UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE

FISHERY BULLETIN

OF THE

FISH AND WILDLIFE SERVICE

VOLUME 59

SH
11
.A25
v.59

BULLETINS 145 through 155
ISSUED BY THE FISH AND WILDLIFE SERVICE
1959

7897

National Oceanic and Atmospheric Administration

ERRATA NOTICE

One or more conditions of the original document may affect the quality of the image, such as:

Discolored pages
Faded or light ink
Binding intrudes into the text

This has been a co-operative project between the NOAA Central Library and the Climate Database Modernization Program, National Climate Data Center (NCDC). To view the original document, please contact the NOAA Central Library in Silver Spring, MD at (301) 713-2607 x124 or www.reference@nodc.noaa.gov.

LASON
Imaging Contractor
12200 Kiln Court
Beltsville, MD 20704-1387
March 21, 2005

UNITED STATES DEPARTMENT OF THE INTERIOR

FISH AND WILDLIFE SERVICE

BUREAU OF COMMERCIAL FISHERIES

TITLE PAGE AND INDEX

VOLUME 59

ISSUED 1962

UNITED STATES GOVERNMENT PRINTING OFFICE • WASHINGTON, D.C. • 1962

CONTENTS OF VOLUME 59

Bulletin No.		Page
145.	Morphology of the white shrimp, *Penaeus setiferus*, (Linnaeus 1758). By Joseph H. Young. (Issued April 1959.)	1–168
146.	Decline of the yellowtail flounder (*Limanda ferruginea*) off New England. By William F. Royce, Raymond J. Buller, and Ernest D. Premetz. (Issued June 1959.)	169–267
147.	Some uses of statistical analysis in classifying races of American shad (*Alosa sapidissima*). By Donald R. Hill. (Issued April 1959.)	269–286
148.	Sexual maturity and spawning of albacore in the Pacific Ocean. By Tamio Otsu and Richard N. Uchida. (Issued May 1959.)	287–305
149.	Grayling of Grebe Lake, Yellowstone National Park, Wyoming. By Thomas E. Kruse. (Issued May 1959.)	307–351
150.	Study of age determination by hard parts of albacore from Central North Pacific and Hawaiian waters. By Tamio Otsu and Richard N. Uchida. (Issued April 1959.)	353–363
151.	Fluctuations in the population of yellow perch, *Perca flavescens* (Mitchill), in Saginaw Bay, Lake Huron. By Salah El-Din El-Zarka. (Issued July 1959.)	365–415
152.	Young jack crevalles (*Caranx* species) off the southeastern Atlantic coast of the United States. By Frederick H. Berry. (Issued December 1959.)	417–535
153.	Life history of the threespine stickleback, *Gasterosteus aculeatus* Linnaeus, in Karluk Lake and Bare Lake, Kodiak Island, Alaska. By John Greenbank and Philip R. Nelson. (Issued June 1959.)	537–559
154.	Life history of the sea lamprey of Cayuga Lake, New York. By Roland L. Wigley. (Issued September 1959)	561–617
155.	Early development and metamorphosis of the ten-pounder, *Elops saurus* Linnaeus. By Jack W. Gehringer. (Issued September 1959.)	619–647

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*
FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

MORPHOLOGY OF THE WHITE SHRIMP *Penaeus setiferus* (Linnaeus 1758)

BY JOSEPH H. YOUNG

FISHERY BULLETIN 145
From Fishery Bulletin of the Fish and Wildlife Service
VOLUME 59

UNITED STATES GOVERNMENT PRINTING OFFICE • WASHINGTON • 1959

For sale by the Superintendent of Documents, U. S. Government Printing Office
Washington 25, D. C. . Price $1

The Library of Congress has cataloged Fishery Bulletin 145 as follows:

Young, Joseph Hardie, 1918–

Morphology of the white shrimp *Penaeus setiferus* (Linnaeus 1758) Washington, U. S. Govt. Print. Off., 1959.

iv, 168 p. illus. 30 cm. (U. S. Fish and Wildlife Service. Fishery bulletin 145)

"From Fishery bulletin of the Fish and Wildlife Service, volume 59."

Bibliography: p. 160–169.

1. Shrimps. I. Title. (Series: U. S. Fish and Wildlife Service. Fishery bulletin, v. 59, no. 145)

SH11.A25 vol. 59, no. 145 595.3843 59–60272

Library of Congress

The series, Fishery Bulletin of the Fish and Wildlife Service, is cataloged as follows:

U. S. *Fish and Wildlife Service.*

Fishery bulletin. v. 1–

Washington, U. S. Govt. Print. Off., 1881–19

v. in illus., maps (part fold.) 23–28 cm.

Some vols. issued in the congressional series as Senate or House documents.

Bulletins composing v. 47– also numbered 1–

Title varies: v. 1–49, Bulletin.

Vols. 1–49 issued by Bureau of Fisheries (called Fish Commission, v. 1–23)

1. Fisheries—U. S. 2. Fish-culture—U. S. I. Title.

SH11.A25 639.206173 9–35239 rev 2*

Library of Congress [r55e¾1]

CONTENTS

	Page
Introduction	1
Penaeus as comparative material	2
I. Skeletal and muscle systems	3
A. Protocephalon	3
1. Eyestalks	7
2. Antennules	17
3. Antennae	30
4. Labrum	43
B. Gnathothorax	47
1. Mandibles	60
2. Paragnatha	65
3. Maxillae	66
a. First maxillae	66
b. Second maxillae	69
4. Maxillipeds	72
a. First maxillipeds	72
b. Second maxillipeds	74
c. Third maxillipeds	81
5. Pereiopods	87
a. First pereiopods	87
b. Fifth pereiopods	94
C. Abdomen	103
1. Pleopods	115
2. Tail fan	125
II. Nervous system	132
A. Nerves of Supraesophageal ganglion and tritocerebrum	135
B. Ventral nerve cord	139
III Circulatory system	140
A. Heart and pericardium	140
B. Blood vessels of the body	140
C. Appendicular blood vessels	148
D. Venous system	149
E. Respiratory system	149
IV. Digestive system	150
A. Foregut	150
B. Midgut	154
C. Hindgut	154
V. Excretory system	155
VI. Reproductive system	155
Literature cited	160
Bibliography	162

ABSTRACT

In this illustrated morphology of the commercially important white shrimp of the Gulf of Mexico the muscle, nervous, circulatory, excretory, reproductive, and respiratory systems are compared with those of the blue crab, *Callinectes*, a European crawfish *Astacus*, the "coon-stripe" shrimp, *Pandalus*, and other decapod crustaceans. The major portion of the comparative work deals with the muscles, since the muscle systems of a few Decapoda have been reported in much greater detail than other systems.

The comparative studies of muscles and nerves indicates that the Penaeidae represent a generalized anatomical condition in the Crustacea Decapoda, thus verifying the systematic research in this area. Evidently the Penaeidae are relatively close to the decapod stem in the Malacostraca. The generalized condition of Penaeidae is shown again and again by the repetition of functional muscle units. The same units have become simplified in the higher decapods, having been lost, presumably, by the fusion of separate parts. Adhering to the morphological principle that the nerves tend to retain their ancient innervations despite coalescence of parts, shifting of muscle origins, etc., and can therefore be considered as morphologically conservative, the nerves to the repeating muscle units of *Penaeus* are found to have kept their innervations to the same muscles, now fused, in higher Decapoda. The comparative morphology of decapod nerves and circulatory elements is treated only to the extent that research on these systems in other decapods has been published.

Several structures are found in *Penaeus setiferus* which have not been reported previously in the literature. A fibrous circulatory element, the capillary arbor, penetrates the distal optic ganglia. One or more hard concretions embedded in the substance of the antennal portion of the excretory gland are described. Although two pairs of muscles are associated with the labrum of Insecta, muscles have not been described in the labrum of Crustacea. The labrum of *Penaeus* has at least 12 pairs of muscles. A structure, the hindgut gland, is found in the anterior part of the sixth abdominal segment lying dorsal to the rectum. Its function is unknown. Some of the blood vessels of the heavily vascularized branchiostegal region of the carapace run parallel to the margin of the carapace, suggesting "growth rings" by their appearance.

MORPHOLOGY OF THE WHITE SHRIMP *PENAEUS SETIFERUS* (LINNAEUS 1758)

By JOSEPH H. YOUNG, *Department of Zoology, Tulane University*

Penaeus setiferus, the white shrimp of the Gulf of Mexico, represents an important component of the commercial shrimp catch throughout the northern, western, and southern margins of that body of water. With the rise in importance of the commercial shrimp industry to the economy of the Gulf States in the past two decades, information about the life history, morphology, physiology, and behavior of the edible shrimps has become necessary, and even critical, to the continued well-being of the industry.

We know very little about the diet of the penaeid shrimps, how far they travel in search of food and mates, or what constitute barriers to their activities. Our knowledge of digestion, of nervous and glandular control of the processes of molting, reproduction, and coloration is limited for the most part to distant relatives of the Penaeidae. Despite numerous efforts (Müller 1863; Kishinouye 1900; Hudinaga 1935, 1942; Pearson 1939; Johnson and Fielding 1956), the stages of the life cycle of penaeids are not certainly known and consequently we have very little exact ecological information about the larvae. Opinions vary on the life span of adult penaeid shrimps. Whether the adult females reproduce once and then die at the end of a year or reproduce more than once a season, or again, live for 2 years and reproduce each season is not known. The answers to such questions will have a profound effect on the future conduct of the commercial shrimp industry.

This study sets forth in detail the anatomy of *Penaeus setiferus*. Anatomical work as such does not answer the problems suggested above, but as a map to the explorer, anatomy provides the experimental biologist with a guide to the "lay of the land," thereby facilitating his progress. And as a map, the value of an anatomical study to its users hinges upon its accuracy and clarity. To these ends all efforts were bent, the illustrations are large and the structures shaded to give a sense of depth. The anatomical parts are labelled with full words, rather than disguised with cryptographic abbreviations listed below the illustrations or hidden in the text. The plates are defined as diagrams whereby important features may be emphasized by artwork without sacrificing accuracy.

P. setiferus is an omnivorous scavenger dwelling on or near mud-sand bottoms in the littoral zone. The animal is probably restricted to the euphotic stratum in which the light intensities are fairly high. The shrimps are gregarious and move about in large schools. The character of the bottom is probably important to the white shrimp. Evidence from various sources suggests that the animals make use of mud or mud and sand by burrowing into this soft substrate for protection during molting and possibly for other purposes. The white shrimp is a powerful swimmer and capable of migrating great distances. These and other aspects of the life habits of *P. setiferus* have been considered in terms of functional anatomy in the present study.

Several people have made significant contributions to the progress of this study. Credit for initiating the project belongs perhaps most of all to Albert Collier, United States Fish and Wildlife Service, Galveston, Tex. His unfailing cooperation, together with that of T. J. Costello of the same laboratory, contributed greatly to the completion of the anatomical work. Help and encouragement has also come from Dr. Fred R. Cagle, Dr. Royal D. Suttkus, and Dr. George H. Penn, all of the Department of Zoology, Tulane University. Percy Viosca, Louisiana Wildlife and Fisheries Commission; Charles Dawson, of

NOTE.—Approved for publication April 22, 1958. Fishery Bulletin 145. Report of research done under contract between Bureau of Commercial Fisheries and Tulane University (Saltonstall-Kennedy Act).

the Bears Bluff Laboratories, Wadmalaw Island, S. C.; and Dr. Milton Fingerman, Department of Zoology, Tulane University, have all made useful comments about various aspects of the work. I am indebted to Prof. L. B. Holthuis, Rijksmuseum van Natuurlijke Historie, Leiden; Dr. Andre Mayrat, Laboratoire de Zoologie de l'Ecole Normale Superieure, Paris; and Jerome E. Stein, Texas A. and M. College, Galveston, Tex., for helpful criticism of certain parts of the study.

Heartfelt thanks go to the project artist, Raymond Bollinger of New Orleans, La., for the high quality of the plates making up the anatomical study of the white shrimp. Of the 136 figures in this work, all but 10 were finished by Mr. Bollinger from tracings made by the investigator.

METHODS

The anatomical study of *Penaeus setiferus* was made for the most part on white shrimps purchased alive from bait shrimp fishermen. The animals were fixed in Zenker's fluid, dehydrated to 70 percent ethyl alcohol and there stored. Despite difficulties in its use in the field, Zenker's fluid was found to have several advantages over formalin. Zenker's fluid softens or removes the calcareous deposits and leaves the cuticle in a condition similar to thick cellophane. This mixture quickly penetrates to and fixes the internal organs, and in so doing prevents internal maceration caused by the post-morten enzymatic activity of the hepatopancreas. Formalin-fixed material is useless for the study of internal organs. The fixative greatly hardens the cuticle and the external muscles and fails to penetrate to the internal organs.

Dissections were performed under a stereomicroscope. Dissecting needles which were sharpened to fine points in mixtures of strong nitric acid and ethyl alcohol were employed. Locations of muscles and attachments, and other skeletal details were studied on specimens of white shrimps cleared in strong alkali and stained with Van Gieson's Triple Stain (Curtis' Modification). The outlines of whole structures were used as templates within which muscles and other organs were sketched in layers on tracing paper as the dissections progressed. The tracings were transferred to drawing papers on a light box. The drawings were finished in ink and carbon pencil.

PENAEUS AS COMPARATIVE MATERIAL

For purposes of comparative morphology, the Penaeidae enjoy a unique position. Evolution has brought them down to us in an apparently generalized decapod condition. Naturally, we must view with caution any attempt to force a given structure or organ into the generalized category, for all extant animals must be highly specialized in specific instances, if unspecialized in others, for life today. Furthermore, the so-called generalized structure may be the superficies of a well-hidden specialization. Bearing in mind, then, that there may be no such thing as a generalized structure in a modern species, the comparative morphologist can proceed to draw homologies between structures which look alike on phylogenetic and ontogenetic grounds. Information shedding light on the evolution of the decapod crustaceans will be advanced here wherever supporting studies are available.

Unfortunately, very few complete anatomical works exist on decapod crustaceans, and none of these complete works deal with members of the Penaeidae. The present work will have reference to the studies of many workers, but in particular to the extensive studies of Berkeley (1928) on the "coon stripe" shrimp, *Pandalus danae* Stimpson 1857, of Schmidt (1915) and Keim (1915) on *Astacus astacus* (Linn. 1758), and of Cochran (1935) on the blue crab, *Callinectes sapidus* Rathbun, 1896. Other, frequently important, studies will be alluded to in the applicable sections. The greatest handicap to the establishment of a comparative morphology of the Decapoda is our ignorance of the details of the nervous system, the innervations of muscles and other organs. Despite widespread morphological change such as shifting of muscle origins, coalescence of metameres, and other distortions to the primitive body plan, structures tend to retain their ancient innervations. A muscle may move from one segment to another in the evolution of a group. The same nerve will usually continue to innervate it. For the nervous system is morphologically conservative and thus the most informative element in the historical study of metazoan structure. Until a substantial groundwork of neurological facts exists on the decapod crustaceans, homologies between many of the less obvious structures will rest on weak grounds.

When compared externally with the crustaceans mentioned (figs. 1, 2, 3), *Penaeus setiferus* is most similar to *Pandalus danae*, a caridean prawn, and less like *Astacus astacus*. The relationship with the blue crab is obviously distant. The Penaeidae are classed in the Sub Order Natantia together with the Caridae and the Stenopidae. All of these are relatively strong swimmers with light cuticles. Although *Astacus* displays many similarities in form to *Penaeus*, the crawfish is a reptant form with a heavy cuticle. With the lobster, the crawfish has an extensively developed chela on the first walking leg, whereas the white shrimp bears a small chela similar in size to those on the other chelate legs. The antennal scale and the pleopods of the crawfish are much smaller than those of the white shrimp. The former are large in the white shrimp. In other general details, superficially, the white shrimp and the crawfish are substantially similar in structure.

In general, the present anatomical study indicates that the Penaeidae are relatively generalized decapod crustaceans. Compared with the higher decapods, the penaeids tend to have several parts to accomplish a functional end that is carried out by a single part in a higher representative. Expressing this in terms of phylogeny, the lower decapod has lost fewer structures by the fusion of parts than has the advanced form. Since the present study of *Penaeus* is largely grounded upon earlier work on higher decapods, the process of homologizing the structures tends to be reversed from the phyletic order. Homologies must therefore be drawn from the specific to the general. Among the problems thus raised is the matter of functional nomenclature, in particular, of the muscles.

The historical base for the naming of decapod muscles is, for all practical purposes, the work of Schmidt (1915) on *Astacus*. This investigator employed a system of Latinized functional names, handed down to him by earlier anatomists, for the muscles he encountered in the European crawfish. With minor exceptions Schmidt's nomenclature accurately describes the actions of the muscles of *Astacus*. However, the functional muscle names of Schmidt do not describe the actions of the same muscle having a different function in another form. The investigator is therefore faced with the decision either to transfer to a muscle in another animal the functionally inaccurate name of Schmidt, which will simplify comparisons, or to rename the muscle in each case in accordance with its specific function, which will tend to compound the existing confusion in morphological nomenclature. With no great pride I have chosen the latter course in the present study. Until such time as a system of nomenclature having universal validity can be devised, the dilemma is inescapable.

Included in this paper is a section of bibliographical references. These items are primarily systematic, morphological, and experimental papers on Crustacea which contain valuable anatomical information used in the preparation of the present study, but not cited specifically. Since workers in many fields have to resort to anatomical studies in the course of their research, the anatomical information is necessarily disguised under titles which reflect the primary objects of their research. The student of crustacean morphology therefore, finds bibliographical compilations of works from diverse sources very helpful. The bibliography is in no sense complete.

I. SKELETAL AND MUSCLE SYSTEMS

The great mass of the shrimp body is comprised of skeleton and, in particular, muscle; accordingly, the bulk of the present anatomical study is devoted to a consideration of these elements. The description is presented in the order of the three natural body regions of the animal, the simple head, or protocephalon, the gnathothorax, and the abdomen. The skeleton falls easily into these divisions. The muscles, of course, do likewise, but not so obviously, since many of them cross skeletal subdivisions for mechanical reasons. In some anatomical works, the arthropod appendages are treated separately, as if these organs were attached to the animal in a kind of evolutional afterthought in the arthropod line. The appendicular muscles would, indeed, so indicate, but the skeleton, the nervous system, and the innervations of the muscles tell us that the arthropod appendage is an ancient structure. The appendages, then, will be taken up with the tagmata to which they belong.

A. Protocephalon

The protocephalon is that morphologically separable pregnathal group of segments so designated by Snodgrass (1951). This simple head includes, in the order of their occurrence in the adult, the eyes, antennules, antennae, and labrum.

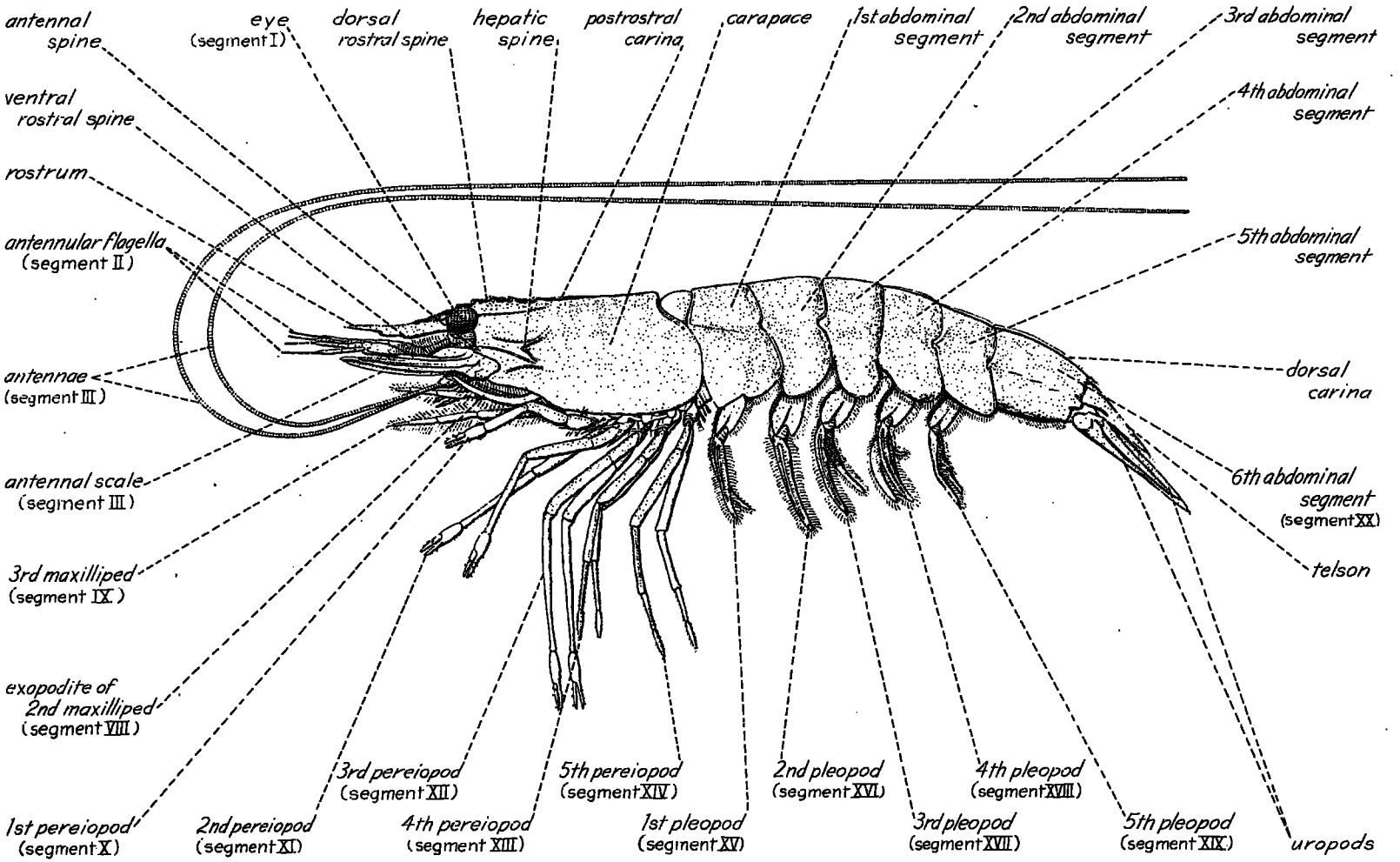

FIGURE 1.—*Penaeus setiferus*. **Lateral view of adult female.**

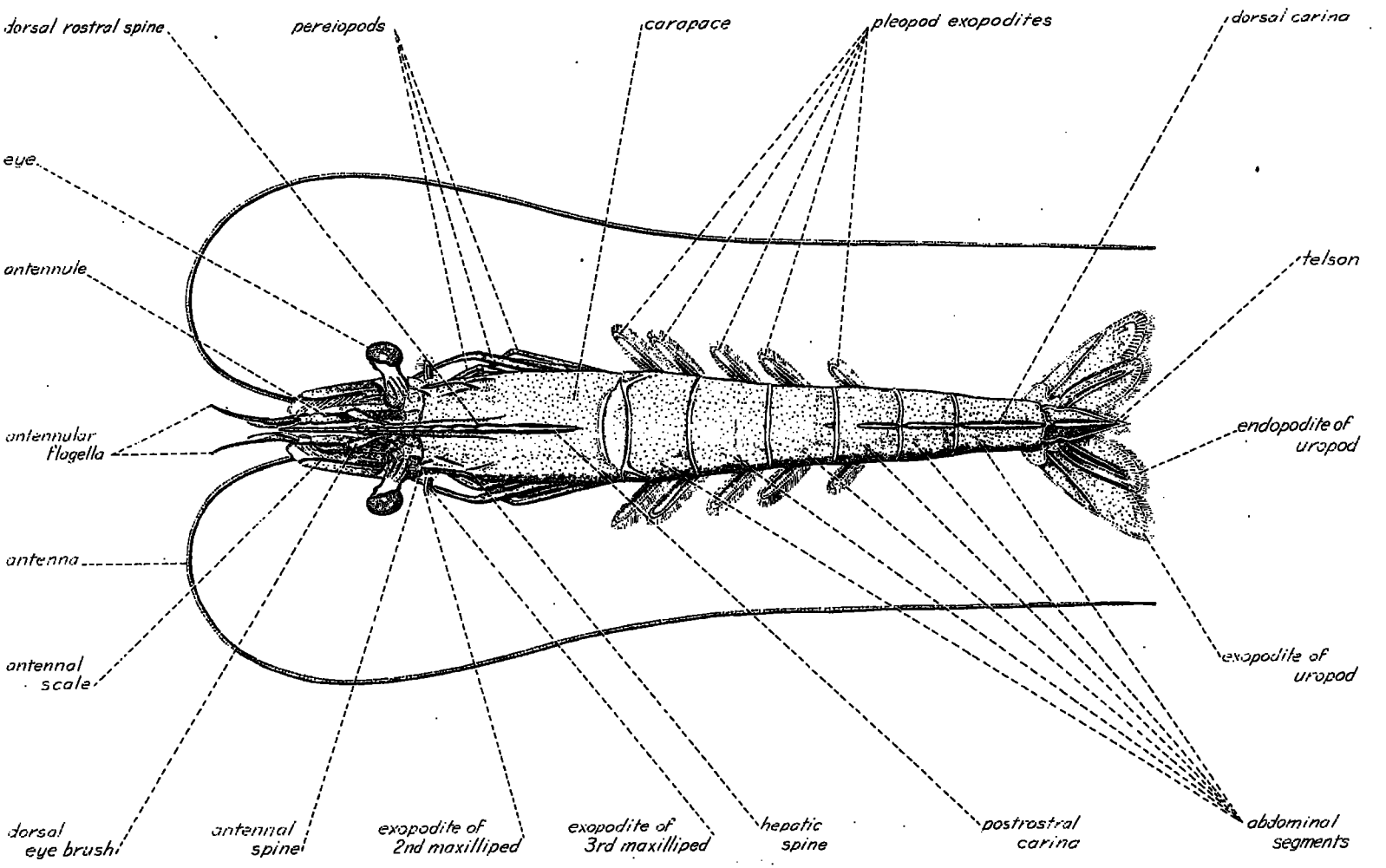

FIGURE 2.—Dorsal view of adult female.

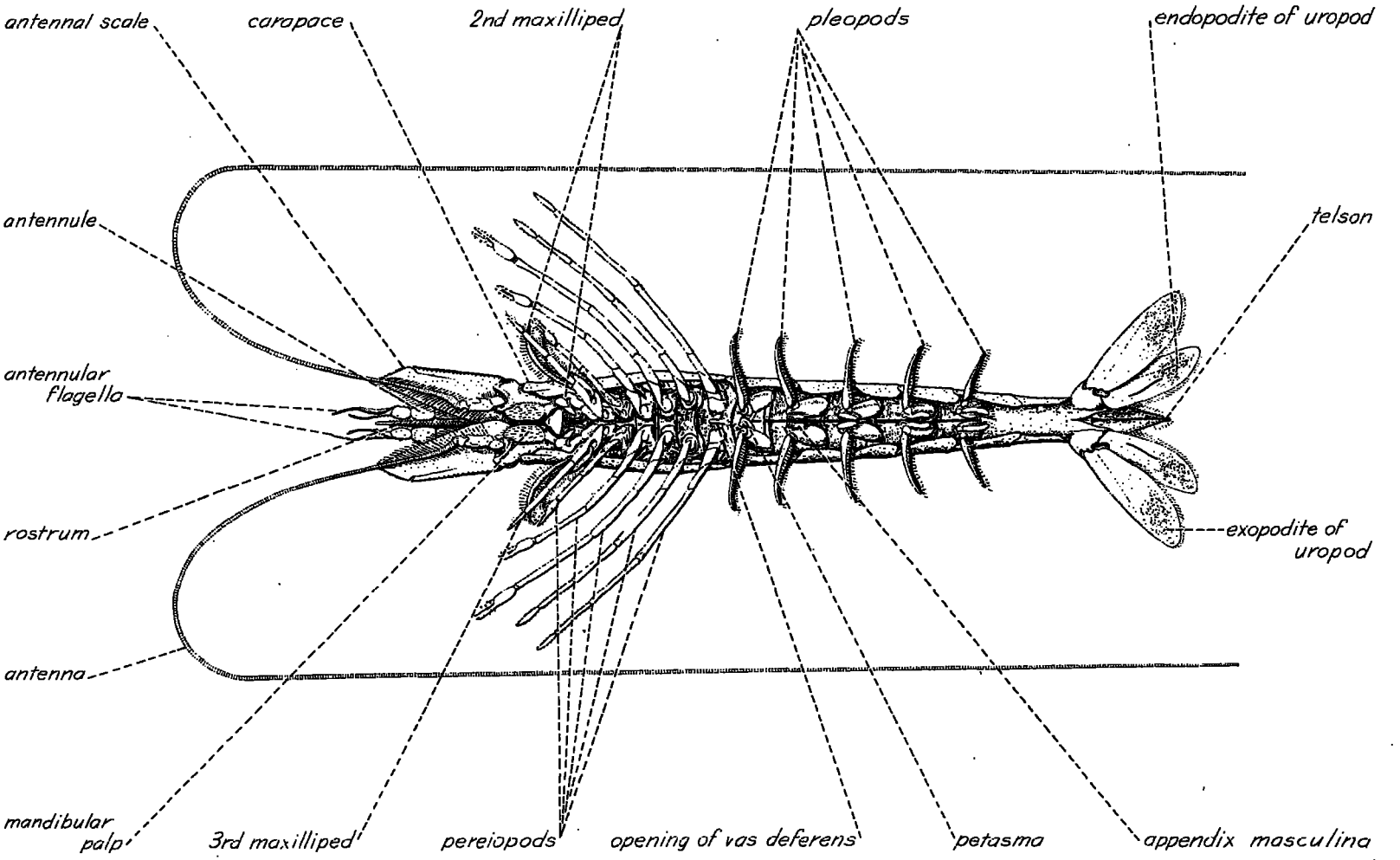

FIGURE 3.—Ventral view of young male.

The protocephalon is clearly distinct from the succeeding gnathothoracic and abdominal tagmata, and in *Penaeus setiferus*, and other species of the genus (Grobben 1917) is independently movable. Grobben, incidentally, described the area as the "sincipit," a term apparently discarded by Snodgrass in favor of the term, "protocephalon." In the section below on the eyestalks, a consideration of the muscles which move the protocephalon on the gnathothorax will be found. A discussion of the primitive order of the head segments follows in the section on the labrum.

SKELETAL ELEMENTS

The protocephalon is constructed roughly on the plan of a vertically placed hemisphere confluent posteriorly with the gnathothoracic hemocoele. The skeleton is flattened dorsally in the region of the ocular plate (fig. 4) or lobe from which the foramina of the eyestalks are perforated. The large, paired foramina of the antennules and antennae and the mesal foramen of the labrum occupy almost the entire anterior and ventral surface of the protocephalic skeleton. The latter regions are heavily sclerotized and deeply indented between the antennular and antennal foramina by the medial stem of the Y-shaped epistome (figs. 28, A; 30). The top, or posterior portion of the epistomal Y, divides across the anterior face of the labral foramen and the posterior side of the large antennal foramina. Upon the lateral epistomal bars, as shown by Snodgrass (1951), the medial mandibular condyles are located.

