (Smith 1979a; Gauldie and Johnston 1980). In many of the latter cases, it has been suggested that natural selection is the underlying cause of the shift in allele frequencies with age. Our analysis of the pink snapper data (Table 4) revealed that both alcohol dehydrogenase and Ldh-C exhibited significant differences in allele frequency between young and old fish. However, we do not have any direct information that these changes are due to natural selection.

There have been few electrophoretic studies of commercial fishes which have addressed the question of temporal stability of allele frequencies. In the American eel, *Anguilla rostrata*, data for 4 successive years revealed that patterns of genetic differentiation were generally unchanged through time (Koehn and Williams 1978). On the other hand, studies of pink salmon (Aspinwall 1974) have demonstrated substantial temporal heterogeneity in allele frequencies due to the existence of distinct spawning stocks isolated in time. Temporal differences in gene frequencies related to different spawning stocks have also been suggested by Kornfield et al. (1982) for Atlantic herring. The present analysis of opakapaka allele frequencies through time (Table 5) revealed no temporal differences.

There can be no doubt that the Hawaiian Islands offer a sharply discontinuous distribution of adult habitats for *Pristipomoides filamentosus* given that the species is almost completely restricted to water depths of 50-200 m in Hawaii (Ralston 1980) (200 m contour lines in figure 1 of Shaklee and Samollow 1984). Furthermore, there is no reason to believe that adult pink snapper—strictly demersal fish—migrate through the open, oceanic waters between islands. It is therefore somewhat surprising that no evidence of genetic subdivision of opakapaka among localities within the Archipelago was observed. This seems particularly surprising given that there are several reports of stock heterogeneity in other demersal marine fishes such as Atlantic cod (Jamieson 1975; Cross and Payne 1978; Jamieson and Turner 1978), walleye pollock (Grant and Utter 1980), New Zealand snapper (Smith et al. 1978), and two species of flatfishes (Fairbairn 1981a, b). The genetic homogeneity observed for pink snapper in the present study would seem a singular exception when compared with the above results were it not for the fact that numerous other demersal species exhibit similar patterns of apparent genetic homogeneity, e.g., plaice (Purdom et al. 1976; Ward and Beardmore 1977), hake (Smith et al. 1979), ling (Smith 1979b; Smith and Francis 1982), and New Zealand hoki (Smith et al. 1981). However, it must be remembered that the embryonic and larval stages of *P. filamentosus* and most, if not all, of these other species are pelagic and, therefore, serve as a dispersal phase. Given that this pelagic stage apparently lasts for 1-2 mo in pink snapper, it would not seem unreasonable that larval dispersal among localities due to wind-driven currents within the Hawaiian Islands would be of sufficient magnitude to ensure adequate gene flow among adult populations to prevent detectable genetic differentiation (Lewontin 1974).

If this interpretation is correct, it would mean that although the total pink snapper harvest in Hawaii is derived from numerous small geographically separated fisheries, each associated with discontinuous patches of suitable habitat (islands, reefs, and banks), the pink snappers themselves are all members of a single, large panmictic population distributed throughout the Hawaiian Archipelago. Based on the above information, it seems appropriate to manage the pink snapper fishery in Hawaii as a single unit stock—including both the main Hawaiian Islands and NWHI. However, since the observed genetic homogeneity does not unambiguously establish the existence of a unit stock (it is merely consistent with this hypothesis), this management policy must remain open to reevaluation in the future especially if data of another kind should suggest stock heterogeneity.