1. EYESTALKS

Most of the following section on the eyestalks was previously published by the writer (Young 1956).

In some of the lower and in many of the higher Crustacea, the compound eyes are set upon movable stalks or peduncles. Their presence at the ends of extensions has excited speculation for many years. Carcinologists have long discussed the reasons for the eyestalks, their similarity with other appendages (Calman 1909), and the nature of vision in a stalked-eyed animal, among other things. Yet little has been written about the mechanics of the eyestalk with respect to vision. No one has proposed any useful explanation for the fine adjustments presumably available to a compound eye which has as numerous oculomotor muscles as the crustacean stalked eye.

The presence of a set of muscles to move the corneal surface of the compound eye on the eyestalk, and of muscles to move the eyestalk about with respect to the body suggests the importance of the position of the corneal surface relative to the environment. By contrast, adjustments of corneal position in an arthropod without eyestalks suggests a function of head and "neck" muscles for activities other than feeding, if we assume any importance to the arthropod of corneal position adjustments.

Recently, the eyestalk nerves of a few crustaceans have been shown to contain neurosecretory elements which evidently proliferate hormone systems controlling such processes as molting (Passano 1953), retinal pigment migration (Welsh 1941), and chromatophore movements (Perkins 1928). In view of the concentrated attention currently being paid to matters of neurohormonal control of physiological functions in the arthropods, an understanding of the relation of vision to neurosecretion appears to be near at hand.

The white shrimp, *Penaeus setiferus*, carries its eyestalks at an angle of about 75° to the median sagittal plane and at an angle of about 10° to 15° to a frontal plane at the ocular plate (fig. 4). Only rarely are the eyes brought forward to lie in the optic depressions of the antennules, and then but for an instant for protection or possibly cleaning against the long plumules surrounding the depressions. Normally, therefore, in *P. setiferus* and many other species of shrimps, the eyes and stalks are widely spread and slightly upturned, a situation not understood by morphologists who, working with preserved materials, have described the eyestalks as projecting anteriorly. Had previous workers taken into account the lateral position of the eyestalk in the shrimps, and for that matter in the crawfishes, a certain amount of confusion in the naming of eyestalk musculature might have been avoided. For in fact, medial muscles are anterior and lateral muscles are posterior. In the interests of uniformity, however, certain of the incorrect names are here employed.

P. setiferus is a bottom feeder. According to an unpublished observation by Charles Dawson, Bears Bluff Laboratories, Wadmalaw Island, S. C., schools of penaeid shrimps are frequently found on muddy bottoms. This worker describes placing several *P. aztecus* Ives, 1891, in aquaria with an inch or two of mud on the bottom, into

which the animals immediately burrow, except for the eyes. Such behavior suggests that the long eyestalks are among the organs enabling the penaeid shrimp to make use of mud for protection, especially after molting.

In the past, observers have described square corneal facets in the eyes of several species of decapod crustaceans (Huxley 1906; Calman, 1909). A study of slides made of the corneal cuticle shows that the corneal facets in the compound eye of *Penaeus setiferus* are also square. Likewise, the underlying crystalline cone cells are square in the white shrimp and total four per ommatidium, as determined by the study of tangential sections of the eye from which the corneal cuticle had been removed. Ramadan (1952) reports a similar situation in a species of *Metapenaeus*. In longitudinal section the ommatidium of *P. setiferus* is like that of *Astacus*, as described by Bernhards (1916), with comparatively elongate crystalline cone and short rhabdom cells. If anything, the cone cell is longer in the white shrimp than in the crawfish. A light pink substance which gives the dark-adapted shrimp eye its bright color in strong light is the tapetum (Ramadan 1952). It is associated with the proximal or retinal pigment of the ommatidia.

SKELETAL ELEMENTS

The ommatidial surfaces arise from a sclerotized cup, previously named the optic calathus, or basket (Young 1956), to avoid confusion with the optic cup of the vertebrate embryo (fig. 4). The optic calathus rests upon the elongate stalk segment in a structural relation permitting universal movements, although the degree of movement varies in different planes.

Two points of articulation in the dorsoventral plane allow the optic calathus considerable horizontal movement around the distal end of its supporting stalk. These dorsoventral hinges are, however, sufficiently loose to permit vertical and rotational calathus movements, but to a lesser extent than horizontal movements. The long stalk is comprised externally of several longitudinal sclerotized bars which are separated by pliable cuticle. Two of the bars give support to the dorsoventral points of articulation (fig. 11) and others to less well-defined points of articulation between the stalk and calathus, and between the stalk and basal segment.

The stalk is movable upon the short, boxlike, basal segment in the horizontal plane. Vertical movements between the basal segment and the stalk are restricted. With respect to the structure here labelled the median tubercle (fig. 4), Anderson and Lindner (1943) and Voss (1955) state that shrimps of the subfamily Penaeinae have no distinct median tubercle on the ocular peduncle. However, many of the shrimps of this group do possess large, blunt, median tubercles, similar to those in *Penaeus setiferus*.

Set between the basal segments is the ocular plate or lobe, a broad, roughly rectangular sclerotized structure which encloses laterally the medial parts of the basal segments (fig. 4). The ocular plate is the dorsal-most region of the protocephalon. Movements between the basal segment and the ocular plate are similar in extent to those between the stalk and the basal segment. Horizontal movements are limited to an arc of about 15° or 20°.

MUSCLE ELEMENTS

PROTOCEPHALON MUSCLES OF THE OCULAR REGION

Taking origin from either the epistomal invagination or the dorsal surface of the carapace and inserting upon basal parts of the eyestalks are four pairs of muscles. The basal regions of the eyestalks will be assigned here to the dorsal part of the protocephalon.

ANTERIOR PROTOCEPHALON LEVATOR MUSCLES

FIGURES 34, 35

The tiny anterior protocephalon levator muscles are probably the muscles designated by Grobben (1917, 1919) as the protocephalon levators (musculus levator sincipitis) in a European penaeid and in other species of higher Crustacea. These muscles are difficult to make clear, either by dissection, or by illustration, since they take origin on the carapace, on the nearly vertical sides of the rostral base. During removal of the carapace and the underlying layers of tough, fibrous epidermis and connective tissue, these muscles are torn away. The anterior protocephalon levators insert in the heavy connective tissue associated with the posterior edge of the protocephalon. Their actual levation of the protocephalon is negligible, since they are not only minute in cross section, but

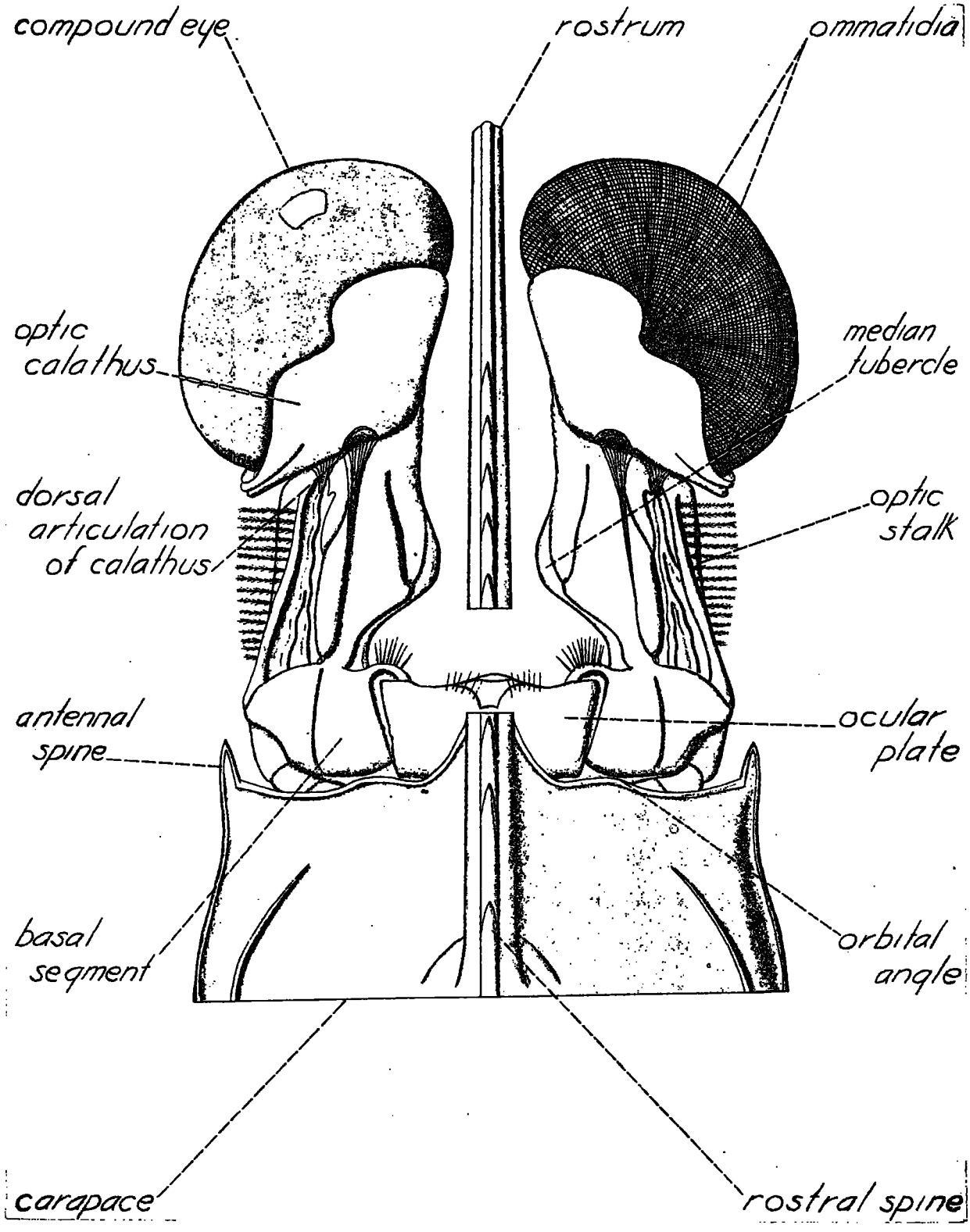

FIGURE 4.—Dorsal view of eyestalks in anterior position. Rostrum cut away to show ocular plate.

short in length. No counterpart of the anterior protocephalon levator muscles was described by Schmidt (1915) in *Astacus*, or by Berkeley (1928) in *Pandalus*. However, Grobben (1917) illustrates a protocephalon levator in *Astacus* and theoretically one would expect to find the muscle in *Pandalus*.

POSTERIOR PROTOCEPHALON LEVATOR MUSCLES

FIGURES 5, 6, 34

The function of moving the protocephalon dorsally is performed by a pair of large muscles, the posterior protocephalon levator muscles, which originate close together at the dorsal midline of the carapace somewhat posterior to the origin of the anterior protocephalon levator muscles and which run forward and downward to attach on a nearly vertical transverse plate, posterior to the postocular region of the eyestalk base (fig. 6). The muscle inserts ventrally to the insertion of the anterior levators. The contraction of the posterior protocephalon levators may also act to rotate posteriorly the eyestalk base and hence raise the extended eyestalks.

Possible homologs of the posterior protocephalon levator muscles are the median dorsal muscles designated as the musculus oculi basalis posterior. In *Astacus*, Schmidt (1915) found that these muscles arise on the median dorsal surface of the carapace and are attached by short tendons to the much longer tendons of other, more anteriorly placed muscles, the musculus oculi basalis anterior. The anterior eye base muscles, to anglisize freely, are attached to the median dorsal region of the eyestalk base (Schmidt 1915). More will be said of the latter muscles below.

The posterior eye base muscles, it should be emphasized, do not attach to the eyestalk base in *Astacus*, but if the assumption is made that, due to the immovable protocephalon in *Astacus*, the attachment of the muscles to the eyestalk base has moved in that animal to the tendons of the anterior eye base muscle, then a homology with the posterior levators in the white shrimp may be proposed. However, the extensive rearrangement of muscle attachments upon which the assumption is based weakens the proposal.

Even more significant, muscles exist in *Penaeus setiferus*, as will be shown later, which are more likely to be the homologs of the anterior and posterior eye base muscles in *Astacus*, *Pandalus*, and *Callinectes* than are the posterior protocephalon levator muscles. If the latter is true then the posterior protocephalon levators have been lost during the evolution of *Astacus*, *Pandalus*, and *Callinectes*, in which forms no trace of the muscles appears (Schmidt 1915; Berkeley 1928; Cochran 1935).

OCULAR PLATE DEPRESSOR MUSCLES

FIGURES 5, 6, 7

The ocular plate depressor muscles originate on the posterior surface of the epistomal invagination. They run anterodorsally, passing beneath the insertions of the posterior protocephalon levator muscles, and insert broadly on the posterior edge of the ocular plate (figs. 5, 6, 7). On contraction, the ocular plate depressors draw the ocular plate posteriorly and ventrad. Based on the attachment points of the muscles in *Penaeus setiferus*, they may have given rise by partial fusion to the anterior eye base muscles (musculus oculi basalis anterior) as they are found in the European crawfish, where the muscles are attached ventrally to the epistomal region by a long tendon and run dorsad to the edge of the eyestalk base. Cochran (1935) describes in *Callinectes* a pair of anterior eye base muscles which arise from a kind of epistomal invagination rather like that in the white shrimp, but instead of fusing as in the European crawfish, they diverge slightly laterad in the blue crab in probable accompaniment with the general broadening of the body in the Brachyura.

The ocular plate depressor muscles apparently are homologous with the musculus oculi basalis anterior in *Pandalus*, the name for which Berkeley (1928) has taken from Schmidt (1915). In *Pandalus*, these muscles are similar to those in *Penaeus*, except that they are slightly separated, whereas in *P. setiferus* they are close together.

PROTOCEPHALON ATTRACTOR MUSCLES

FIGURES 5, 6, 7, 8

The protocephalon attractor muscles are two very large muscles which take broad L-shaped origins on the carapace and run anteriorly to insert on two pairs of large apodemes and on other parts of the protocephalon. The largest apodeme, on which the ventral-most part of the protocephalon attractor muscles inserts, arises from the ventral surface of the antennular foramen, broadening posteriorly into a large vertical sheet

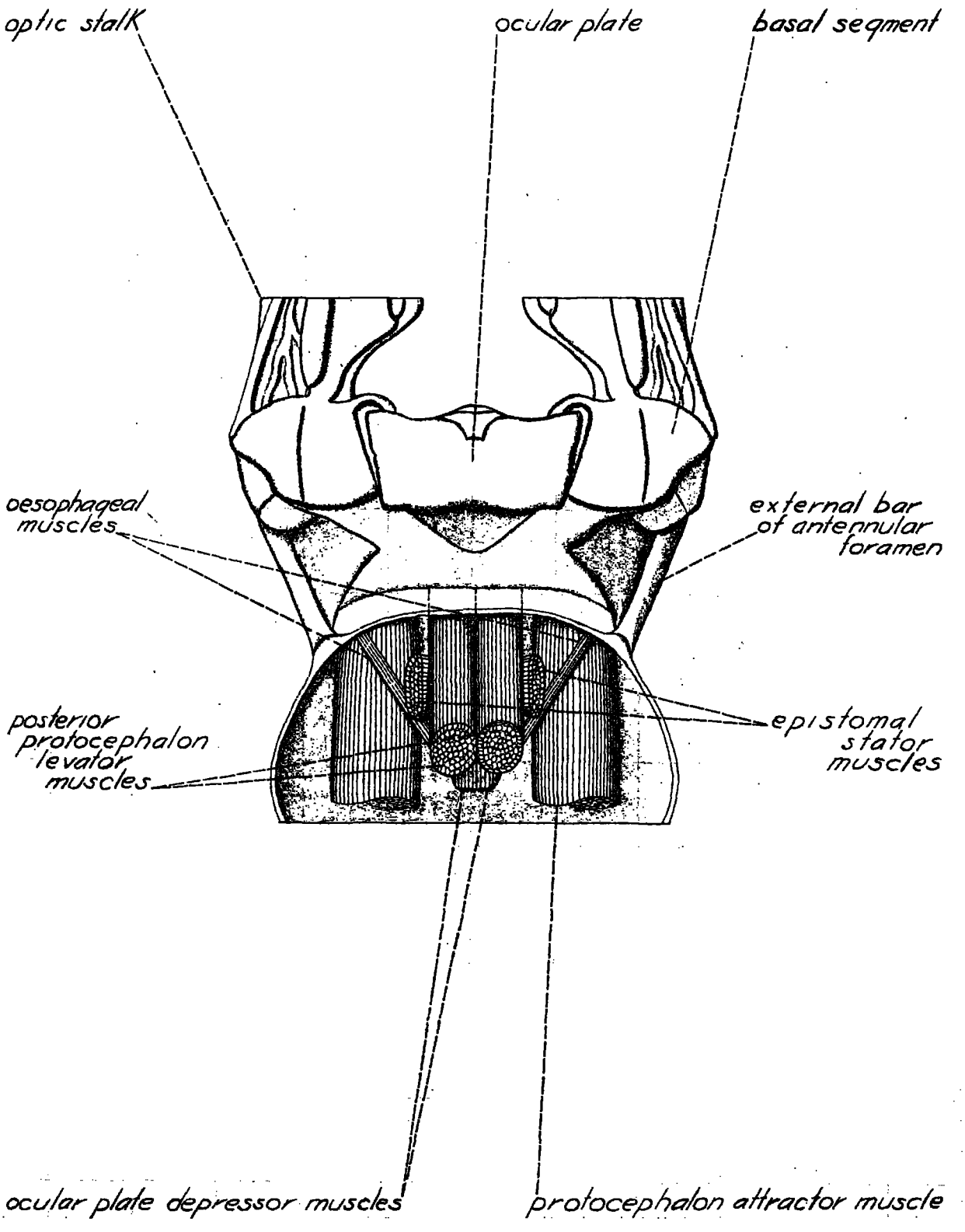

FIGURE 5.—Dorsal view of protocephalon, carapace removed, to show muscles of postocular region.

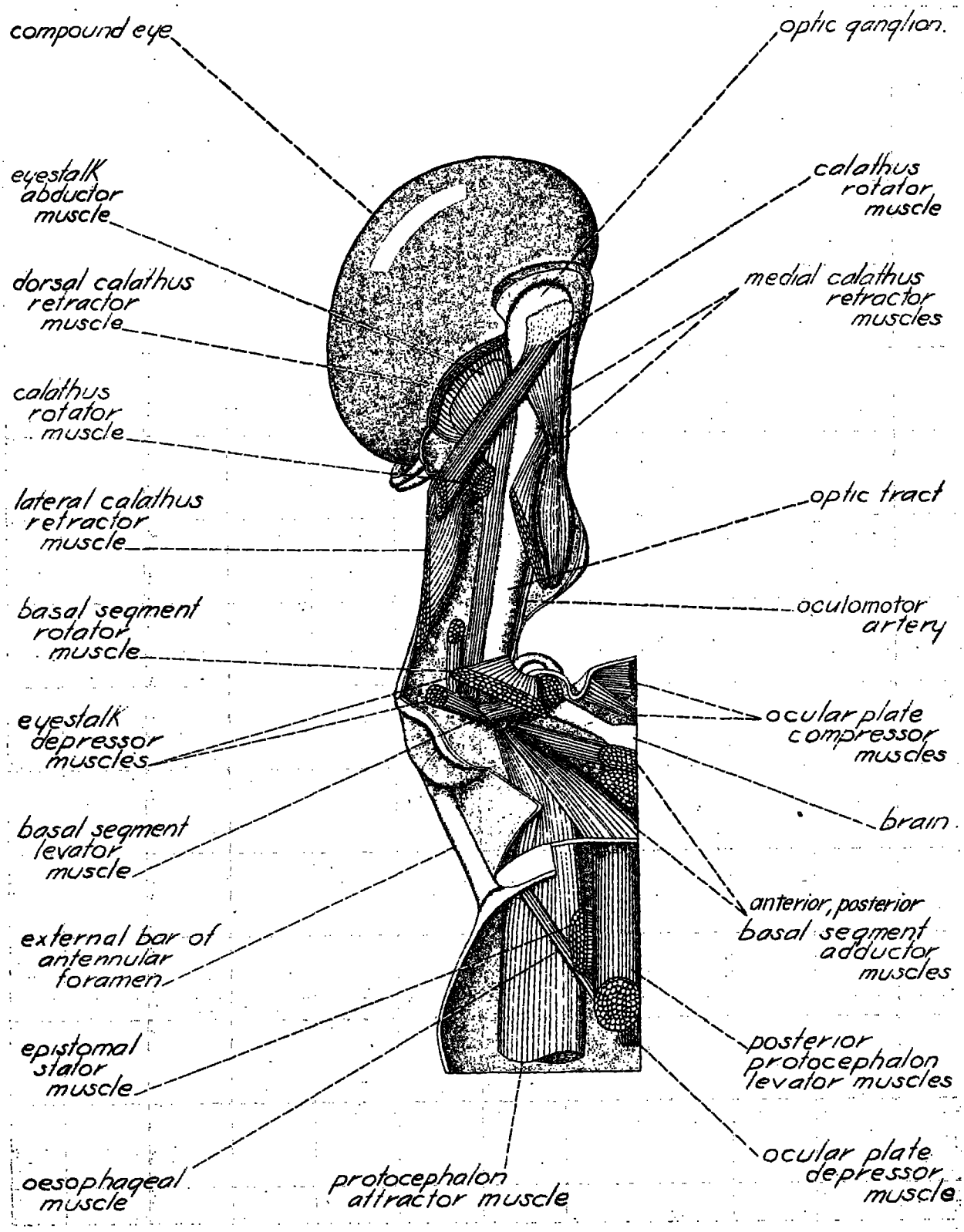

FIGURE 6.—Dorsal view of left eyestalk. Dorsal cuticle and carapace removed to show muscles.

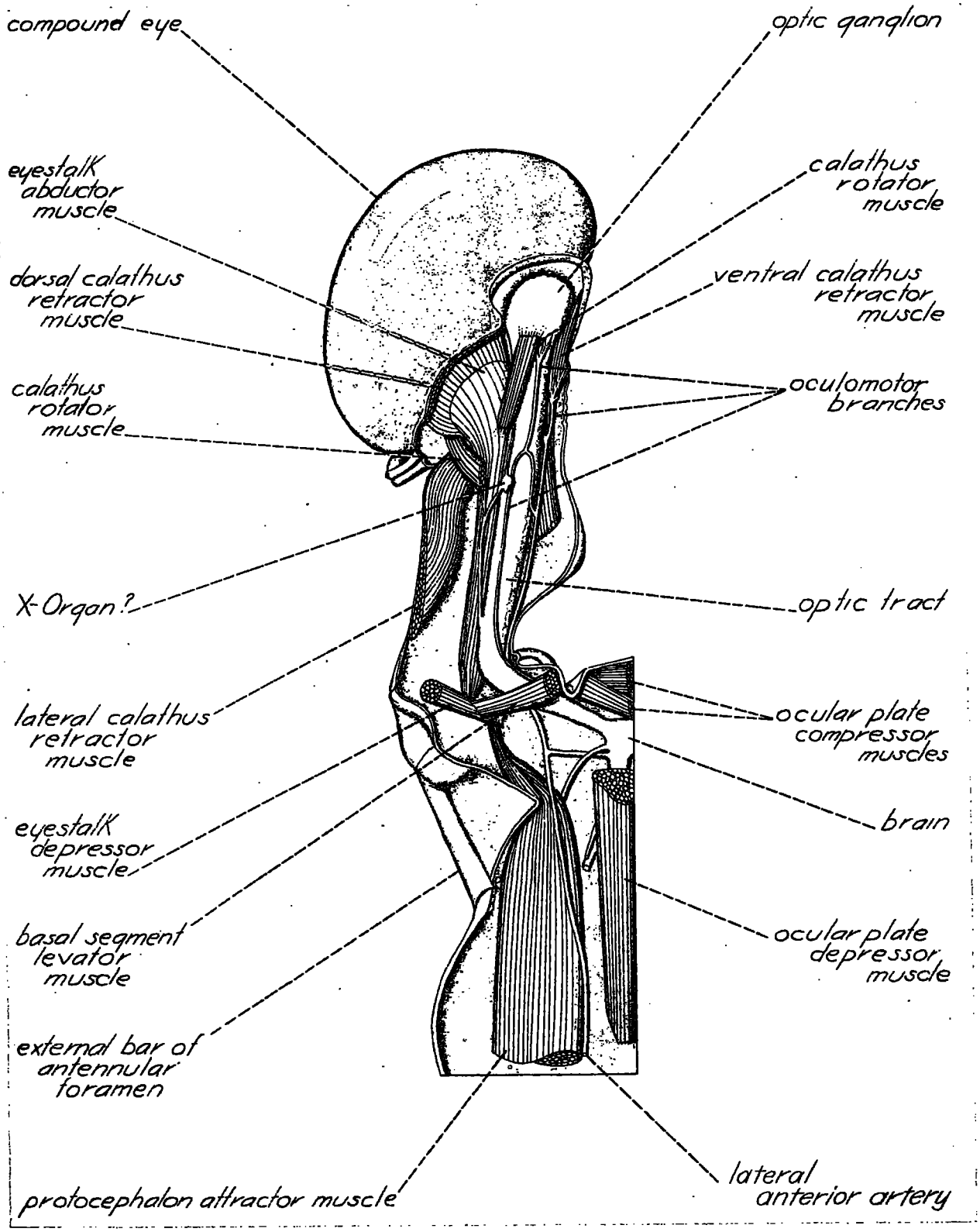

FIGURE 7.—Dorsal view of left eyestalk. Dorsal muscles removed to show branches of nerves and arteries.

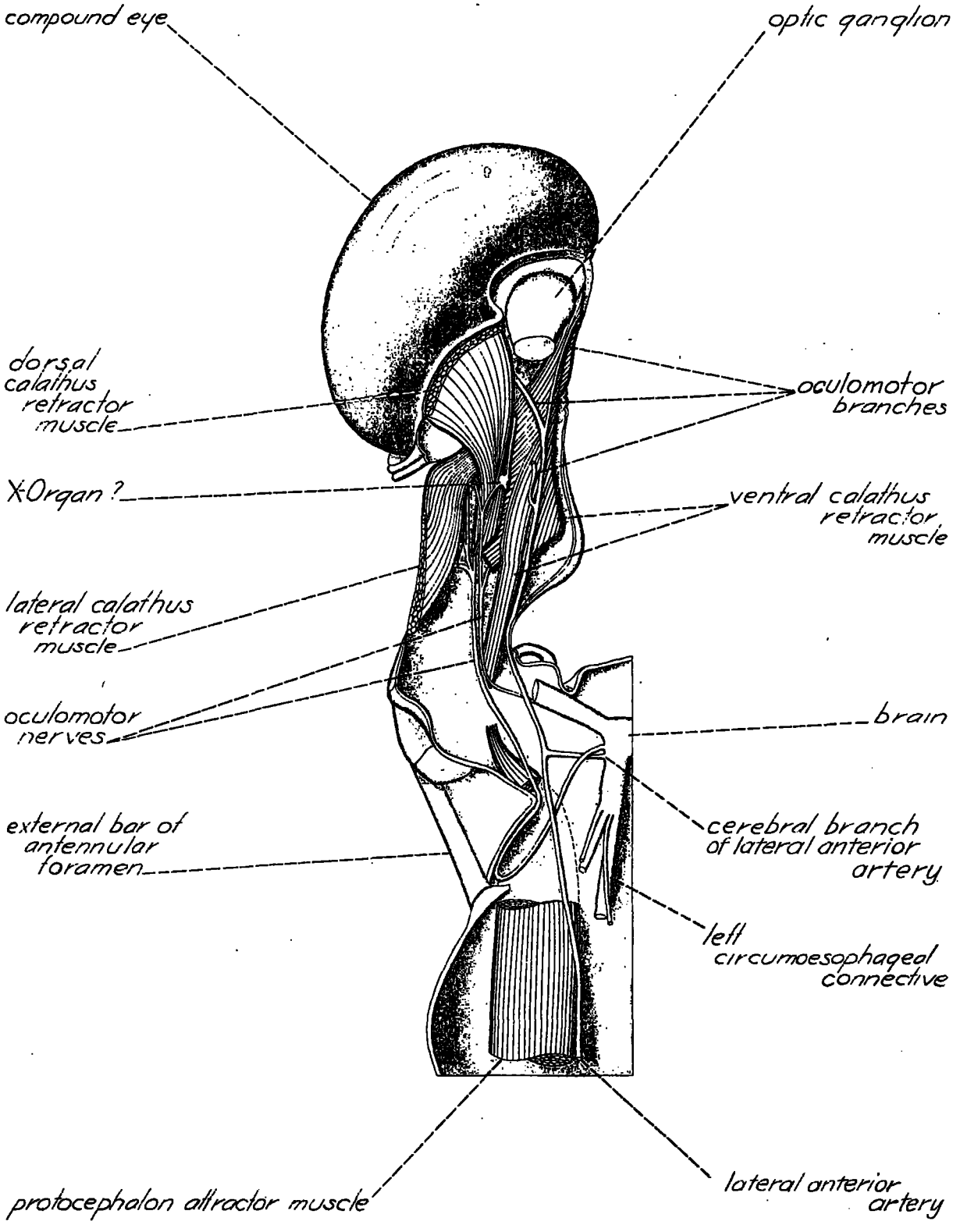

FIGURE 8.—Dorsal view of left eyestalk. Dorsal muscles and optic tract removed to show ventral muscles and branches of nerves and arteries.

of cuticular material. Slightly anterodorsal to the antennular apodeme, in the same parasagittal plane, is an apodeme which invaginates from the ventral floor of the basal segment of the eyestalk and projects through the ventrolateral side of the eyestalk foramen into the thoracic hemocoele. This apodeme, like that near the antennule, broadens vertically. By virtue of apodemal position, that part of the protocephalon attractor muscle attaching upon the eyestalk apodeme is somewhat longer than is the part inserting on the antennular apodeme.

The longest and most dorsal part of the protocephalon attractor muscle extends anteriorly beyond the antennular and eyestalk apodemes, to insert slightly laterad in connective tissue at the ventral surface of the basal segment of the eyestalk (figs. 7, 8).

To these comparatively huge protocephalon muscles we may ascribe at least two functions, namely, (1) attraction of the protocephalon, and (2) adduction of the eyes. The largest of the three inserting bodies of the muscle is the ventral-most part inserting on the antennular apodeme, described above. From a study of the points of articulation between the carapace and the protocephalon, dorsally, and the mandibular segment and the protocephalon, ventrally, the primary result of contraction of the ventral muscle body would be to draw the protocephalon directly posterior. The muscle was described as a protocephalon depressor (musculus depressor sincipitis) by Grobben (1917) in a number of Decapoda and in the stomatopod *Squilla*. This worker has shown that the protocephalon attractors, or depressors, are missing in those forms, like *Astacus*, in which the protocephalon is immovably fused to the thorax. The point of Grobben's discussion, that the protocephalon is movable on the gnathal tagma in the generalized crustacean, is not changed by a difference of opinion over the function of the muscle under consideration.