Genetic aspects of population structure have now been studied in four marine species throughout the Hawaiian Archipelago. In three of these

species—a spiny lobster, *Panulirus marginatus* (Shaklee and Samollow 1984), a damselfish, *Stegastes fasciolatus* (Shaklee 1984), and the pink snapper discussed in the present report—no evidence of subpopulation or stock heterogeneity was found. This lack of demonstrable population subdivision occurs in spite of the fact that 1) a range of over 2,400 km in length was sampled, 2) adult habitats for all three species are clearly discontinuous and, in places, separated from one another by extensive, deep-water expanses, 3) one of the species (*Panulirus marginatus*) is endemic to the Hawaiian Islands (implying a somewhat limited dispersal ability), and 4) one species (*Stegastes fasciolatus*) has demersal eggs, a relatively short-lived pelagic larval stage (possibly as short as 20 d), and is territorial as an adult. That not all marine organisms in the Hawaiian Archipelago are characterized by single, large, panmictic populations is dramatically illustrated by the fourth species, a limpet *Cellana exarata*. This species exhibits extensive population subdivision both between the NWHI and the main Hawaiian Islands and within each of these major areas (Shaklee and Samollow 1980; Shaklee 1983; Samollow 1984[6]). Together, the patterns of population structure exhibited by these four species in the Hawaiian Islands provide some insight into the extent and pattern of subpopulation differentiation in marine organisms in an archipelagic system. However, it seems apparent that considerably more investigation will be necessary before a comprehensive picture of patterns of subpopulation differentiation, not to mention an understanding of their underlying bases, becomes clear.

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[6]Samollow, P. B. 1984. Genetics of Hawaiian limpets. I. Population structure of the blackfoot 'opihi, *Cellana exarata*. Unpubl. manuscr., 22 p. Southwest Center for Biomedical Research, P.O. Box 28147, San Antonio, TX 78284.

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NOTE

DISTRIBUTION AND ABUNDANCE OF *SICYONIA PENICILLATA* LOCKINGTON, 1879 IN THE GULF OF CALIFORNIA, WITH SOME NOTES ON ITS BIOLOGY[1]

Penaeid shrimp on the continental shelves of México are heavily exploited and represent one of the major sources of seafood. It is also an important source of revenue as most of the catch is exported. Of the different species which are commercially fished, the genus *Penaeus* constitutes practically the entire catch (Dilio-Fuentes et al. 1976; Klima 1981; Mathews 1981). In the Gulf of California, on the Pacific side of México, there is a very important trawl fishery for *Penaeus* (*Farfantepenaeus*) *californiensis* Holmes and, to a lesser extent, for *P.* (*Litopenaeus*) *vannamei* Boone and *P.* (*L.*) *stylirostris* Stimpson which are both predominantly caught in coastal lagoons. Small catches of *P.* (*F.*) *brevirostris* Kingsley are also taken in the southern Gulf of California (Edwards 1978; Mathews 1981). In the area, however, the fisheries for *Penaeus* shrimp have shown a steady fall in catch since 1962 (Lluch-Belda 1974; Rodríguez de la Cruz 1981a). One of the major consequences has been an increasing but still limited interest for the bycatch of *Penaeus* shrimp and more attention has recently been given to other species or genera that were previously considered too small or not abundant enough (Hernández-Carvallo 1976; Grande-Vidal and Díaz-López 1981; Paul 1981). Thus, other contributors to the total catch are *Xiphopenaeus riveti* Bouvier, which has been increasingly important in the Gulf of California fishery since 1972 (Hernández-Carvallo 1976), and *Trachypenaeus pacificus* Burkenroad, which occasionally appears in local markets, and has effectively occupied a secondary part in recent fisheries (Rodríguez de la Cruz 1981b; Mathews 1981).

Although there are 19 species of *Sicyonia* reported from American waters, little information has been published on the relative importance that the genus has or might have for fishery development. Commercial catches have been reported for *S. brevirostris* Stimpson along the coast of the southeastern United States (Pérez Farfante 1980) and in the Gulf of México (Arreguín-Sánchez 1981), and this species seems to be one of the most abundant decapod crustaceans in these areas (Kennedy et al. 1977; Huff and Cobb 1979; Soto 1980; Wenner and Read 1982). Comparatively, on the Pacific coast of America, two species have been occasionally caught in large quantities. *Sicyonia ingentis,* the only species of the genus found north of México, is actively fished off the coast of California (Frey 1971; Mearns and Greene 1974), while in the Southern Hemisphere, the importance of rock shrimp in fishery activities has recently increased and *S. disdorsalis,* one of the four species occurring in the area, represented about 5.8% of the total catch of penaeid shrimp in northern Perú in 1977 (Arana and Méndez 1978). *Sicyonia disdorsalis* is also the dominant species in the southeastern Gulf of California (Hendrickx et al. 1982) and is commonly found as a member of the *Penaeus* bycatch (Paul and Hendrickx 1980).