Furthermore, these muscles are not antennular in any way, having, as brought out by Snodgrass (1951), origins on the carapace. They are also, to say the least, not strictly antennal, since a portion of the muscle inserts in the eyestalk. Although the protocephalon attractor muscles in *Penaeus brasiliensis* Latreille, 1817, may be widely different from those in *P. setiferus*, the statement of Knowles (1953) that the two muscles lying just beneath the anterolateral side of the carapace are antennal is probably in error. From his figures the external-most muscle is properly a remotor of the antennal scale, while the large inner muscle is the protocephalon attractor muscle.

The two anterodorsal parts of the protocephalon attractor muscles which find insertions in the eyestalks have, in addition to attraction, the function of eyestalk adduction. Upon contraction of the whole muscle, these dorsal fibers in the eyestalk draw the ocular plate and attached eyestalk segments posteriorly toward the carapace. The posterior side of the basal segments makes contact with a condylic thickening on the anterior edge of the carapace, at a point known as the orbital angle (fig. 4), thereby swinging the eyestalks forward in a horizontal plane into the ocular depressions on the antennules. As suggested in introductory comments, the movement is a quick one, much faster than the return of the eyes to the spread position. In *Penaeus setiferus* other muscles exist which function to adduct the eyes, but their effect is negligible when compared to that of the much larger protocephalon attractor muscles.

The protocephalon attractor muscles appear in *Pandalus*, designated by Berkeley (1928) as the depressor muscles *c* of the antennae, on grounds of their attachment to the basipodites of those structures. At the same time this worker ascribes to the depressor muscles *c* the function of adduction and rotation, rather than the depression of the antennae. Berkeley's name for the muscles obviously was taken from the work of Schmidt (1915) on *Astacus*, in which form the antennal depressor muscles *c*, while small, nonetheless depress the antennae. Although proof must wait upon a study of the nerves in *Penaeus* and *Pandalus*, Berkeley has homologized the so-called depressor muscle *c* of *Pandalus* and *Astacus* on the basis of their dorsolateral origins on the carapace and their insertions on the mediodorsal edge of the antennal basipodite (in *Pandalus*) and coxopodite (in *Astacus*).

That the depressor muscles *c* in *Pandalus* and the protocephalon attractors in *Penaeus* are homologous seems fairly certain, despite the apparent change of insertion in the former. A review of cleared and stained exoskeletons of *Pandalus* might show multiple insertions of the muscle as in *Penaeus*. The homology of the protocephalon attractor muscles in *Peneaus* with the depressor muscles *c* in *Astacus* is less certain. In *Callinectes*, Cochran (1935) figures a pair of

ocular attractor muscles which originate on the carapace. Their phylogenetic relation to the protocephalon attractor muscles in *Penaeus* is unlikely.

OCULAR PLATE MUSCLES

Arising in the ocular plate or postocular region dorsal to the brain are several pairs of muscles and a muscle group. Some of these muscles insert inside and some outside of the ocular plate.

OCULAR PLATE COMPRESSOR MUSCLES

FIGURES 6, 7

Attached about the shallow anterodorsal groove of the ocular plate is a group of muscles which runs to the lateral wall of the ocular lobe (figs. 6, 7), the ocular plate compressor muscles. They function to draw the sides of the head lobe and ocular plate mesad, and to depress slightly the center of the ocular plate.

ANTERIOR BASAL SEGMENT ADDUCTOR MUSCLE

FIGURE 6

The anterior basal segment adductor muscle originates on the ocular plate dorsal to the brain and attaches to connective tissue and apodemal material in the ventral part of the basal segment (fig. 6). Contractions of the muscle turn the basal segment toward the ocular plate in a horizontal plane.

POSTERIOR BASAL SEGMENT ADDUCTOR MUSCLE

FIGURE 6

The posterior basal segment adductor muscle inserts in the basal segment at the same point as the anterior basal segment adductors, but originates on the anterior side of the vertical transverse plate posterior to the postocular region (fig. 6). It, too, draws the anterior edge of the basal segment toward the ocular plate. The origins of these muscles are so widely separated that we may conclude that they have never been the same muscle. How the basal segment adductors may be homologized with muscles in *Pandalus* and *Callinectes*, in which forms no knowledge of muscle innervations exists, will be speculation. The ocular adductor muscles of *Astacus* and *Pandalus* may well be the homologs of the anterior adductor muscles of *Penaeus*, but hardly with the ocular adductors of *Callinectes*, in which animal the muscles are located in the distal end of the long stalk segment. Phylogenetic relationships of the posterior basal segment adductor muscle are even more uncertain, although possibly it is the same muscle as the ocular attractor muscle in *Pandalus* and *Astacus*. The basal segment adductor muscles do not appear in *Callinectes*.

BASAL SEGMENT LEVATOR MUSCLE

FIGURE 6

The basal segment levator muscle originates at the anterodorsal corner of the ocular plate and runs ventrally to the connective tissue and apodemal cuticle on the ventral surface of the basal segment (fig. 6). In the normal spread condition of the eyestalk, contraction of the muscle tends to raise the basal segment and with it the extended eyestalk.

BASAL SEGMENT MUSCLES

In the functional descriptions of the muscles which follow, the eyestalks will be considered as in their lifelike, lateral positions.

BASAL SEGMENT ROTATOR MUSCLE

FIGURE 6

The basal segment rotator muscle is a short, broad structure originating on the anterodorsal edge of the basal segment and inserting on the anteroventral edge of the same segment. Upon contraction, the muscle pulls the dorsal surface of the basal segment anteriorly, thus rotating the entire eyestalk forward.

EYESTALK DEPRESSOR MUSCLES

FIGURE 6

Two very small muscles, the eyestalk depressor muscles, one slightly lateral to the other (fig. 6), function to draw the eyestalk ventrally.

EYESTALK MUSCLES

EYESTALK ABDUCTOR MUSCLE

FIGURE 6

All of the muscles of the eyestalk and optic calathus are associated with retraction and rotation of the optic calathus on the eyestalk, except the long eyestalk abductor muscle (fig. 6). The proximal end of the eyestalk abductor muscle is attached in connective tissue in the ventral region

of the basal segment. The muscle runs the length of the eyestalk to insert in connective tissue near the dorsal calathus retractor muscle. Contraction of the muscle swings the eyestalk horizontally to a lateral position. The eyestalk abductor muscle of *Penaeus* is very likely homologous with the abductor muscle described for *Astacus* and *Pandalus*, and possibly with the lateral branch of the ocular abductor muscle in *Callinectes*.

CALATHUS RETRACTOR MUSCLES

The muscles in *Penaeus* which retract the optic calathus appear to be clearly represented by the retractor muscles of the eyes of *Astacus*, *Cambarus bartoni* (Fabricius 1798), *Pandalus*, and *Callinectes*. Phylogenetically, the situation in *Penaeus* is somewhat more generalized than in the other forms which we are considering, in that several of the calathus retractor muscles in *Penaeus* have more than one part. In addition, *Penaeus* has a number of apparently independent rotator muscles, none of them previously described, which function to twist the optic calathus about a longitudinal axis through the eyestalk.

DORSAL CALATHUS RETRACTOR MUSCLE

FIGURES 6, 7, 8

The dorsal calathus retractor muscle arises in connective tissue near the ventral surface of the eyestalk and attaches to the dorsal edge of the calathus.

LATERAL CALATHUS RETRACTOR MUSCLE

FIGURES 6, 7, 8, 9

The lateral calathus retractor muscle, really the posterior retractor, originates on sclerotized material along the lateral, or actually posterior, blood sinus running the length of the eyestalk. The larger portion of this muscle attaches on the lateral edge of the calathus, the lesser part turning ventrally and running across the ventral edge of the calathus, just dorsal to the ventral retractor muscles (fig. 9). When this muscle contracts it not only retracts the calathus, but rotates the calathus about an axis longitudinal to the eyestalk.

VENTRAL CALATHUS RETRACTOR MUSCLE

FIGURE 9

The ventral calathus retractor muscle originates on several sclerotized regions on the ventral surface of the eyestalk. One part of the muscle is long and slender, while the others are short and arise from broad origins (fig. 9). The muscle is inserted over a wide area on the ventral edge of the calathus.

MEDIAL CALATHUS RETRACTOR MUSCLE

FIGURE 6

The medial calathus retractor muscle originates on two points in the region of the median tubercle, and actually is comprised of two muscles (fig. 6). The larger muscle originates in the median tubercle and inserts in connective tissue dorsal to the distal optical ganglionic mass. The smaller muscle originates dorsal to the larger muscle and inserts on a ventromedial point on the calathus. The contraction of both muscles results in medial retraction of the calathus; functioning in opposition, the muscles retract the calathus in a vertical plane, reinforcing the action of the dorsal and ventral retractor muscles.

CALATHUS ROTATOR MUSCLES

FIGURES 6, 7

At least three calathus rotator muscles may be seen in the eyestalk of *Penaeus setiferus*. Rotator muscles of this type have not been described for *Pandalus*, *Astacus*, *Cambarus*, or *Callinectes*. The calathus rotators bear a certain similarity to one another, in that they are all superficial in position and insert in the heavy connective tissue underlying the thick cuticle of the calathus.

2. ANTENNULES

The antennules, or first antennae, are said to belong to the second segment of the body of Crustacea, following the eyes. In the company of the eyes, the antennae, and the labrum, the antennules are attached to the body tagma that has been termed by Snodgrass (1951a; 1952) the protocephalon. Whereas the appendicular nature of the eyestalk generally has been questioned, the status of the antennules as true crustacean appendages has rarely been attacked, despite controversy over the homologies of the component segments.

The antennule of *Penaeus setiferus* is comprised of a proximal stem divided into three basal segments, called the protopodite by Huxley (1906), and two distal flagella. Proponents of theories such as Huxley's (1906) suggesting correspondence of parts between the segments of the anten-

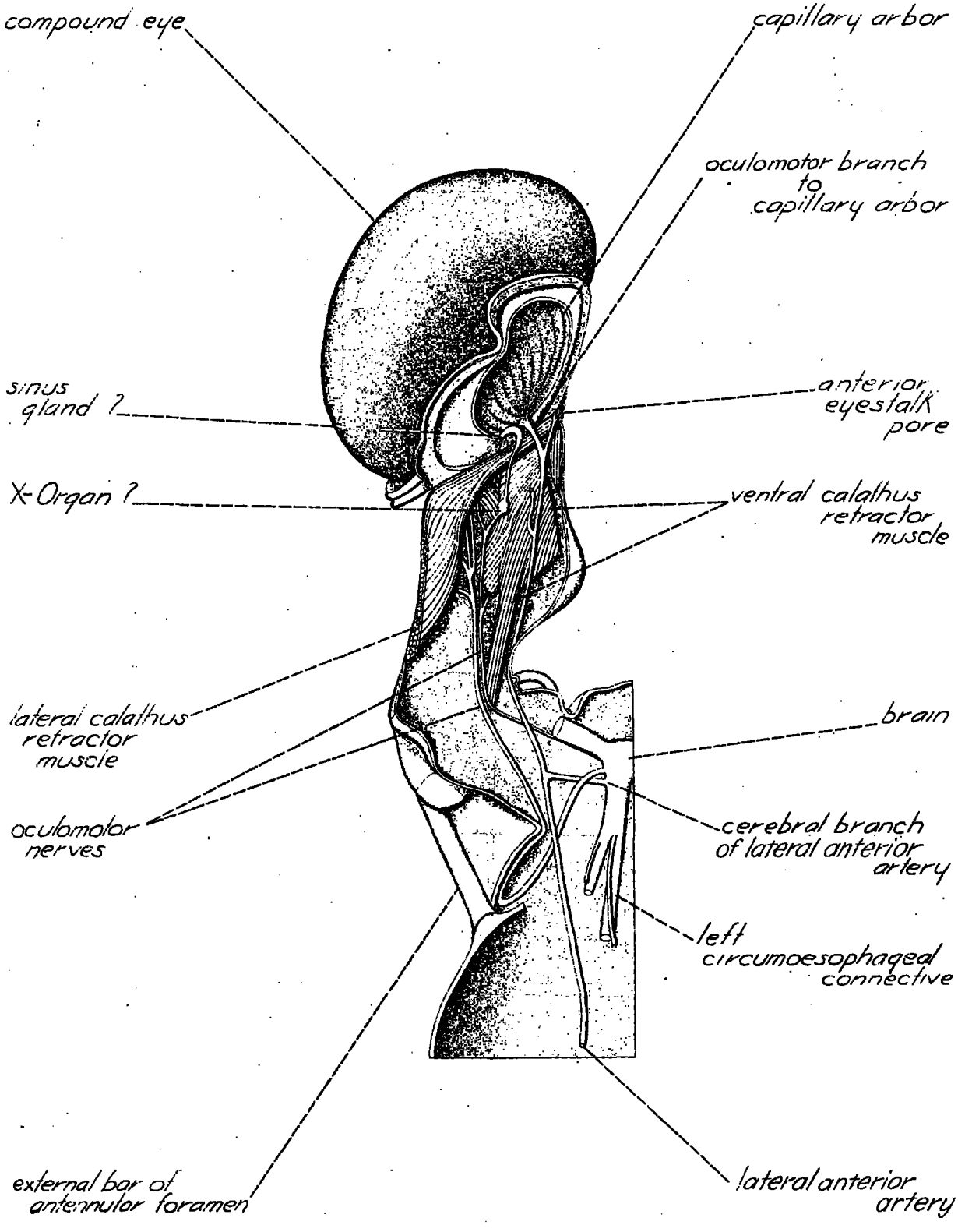

FIGURE 9.—Dorsal view of left eyestalk. Dorsal muscles and optic tract removed to show brain, branches of nerves, arterial capillary supply to distal optic ganglia, neurosecretory glands, and location of anterior eyestalk pore.

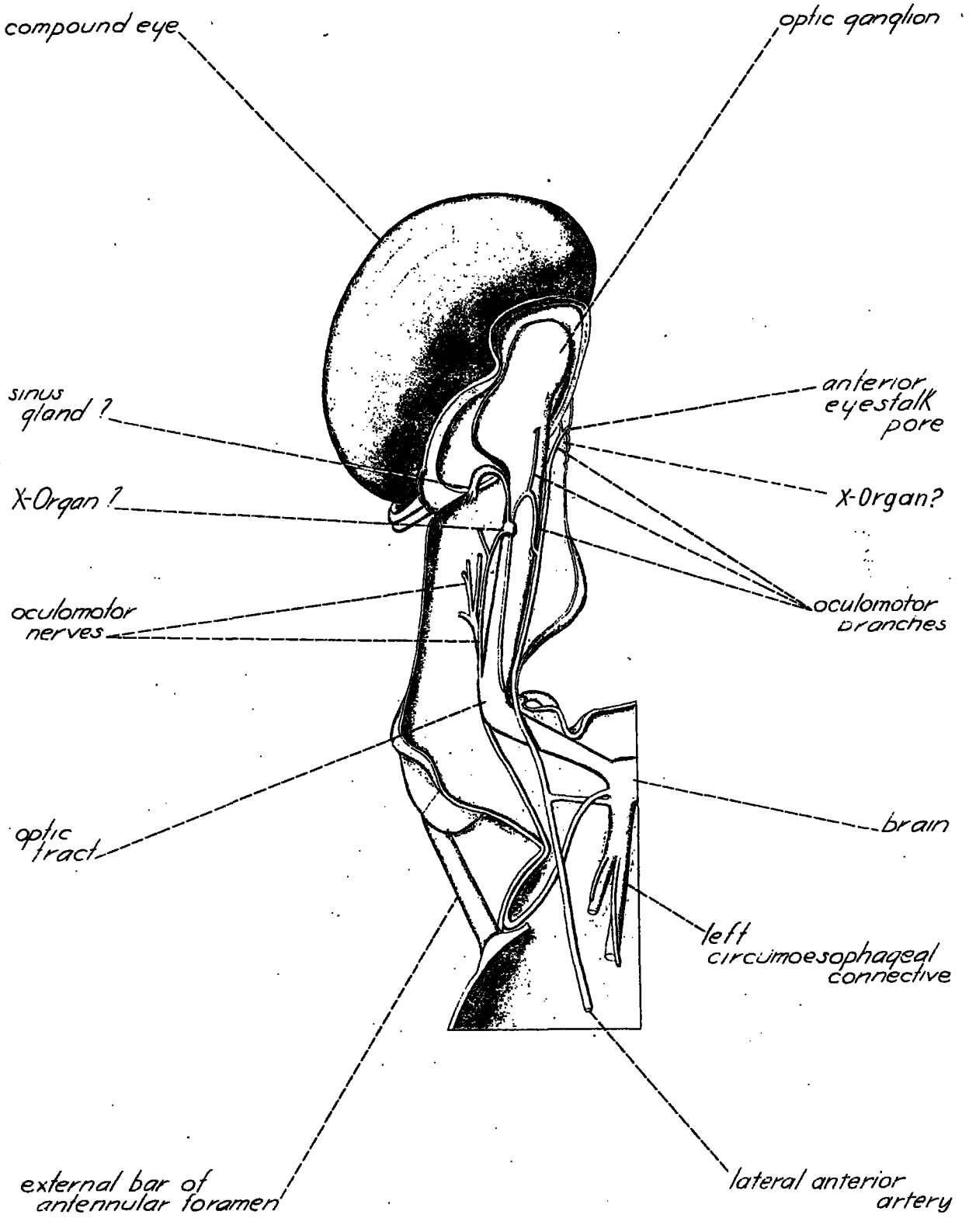

FIGURE 10.—Dorsal view of left eyestalk. Muscles removed to show optic tract, oculomotor nerves, neurosecretory glands, and branches of lateral anterior artery.

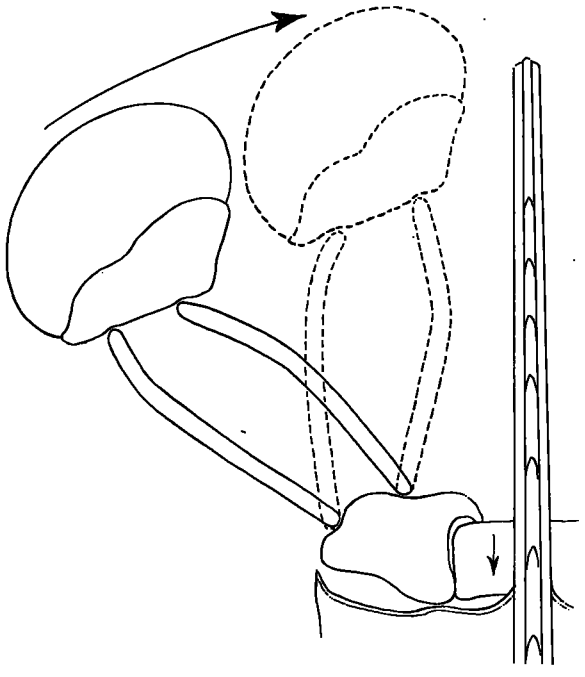

FIGURE 11.—Dorsal view of left eyestalk. Diagrammatic. The skeletal bars of the eyestalk are so arranged that the position of the ommatidial surface is maintained whatever the angle of the eyestalk with respect to the long axis of the shrimp.

nule and those of the typical crustacean appendage have not received support. Most carcinologists consider the parts of the antennule so extensively modified from the usual plan as to defy identification. At the same time, the clearly segmented structure of the antennule marks it as a true appendage, in the opinion of many workers.

The form and function of the crustacean antennule usually is said to be constant among the Decapoda, relative to the extraordinary variability in the appendage occurring in the lower Crustacea. Nonetheless, among the decapods wide differences are found. The outer or lateral flagellum is split in many of the Caridea, giving the impression that the antennule bears three flagella. Among the tribe Penaeidae, the outer flagellum is prehensile in certain genera of the Family Sergestidae. In the Solenocera each flagellum is semitubular, thus forming a siphon (Calman 1909). The antennule is small and reduced in the Brachyura.

Despite infrequent anatomical treatment of the decapod antennule, the available work suggests that a marked uniformity exists in the appendage and its parts over a broad spectrum of the Decapoda. From the standpoint of comparative morphology this feature of similarity would appear to simplify the process of homologizing part to part, and does, except for the matter of muscle names, a problem discussed earlier.

SKELETAL ELEMENTS

In dorsal view the antennule is shaped in a long wedge pointing anteriorly, the broadest portion being the proximal part of the first segment at the region of attachment of the antennule with the skeleton of the body. Each successive distal segment gradually becomes narrower. The mesial edge of the basal segments is straight and flat where the appendage rests against the other antennule. The first, or proximal, antennular segment (fig. 12) is relatively larger and more complex than the segments distal to it. The first segment is attached by a large articular foramen to the protocephalon, the tagma to which the antennules belong. Here, dorsal and ventral points of articulation, or condyles, afford the first antennular segment limited horizontal movement.

Centered in the posterior region of the first antennular segment is the statocyst, the organ that is thought to mediate the special sense of equilibration (figs. 12 to 16). Earlier workers termed the structure an otocyst, having ascribed to it an auditory function (Huxley 1906). The statocyst is constructed like an incomplete sac that has dorsal and anterior openings. Hairs, presumably sensory, project from the inner surface of the cuticular sac into the lumen of the statocyst. The hairs are arranged in regular rows. The rows of hairs are confined to oddly shaped patterns located at various places on the inner surface of the statocyst. Nerves from the sensory hairs coalesce ventrad of the sac into a broad, flat nerve tract that enters the brain at a point ventral to the optic tract (fig. 14).

The dorsal opening of the statocyst is partially covered by a fleshy, heavily setose lobe, the dorsal closing lobe (figs. 12, 15). In fresh material the dorsal closing lobe may be lifted from the dorsal opening of the statocyst without great difficulty. The saccular statocyst is shut anteriorly by a thin, curled sheet of cuticle that arises vertically by evagination from the ventrolateral floor of the antennular eye depression. The sheet is designated here as the anterior closing plate (figs. 12 to 15). Neither the dorsal closing lobe nor the anterior closing plate effect complete obturation of the statocyst. As a result, water circulates through

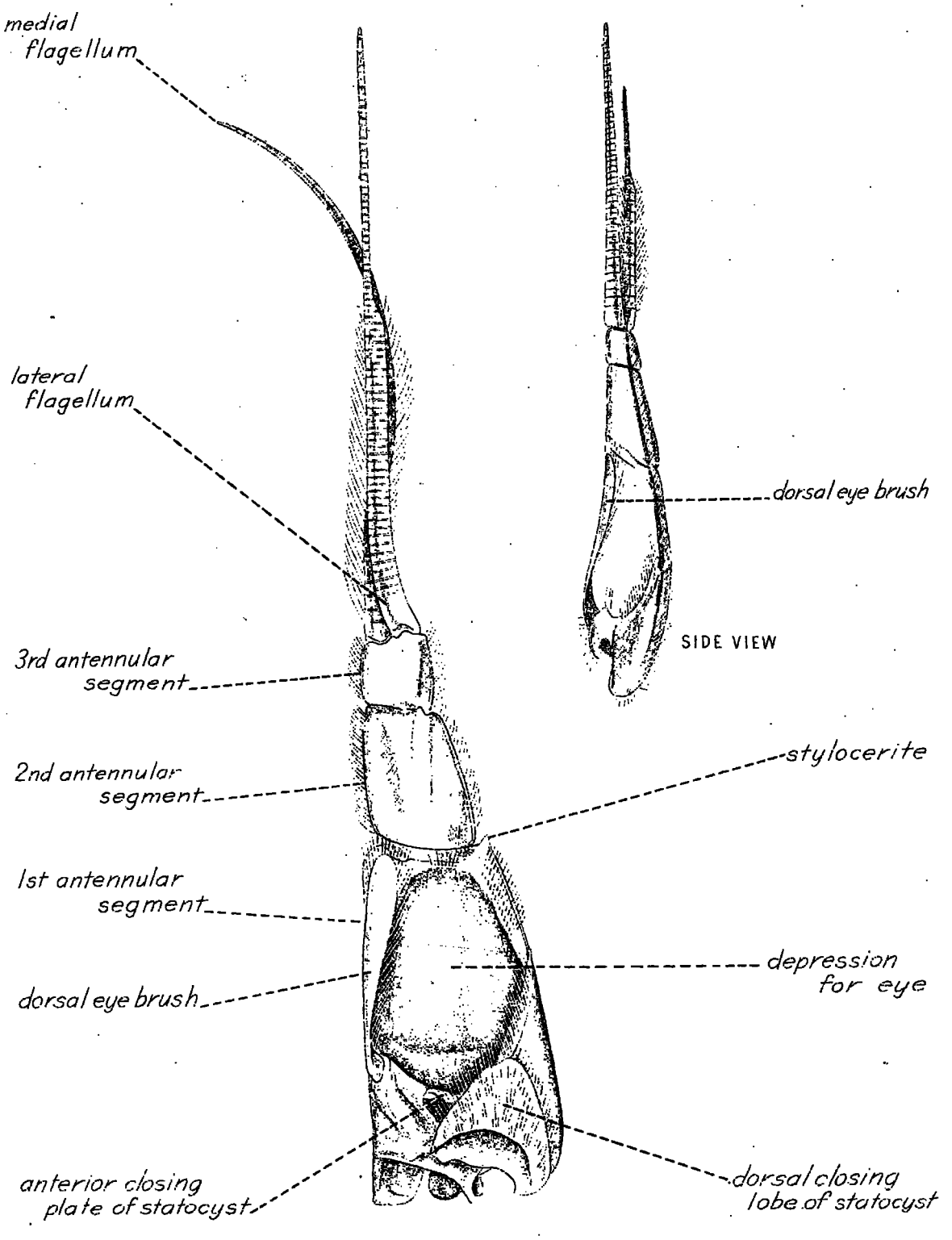

FIGURE 12.—The larger figure is a dorsal view of the right antennule, the smaller a lateral view of the right antennule.

the statocyst at all times, to the extent that the heavy investment of hairs in the area permits.

In living shrimps, as has been shown by Burkenroad (1939), the open statocyst contains sand grains. The sand probably functions as statoliths, if the statocyst is indeed equilibratory. These statoliths are obtained by the shrimp from the substrate through activities of the animal that are either directed or incidental to their collection. Cursory examination of the statocyst does not reveal bodies that have obviously been secreted by the shrimp. Burkenroad (1939), however, finds that the statocyst of penaeids contains statoliths secreted by the animals. Since the statocyst is open to the water and to the substrate into which the shrimp is known to burrow, the possibility exists that the statocyst contents may undergo continual replacement during intermolt periods. However, since the shrimp loses the statocyst with its contents at each ecdysis, the statoliths are probably replaced in large measure at the time. That the animals burrow into the substrate for protection, statolith replenishment, and rest following the molt is supported by negative information provided by observing shrimps in clean aquaria at ecdysis. Upon shedding in this unnatural environment, the shrimp is unable to navigate properly and soon perishes, even if kept alone. The statocysts are found to be empty of statoliths.

The largest region of the first antennular segment is the eye depression. Beginning at the anterior closing plate and extending to the margins of the first antennular segment distally and to the sides is a broad, deep concavity into which the corneal surface of the compound eye may rest (figs. 12, 13). The eye depression is confined proximally by the anterior closing plate of the statocyst and the skeletal structures that surround the statocyst. The dorsal closing lobe projects out slightly, dorsal to the depression. A large, wedge-shaped, fleshy lobe arising in the posterolateral region of the first segment extends anteriorly along the lateral margin to a point. At the anterolateral corner of the first antennular segment is a small, sharp stylocerite (fig. 12), a structure common to the Tribe Penaeidae (Voss 1955). Along the mesial margin of the first segment lies the dorsal eye brush, or prosartema (figs. 12, 13), a long, thin lobe arising dorsally from the proximal region of the segment and extending anteriorly to the anteromesial corner of the segment.

Most of the structures lining the eye depression are heavily setose, to a degree that would make their outlines obscure if illustrated faithfully. For this reason only a fraction of the true covering in hair of the dorsal side of the antennule has been shown. The presence of this extensive investment of hair probably can be explained as a system of brushes to clean the corneal surfaces of the compound eyes. Many stalk-eyed crustaceans carry the eyes laterally and never for any length of time in the eye depressions of the antennules. However, the eyes are brought frequently into and out of the depressions, and thus through the long hairs lining the depression.

The second antennular segment (fig. 12), a far simpler structure than the first segment, is attached to the latter distally. The second segment articulates with the first segment allowing limited horizontal movements of the antennular segments distal to the first segment. The second segment is a rectangular box in shape and modified for the actions of the muscles which it contains.

The third antennular segment (fig. 12) is a small, square structure articulated with the second segment. Movement of the third segment and the flagella on the second segment is limited to an attenuated horizontal arc. No special sense organ appears in the third antennular segment.

Two flagella, the medial flagellum and the lateral flagellum (fig. 12), articulate independently with the third antennular segment. The points of articulation between the flagella and the third segment are so arranged that the flagella may move through a broad arc in the frontal plane. Each articulates with the third segment in slightly different horizontal planes. The lateral flagellum is attached dorsad of the medial flagellum. The flagella are composed of many short articles of light construction connected by rings of thin cuticle, thus permitting bending in all planes. The length of the articles differs in the two flagella, those of the lateral flagellum being shorter than the articles of the medial flagellum. Other differences between the flagella include variation in cross-sectional shape and in the types of setae and processes projecting from the articles.

Numerous studies have been made on the function of the antennular flagella and the variety of hairs and processes that they bear. These investi-

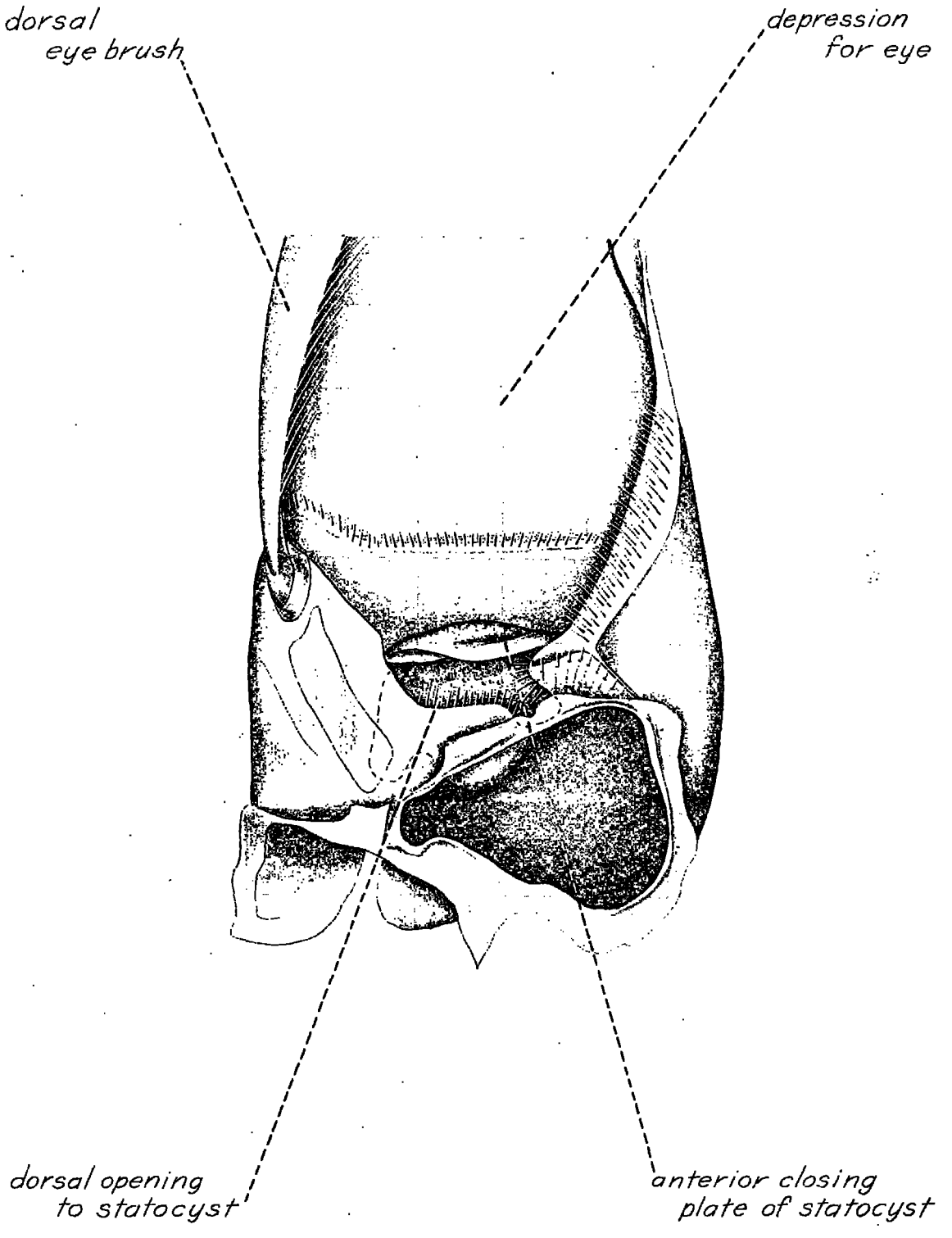

FIGURE 13.—Dorsal view of proximal region of first antennular segment, right antennule. Cleared specimen showing entrance to statocyst. Dorsal closing lobe removed.

gations show that the flagella are involved in chemoreception (Doflein 1911; Balss 1913; Bell 1906; Lissman and Wolsky 1935; Spiegel 1927). The olfactory nature of the antennular flagella is related to an interesting structural modification. This modification is the apparent sexual dimorphism of the medial flagellum in the adult male of *Penaeus setiferus* (fig. 17). The change to the medial flagellum, which is easily visible to the naked eye, results in a pronounced dorsoventral flattening, together with the appearance of numerous, stout processes of two sizes on the dorsal margin. That these processes may be predominantly proteinaceous is suggested by their loss following treatment of the preserved material in strong alkali, for as is well known strong alkali degrades the glucosamine of chitin but does not immediately remove it, whereas the alkali-soluble proteins of the internal organs and cuticle are rendered soluble and washed out (Richards 1951).

Other changes to the condition of adult maleness probably occur during the same molt that modifies the medial flagellum. The most obvious secondary sexual character is the mesial joining of the previously free wings of the modified pleopod endopodities of the first abdominal segment to form the definitive and functional petasma, or sperm-transfer organ.

Since the antennular flagella are olfactory, the sexually dimorphic medial flagellum of the male *Penaeus setiferus* probably functions to enable the male to find the sexually mature female during the time of mating. The occurrence of secondary sexual modifications of the antennular flagella are widespread among the Crustacea Decapoda. Meredith (1954) describes a modified outer antennular flagellum in the adult male of *Crangon vulgaris* and suggests that the structure may function in mating. This worker finds that the character is of use in identifying adult males in the field. The most extensive treatment of the subject of sexual dimorphism in Crustacea is that of Rioja (1939a, 1939b, 1940a, 1940b, 1940c, 1941a, 1941b, 1942a, 1942b), who has described in detail the sexually modified medial flagellum of *Penaeus setiferus* and several other species of penaeid shrimps. This worker considers the character to be constant in occurrence and sensory in function, and closely related to the sexual activities of the shrimps.

In the opinion of the present writer, the modified medial antennular flagellum is a constant character in the sexually mature male of *Penaeus setiferus*. However, the subject needs further study. A large, statistically significant number of male and female *Penaeus setiferus* shown to be sexually mature by the histological methods of King (1948) should be examined to prove the point. In the present study 10 adult males and 8 adult females were considered in connection with the character.

MUSCLE ELEMENTS

The antennule of *Penaeus setiferus* contains 13 muscles, as contrasted with 12 for the caridean *Pandalus*, and 9 for the antennule of *Astacus*. Cochran (1935) lists 9 for *Callinectes*, including a double antennular promotor muscle and a double antennular remotor muscle. If these divided muscle bodies are actually 2 promotor and 2 remotor muscles, then the antennule of *Callinectes* can be said to have 11 muscles.

ANTENNULAR ABDUCTOR MUSCLE

FIGURE 14

The antennular abductor muscle of the first antennular segment is attached posteriorly to an apodeme that arises from the ventrolateral margin of the articular foramen by which the antennule is connected to the protocephalon. The plane of orientation of this apodeme is vertical. The antennular abductor runs anteriorly a brief distance and divides into two large branches that attach to sclerotized bars supporting the posterior region of the first antennular segment in the neighborhood of the statocyst. Contraction of the first segment abductor muscle swings the first antennular segment, and with it the distal antennular segments, outward from the mid-sagittal plane of the body in the limited horizontal motion possible to the first segment. The antennular abductor of *Penaeus* is homologous with the musculus promotor I antennae of *Astacus*, *Pandalus*, and possibly to the first segment promotor muscles of *Callinectes*, judging from the origins, insertions, and arrangements of the muscles.

However, the functions of the homologous muscles are different, as often happens. The difference lies primarily in the restriction of antennular movement created by the presence of the antennal scales ventral to the antennules in *Penaeus*. In the white shrimp, the scales are relatively large and, when lying in their usual longitudinal posi-

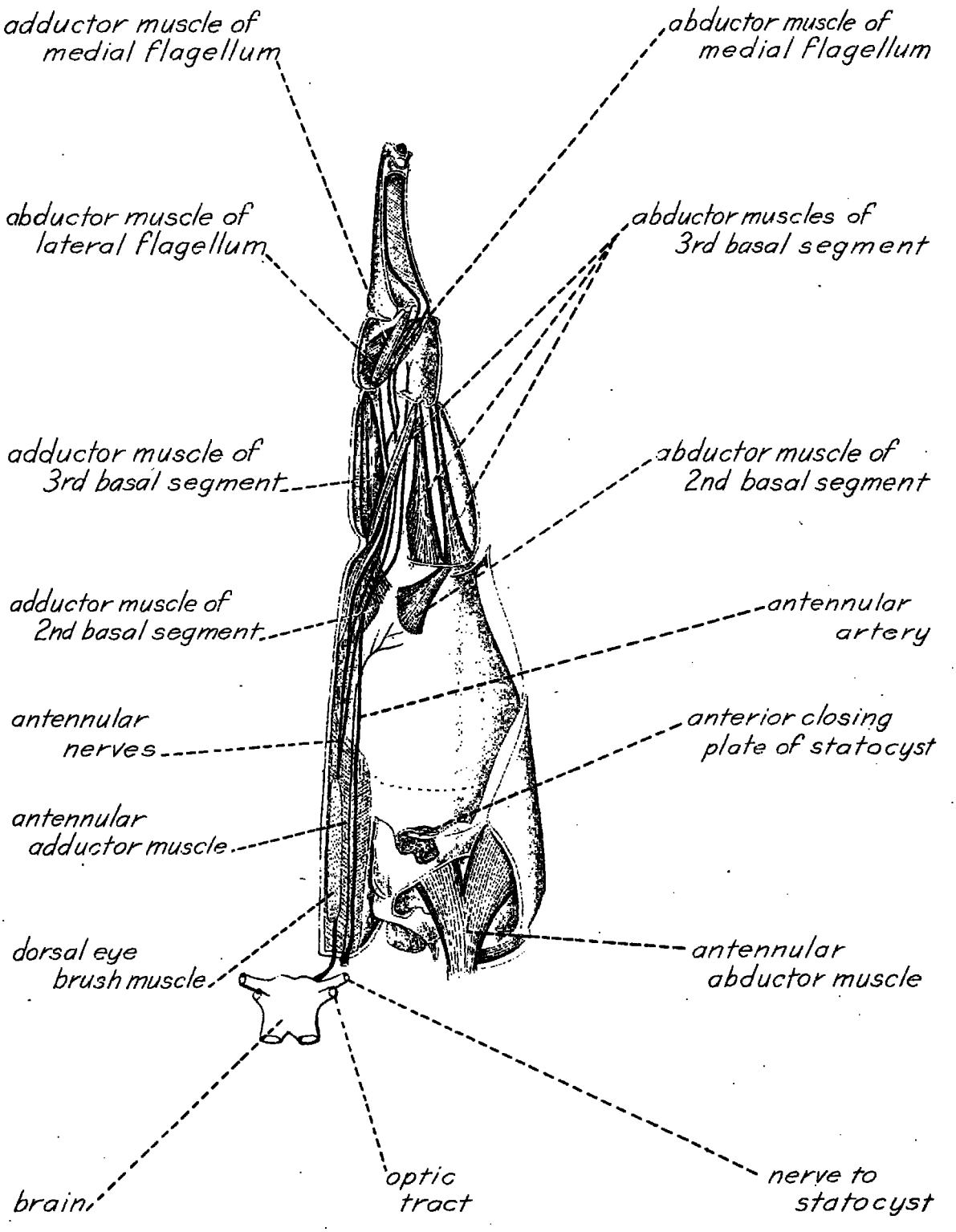

FIGURE 14.—Dorsal view of right antennule showing dorsal muscles. Dorsal cuticle removed.

tion, their mesial margins overlap beneath the antennules. Movements of the antennules ventrad are thereby prevented. In *Pandalus* and *Astacus* the first antennular segments may be raised and lowered about a transverse axis through the articular foramina of the antennules, in the sagittal plane. That Schmidt (1915) in his study of *Astacus* named the muscle a "promotor" is open to question. The muscle might better be described as a levator of the first antennular segment. Berkeley (1928) and Cochran (1935) adopted the terminology of Schmidt for this muscle in *Pandalus* and *Callinectes*, although, in *Callinectes* the musculus promotor I antennae apparently moves the antennule toward the midline of the animal.

ANTENNULAR ADDUCTOR MUSCLE

FIGURE 14

The antennular adductor muscle of the first antennular segment originates on a vertically-oriented apodeme arising from the ventromesial region of the articular foramen between the antennule and the protocephalon. The muscle courses anteriorly along the mesial margin of the first antennular segment, inserting in the cuticle at many points along the mesial edge of the first segment (fig. 14). The antennular adductor muscle functions to turn the first antennular segment toward the mid-sagittal line of the shrimp.

The musculus remotor I antennae described by Berkeley (1928) in *Pandalus*, by Schmidt (1915) in *Astacus*, and by Cochran (1935) in *Callinectes* are in all probability the homolog of the first segment adductor muscle in *Penaeus*. In the case of the former three animals, two musculi remotor I antennae have been found in the antennule of each, a remarkable uniformity in animals as distantly related as these. *Penaeus*, too, has these muscles, but the dorsal-most, discussed in the following section, appears to have a function different from that of remotion or adduction.

DORSAL EYE BRUSH MUSCLE

FIGURE 14

The dorsal eye brush muscle, or prosartema muscle, lies upon the adductor muscle of the first antennular segment, and is almost certainly the homolog of the musculus remotor *b* I antennae found in the antennules of *Pandalus*, *Astacus*, and possibly of *Callinectes*. However, instead of taking part in the adduction of the first antennular segment, the eye brush muscle in *Penaeus* serves to stiffen the dorsal eye brush (figs. 12, 13). Fibers of the muscle enter the eye brush at its point of attachment to the first antennular segment, and their contractions presumably enhance the function of the brush as an eye cleaner.

ABDUCTOR MUSCLE OF SECOND BASAL SEGMENT

FIGURE 14

The second antennular segment is turned away from the midline on its points of articulation with the first antennular segment by contractions of the abductor muscle of the second basal segment (fig. 14). This muscle originates on the anteroventral part of the first antennular segment at about the midpoint between the anterior margins of the segment. The muscle runs a short distance anterolaterally to insert on a posterolateral apodeme of the first antennular segment.

The second basal segment abductor muscle of *Penaeus* has a homologue in the musculus productor$_2$ I antennae of *Pandalus*, *Astacus*, and *Callinectes*, although the use of the term "productor" for the action of the muscle in *Callinectes* is questionable. In the blue crab musculus productor$_2$ I antennae is said by Cochran (1935) to pull the second antennular segment downward, indicating that the muscle functions as a depressor.

ADDUCTOR MUSCLE OF SECOND BASAL SEGMENT

FIGURES 14, 15

The adductor muscle of the second basal segment originates ventrally in the anteromesial corner of the first antennular segment and inserts on a small apodeme at the posteromesial corner of the second antennular segment (figs. 14, 15). Contraction of the adductor muscle turns the second antennular segment, together with the distal elements of the antennule, toward the mid-sagittal plane of the animal. The second basal segment adductor muscle of *Penaeus* has a counterpart in the musculus reductor$_2$ I antennae of *Pandalus*, *Astacus*, and *Callinectes*. The muscle functions in *Pandalus* and *Astacus* to depress the distal antennular segments and flagella, while in *Callinectes* the distal elements are raised toward the midline by the action of the musculus reductor$_2$. The muscle might better have been called a second segment levator in the blue crab.

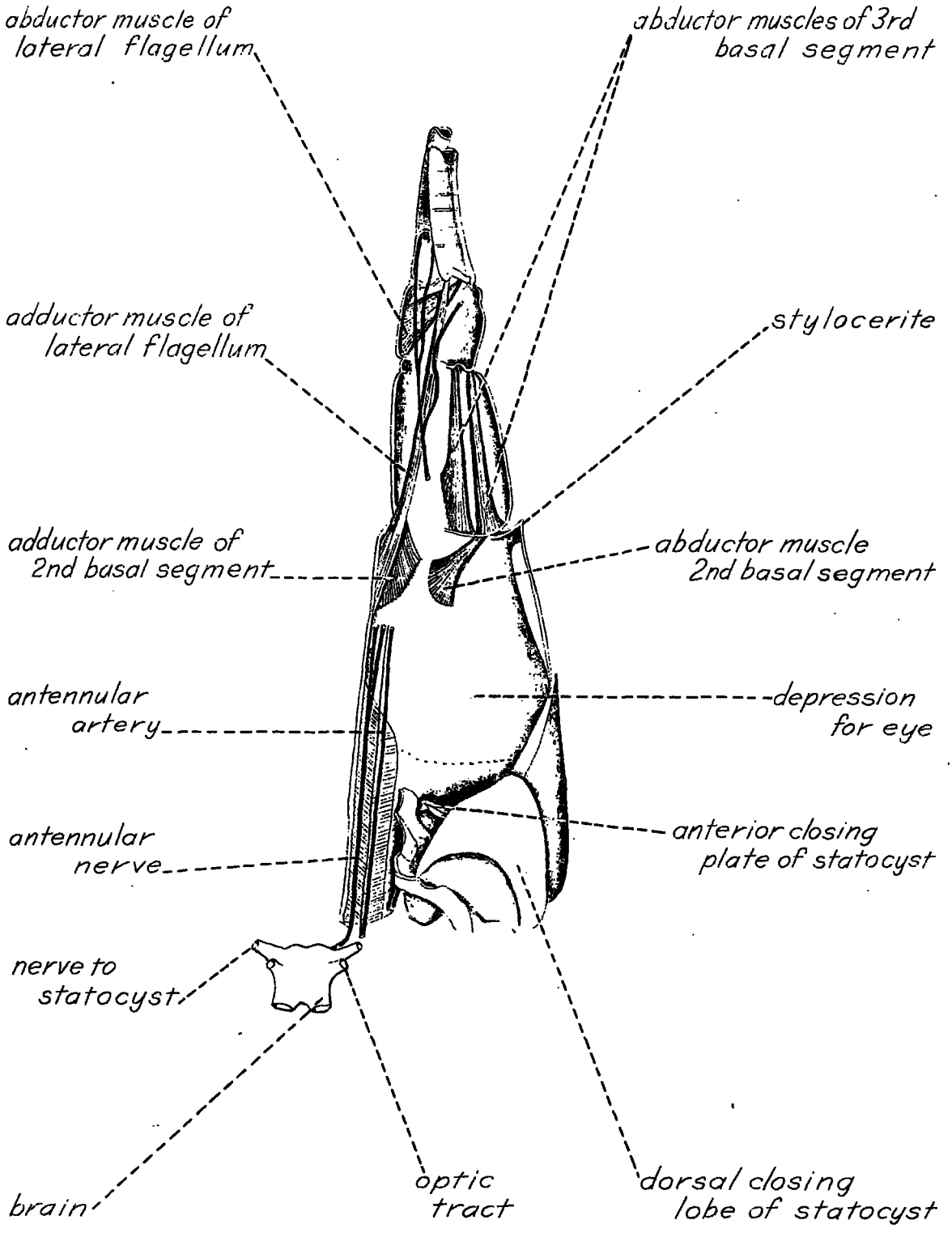

FIGURE 15.—Dorsal view of right antennule showing ventral muscles.

ADDUCTOR MUSCLE OF LATERAL FLAGELLUM

FIGURE 15

Arising from the anteromesial margin of the first antennular segment, just dorsal to the origin of the second basal segment adductor muscle, is the long, slender adductor muscle of the lateral flagellum. The muscle courses anteriorly through both the second and third antennular segments to insert on an apodeme arising from the mesial edge of the lateral flagellum base. Upon contraction of the lateral flagellum adductor the lateral flagellum is turned on its points of articulation toward the mid-sagittal plane. The muscle has a probable homolog in the musculus adductor I antennae of *Pandalus*, although in the latter the muscle inserts in the ventral part of the third antennular segment rather than on a flagellum. A lateral flagellum adductor muscle does not occur in the antennule of *Astacus* or *Callinectes*. Cochran (1935) describes a musculus adductor$_2$ I antennae for *Callinectes* that functions somewhat like the musculus adductor I antennae found by Berkeley (1928) in *Pandalus*, but which is not homologous with the latter muscle or with the lateral flagellum adductor muscle in *Penaeus*. A study of the nerves might show that the musculus adductor$_2$ I antennae in *Callinectes* is part of the musculus reductor$_2$ I antennae (second segment adductor muscle of *Penaeus*).

ADDUCTOR MUSCLE OF THIRD BASAL SEGMENT

FIGURE 14

The relatively large adductor muscle of the 3d basal segment originates in the posteromesial corner of the second antennular segment and runs directly anterior to insert on an apodeme in the posteromesial corner of the first antennular segment. Contractions of this muscle turn the third antennular segment and the flagella mesad, reinforcing the action of the proximal antennular adductors. The third basal segment adductor of *Penaeus* has homologs in the musculus reductor$_3$ I antennae of *Pandalus*, *Astacus*, and *Callinectes*. Cochran's (1935) use of the name "reductor" for the muscle in *Callinectes* is unfortunate. The reductor muscle of the third antennular segment in the blue crab appears to function virtually opposite to the muscle of the same name in *Pandalus* and *Astacus*, a situation that underlines the impropriety of transferring functional muscle names from one animal to another.

ABDUCTOR MUSCLES OF THIRD BASAL SEGMENT

FIGURES 14, 15

The second antennular segment of *Penaeus* contains three abductor muscles of the 3d basal segment. The lateral abductor muscle originates in the posterolateral corner of the second antennular segment and runs directly anterior to its point of insertion on a small apodeme of the posterolateral corner of the third antennular segment. Just mesad of the lateral, or first, abductor, a second abductor muscle originates broadly on the ventral surface of the posterior region of the second segment. This second abductor muscle courses anteriorly, parallel to the lateral-most abductor muscle, and inserts on a short apodeme slightly mesad of the insertion of the lateral-most muscle (figs. 14, 15). The mesial third basal segment abductor muscle originates in the posteromesial corner of the second antennular segment dorsal to the origin of the third basal segment adductor muscle. The mesial abductor runs diagonally to the anterior to insert on the apodeme of one of the lateral abductor muscles (fig. 14). Contractions of the third segment abductor muscles turn the third segment and the flagella away from the mid-sagittal plane. Their action reinforces that of the first and second segment abductor muscles.

The lateral-most abductor muscle of the third antennular segment of *Penaeus* is homologous with the musculus productor$_3$ I antennae of *Pandalus*, *Astacus*, and possibly *Callinectes*. In *Pandalus* and *Astacus* the musculus productor$_3$ swings the third segment dorsally in the sagittal plane, while in *Callinectes* the muscle named by Cochran (1935) a "productor" appears to flex the third segment. The second lateral third-segment abductor muscle in *Penaeus* has homologs in the musculus abductor$_3$ I antennae of *Pandalus* and *Astacus*. The muscle has been lost in *Callinectes*. The mesial third-segment abductor muscle of *Penaeus* does not appear in the antennule of any of the crustaceans to which reference has been made here.

ABDUCTOR MUSCLE OF LATERAL FLAGELLUM

FIGURES 14, 15

The abductor muscle of the lateral flagellum has its origins along most of the mesial side of the third antennular segment. The muscle nar-

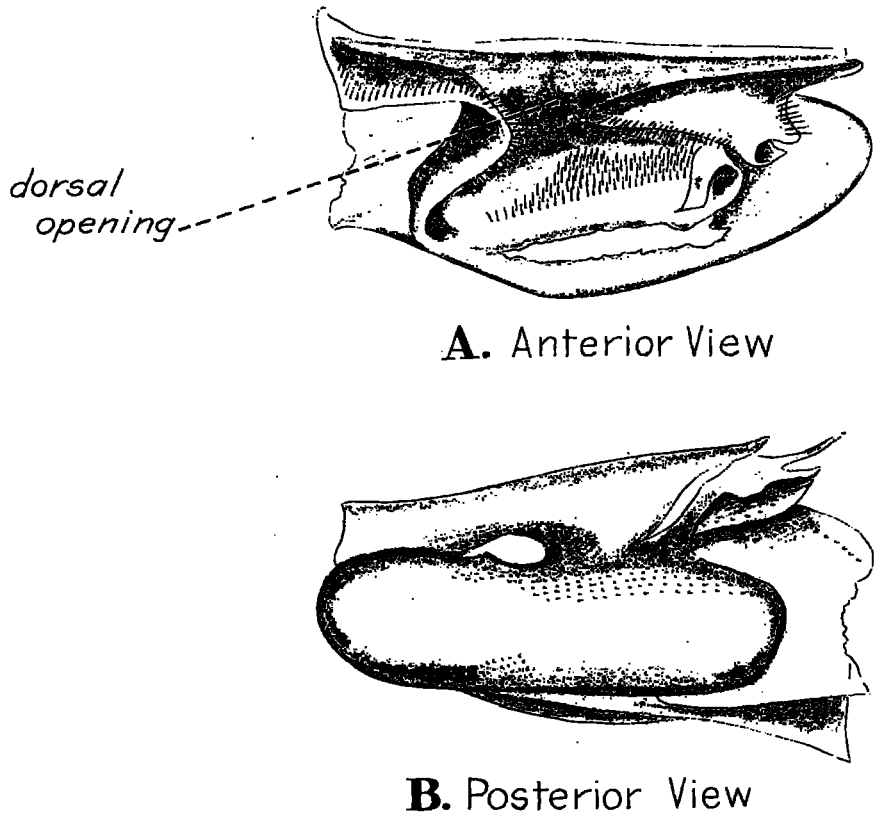

FIGURE 16.—Cleared statocyst. *A*. Anterior view. *B*. Posterior view.

rows as it runs anterolaterally, ventral to the lateral flagellum adductor muscle, to insert on an apodeme on the lateral edge of the base of the lateral flagellum (fig. 15). The lateral flagellum abductor muscle turns the lateral flagellum away from the midline in the horizontal plane. The muscle in *Penaeus* is very likely homologous with the musculus reductor$_4$ I antennae of *Pandalus*, *Astacus*, and *Callinectes*, although evolutional rearrangements have given rise to several changes. Berkeley (1928) describes the reductor$_4$ muscle in *Pandalus* as consisting of two parts, inserting on two opposite margins of the base of the lateral flagellum, and having at times an antagonistic action to one another. Such action suggests very strongly the existence of two muscles, rather than one with two functions.

ADDUCTOR MUSCLE OF MEDIAL FLAGELLUM

FIGURE 14

Originating in the posteromesial corner of the third antennular segment is the small adductor muscle of the medial flagellum. The adductor muscle courses anteriorly and inserts on an apodeme on the mesial edge of the flagellum base. Contractions of the muscle turn the medial flagellum toward the midline in the horizontal plane. No counterpart of this muscle in *Penaeus* is described for the antennule of *Pandalus*, *Astacus*, or *Callinectes*.

ABDUCTOR MUSCLE OF MEDIAL FLAGELLUM

FIGURE 14

The abductor muscle of the medial flagellum originates ventral to the origin of the medial flagellum adductor muscle and inserts on the medial flagellum by a short apodeme located at the lateral margin of the flagellum base. The muscle turns the medial flagellum outward from the midline in a horizontal plane. The medial flagellum abductor muscle of *Penaeus* has been lost in the antennule of the other crustaceans referred to in this study.

3. THE ANTENNAE

The antennae, or as they are frequently termed, the second antennae, display wide variations among the Crustacea. In certain of the Copepoda and other groups in the lower Crustacea they are large swimming organs. They are modified for clinging in other copepods. Frequently the antenna of the male crustacean is modified as a sexual clasper. Sexual dimorphism of the antennae is widespread in the lower Crustacea, the appendage of the adult male being more highly developed than that of the female. In several groups the structures may be extremely reduced or even lost in the adult animals.

The antenna of the higher Crustacea is fairly uniform, although exceptions do occur. The malacostracan antenna is said to consist of a 2- or 3-segmented protopodite, an endopodite of 2 or 3 segments, the distal-most bearing a flagellum, and an exopodite reflected into a flat scale. The protopodite usually is comprised of the coxopodite and basipodite, but some forms may have a proximal pre- or sub-coxa in addition (Calman 1909). Carcinologists use the expression "peduncle" to refer to the total number of endopodite and protopodite segments, usually 5 or 6, in the Malacostraca. Representatives of the lower Decapoda, like *Penaeus setiferus*, have a 5-segmented antennal peduncle, made up of the coxopodite and basipodite in the protopodite, and 3 proximal endopodite segments. The exopodite is scalelike. The scale is often missing or reduced to a spine in the higher decapods and the endopodite and flagellum may be relatively small.

Functionally, the antennae have always been thought to be sensory. More specifically, the antennal flagella are said to be centers of tactile sensation, whether pressure or simple touch is not known. No experimental data to support these contentions exist. The functions of the antennal scale would appear to be varied, in accordance with its great variation in size. The scale is missing in the Brachyura and small in the crawfishes and other Astacura, making its function somewhat difficult to determine by observational means. The organ is very large in the swimming decapods of the Natantia. The suggestion has frequently been made that the scale is an anterior swimming plane in the latter group.

Some attempt has been made to ascertain the function of the antennal scale in the swimming of the white shrimp. Normally the scale is carried in a directly anterior position, rotated slightly on its longitudinal axis. The rotation is such that the thin mesial margins of the scale lie somewhat ventrad of the heavy lateral margins. The effect produced is that of a ship's bow. Shrimps in an aquarium were lightly secured by a loop of string to the end of a rod. Lifted from the bottom in this position, the animals are stimulated to swim forward. Jets of water from a pump were directed at the motionless shrimps from various directions to see whether the antennal scale was used as an anterior steering device. No compensatory movements of the scale were observed. The organs appeared simply to cleave the water ahead. During normal movements about an aquarium, the scales are occasionally spread widely, but are never kept in the spread condition for more than a moment.

The antenna in *Penaeus setiferus* is typical of the natant Decapoda. The antennal scale is broad and strong and extends as far as the anterior tip of the rostrum. The protopodite is comprised of two segments, a short, incomplete coxopodite and a very large basipodite. To the large basipodite is articulated the exopodite, or scale, and the basal segments of the antenna. The size of the basipodite reflects its support of the heavy scale rather than that of the smaller antennal segments. The long antennal flagellum is carried laterally, from which position the movements of the shrimps through the water cause the flagellum to drag alongside and some distance behind the animal. The flagellum is approximately twice the body length in the white shrimp.

SKELETAL ELEMENTS

The first antennal segment, or coxopodite (fig. 18), is an incomplete ring by which the antenna is attached to the protocephalon. The foramen of the antenna at which the first antennal segment articulates with the protocephalon is by far the largest of the head foramina. At its broadest portions, muscles insert upon the first antennal segment.

The basipodite, or second antennal segment (figs. 18, 23), is a large, heavily sclerotized article connected firmly to the first antennal segment proximally and articulating distally with the third antennal segment, or ischiopodite, of the endopodite, and with the antennal scale, or exopodite. At

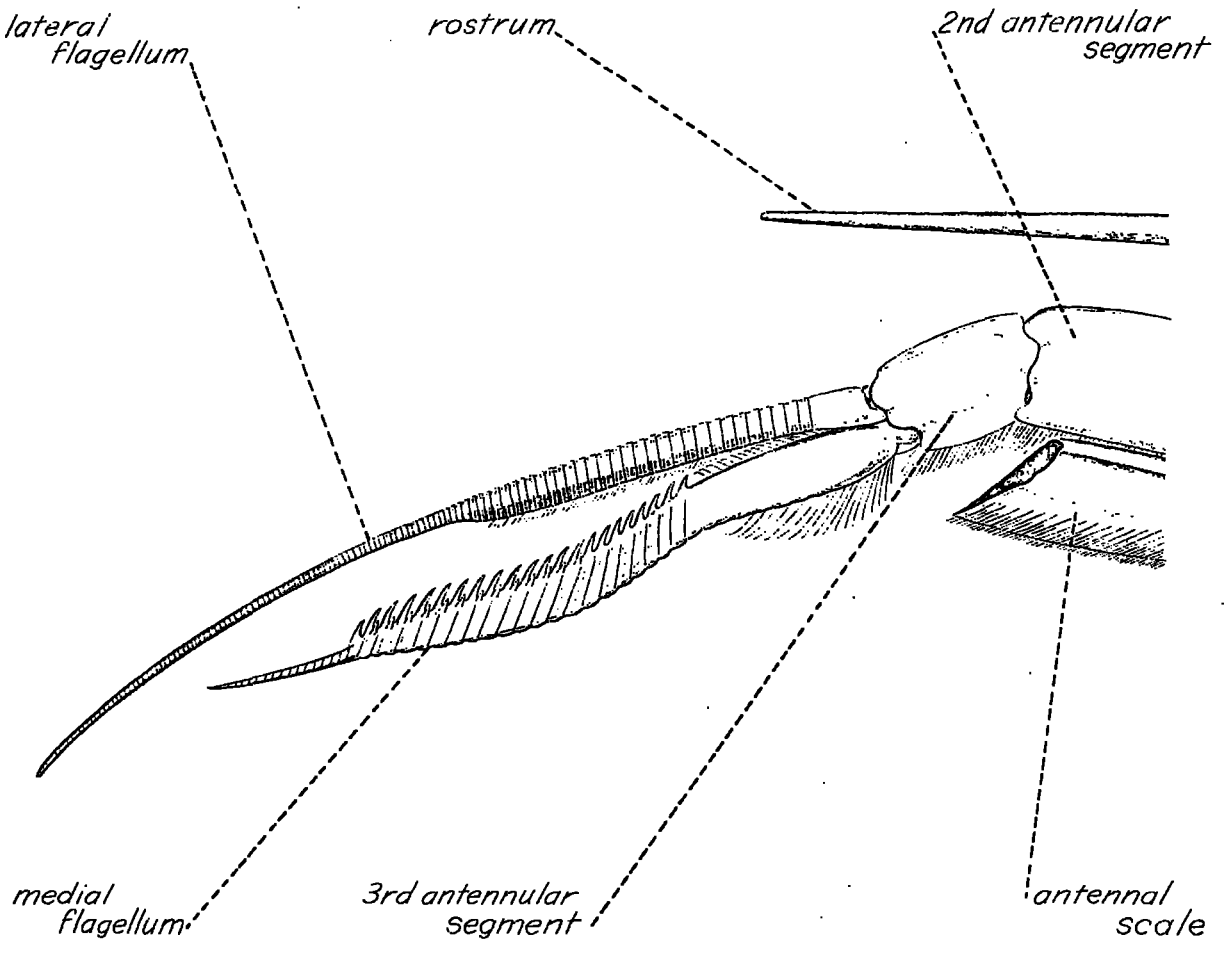

FIGURE 17.—Enlarged view of left antennular flagella showing sexual modification to medial flagellum in adult male.

the point of articulation with the antennal scale, the second antennal segment is deeply notched anteriorly providing an articular foramen for the large antennal scale. Strong dorsal and ventral points of articulation, or condyles (figs. 18, 22, 23) on the rim of the scale foramen permit the scale considerable horizontal movement. As brought out earlier, the great weight and strength of the second antennal segment exists as support for the antennal scale, rather than for the long, slender antennal flagellum. The second antennal segment articulates with the third antennal segment, or ischiopodite, by a small foramen located ventromesially (figs. 18, 23). The extent of movement between the second and third antennal segments is very limited.