The information in this paper was obtained while processing the material collected during a 2-wk cruise in the Gulf of California, and it is presented as a contribution to the study of the biology and fishery of *S. penicillata* on the Pacific coast of México. Information related to the distribution, abundance, and habitat of the species in the Gulf of California, biometric data, and natural diet is also included.

Material and Methods

Samples of benthic fauna were collected in May 1982 at 32 different sampling stations on the continental shelf of the Gulf of California, México (Fig. 1). Of these 32 collections, 28 were made with an 11 m headrope commercial otter trawl, with a stretched mesh of 6.5 cm, equipped with a 2.5 cm bar mesh inner cod end bag. Four samples were made with a 3 m wide rectangular oyster dredge equipped with 2.5 cm bar mesh collection bags. Tows were made from the 50 m RV *El Puma,* of the Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, at speeds of between 2 and 4 km/h and were about 30 min in duration. At the end of each tow, samples were first sorted into major groups (mollusks, crabs, shrimp, echinoderms, and fish) and fresh weights for each group were obtained to the nearest 100 g with

[1]Contribution No. 341 of the Instituto de Ciencias del Mar y Limnología, UNAM.

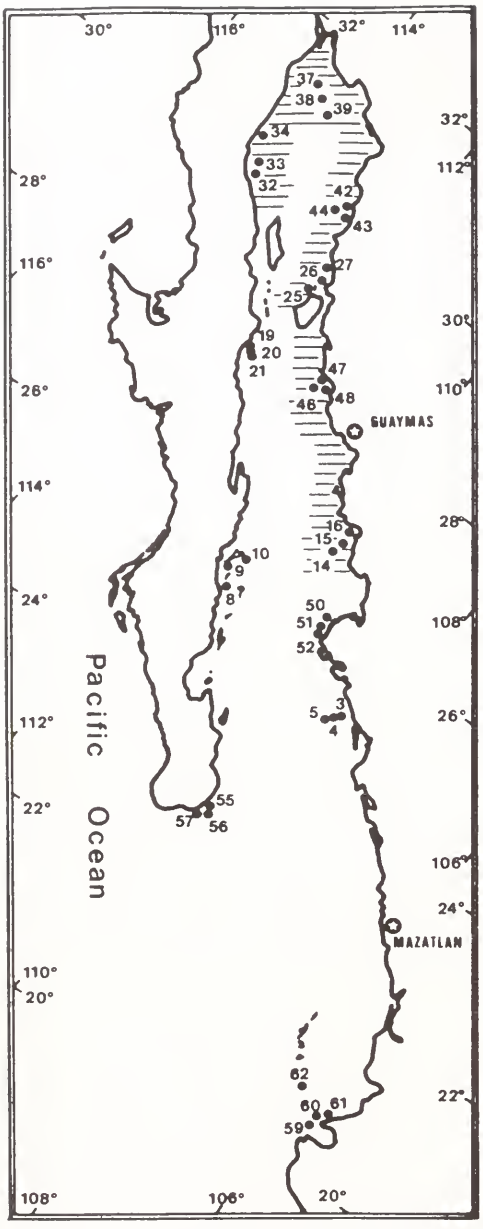

FIGURE 1.—Location of the sampling stations (solid circles) and distribution of *Sicyonia penicillata* (striped area) according to the occurrence of this species in the samples.

spring balances. Whenever members of one species or genus accounted for a large part of the total catch, they were weighed apart from the rest of the catch.

Samples were immediately fixed with a 8% seawater solution of Formalin[2], except for the *Sicyonia* samples that were stored in the deep freezer of the vessel at a temperature of −25°C. Frozen samples of *S. penicillata* were later used in the laboratory to determine individual weights (W) with a top pan electric balance (± 0.05 g precision). Total length (TL: rostrum tip to telson tip) and carapace length (CL: orbital margin to mid-posterodorsal margin of carapace) of the shrimps were obtained with a dial caliper to the nearest 0.1 mm. Determination of linear and exponential relationships, TL-CL and W-CL, followed the method of Sokal and Rohlf (1969).

The analysis of the foregut contents was done with a series of 20 specimens that were selected at random from among the material obtained during trawling activities. The foreguts were removed by dissection, their contents analyzed under magnification, and the frequency of occurrence of each food item was calculated and expressed as a percentage of the total number of foreguts examined.

Results and Discussion

Geographic Distribution

Sicyonia penicillata was first described by Lockington (1879) from Bahía Bolinas (sic), Baja California (?Bahía Ballenas) and Bahía de Los Angeles in the Gulf of California. Brusca (1980) reported the species as the most common rock shrimp from the Gulf of California (Gulf) and from the west coast of Baja California where it was found as far north as the Laguna Ojo de Liebre (lat. 27°45′ N). It also occurs in bays of the western side of the Gulf (Burkenroad 1934, 1938).

During the present study, *S. penicillata* was found in the northern part and along the east coast of the Gulf, south to Punta Arboleda (lat. 26°45′ N), and was captured at 13 of the 32 sampling stations (Fig. 1). Although a wide continental shelf runs uninterruptedly from this latter locality south to Bahía Banderas, at the southern tip of the Gulf, the species seems to be absent from the southeastern part of the Gulf. Indeed, monthly sampling made in Bahía de Mazatlán over a 2-yr period and intensive trawling operations made on the continental shelf of southern Sinaloa (lat. 22°14′ to 23°37′ N) on three occasions during a period of 1 yr did not bring up a single specimen of *S. penicillata*, and the dominant species for this

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

area appears to be *S. disdorsalis* (Hendrickx 1984). Although several species of *Sicyonia* from the Pacific coast of America have a wide distribution range, *S. penicillata* seems to be restricted to the southern half of Baja California and the central and northern Gulf of California (Hendrickx 1984).

Abundance

A total of 3,502 specimens were collected during the sampling operations, including 1,919 females (55%) and 1,583 males (45%). Generally *S. penicillata* was rare or uncommon at most of the trawl stations. Most of the catches were <1 kg/h and commercial-size catches were obtained only twice during the survey (33 and 66 kg/h). The largest catches of all were from the northernmost part of the Gulf at stations 38 and 39 (Table 1) and represented 97 and 88% of the crustacean catch and 6 and 69% of the total catch, respectively. All of the sampling was done during daytime or at dusk. Nighttime captures might prove to be much higher as has been the case with *S. brevirostris* on the Florida's West Central Shelf (Huff and Cobb 1979).

TABLE 1.—Sampling conditions and abundance (kg/h of trawling) of *Sicyonia penicillata* in the Gulf of California during the survey (catch = 0 for the rest of the stations).

Sampling station	Depth (m)	Abundance (kg/h)	Substrate	Sand	Silt	Clay
				(% by weight)		
15	53	1	Fine sand with shell fragments	69	23	8
25	75	1	Very coarse sand with shell fragments	100	—	—
27	30	1	Sand	100	—	—
32	39	1	Green mud	24	43	34
33	80	1	Compact green mud	2	46	52
34	26	2.2	Green mud	8	42	50
37	35	1	Fine sand; silty (brown to grey mud)	79	12	9
38	60	66.4	Fine sand; silty (brown to grey mud)	75	18	7
39	100	33	Very fine sand	72	17	10
43	73	1	Silty sand	—	—	—
44	100	1	Silty sand	54	29	17
47	49	1	Fine sand	83	10	7
48	54	1	Fine sand	78	14	8

Bathymetric Range and Substrate

The species seems to occupy a wide bathymetric range. It has been reported by Burkenroad (1938) from the beach level (under stone) down to a depth of 72 m. In the present study, the shrimp were collected at depths between 26 and 100 m (Table 1). Information on bottom substrates was obtained from samples collected during the same cruise and processed by the Laboratorio de Geología Marina of the Marine Station of Mazatlán and have been summarized in Table 1. Maximum abundance was found at stations with smooth bottom made of compact mud and of very fine sand, although specimens were also collected in small numbers on bottoms made of coarse sand and of crushed shell-sand.