The third antennal segment (figs. 18, 23) is a small, heart-shaped structure whose apex is directed posteriorly. Its small vertical movement, at right angles to its long axis, against the second antennal segment permits some rotation of the distal antennal segments. Movements of the little shield-shaped fourth antennal segment (figs. 18, 23) against the third antennal segment are, on the other hand, extensive. The fourth antennal segment attaches laterally to the third segment at about a 45° angle. By means of a dicondylic articulation, the fourth segment rotates through an arc of nearly 90°, and with it the distal antennal parts.

According to Schmidt (1915), the third antennal segment represents the fusion of the ischiopodite and meropodite and he evidently has morphological support for this view in *Astacus*. Curiously, no trace of a division is apparent in the third antennal segment of *Cambarus*, nor does Berkeley (1928) find one in the caridean *Pandalus*. No evidence for the fusion of the ischiopodite and meropodite can be seen in *Penaeus setiferus*.

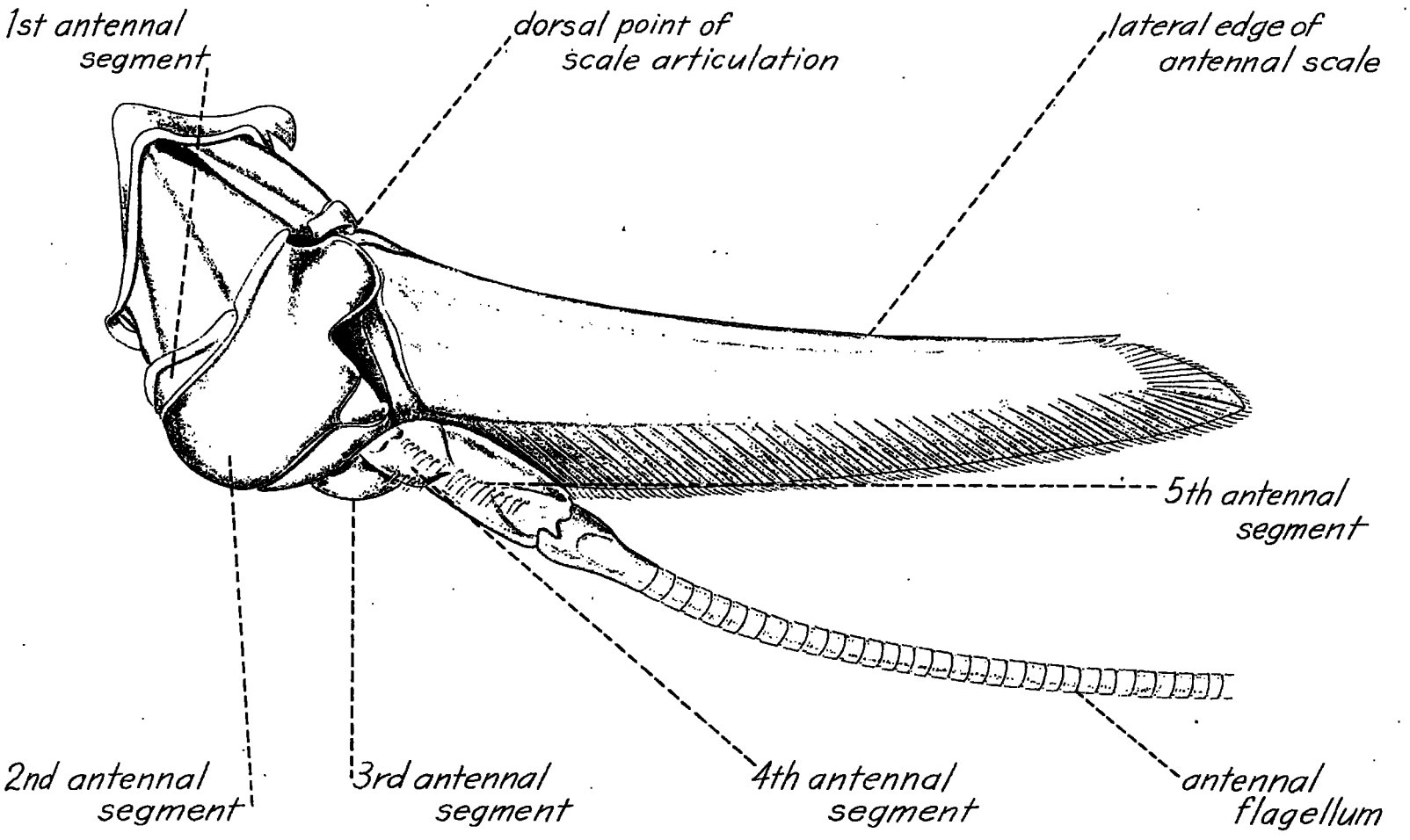

FIGURE 18.—Lateral view of right antenna.

The fifth antennal segment (figs. 18, 23) lies on the axial line distal to the fourth antennal segment and is connected to the pointed fourth segment by a broad V-shaped surface in the proximal end of the fifth segment. Two condyles in the vertical plane located at the apex of the V-shaped surface permit limited horizontal movements of the fifth segment on the fourth antennal segment. The relatively large fifth antennal segment bears the base of the long flagellum on its distal end. Strong dorsoventral condyles allow the flagellum to turn through an arc of more than 90° and the size of the fifth segment is probably an evolutional response to the long muscles needed to operate the flagellum. In living shrimps, the distal part of the flagellum is carried at right angles to the fifth antennal segment, the rest of the long flexible flagellum floating behind the animals. The antennal flagellum (figs. 23, 25) owes its flexibility to its annular construction. Each small annulation is capable of a little movement with respect to its neighbors.

An enlargement of the flagellar rings (fig. 25) shows probable sensory structures. On the dorsal surface of each ring (fig. 25, *A*) may be seen a pair of dorsal setae. On the ventral surface (fig. 25, *B*) a pair of plumose ventral setae project anteriorly from the distal portion of each annulation. Between the bases of the ventral setae is a ventral pit. The interior of the flagellum consists of blood vessels and nerves.

MUSCLE ELEMENTS

The skeletal parts of the antenna of *Penaeus setiferus* are operated by 12 types of muscles, including at least 26 individual muscles. Berkeley (1928) describes 15 types of muscles in *Pandalus*. Schmidt (1915) lists 18 muscle types in the European crawfish, the appendage containing 21 separate muscles to carry out its complex movements. The reduced antenna of *Callinectes* has only 8 muscles (Cochran 1935). The evolutional trend of reduction of the number of muscles and muscle types has apparently been reversed in the case of the crawfish antenna, in which form much more complicated antennal activities are displayed by the living animals than in *Penaeus* or *Pandalus*.

FIRST ANTENNAL SEGMENT ADDUCTOR MUSCLE

FIGS. 21, 24

Attaching on the median rim of the coxopodite foramen, the first antennal segment adductor muscle inserts in the first antennal segment near the external opening of the excretory apparatus (fig. 21). Contractions of this short, powerful muscle turn the coxopodite and hence the antenna mesad. Homologs of this muscle in *Astacus* and *Pandalus* are difficult to determine without full information on the nerves. Allowing for functional differences in the antennae of the various crustaceans here considered, the most likely homolog of the first segment adductors in *Astacus* is the musculus depressor *a* II antennae. Berkeley (1928) designates two medial antennal base muscles as the musculus depressor *a* and *b* II antennae, after Schmidt (1915). From her illustrations of the antenna in *Pandalus*, the antennal depressor muscle *a* appears to be the same muscle as the first antennal segment adductor in *Penaeus*. The muscles in the latter two forms are similar, strongly suggesting an homology. The antennal depressor muscle *a* in *Astacus* is much less suggestive of phylogenetic similarity.

SECOND ANTENNAL SEGMENT PROMOTOR MUSCLES

FIGS. 19, 22

Far and away the heaviest musculature of the anterodorsal region of the white shrimp is that concerned with the antennae. The dorsal-most of these is a large, flat muscle originating in connective tissue slightly laterad of the postrostrum (fig. 19). This muscle, a second antennal segment promotor muscle, runs anteriorly and laterally to insert in what appears to be a free apodeme just beneath the dorsal rim of the coxopodite. This apodeme is not connected to the coxopodite, but instead (fig. 19) consists of a transverse fascia in which the distal second antennal segment promotor muscle originates. The presence of the free apodeme of the proximal second segment promotor muscle may indicate that the muscle is in reality a first antennal segment (coxopodite) promotor. The free apodeme, however, produces a functional second antennal segment (basipodite) promotor and the muscle is therefore so described. The proximal second segment promotor is evidently the homolog of the musculus promotor II antennae in *Astacus*, *Pandalus*, and *Callinectes*, although in these forms the muscle clearly attaches to the dorsal margin of the coxopodite.

The distal second antennal segment promotor muscle extends the functional connection of the muscle group to the dorsal edge of the second an-

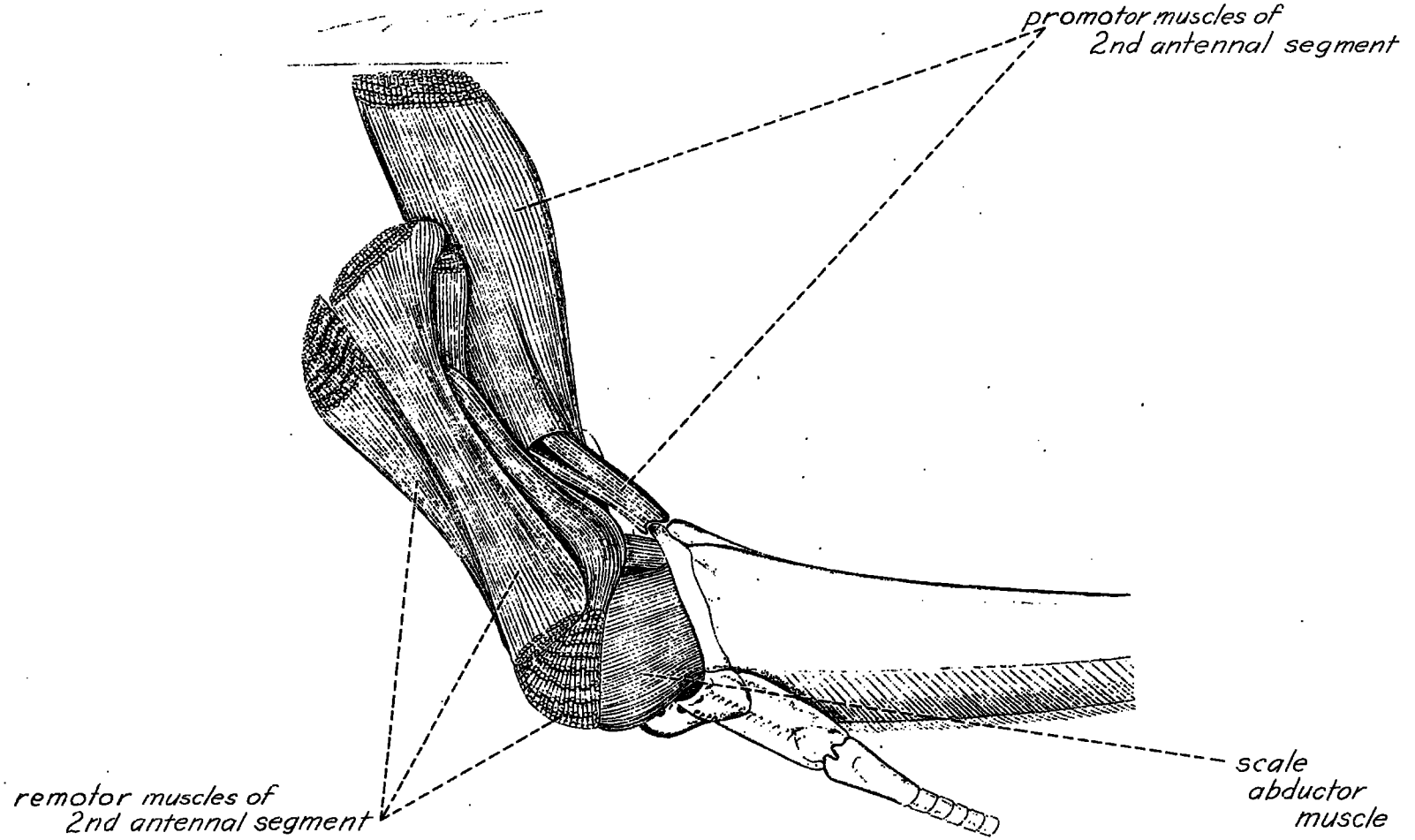

FIGURE 19.—Lateral view of right antenna, carapace and cuticle removed to show muscles.

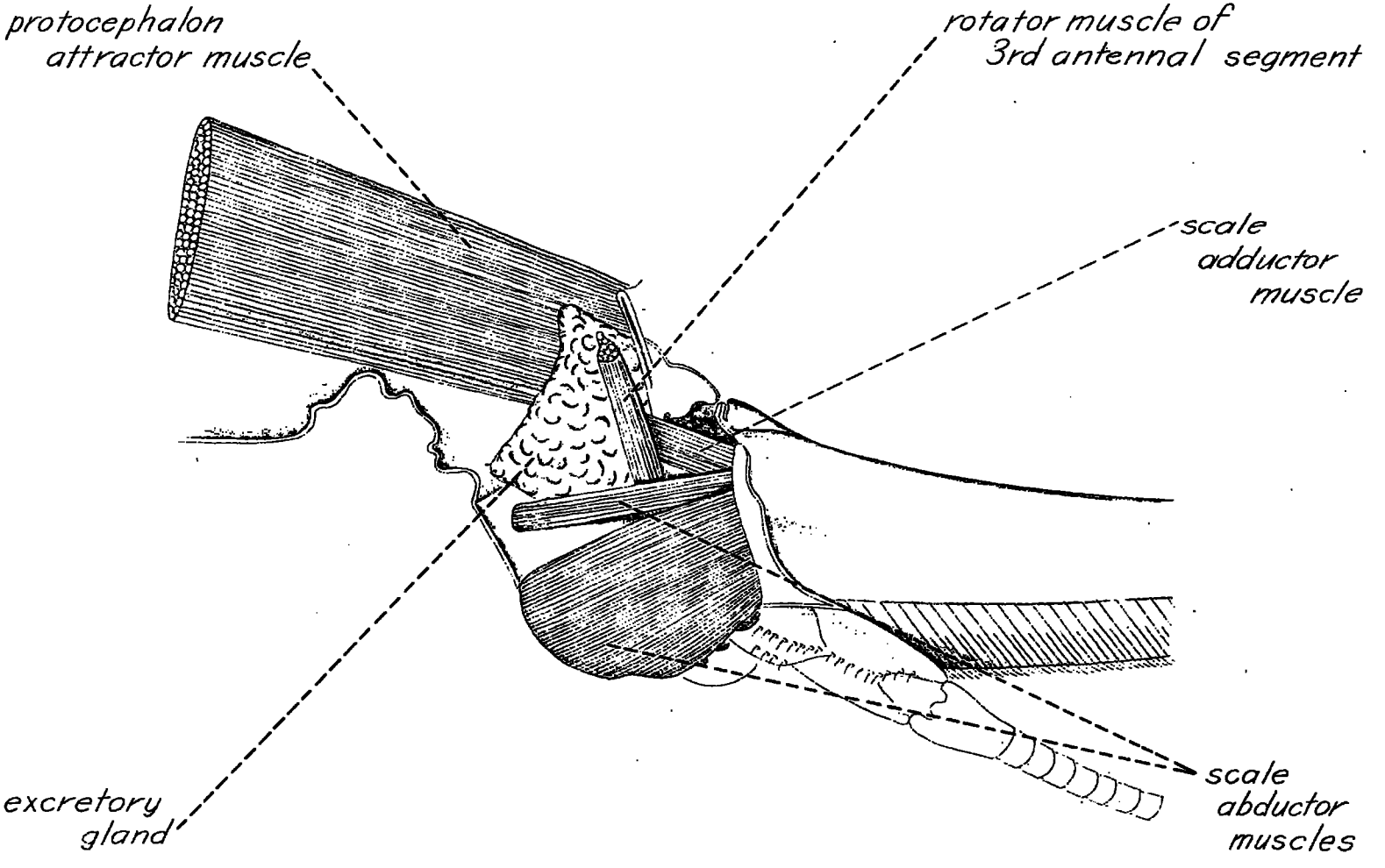

FIGURE 20.—Lateral view of right antenna. Lateral muscles removed to show excretory gland.

tennal segment, or basipodite. Upon contraction the promotor muscles raise the antennal scale and endopodite segments dorsally. The muscles actually function as levators. Without information about the innervation, no homolog of the distal promotor muscle is here suggested.

SECOND ANTENNAL SEGMENT REMOTOR MUSCLES

FIGS. 19, 24

At least three large antennal muscles arise on the dorsolateral carapace just anterior to the hepatic spine. These muscles, here considered the second antennal segment remotor muscles (figs. 19, 24), run anterolaterally to extensive insertion areas in the lateral and posterior regions of the second antennal segment (basipodite). The lateral- and posterior-most of these muscles might be thought to insert on the ventral margin of the first antennal segment, in which case the two muscles would be first segment, or coxopodite, remotor muscles. Repeated dissections in the area indicate otherwise, however, and for this reason the muscles are assigned to the basipodite. The posterior-most remotor displays a definite torsion as it passes from its lateral point of origin to a posterior and even slightly medial insertion area. While the function of all three remotor muscles is actually the depression of the large scale, that of the posterior remotor muscle may also include adduction of the scale, together with depression. Since the antennal scale of *Penaeus* bears a major portion of the weight of water striking the anterior end of the animal, large remotor (depressor) muscles are needed to maintain the scale in position.

The homologies of the second antenna segment remotors is made confusing by the functional muscle nomenclature. A comparison of the function of the antennae in the crawfish and *Penaeus* shows wide differences. The crawfish antennal segments are constructed to permit extension movements of the comparatively short, stiff flagellum. One kind of extreme of this modification has been achieved in the antenna of *Palinurus*, in which form movability is combined with great size and power for the protection of the animal. As has been suggested, the antennal movements of *Penaeus* are comparatively limited by virtue of segmental architecture, particularly in the segments of the protopodite. The heavy musculature of carapace origin is in reality associated with the simple movements of the scale; the muscles of the distal antennal segments of the endopodite are comparatively small.

As a consequence of the many antennal functions in different crustaceans, homologous muscles have different functions and nomenclature. At least part of the second antennal segment remotor muscle mass in *Penaeus* is undoubtedly homologous with the musculus remotor II antennae in *Astacus*, *Pandalus*, and *Callinectes*. Part also may be homologous with the musculus depressor *c* II antennae in *Astacus* and perhaps even with a part of the large musculus depressor *c* II antennae in *Pandalus*, although certainly the major part of the antennal depressor *c* in *Pandalus* is the protocephalon attractor muscle. The other antennal depressor muscles, *a*, *b*, and *d* (*d* is not found in *Pandalus*) in *Astacus* and *Pandalus* are not evident in *Penaeus*.

SCALE ABDUCTOR MUSCLES

FIGURES 19, 20, 24

Taking origin from large areas to the posterior, ventral, and medial region of the second antennal segment (basipodite), the proximal scale abductor muscles (figs. 19, 20, 24) insert on the lateral margin of the antennal scale (exopodite), lateral to the dorsoventral scale condyles. In addition to the huge ventral scale abductor, at least two and probably three small-scale abductors (figs. 20, 24) are found in the second antennal segment of *Penaeus*. A long, distal scale abductor muscle (fig. 24, *B*), originating in the distal part of the scale, runs proximally along the lateral margin of the scale to insert on the lateral margin of the basipodite foramen, lateral to the axis of the scale condyles. When the scale abductor muscles contract, the large scale is swung laterally some distance. The functional reason for this movement is not clear. Shrimps in an aquarium occasionally spread the scales, at times in association with cleaning activities of the head appendages and a sudden flushing out of the gill chamber.

The proximal scale abductor muscles of *Penaeus* are probably homologous with the second antennal exopodite abductor muscles *a*, *b*, and *c* in *Astacus* and with the single exopodite abductor in *Pandalus*. The scale is reduced in *Callinectes*. Schmidt (1915) does not show a distal scale abductor muscle in *Astacus* such as exists in *Penaeus*, and Berkeley (1928) makes no mention of the muscle

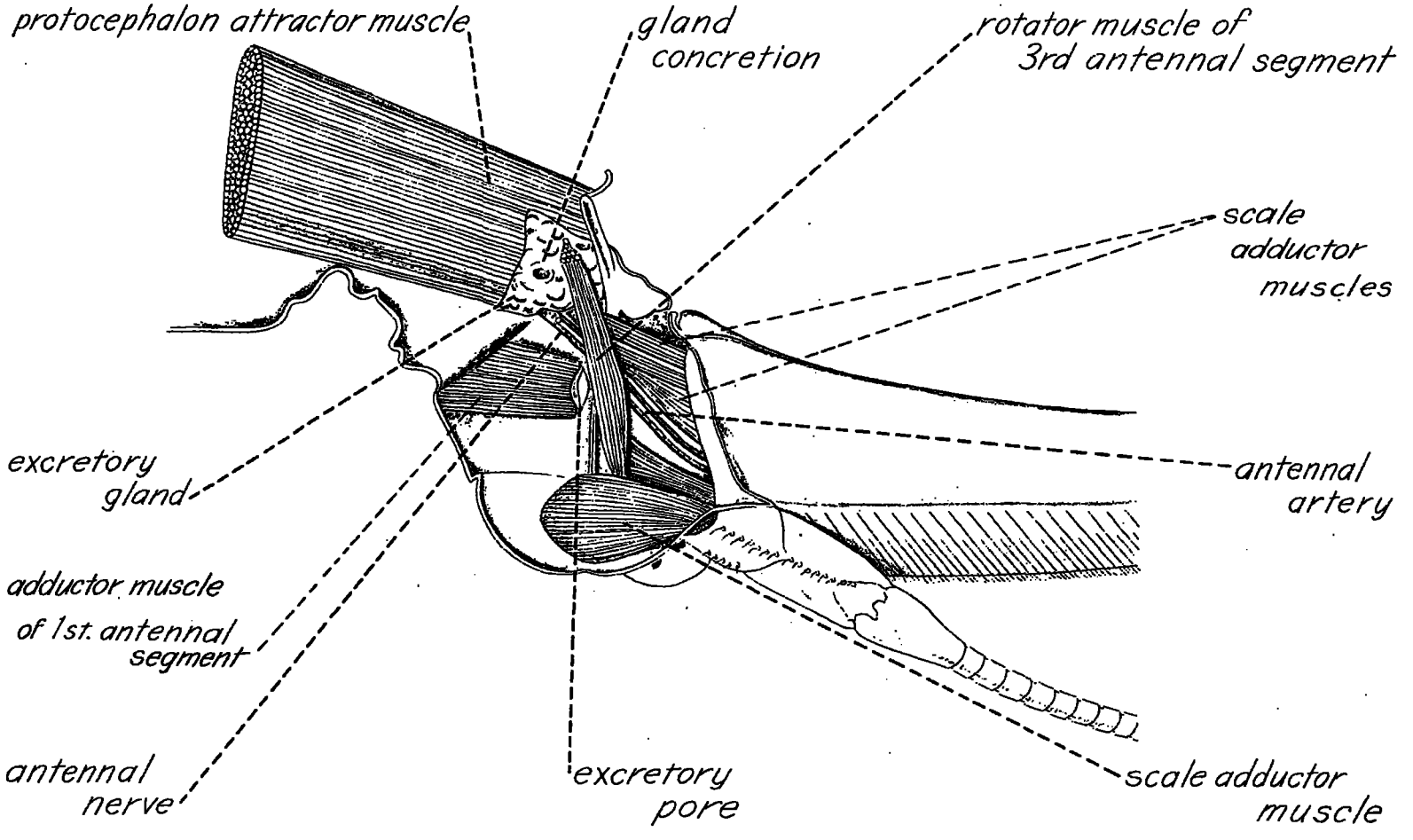

FIGURE 21.—Lateral view of right antenna. Lateral muscles removed to show medial muscles, nerves, and arteries. Part of excretory gland removed to show gland concretion.

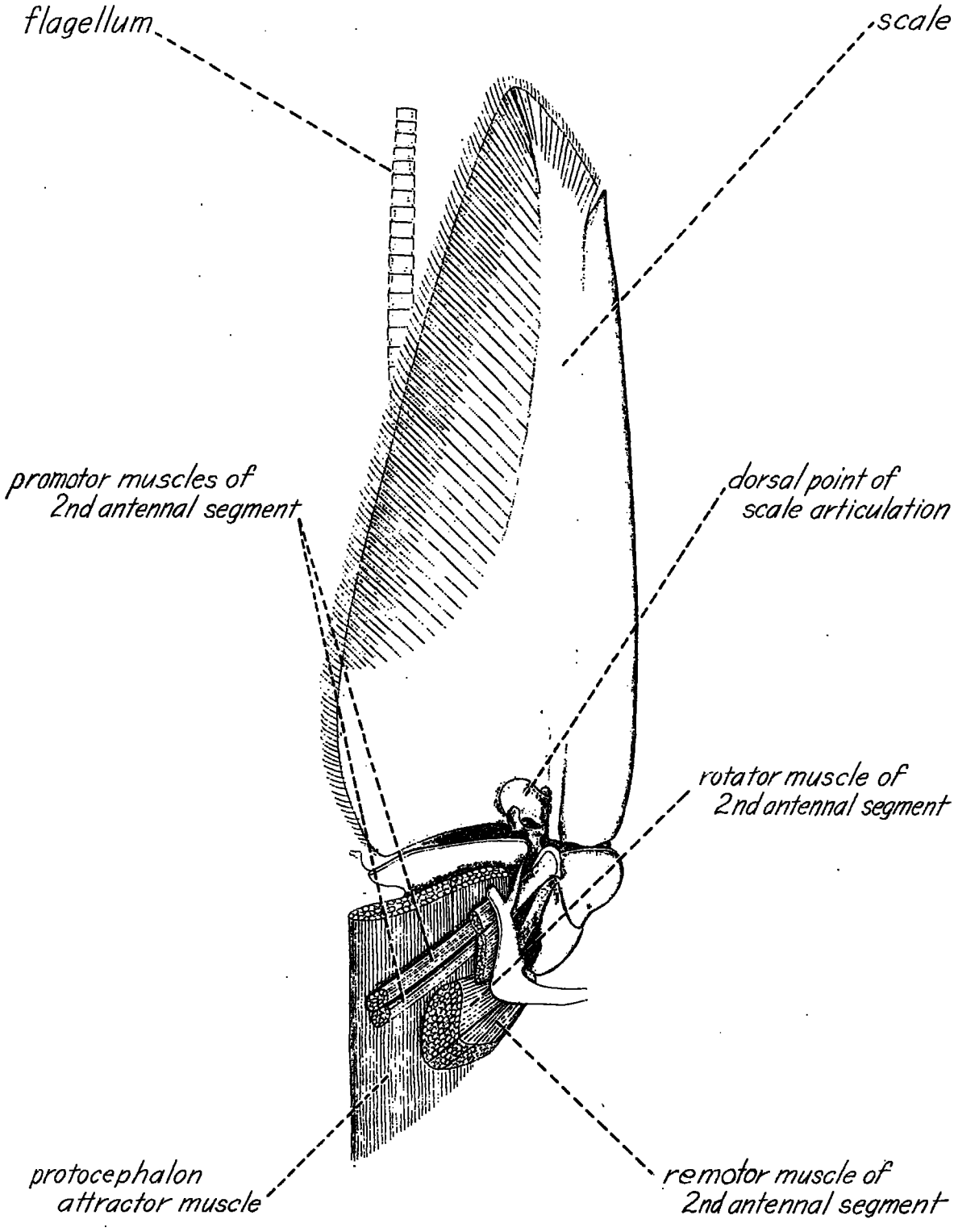

FIGURE 22.—Dorsal view of right antenna showing antennal scale and protopodite muscles. Carapace removed.

in *Pandalus*. However, Berkeley illustrates a distal scale muscle which she designates as the musculus adductor exopoditis *b* II antennae and which from the standpoint of its arrangement appears to be the distal scale abductor muscle in *Penaeus*. A careful review of the insertion of Berkeley's exopodite adductor muscle might show that it is in reality an abductor muscle.

SCALE ADDUCTOR MUSCLES

FIGURES 20, 21, 24

Two types of scale adductor muscles (figs. 20, 21, 24) are found in the antenna of *Penaeus*. At least two scale adductors originate on the medial wall of the second antennal segment ventral to the excretory pore (fig. 24, *B*), and run diagonally to insertion points on the ventral and medial margins of the scale foramen. Their insertions are mesad of the axis of the scale condyles. The distal scale adductor muscle (fig. 24, *B*), like the distal scale abductor, is located in the body of the scale. It originates in the distal region of the exopodite and runs caudad parallel to the distal scale abductor to insert on the margin of the basipodite foramen mesad of the scale articles. Upon contraction, the scale adductor muscles move the antennal scale inward toward the median line of the shrimp, in opposition to the action of the scale abductors.

THIRD ANTENNAL SEGMENT ROTATOR MUSCLE

FIGURES 20, 21, 24

Arising on the dorsomedial rim of the first antennal segment (coxopodite) foramen and running ventro-medially, the third antennal segment rotator muscle (figs. 20, 21, 24) inserts on an apodeme located on the lateral margin of the third antennal segment (figs. 23, 24). Contractions of the muscle accomplish the movement described in the section on the skeletal elements, namely, lateral rotation of the third antennal segment and the antennal parts distal to the third segment.