The distribution pattern of the species in the Gulf indicates a preference for the shelf of the northern Gulf and the eastern central Gulf. No specimens were found at station 19 and southward, along the Baja California coast, where sand and gravel were observed. The absence of *S. penicillata* from the southeastern Gulf platform, where substrate varies with depth from fine sand to mud (mostly silty mud mixed with clay), is probably due to other factors such as water temperature or dissolved oxygen level which can be lower than 1 ml/l at bottom level in this area (January and April data) (Hendrickx et al. 1984), or to competition with *S. disdorsalis*.

Natural Diet

As in other penaeid shrimp, food in the stomach of *Sicyonia* is usually finely triturated, making difficult identification of the components of the diet (Cobb et al. 1973). Relative importance of various food items in the diet is listed in Table 2 (20 stomachs).

All stomachs examined were at least 30% full and 12 of them were at least 50% full. Sampling was done in late afternoon, and the degree of stomach fullness indicates that the species feeds during daytime. Crustaceans were the most frequent item in the diet, followed by small mollusks and polychaetes. Unidentifiable organic matter was present in almost every stomach (80%) and, in

TABLE 2.—Food items in the diet of *Sicyonia penicillata* (20 stomachs).

Food items		% Frequency of occurrence
Algae		15
Foraminifera		15
Nematoda		10
Polychaete fragments		40
Mollusca:	Gastropoda	20
	Fragments	40
Crustacea:	Copepoda	5
	Isopoda	10
	Amphipoda	35
	Fragments	70
Fish scales		30
Pellets		45
Unidentifiable organic matter		80
Sand, silt, etc.		20

many cases, it accounted for a large fraction of the content. *Sicyonia penicillata* seems to be a generalized carnivore, feeding on small benthic crustaceans, mollusks, and polychaetes.

Biometric Relationships

Biometric relationships were obtained from a series of 82 specimens selected from the total catch at station 38. Carapace length/total length relationships were assessed for 24 males (TL: 85-49 mm) and 58 females (TL: 97-43 mm). The male relationship was TL = 4.73 + 3.74 CL ($r = 0.992$) and the female relationship was TL = 4.51 + 3.63 CL ($r = 0.991$). Relationships assessed for each sex were significantly different from one another (t-test on slope; $P < 0.001$). Carapace length/weight relationships were also assessed for each sex and the following equations were obtained: male $W = 1.1 \times 10^{-3}\ CL^{2.9775}$ ($r = 0.978$) and female $W = 1.7807 \times 10^{-3}\ CL^{2.7733}$ ($r = 0.985$) (Fig. 2).

Fishing Potential

Commercial concentration of *Sicyonia penicillata* were found at two localities only (33 and 66.4 kg/h). These values are comparable with the catch reported for *Sicyonia* spp. by Cobb et al. (1973) off the northeast coast of Florida (up to 46 kg/h). There is little information available on commercial catch in the Gulf of California. Unpublished data obtained from the Mexican Fishery Institute (Instituto de Pesca) indicate total catch between 40 and 1,572.5 t/yr for the period of 1977-82 in the northern and central Gulf (data are for the fishing harbor of Guaymas, Sonora, for five consecutive fishing seasons: 1977-78, 40 t; 1978-79, 610.3 t; 1979-80, 1,572.5 t; 1980-81, 167.5 t; 1981-82, 207.0 t). These catches corresponded to mixed captures of rock shrimp where *S. penicillata and S. aliaffinis* seemed to predominate. In 1979-80, when the peak catch was obtained, large quantities of *Sicyonia* were brought by truck to Es- were dried in huge chile-ovens, peeled, and sold as appetizer or seasoning (D. Castro[3]).