The homologs of this muscle in the other crustaceans referred to are not clear. The best possibility in *Astacus* is one or both of the meropodite muscles *a* and *b*. On the basis of area of insertion, the most likely homologs is the musculus meropoditis *a*, although the third segment rotator in *Penaeus* and the meropodite muscle *a* in *Astacus* have different origins, the latter being in the basipodite of the crawfish antenna. The meropodite muscle in *Pandalus* is more nearly similar to the situation in *Penaeus* than in *Astacus*. In both *Astacus* and *Pandalus*, Schmidt (1915) and Berkeley (1928) illustrate a muscle, the musculus reductor ischiopoditis II antennae, said to oppose the action of the meropodite muscles *a* and *b*. No similar muscle has been found in *Penaeus*, although the shrimp may have a functional analog in the fourth antennal segment adductors.

FOURTH ANTENNAL SEGMENT ADDUCTOR MUSCLE

FIGURE 24

The fourth antennal segment adductor muscle (fig. 24) originates in a broad fan on the ventral surface of the basipodite. The muscle runs anterodorsally, narrowing to its apex at its point of insertion on a small, movable article presumed to be a part of the fourth antennal segment. Certainly a muscle originating on the basipodite and inserting on the fourth antennal segment is unusual. Controversy could be avoided by assigning the small, movable article to which this muscle inserts to the third antennal segment; however, the movable article appears to be widely separated from the third segment and instead is lateral to the fourth segment and clearly connected to it. When the fourth segment adductor muscle contracts, the movable article is drawn posteroventrally with the result that the fourth antennal segment is rotated upon the third segment and turned a short distance mesad. As such, the fourth segment adductor represents in part an opposing muscle to the third segment rotator muscle. The homology of this muscle is uncertain.

FOURTH ANTENNAL SEGMENT ABDUCTOR MUSCLE

FIGURE 24

Originating from a broad area slightly posterior to the origin of the fourth segment adductor muscle, the fourth antennal segment abductor muscle (fig. 24) runs to an insertion on the same small movable article of the fourth antennal segment to which the fourth segment adductor attaches. The fourth segment abductor is much larger than the fourth segment adductor. Upon contraction the fourth antennal segment abductor reinforces the action of the fourth segment ad-

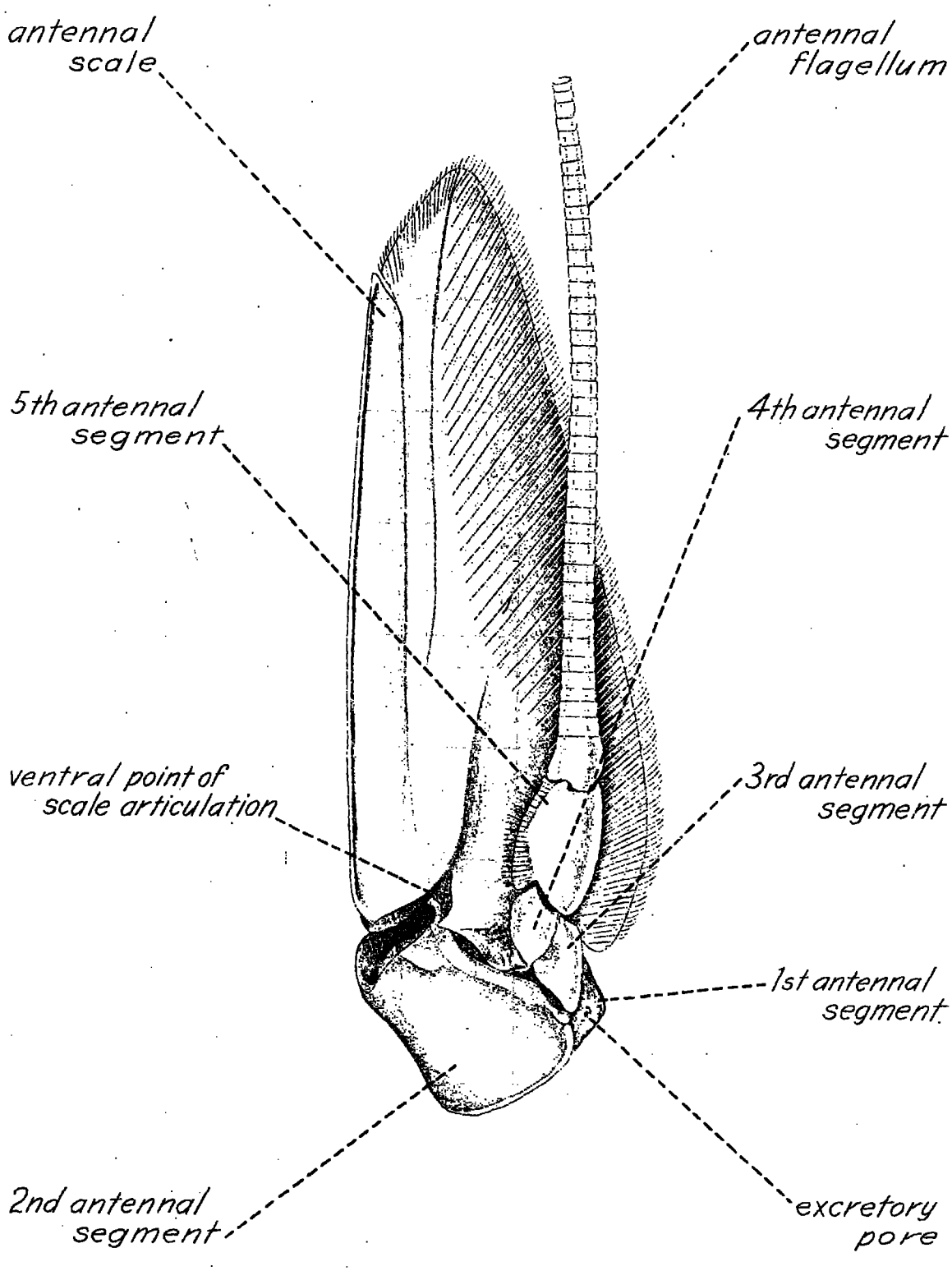

FIGURE 23.—Ventral view of right antenna showing skeletal elements.

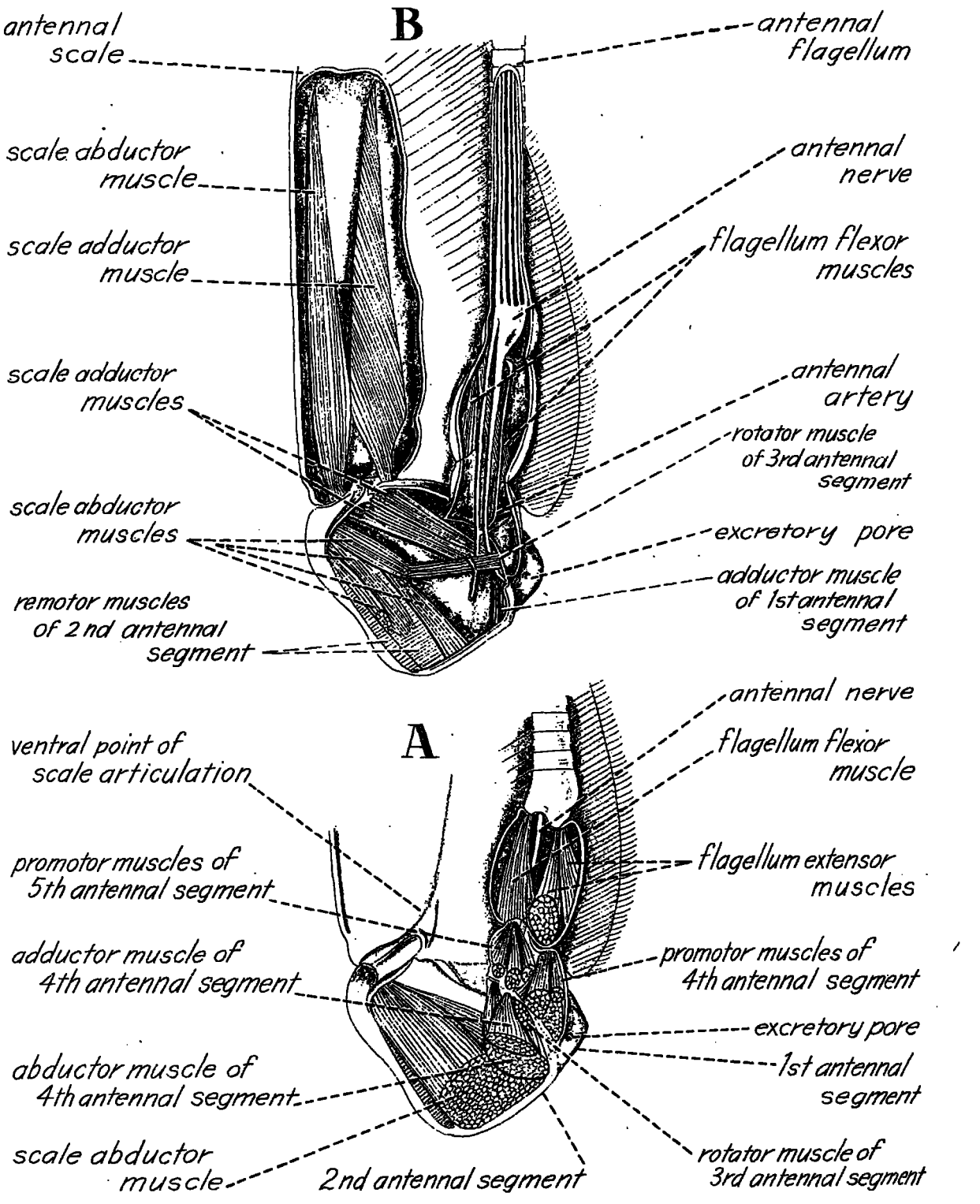

FIGURE 24.—Ventral view of right antenna showing ventral muscles, nerves, and blood vessels. Ventral cuticle removed. *A*. Superficial ventral elements. *B*. Dorsal elements.

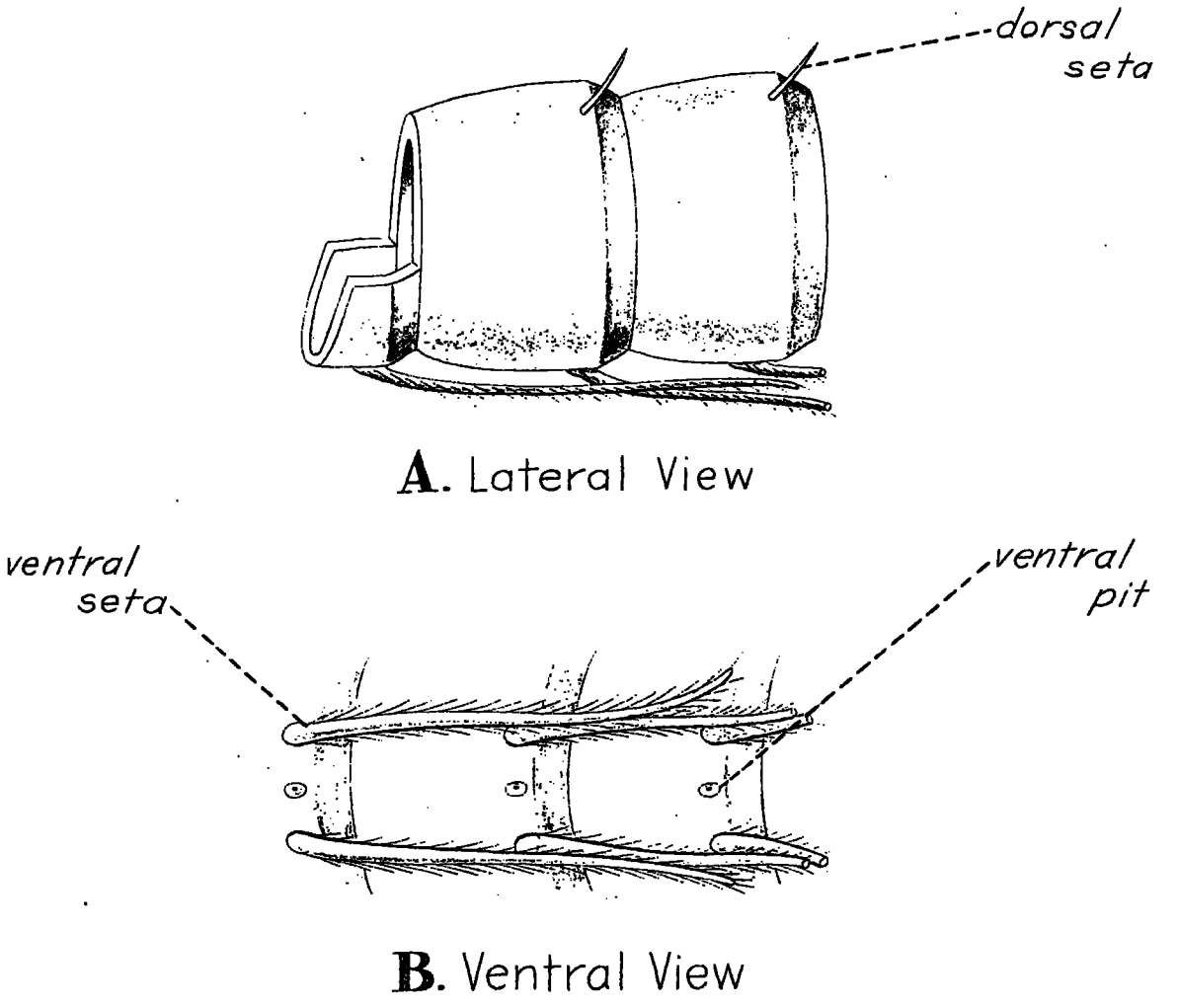

FIGURE 25.—Enlargement of proximal segments of antennal flagellum showing sensory structures.

ductor muscle in rotating the fourth segment on the third segment. In opposition to the fourth segment adductor, the fourth segment abductor turns the fourth antennal segment laterad a short distance. No homolog of this muscle is here advanced.

FOURTH ANTENNAL SEGMENT PROMOTOR MUSCLES

FIGURE 24

The fourth antennal segment promotor muscles (fig. 24) are situated within the body of the third antennal segment. At least three of these muscles occur in *Penaeus*. The short, thick promotors originate throughout the ventral surface of the third antennal segment and insert at their narrow apical tips on an apodeme of the fourth antennal segment. Contractions of the fourth antennal segment promotors move the fourth segment and the distal antennal parts anteriorly. How these muscles are represented in the other crustaceans referred to in this paper is uncertain.

FIFTH ANTENNAL SEGMENT PROMOTOR MUSCLES

FIGURE 24

The fifth antennal segment promotor muscles (fig. 24) are comprised of a tuft of at least four small muscles restricted to the fourth antennal segment. The muscles originate on the lateral and posterior margin of the fourth article and attach to an apodeme arising from the posterior

groove of the fifth antennal segment. Contractions of the fifth segment promotors move the fifth antennal segment anteriorly in a limited way. The homolog of these muscles in *Astacus* is very like the musculus extensor propoditis II antennae. Berkeley (1928) does not find the muscle in *Pandalus*.

FLAGELLUM EXTENSION MUSCLES

FIGURE 24

The fifth antennal segment of *Penaeus* contains two flagellum extensor muscles (fig. 24), occupying the medial half of the segment. One of the flagellum extensors originates on the medial side of the fifth segment and runs distally to insert on the large extensor apodeme on the medial side of the flagellum base. The second extensor takes origin on the posteroventral region of the fifth segment, runs distally, and inserts on the large extensor apodeme on the flagellum. These muscles bring the base of the flagellum directly anterior to the proximal antennal segments. One or both of these muscles is undoubtedly homologous with the antennal dactylopodite extensor muscle as shown by Schmidt (1915) in *Astacus* and by Berkeley (1928) in *Pandalus*. The related muscle, if any, in *Callinectes* is uncertain without adequate information about the nerves.

FLAGELLUM FLEXOR MUSCLES

FIGURE 24

Three flagellum flexor muscles in the fifth antennal segment of *Penaeus* turn the antennal flagellum to its normal position at right angles to the proximal antennal segments. The largest and ventral-most of these muscles originates broadly along the proximal groove of the fifth segment and inserts on the flexor apodeme on the flagellum base. Dorsal to the large muscle, two flagellum flexor muscles insert on the same flexor apodeme on the flagellum. The dorsolateral flagellum flexor originates in the lateral corner of the fifth segment, the dorsomedial flexor originating in the medial corner of the fifth antennal segment. At least one of these muscles in *Penaeus* is the homolog of the musculus flexor dactylopoditis II antennae in *Astacus* and *Pandalus*. Whether homologs exist in *Callinectes* is not known.

4. LABRUM

The labrum is the final component of the protocephalon to be considered. In all arthropods the labrum is a lobe or sac suspended over the mouth from a sclerotized region of the head known as the epistome (the hexapod clypeus). Crustacean morphologists ordinarily do not consider the labrum an appendage. Most workers consider the labrum an unpaired structure. Some students of Crustacea place the epistome as the ventral element of a preoral, premandibular segment, behind the eyes, antennules, and antennae, in the order of their occurrence in many adult crustaceans. Others have even assigned the epistome to the sternum of the antennal or mandibular segments, giving the labrum an utterly indefensible postoral position.

The position of the epistome and labrum in adult arthropods is variable. In some crustaceans, like the adult isopods and amphipods, and in most insects, the epistome is anterior or facial (Snodgrass 1951). The labrum thus is ventral or anterior to it. However, in most crustaceans, some chilopods, and a few insects the head segments have thrust forward, overgrowing the epistome anteriorly. The result is a secondary ventral position of the epistome and labrum in some arthropods. In point of fact, the labrum is the anterior end of the arthropod. I am in full agreement with Snodgrass (1951) in this view. Furthermore, the labrum is here considered not only the most anterior part of the arthropod, but also the anterodorsal "upper lip" of these forms, and as such the dorsal part of the first segment. Considerable support for this interpretation has been adduced by Ferris (1947) and Henry (1948a), based on the study of the labral nerves.

If we accept the view of various workers, including Henry (1948a), that the tritocerebrum of arthropods is in reality the first ganglion of the ventral nerve cord, whatever its fate in the adult, then we are bound to regard structures innervated by tritocerebral nerves as primitively anterior. Since the labrum of *Penaeus* is clearly innervated by a pair of nerves from the tritocerebral ganglia (figs. 27, 76), similar to the situation in other Crustacea and Insecta (Henry 1948a, 1948b), then the labrum is segment 1 in *Penaeus*.

No evidence is here advanced to suggest that the labrum is a reduced appendage. Indeed, this ancient "upper lip" was probably never an arthroappendage in the true sense at any time in its history. The labrum is, however, very likely paired. In support of this is the morphology of the nerves and muscles. The labral nerves are paired and arise from the clearly bilateral trito-

cerebral ganglia. Each nerve enters the sac of the labrum and innervates only those sensoria and muscles in half the labrum from the medium sagittal plane laterad. In *Penaeus* no nerve can be seen crossing the median sagittal plane. Furthermore, the embryonic labrum of many higher arthropods (Johannsen and Butt, 1941; Young 1953) develops as a paired structure, with paired coelomic sacs.

SKELETAL ELEMENTS

FIGURES 26, 27

In *Penaeus setiferus* the labrum is a soft, lightly sclerotized sac attached between the widely spread posterolateral bars of the epistomal Y (fig. 28, *A*). It may be noted in passing that these lateral epistomal bars are morphologically anterior, although due to rearrangements of the head segments, discussed above, the position of the epistome is reversed in the head of many crustaceans. The anterior or medial bar of the epistome, dividing the antennal foramina, curves anterodorsally to form a deep ventral pit, best seen in lateral view (figs. 28, *A*; 30) of a cleared anterior skeleton cut along the median sagittal plane. To the epistomal invagination, or apodeme, is attached a pair of muscles to be discussed below.

The labrum is shaped to fit between the antennal bases anteriorly and the incisor and molar surfaces of the mandibles posteriorly (figs. 26, *A*, *B*). Various auricles and lobes project from the labral surface to enhance its function as an aid in feeding. A toothed structure, the posterior feeding process (figs. 26, 27), projects directly into the mouth aperture.

MUSCLE ELEMENTS

EPISTOMAL STATOR MUSCLES

FIGURES 5, 6, 30, 34

Originating on the dorsal surface of the carapace, lateral to the posterior protocephalon levator muscles, and converging on the anterior side of the epistomal invagination is a pair of small muscles which are named in the present work the epistomal stator muscles (figs. 5, 6). The name derives from the fact that contractions of the muscles would appear to hold the epistomal invagination in position during the contraction of other muscles in the area. The epistomal stator muscles are homologous with the musculus oculi basalis posterior in *Pandalus*, *Astacus*, and probably in *Callinectes*.

Giving the name, epistomal stators, to these muscles may be adding confusion to the morphological scene, since these muscles are undoubtedly the musculus attractor sincipitis described by Grobben (1919) in the stomatopod *Squilla mantis* and the muscle attracteur du synciput illustrated by Mayrat (1955, 1956a, 1956b) in *Praunus flexuosus* O. F. Müller. The "sincipit" (Mayrat spells it "synciput") of Grobben (1917) is of course the protocephalon of Snodgrass (1951) as applied to the Crustacea. No great objection is offered here to designating the muscles in *Squilla* and *Praunus* as the synciput attractors. The muscles are indeed synciput or protocephalon muscles apparently functioning in certain forms to draw the protocephalon posteriorly. However, the same muscles in *Penaeus* do not attract the protocephalon. Furthermore they insert on a specific region of the protocephalon, the epistome, and so deserve as special a name as possible. The problem can be resolved by a study of the nerves, for if the epistomal stator muscles belong to the epistome, they should be innervated by epistomal or clypeal nerves.

LABRAL MUSCLES

FIGURE 27

One of the most astonishing features of the anatomy of *Penaeus setiferus* is the musculature of the labrum. In the generalized insect labrum, the structure is moved by two pairs of extrinsic muscles, the anterior and posterior labral muscles arranged for production and reduction. To the intrinsic labral compressor muscles of insects may be assigned various functions. In contrast, a review of general and special accounts of the anatomy of Crustacea has shown no reference to labral muscles in this class. Yet the labrum of *Penaeus* (fig. 27) is operated by at least 12 pairs of intrinsic muscles, bilaterally situated, and at least 1 intrinsic muscle running across the entire lobe. From their arrangement, the labral muscles obviously distort the labrum in all sorts of ways in the function of the organ as a tongue. In addition, at least 2 pairs of extrinsic muscles insert on the edge of the labral foramen to move the entire organ. No attempt has been made here to assign functional muscle names to the individual labral muscles.

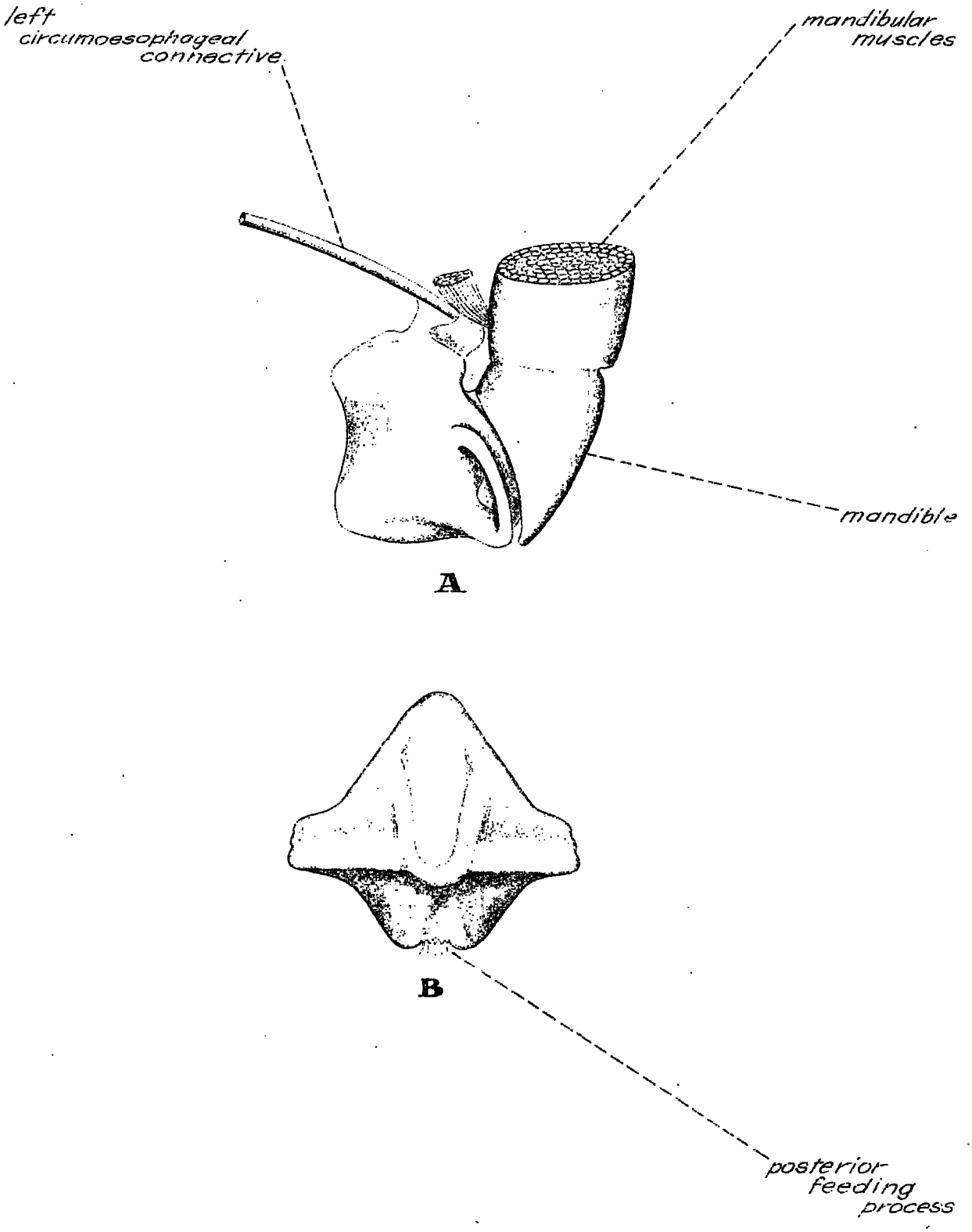

FIGURE 26.—Labrum. *A*. Lateral view of labrum from the left side showing relation of labrum to mandible. *B*. Ventral view of labrum showing posterior feeding process.

468059 O—59——4

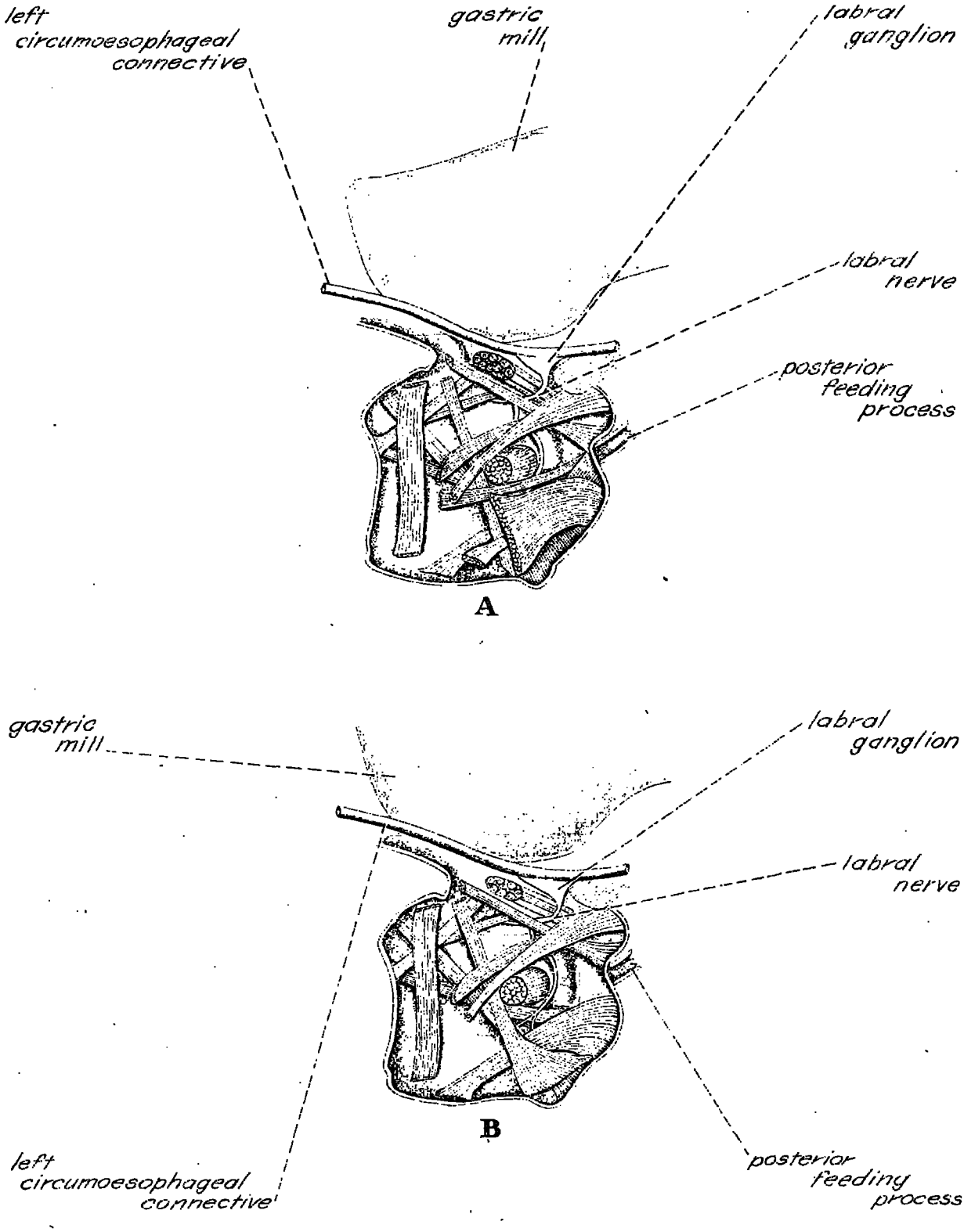

FIGURE 27.—Lateral views of labrum from the left side showing muscles and nerves. *A*. Cuticle removed to show superficial lateral muscles of left side. *B*. Interior muscles of labrum.

Although not shown in the illustrations of the labrum, material of a glandular nature is found in median ventral regions of the structure. Gland cells in the crustacean labrum have been described in the past.

B. Gnathothorax

The gnathothorax will be considered here as those segments following the protocephalon involved primarily with feeding and walking. The latter are not truly separable as body tagmata in the Crustacea, since after the mandibles and maxillae, varying numbers of walking legs may be adapted for feeding (Snodgrass 1951). Walking legs adapted for feeding are referred to as maxillipeds. In the Crustacea Decapoda, the gnathothorax is comprised of the mandibles, paragnatha, 2 pairs of maxillae, 3 pairs of maxillipeds, and 5 pairs of walking legs. In the present study, the gnathal segments will include the maxillipeds, and to the thorax will be assigned the five walking legs, without implying any morphological rigidity to the division. Above and to the sides, the gnathothorax is protected by the large dorsal shield, or carapace. Nearly all trace of segmentation has disappeared from the dorsal regions of the gnathothorax and the carapace. The few remaining sutures and markings of the carapace are not well understood in the Crustacea; consequently systematic nomenclature which has grown up around these devices is highly artificial.

The gnathothorax is constructed in the form of a rather special box arranged to provide both rigidity and movability. The immobile carapace is heavily sclerotized for protection of the internal organs and support of muscle origins, and extends ventrad in a deep fold of the tergum to cover completely the laterally placed gills (figs. 30, 31). The lateral carapace is called the branchiostegite, since the structure forms a chamber for the gills. The deep fold of the rigid carapace forming the branchiostegite permits movement between the carapace and the architecture of the ventral gnathothorax. The whole is reminiscent of a modern sedan in which a rigid body above is attached to a chassis able to respond to imperfections in the road surface. Upon the dorsal carapace orginate numerous important muscles, including some of those of the protocephalon appendages, the mandibles, maxillae, gastric mill, and dorsal and ventral abdominal muscles.

Compared to the ventral skeleton of Astacura and Brachyura, that of *Penaeus* is very lightly sclerotized (Snodgrass 1952; Huxley 1906). In the crawfishes, the median sternal elements are rigidly fused together, except for the sternum of the last thoracic segment, and thus provide a rigid keel from which the pleurosternal arms arise. Pleural (laterotergal) and sternal apodemes arise from the invaginations between the fused arms of two adjacent segmental units. Similar apodemes occur in the same locations in the ventral skeleton of *Penaeus*, but the ventral sternal element of each segmental unit is separated from its neighbors by a transverse slit of thinly developed cuticle (fig. 28). The slits permit movements between segments along the anteroposterior axis of the thorax, even though the lateral pleurosternal arms are fused.

The ventral skeleton of the gnathothorax in *Penaeus* (figs. 28, 30) consists of a series of sclerotized units which are slightly movable with respect to one another, but not articulated (fig. 28). Each unit bears the paired foramina and muscle apodemes of the jointed appendages attached thereto. The typical segmental unit contains contributions from two sources: The tergum, in the form of the dorsal tergum, and the vertical, laterotergal pleural plates (Snodgrass 1952), dorsal to the leg bases, and the sternum which comprises the ventral region between the leg bases. The dorsal condyles of the coxopodites are situated on the laterotergal plates while the ventral coxopodite condyles are sternal. In the anterior region of the gnathothorax of *Penaeus*, the pleural plates lie horizontally to become the roof of the gill chamber, similar to the arrangement in *Cambarus longulus* Girard as shown by Snodgrass (1952).

The delicate nature of the ventral skeleton in *Penaeus* is even more noticeable in lateral view (fig. 28, *A*). From here the pleurosternal arms may be seen to bifurcate in the pleural region and those of each segmental unit tend to unite dorsally in the form of a reverse-curve, or ogee, arch of the architect. Again, compared to the composite pleura of the crawfishes (Snodgrass 1952), those of *Penaeus* appear to have been retained in a somewhat more generalized condition, with 7 or 8 pleura clearly distinguishable from one another (figs. 28, 30).

Huxley (1906), Calman (1909), and other students of Crustacea often refer to the system

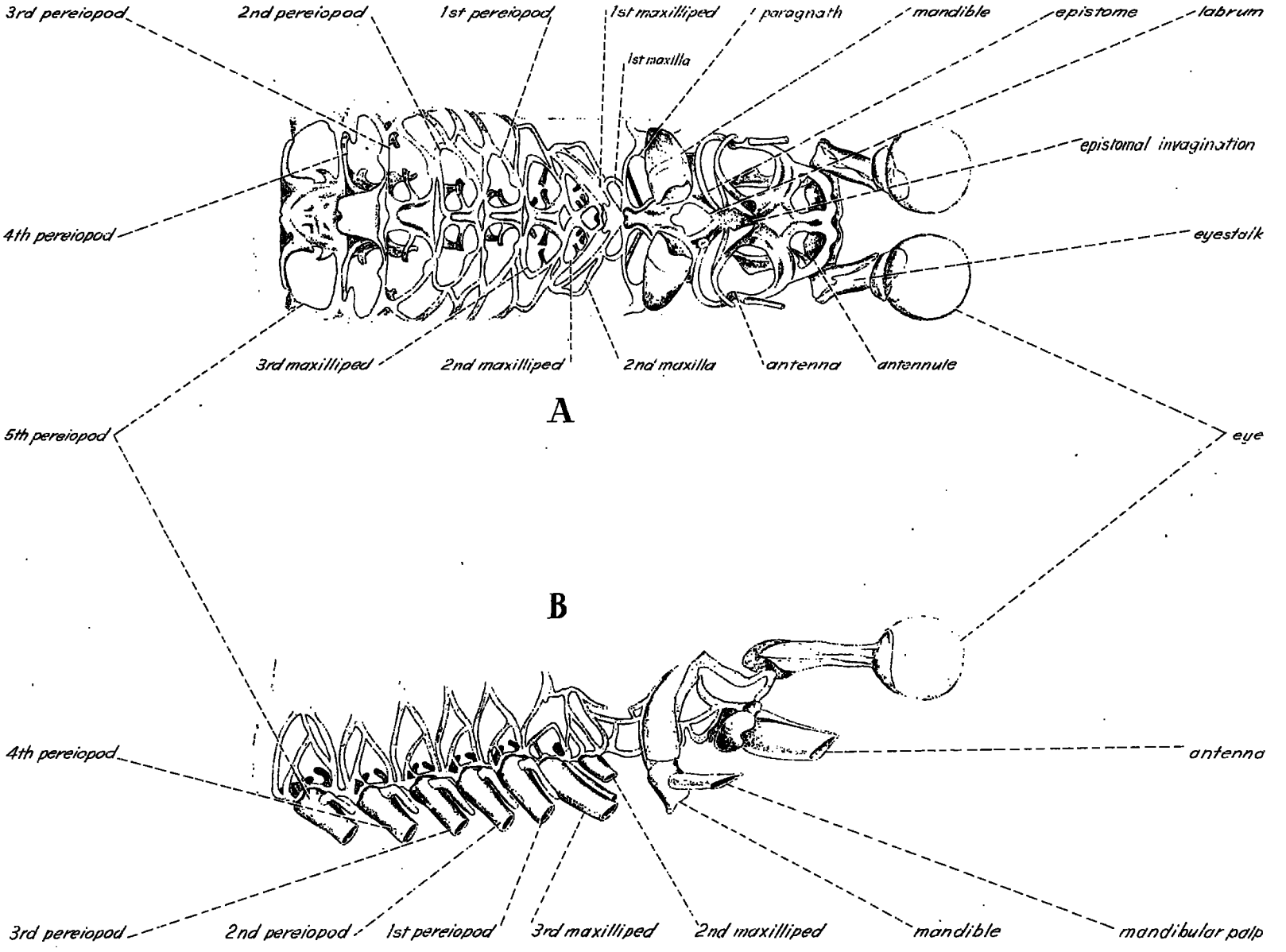

FIGURE 28.—Ventral skeleton of protocephalon and gnathothorax. *A*. Ventral view. *B*. Lateral view of right side.

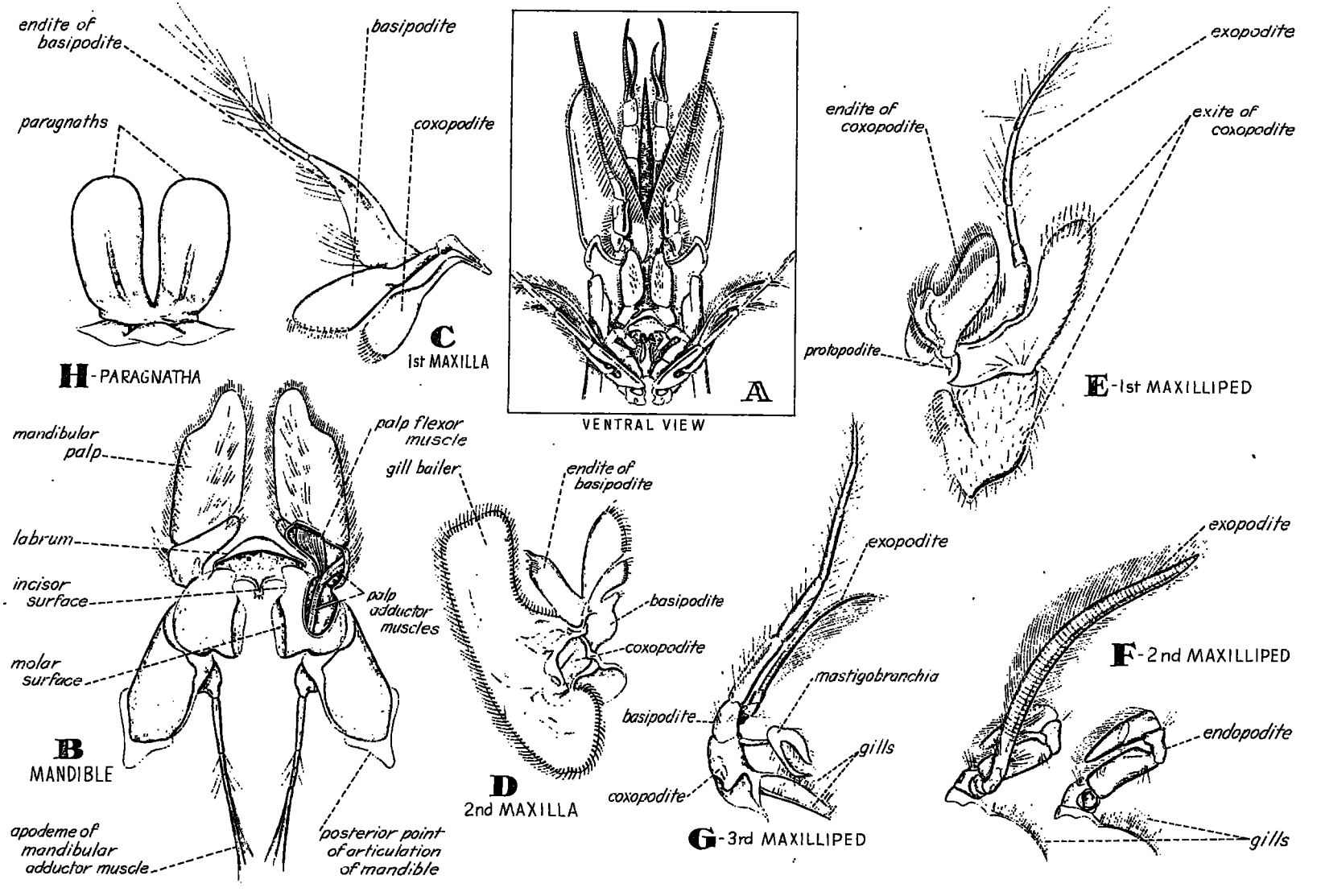

FIGURE 29.—Mouthparts.

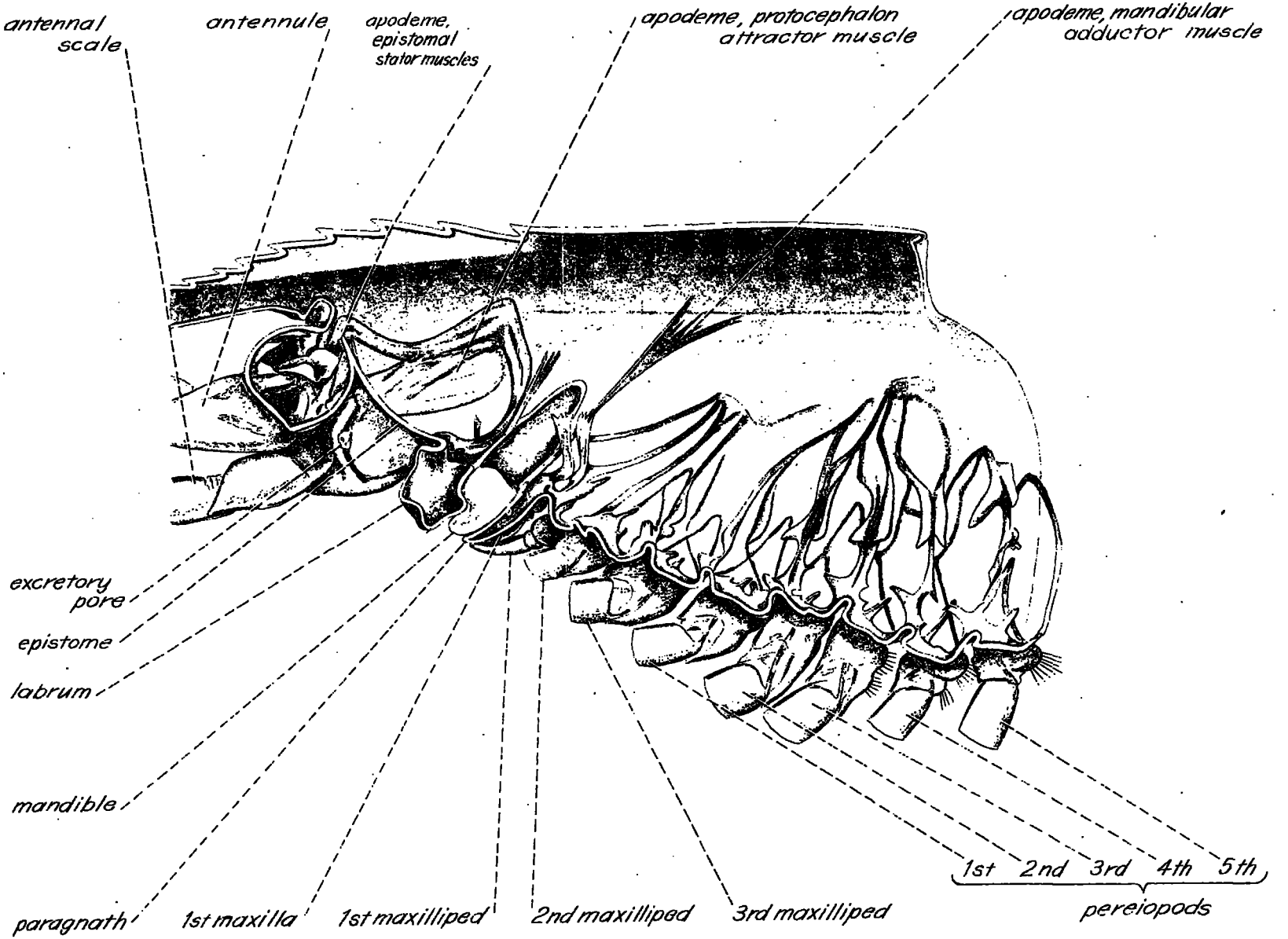

FIGURE 30.—Internal view of right half of protocephalon and gnathothorax.

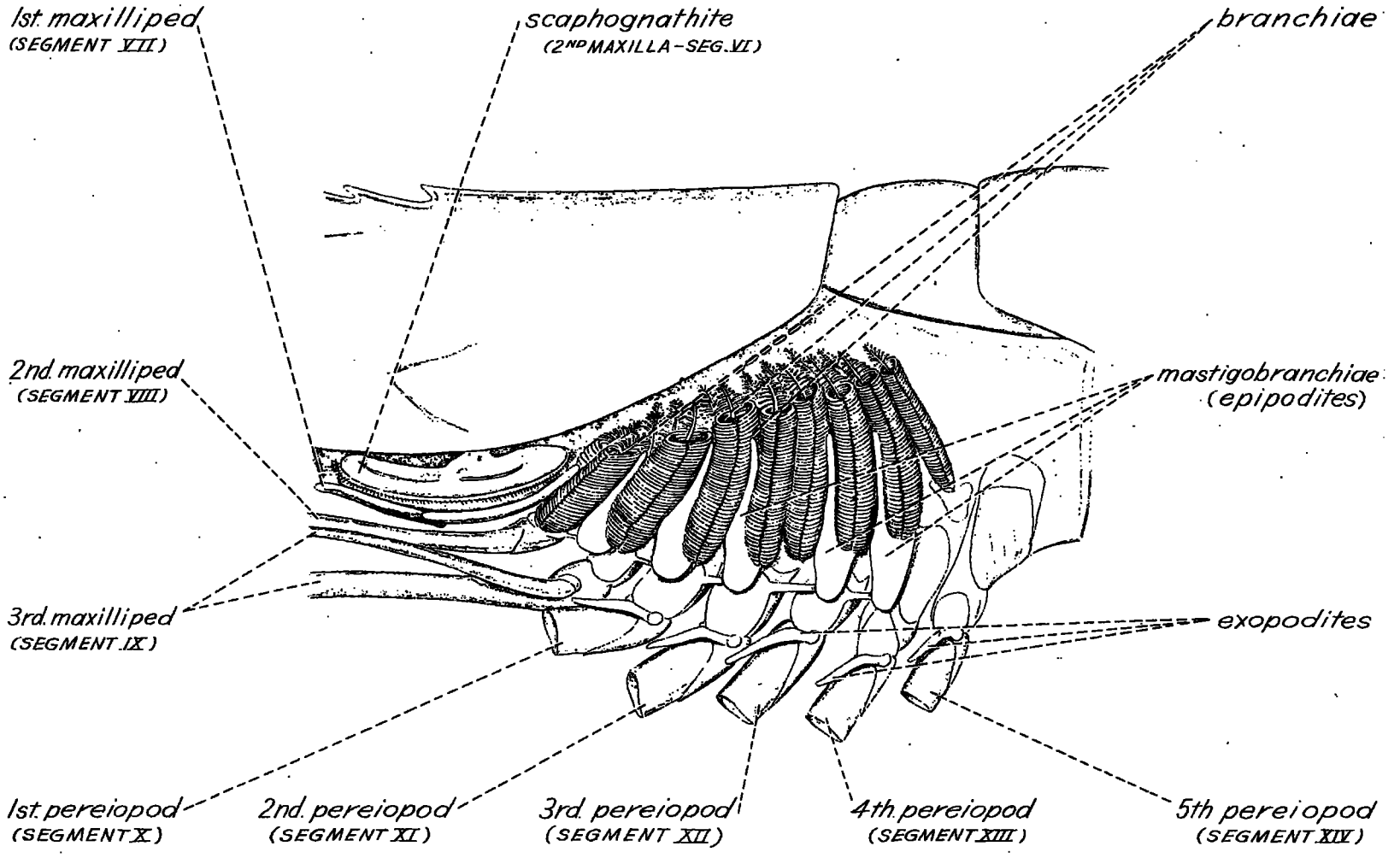

FIGURE 31.—Lateral view of left side of thorax, carapace cut away to show gill chamber, gills, and mastigobranchiae.

of pleurosternal invaginations or apodemes in decapods as the endophragmal system. In Astacura and Brachyura these apodemes fuse internally to form complex endoskeletons consisting of septate structures in the thoracic segments above the ventral nerve cord. The sternal apodemes fuse in the midline to form the sternal furca in the Insecta. In the gnathothorax of *Penaeus* the laterotergal and sternal apodemes are light and do not fuse, consequently no endophragmal system is found, unless we consider the transverse mandibular apodeme (see endosternite, fig. 38) an endophragm of some sort. This structure will be considered more fully in the treatment of the mandibles.

Although the ventral sternal elements of the penaeid gnathothorax are not coalesced into a rigid keel as in Astacura, the sternal plates do broaden from the anterior to the posterior ends of the gnathothorax, and abruptly so in the last three thoracic segments. The sternal plates of the last two thoracic segments are particularly modified in the female to receive the spermatophore from the male (figs. 28, *B;* 89). These structures will be discussed in detail in the section on the reproductive organs, page 155.

Gills

The gills may be exposed by cutting away the branchiostegal region of the carapace along the dorsal-most reaches of the inner lining of the branchiostegite, where the lining joins the laterotergal plates. The gills are thereby found to occupy a chamber (fig. 31), open to the outside ventrally and posteriorly by a narrow slot between the leg bases and thoracic wall on the inside and the extreme margin of the branchiostegite on the outside. The chamber is closed dorsally by the branchiostegal fold. The chamber is rather shallow transversely in its broad, posterior region, but becomes narrow anteriorly and is made much deeper in the region of the second maxilla by the lateral and horizontal reflection of the laterotergal, pleural plates. This narrow, deep, anterior chamber is thus a funnel, closed dorsally by the pleural bridges, medially by the vertical pleural wall, laterally by the branchiostegite, and ventrally by the large, flat coxopodite exites (figs. 29, *E;* 42) of the first maxilliped. Inside the funnel resides a pump, the scaphognathite of the second maxilla (figs. 29, *D;* 31; 41). Details of its mechanical action will be considered when the scaphognathite muscles are described, page 69.

The tightly packed gills or branchiae rise roughly dorsad from their points of origin on the leg bases and pleura (fig. 31). Each gill consists of an axial circulatory rachis from which the individual gill filaments branch. Details of gill structure will be given below in the section on respiration. Interspersed among the gills are six flat, setose, bilobed structures, the mastigobranchiae or epipodites. The lateral margins of the mastigobranchiae may be seen upon removal of the branchiostegite (fig. 31), but they are best seen if the gills are removed (fig. 32). If a shrimp whose branchiostegite has been removed is cooled so that the body processes are reduced but not stopped, the long, fine setae of the mastigobranchiae may be seen to beat in phase with the movements of the scaphognathite, or gill bailer, thus suggesting that the epipodites play a part in the water flow and cleaning of the gills.

The older literature of Crustacea abounds in so-called branchial formulae, the formal study of gill origins. In the decapods the generalized situation is 4 gills for each side of the segment (fig. 32); 1 arises from the laterotergal, pleural plates (pleurobranchia), 2 from an articular element dorsal to the coxopodite (arthrobranchia), and 1 from the coxopodite (podobranchia) (Calman 1909; Snodgrass 1952). The epipodite (mastigobranchia) arises from the coxopodite. As shown by Calman (1909), the use of the gill origins as evolutional landmarks is limited by the practical difficulty of distinguishing between the pleurobranchiae and arthrobranchiae in different species, since ontogenetic changes of gill origin are frequently seen. In fact, evidence exists suggesting that all the gills develop from the appendages, rather than from the limb bases or body wall. Apparently in *Penaeus* the podobranchiae develop embryologically from the mastigobranchiae.

As may be seen in figure 31, the branchial formula for *Penaeus setiferus* consists of 1 tiny arthrobranchia on the first maxilliped (fig. 42); 1 podobranchia, 1 mastigobranchia, and 2 arthrobranchiae on the second maxilliped; 1 mastigobranchia, 2 arthrobranchs, and 1 pleurobranch on the third maxilliped, and the first, second, and third pereiopods; 1 arthrobranchia and 1 pleurobranchia on the fourth pereiopod, and 1 pleurobranch on the fifth walking leg. In a European

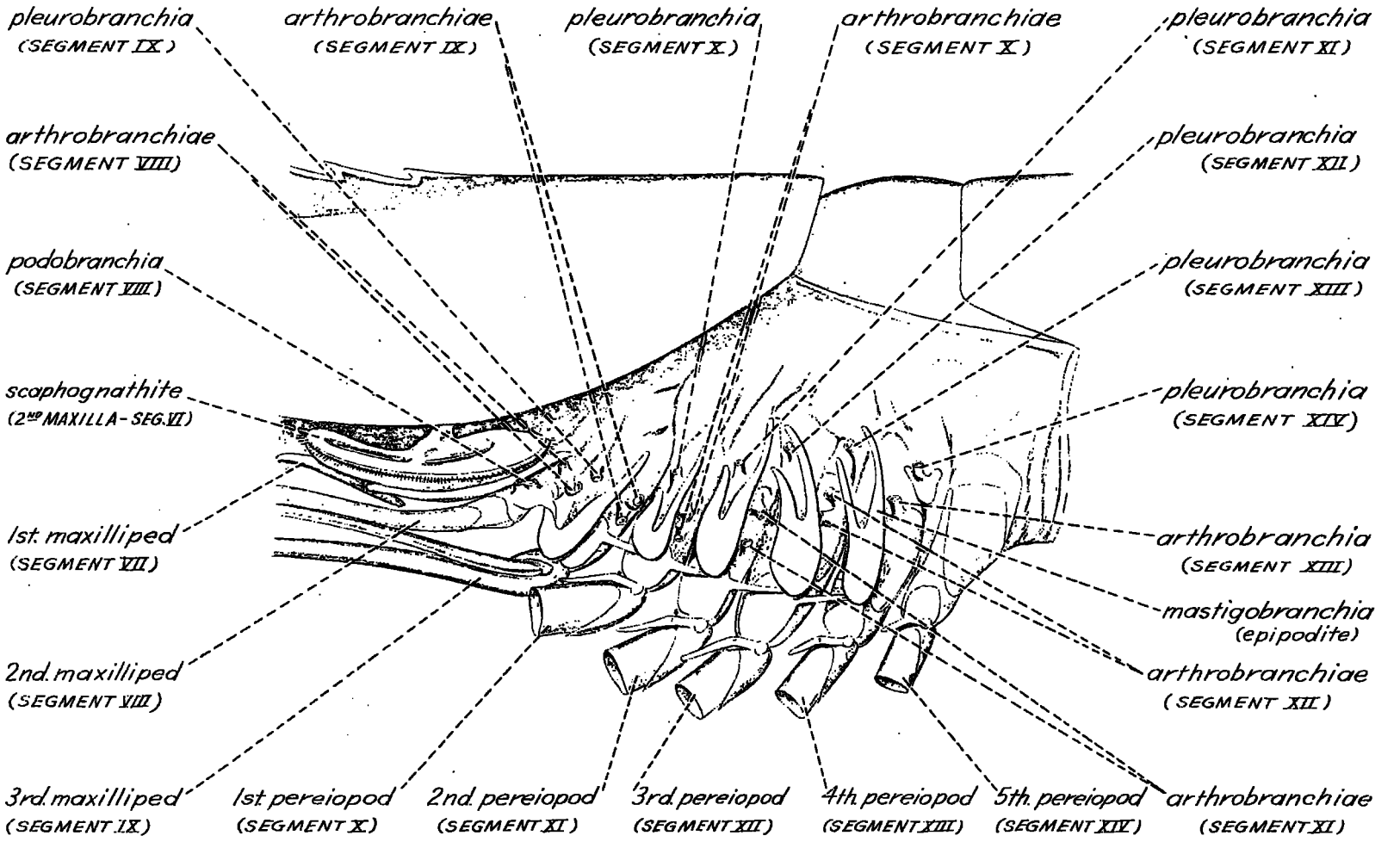

FIGURE 32.—Lateral view of left side of thorax, carapace, and gills removed to show mastigobranchiae and gill attachments.

species of *Penaeus*, Calman (1909) describes a mastigobranchia on the first maxilliped and 1 arthrobranch and 1 pleurobranch on the second maxilliped. Otherwise the branchial formulae of the two penaeids are the same.

MUSCLE ELEMENTS

Of the numerous muscles attaching throughout the gnathothoracic region, many belong to the mouthpart and thoracic appendages and will be taken up when the latter are discussed. Others are protocephalon muscles and have already been considered. Still others are associated with the alimentary canal and heart and will be dealt with in the sections concerned with these organ systems. The many remaining muscles are either small superficial lateral and ventral muscles of the thorax, or large dorsal and ventral muscles. Some of these are morphologically thoracic muscles, and some are morphologically abdominal muscles. In the functional sense, the foregoing muscles may be classified as abdominal musculature, for all of the large muscles taking origin on extensive areas of the dorsal and ventral thoracic skeleton represent the major muscular attachments of the abdomen to the thorax. Substantial movements, especially in the dorsoventral plane, are possible between the thorax and abdomen and it is these muscles which mediate the movements.

SUPERFICIAL LATERAL THORACIC MUSCLES

FIGURE 33

Stretching between the dorsal reaches of the pleural brachia are at least five superficial lateral thoracic muscles. These muscles are extremely thin and weak. Apparently they give rigidity to the thin cuticle of the area during lateral movements of the shrimp along the anteroposterior axis. Schmidt (1915) and Berkeley (1928) do not describe these muscles in *Astacus* and *Pandalus*. The possibility that the epimeral attractor muscles in *Astacus* and *Pandalus* are the superficial lateral thoracic muscles of *Penaeus* is slight.

VENTRAL MUSCLES

SUPERFICIAL VENTRAL THORACIC MUSCLES

FIGURE 36

The superficial ventral thoracic muscles (fig. 36) are situated slightly laterad of the ventral nerve cord. Their median parts are also ventrad of the nerve cord and the ventral (subneural) artery. These muscles are thin and fan shaped, broad anteriorly and narrowing to posterior attachments to thin connective tissue fasciae. In *Astacus* the lateral and ventral pleurosternal apodemes fuse above the ventral nerve cord to produce the mesophragm of the endoskeletal system. The superficial ventral thoracic muscles of the crawfish attach to these mesophragms. Berkeley (1928) finds that the ventral thoracic muscles in *Pandalus* attach to the endophragmal paraphragms, the lateral fusion product of the pleural and sternal apodemes. As stated above, *Penaeus* has neither paraphragm or mesophragm; however, one would expect the superficial ventral muscles to attach to the little pleurosternal apodemes near the limb foramina. Contrary to such expectations, the superficial ventral thoracic muscles in the white shrimp attach to small apodemes on the pleurosternal brachia. The result is to place these muscles ventrad of the nerve cord. Their function of drawing the ventral thoracic segments together is probably the same as in *Pandalus* and *Astacus*.

In *Penaeus* 7 pairs of superficial ventral thoracic muscles are evident compared to 6 for *Astacus* and *Pandalus*. Schmidt (1915), however, finds two superficial ventral thoracoabdominal muscles in *Astacus* compared to one in *Penaeus* and *Pandalus*.

ANTERIOR THORACIC MUSCLES

FIGURES 33 TO 36

By far the largest ventral muscles of the thorax are the lateral and median anterior thoracic muscles (figs. 33 to 36). The anterior-most muscle of these is the lateral anterior thoracic muscle 1 (figs. 33 to 36). This muscle originates by a large, lateral oval in the region just posterior and slightly dorsad of the hepatic spine. In dorsal view (fig. 35) the muscle may be seen to run posteroventrally to join the other anterior thoracic muscles on the ventral surface of the thorax. In this area all the anterior thoracic muscles are interconnected to segmentally arranged fasciae.

The other lateral anterior thoracic muscles (figs. 34, 35), Nos. 2, 3, 4, and 5, may best be seen in ventral view (fig. 36). These muscles take origin from the ventrolateral fascia of each thoracic segment and run posteriorly into the abdominal musculature with the other anterior thoracic muscles.