Prior to this report, information related to fishery grounds, catches, and fishery potential were only available for two American species of *Sicyonia: S. ingentis,* along the coast of southern California, and *S. brevirostris,* in the South Atlantic Bight and in the Gulf of México. Data obtained on *Sicyonia penicillata* indicate that it is the most abundant rock shrimp for the entire Gulf of California. Although the annual rock shrimp catch in the area varied considerably over the past 6 yr (1977-82), it averaged over 500 t/yr. Comparative values for the three species may be found in Table 3. Although these data are not comparable with one another for each year, they clearly demonstrate the relative abundance of *S. penicillata* in the northern Gulf of California.

Sicyonia penicillata is a medium-sized species which average about 90 per kilogram in the northern Gulf of California, compared with *S. ingentis* which averages about 45 per kilogram in the Santa Barbara-Ventura area (Frey 1971). This small size, added to the processing difficulties for hard-shell shrimps, still represents a serious impediment for the development of a fishery.

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TABLE 3.—Landings of *Sicyonia* in three North American fishing areas.

Species	Area	Year	Landings (t)	Author
S. ingentis	Southern California, USA	1961	13.7	Frey 1971
		1967-68	0.2	Frey 1971
S. brevirostris	Contoy, Quintana Roo, México	1971-78	15-300	Arreguín-Sánchez, 1981
(heads off)	South Atlantic and Florida, USA	1979	3,340.0	Pérez Farfante 1980
S. penicillata	Guaymas, Northern Gulf of California, México	1977-82	40-1,572.5	Unpubl. data

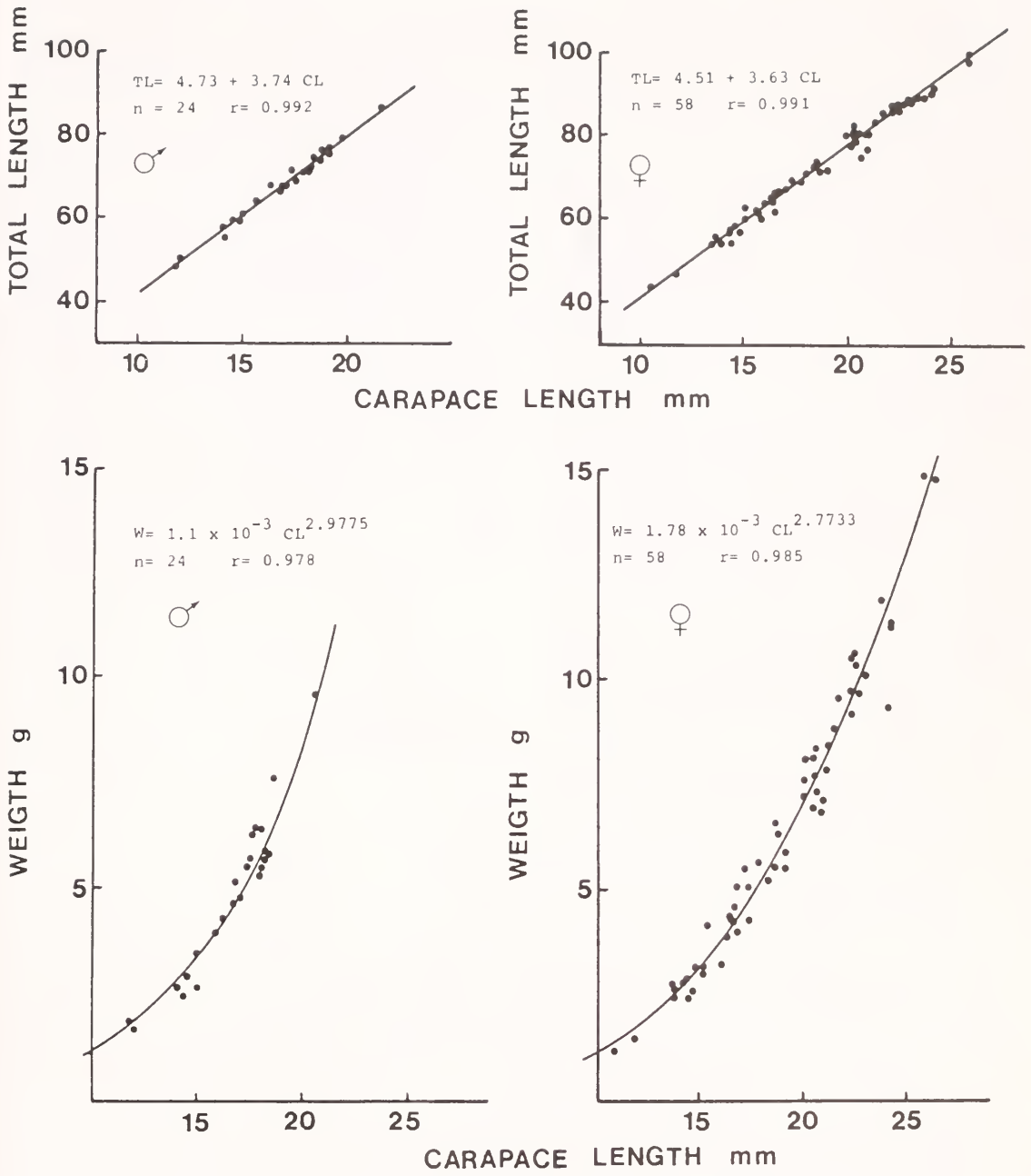

FIGURE 2.—Biometric relationships obtained for *Sicyonia penicillata*.

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INDEX

Fishery Bulletin Vol. 81, Nos. 1-4

NOTICES

NOAA Technical Reports NMFS published during first 6 months of 1984.

Circular

451. Synopsis of biological data on skipjack tuna, *Katsuwonus pelamis*. By Walter M. Matsumoto, Robert A. Skillman, and Andrew E. Dizon. January 1984, iv + 92 p., 77 figs., 20 tables.

Special Scientific Report—Fisheries

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779. Opportunistic feeding of the northern fur seal, *Callorhinus ursinus*, in the eastern North Pacific Ocean and eastern Bering Sea. By Hiroshi Kajimura. February 1984, iv + 49 p., 38 figs., 12 tables, 13 append. figs., 1 append. table.
780. History of scientific study and management of the Alaskan fur seal, *Callorhinus ursinus*, 1886-1964. By Victor B. Scheffer, Clifford H. Fiscus, and Ethel I. Todd. March 1984, iii + 70 p., 14 figs.
781. An annotated checklist of the fishes of Samoa. By Richard C. Wass. May 1984, v + 43 p.

Technical Reports NMFS

1. Synopsis of biological data on the blue crab, *Callinectes sapidus* Rathbun. By Mark R. Millikin and Austin B. Williams. March 1984, iv + 39 p., 9 figs., 11 tables.
2. Development of hexagrammids (Pisces: Scorpaeniformes) in the northeastern Pacific Ocean. By Arthur W. Kendall, Jr. and Beverly Vinter. March 1984, iii + 44 p., 16 figs., 13 tables, 10 append. figs.
3. Configurations and relative efficiencies of shrimp trawls employed in the southeastern United States waters. By John W. Watson, Jr., Ian K. Workman, Charles W. Taylor, and Anthony F. Serra. March 1984, iii + 12 p., 12 figs., 11 tables.
4. Management of northern fur seals on the Pribilof Islands, Alaska, 1786-1981. By Alton Y. Roppel. April 1984, iii + 26 p., 3 figs., 4 tables.
5. Net phytoplankton and zooplankton in the New York Bight, January 1976 to February 1978, with comments on the effects of wind, Gulf Stream eddies, and slope water intrusions. By Daniel E. Smith and Jack W. Jossi. May 1984, iv + 41 p., 12 figs., 22 append. tables.

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