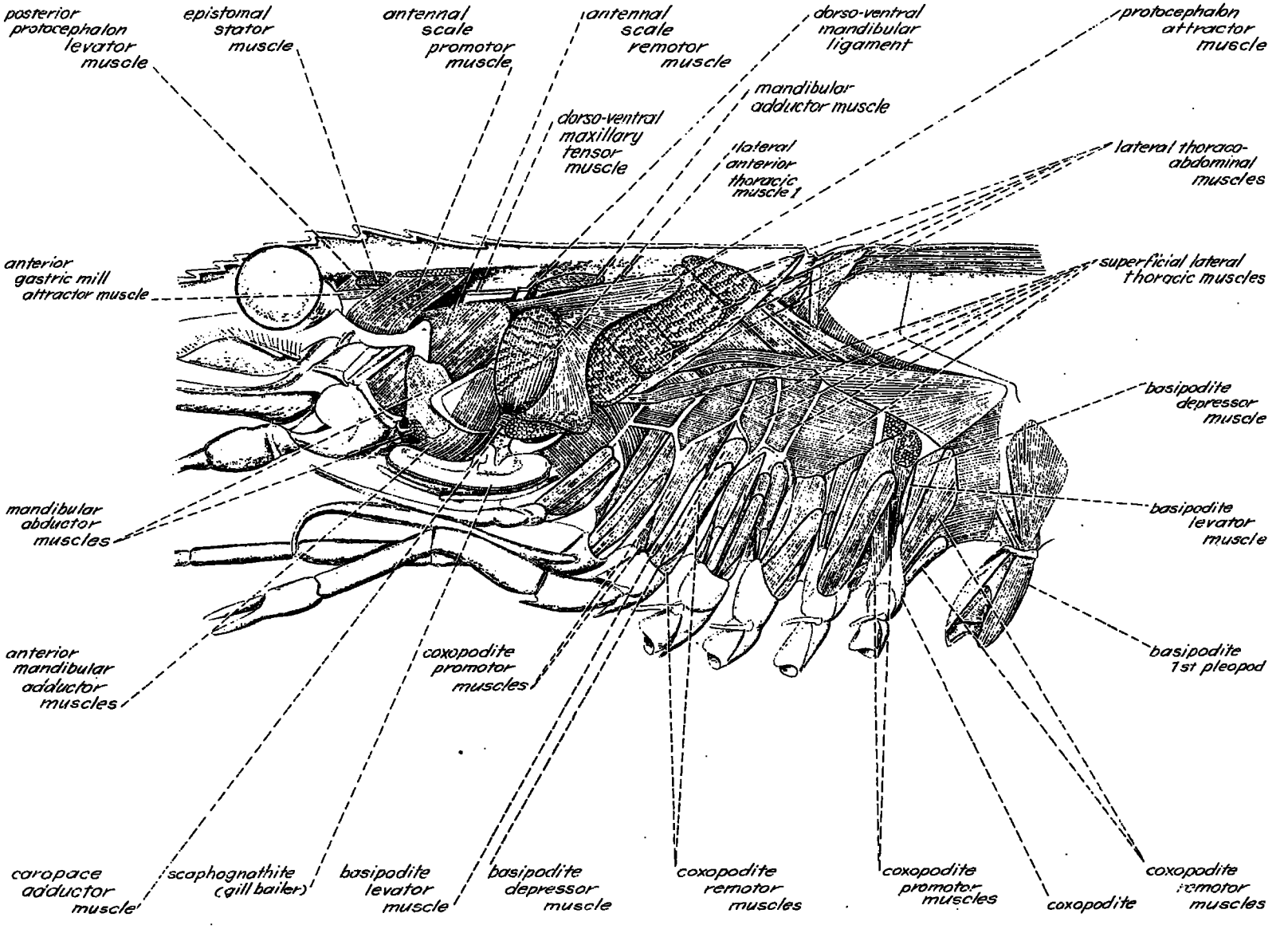

FIGURE 33.—Lateral view of left side of protocephalon and gnathothorax showing muscle origins. Carapace and left body wall removed.

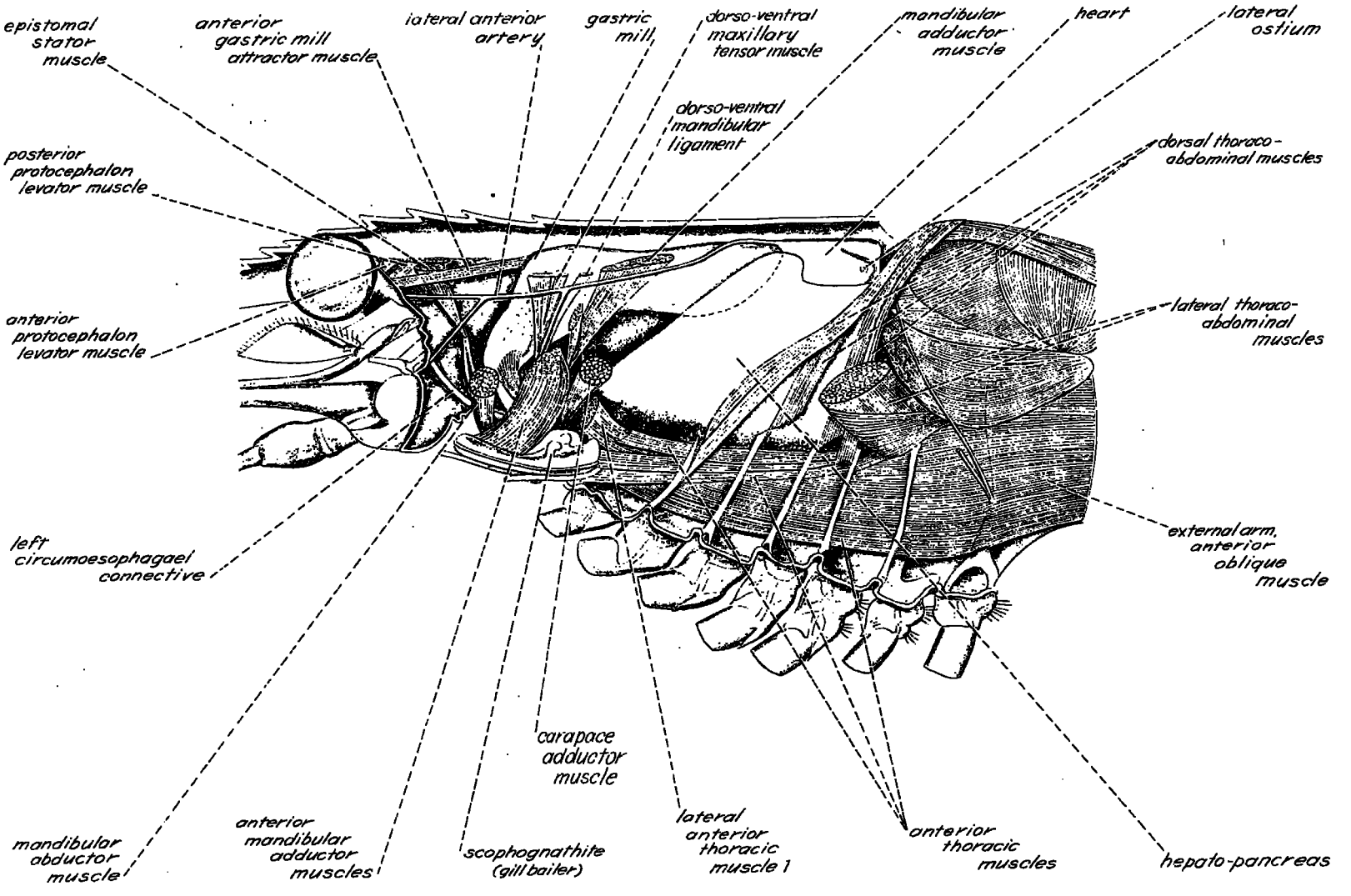

FIGURE 34.—Lateral view of left side of gnathothorax. Lateral muscles removed to show medial muscles and internal organs.

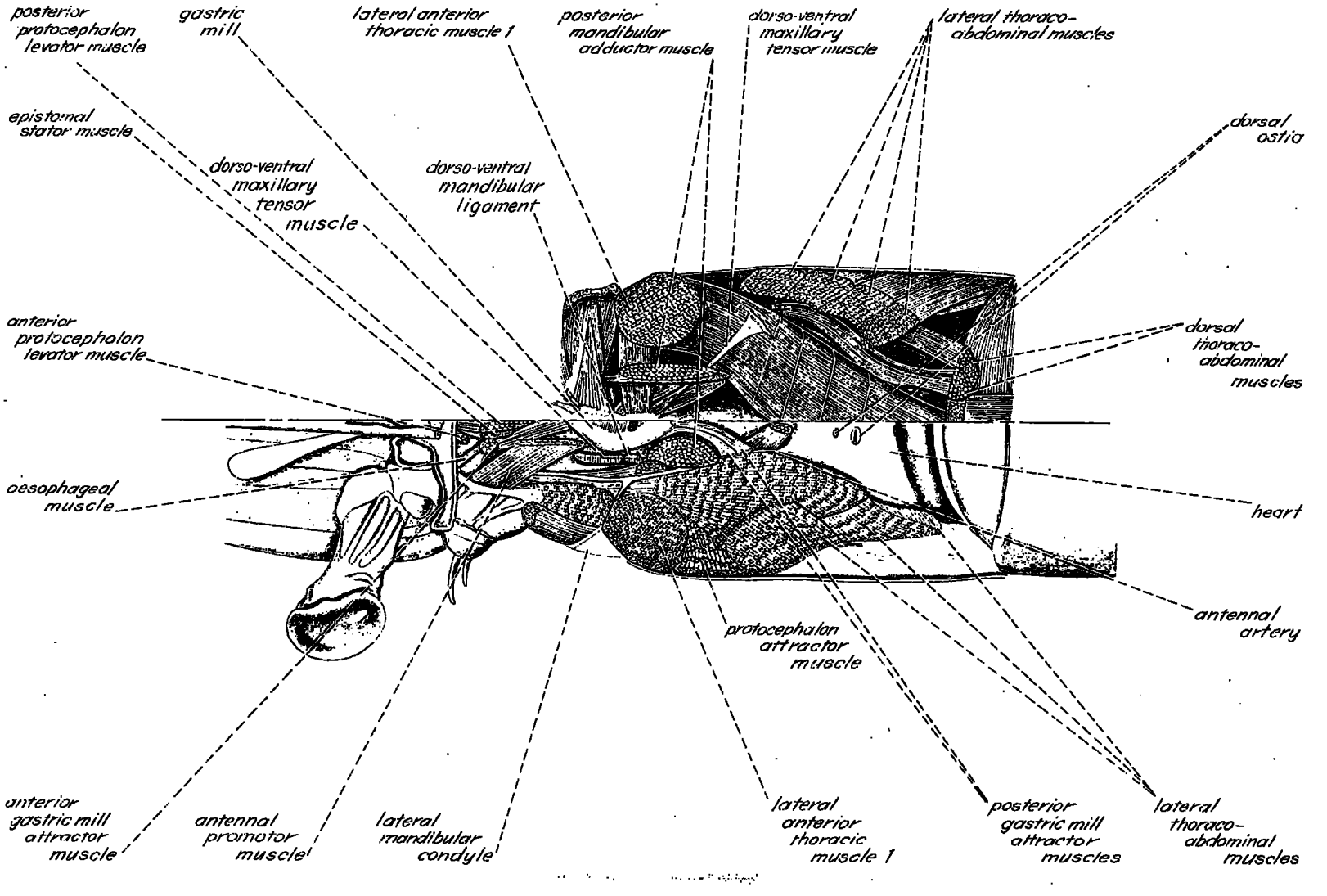

FIGURE 35.—Dorsal views of protocephalon and gnathothorax. Lower section, dorsal muscles. Upper section ventral muscles.

The median anterior thoracic muscles (fig. 36) also originate in segmentally arranged fasciae on the ventral surface. Joined by the other anterior thoracic muscles, the median anterior thoracic muscles pass caudad into the abdominal muscles.

The anterior thoracic muscles play an important part in the powerful flexion of the abdomen on the thorax made by the white shrimps when the animals withdraw suddenly from danger. The anterior thoracic musculature is similar to that in *Pandalus* and *Astacus*, except that in the crawfish these muscles are somewhat smaller. The anterior thoracic muscles are fully homologous in all the forms mentioned here.

VENTRAL HEAD LIGAMENTS

FIGURES 37, 38

The ventral head ligaments are small structures attached between the lateral wings of the epistome and the mandibular endosternite (fig. 37). Apparently they hold the endosternite in position anteriorly. Schmidt (1915) calls these ligaments the ventral head muscles in *Astacus*. Grobben (1917), however, denies the presence of muscle fibers in the structures and suggests the name ligament for muscle. Berkeley (1928) describes the organs as ventral head muscles in *Pandalus*.

CARAPACE ADDUCTOR MUSCLE

FIGURES 33, 34, 37, 38

The carapace adductor muscle originates on the carapace just ventrad of the most ventral part of the protocephalon attractor muscle (fig. 33). The origin point of the carapace adductor is slightly dorsal to the horizontally turned pleural plates, above the gill pump, or scaphognathite. The muscle runs directly mesad to insert on the posterodorsal midline of the endosternite (fig. 37). The carapace adductor muscle functions as the major position retainer of the endosternite. It may also play a part in necessary distortions of the carapace associated with feeding, molting, and the like.

The carapace adductor muscle appears in many crustacean groups (Grobben 1917). Schmidt (1915) describes it in *Astacus* as the musculus dorsoventralis posterior and Berkeley (1928) has adopted his terminology for the muscle in *Pandalus danae*. Grobben (1917) considers the carapace adductor a useful phyletic character, because of its frequent occurrence, and we are indebted to this worker for the name. Grobben described the carapace adductor muscle (Schalenschliessermuskel) in species of *Penaeus*, *Palaemon*, *Leander*, *Pandalus*, *Galathea*, and *Athanas*.

DORSAL MUSCLES

DORSAL THORACOABDOMINAL MUSCLES

FIGURES 34, 35

Inserting on the anterodorsal tergum of the first abdominal segment and running forward and down to the laterotergal brachia of the thorax are four pairs of long, slender muscles, the dorsal thoracoabdominal muscles (figs. 34, 35). In dorsal view (fig. 35) the area of attachment may be seen on the dorsal part of the first abdominal segment. The muscles divide around the heart and hepatopancreas as they go to the lateral wall of the thorax. Each muscle originates on its own pleural arm, suggesting that the muscles each belong to specific thoracic segments. Upon contraction the dorsal thoracoabdominal muscles extend the first abdominal segment with respect to the thorax, in opposition to the action of the anterior thoracic muscles.

The dorsal thoracoabdominal muscles are evidently the same muscles as those designated as the dorsal thoracoabdominal muscles in *Pandalus* and *Astacus*, although they appear to be relatively larger in size in the caridean shrimp.

LATERAL THORACOABDOMINAL MUSCLES

FIGURES 34, 35

From an area laterad of the heart and the dorsal thoracoabdominal muscles, the lateral thoracoabdominal muscles (figs. 34, 35) originate along a diagonal line just above the dorsal edge of the inner branchiostegal fold and run ventrally and caudad to junctions with abdominal muscles. Very likely the thoracoabdominal muscles are in reality abdominal muscles. Unlike the anterior thoracic muscles, the lateral thoracoabdominal muscles are not segmented. At least four pairs of these muscles covering a broad area laterally are found in *Penaeus*. Functionally, the lateral thoracoabdominal muscles are involved in the flexing of the abdomen, reinforcing the action of the anterior thoracic muscles. Berkeley (1928) suggests that contractions of the muscles on one side may bend the abdomen laterally in *Pandalus*, and such a movement may also take place in *Penaeus*. The lateral thoracoabdominal muscles of *Penaeus* are

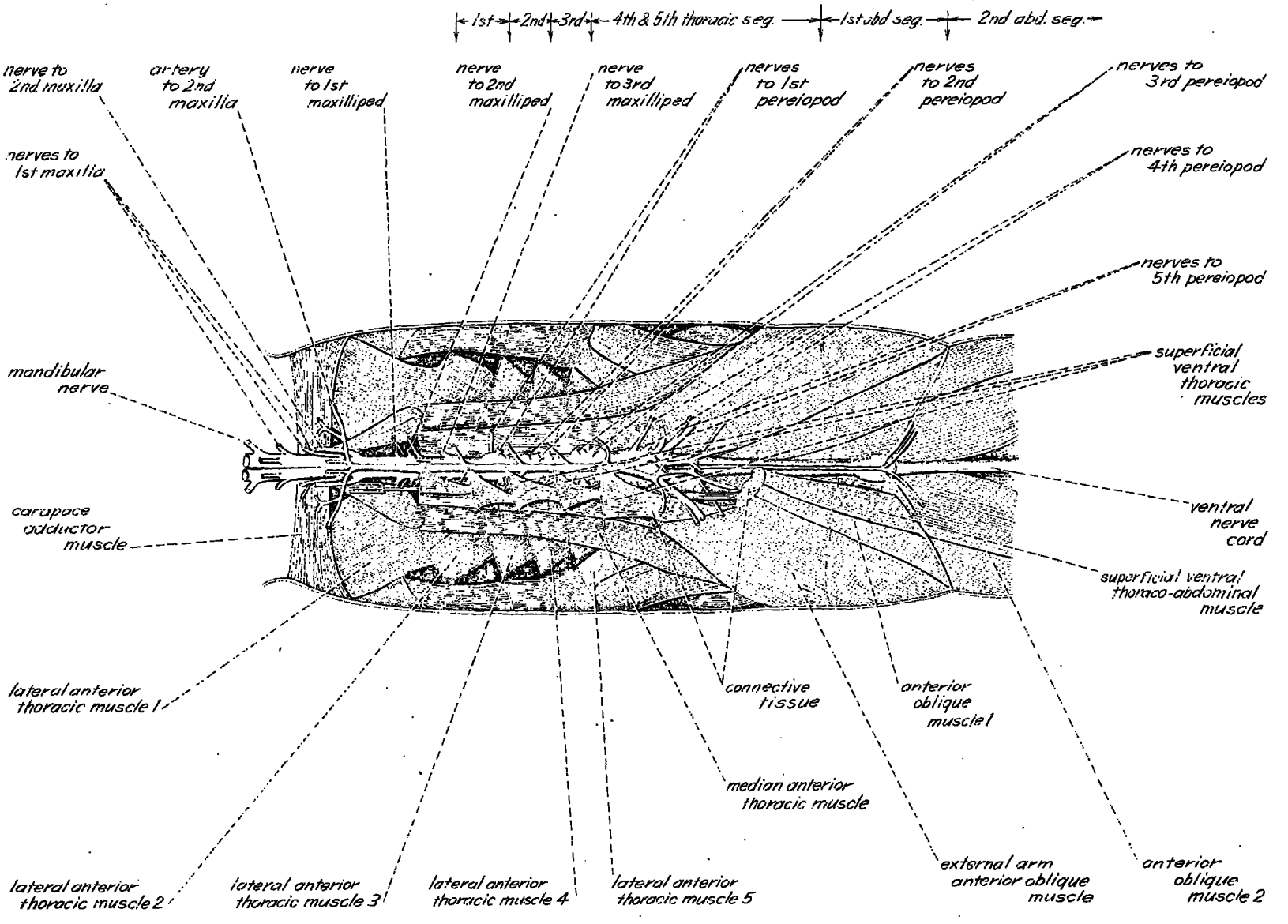

FIGURE 36.—Ventral view of gnathothorax showing muscles, nerves, and blood vessels.

undoubltedly homologous to the musculi laterales thoracoabdominales of *Astacus* and *Pandalus*.

APPENDAGES OF THE GNATHOTHORAX

The generalized limb of Crustacea is thought to consist of a basal protopodite, made up of a proximal coxopodite and a distal basipodite, bearing two rami, the exopodite and endopodite. This simple arrangement has been retained in the pleopods of Crustacea, notably the Natantia. The typical gnathothoracic limb of *Penaeus*, if one can be said to exist, has the basal coxopodite and basipodite, the latter with a well-developed endopodite and a reduced exopodite. The coxopodite of the white shrimp is attached to the limb base by means of diametrically placed condyles, the axis of the condyles varying in accordance with the location and function of the appendage. The basipodite is attached to the coxopodite by dicondyles whose axis is at right angles to that of the coxal condyles. Distally, the endopodite is divided into the typical five articles: the ischiopodite, meropodite, carpopodite, propodite, and dactylopodite. The coxopodite may give rise to lateral epipodites and in some cases gills.

The exopodite may be modified to long, frond-shaped filaments (second and third maxillipeds) or reduced to a small finger projecting from the basipodites (fig. 31). The gnathal appendages, excluding the second and third maxillipeds, tend to be modified substantially from the typical plan given above.

1. MANDIBLES

SKELETAL ELEMENTS

Of the gnathothoracic appendages, the mandibles are perhaps the most difficult to understand. For one thing the dorsal and internal manifestations of this and other gnathal segments are coalesced or obliterated. In addition, the mandible is complicated by the presence of a true endoskeleton (figs. 37, 38), lying transversely in the gnathothorax above the nerve cord and supporting the gastric mill. Nevertheless, Snodgrass (1951b) adduces strong evidence in support of the evolution of the mandibles from a typical limb on the basis of a comparative study of the skeleton and muscles of the arthropod mandible.

The sclerotized parts of the mandibles in *Penaeus* are relatively simple. The strongly sclerotized incomplete tube of the mandible, with its ventromedial incisor and molar surfaces and anterior palp, may be seen in ventral view (fig. 29, mandible). The incisor surfaces consist of 2 or 3 sharp ridges used in cutting and tearing food, whereas the flat molar surfaces are for grinding. Both kinds of surface are heavily impregnated with a hardening substance, possibly calcium carbonate, in the form of crystalline stones molded into the cuticle. The stones may be removed by dissection. The tubular part of the mandible, the body, is said to be the coxopodite, whereas the palp is thought to be part of the endopodite (Calman 1909). The subcylindrical body of the mandible is distinctly divided into a large basal portion and a distal lobe, immovably connected to the basal part. In the mandible of *Anaspides*, the basal part is called by Snodgrass (1952) the coxopodite and the distal lobe an endite of the coxopodite. It is interesting to note that the distal gnathal lobe is movable in some arthropods, notably the Diplopoda, and similar to the maxillary lacinia of insects.

The mandibular palp, a part of the endopodite, extends anteriorly from the body of the mandible in the form of a flat, setose lobe shaped to fit around the labrum laterally and anteriorly. The larger part of the broad palp arises from a basal segment, the latter being narrow at its posterior junction with the mandible and broad anteriorly.

The mandible of *Penaeus* is attached to the ventral skeleton by a medial condyle located at a point on the posterior arm of the epistome just laterad of the labrum (fig. 28), and by thin cuticle between the mandible and the lateral extension of the posterior epistomal arm. The mandible has also a lateral condyle on the side of the carapace. Among taxonomists the external manifestation of this lateral mandibular condyle is known incorrectly as the hepatic spine. Snodgrass (1951) erroneously shows two mandibular condyles in *Penaeus* on the laterally spread, posterior bars of the epistome, and does not mention the lateral mandibular condyle. This is curious since, as Snodgrass (1935, 1951b) has shown in earlier work, a significant phyletic series is evident from the study of the arthropod mandible, based upon the evolutional response of the musculature to restriction of mandibular movements. In the course of the work, Snodgrass makes the fact amply clear that in no case is the site of the primary (lateral) condyle ever to be found on the epistome. Rather, the generalized arthropod man-

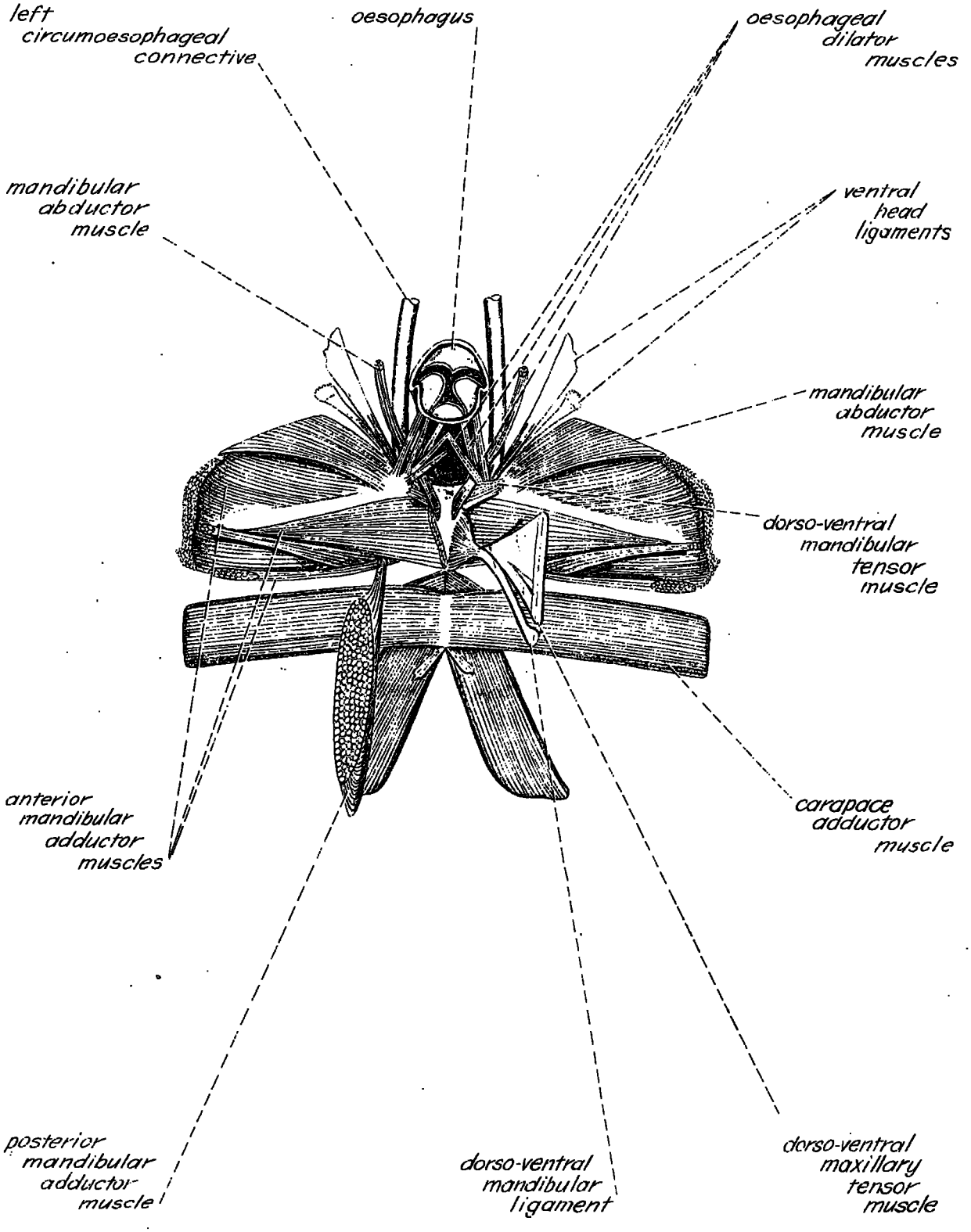

FIGURE 37.—Dorsal view of mandibular musculature.

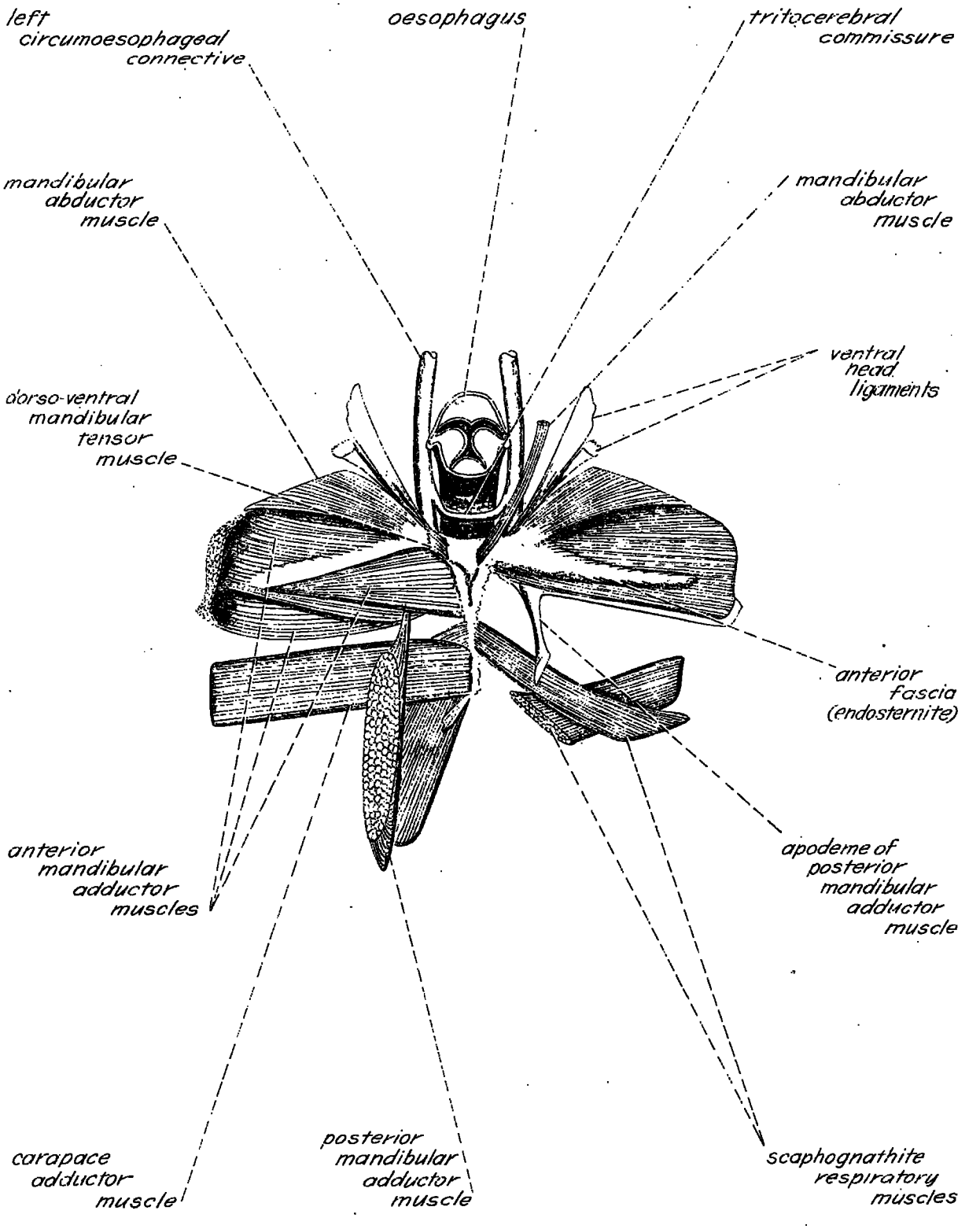

FIGURE 38.—Dorsal view of mandibular musculature, dorsal-most muscles removed.

dible articulates with the mandibular segment at a single point laterally, an arrangement which permits the varied movements of the organ seen at this stage of its evolution.

The monocondylic mandible is found in all the mandibulate arthropods except some higher Crustacea and the pterygote insects (Snodgrass 1935). In the latter forms, a secondary condyle on the epistome is added mesad of the primary lateral condyle. Mandibular movements now become restricted to those about the dicondylic axis. With simplicity, furthermore, comes strength. Snodgrass (1935, 1951b) has described the evolutional simplification of mandibular musculature which follows in groups developing the dicondylic mandible.

A comparison of the mandibular hinges and musculature of the white shrimp with the account of Snodgrass indicates that *Penaeus* represents a transitional form; for, although the shrimp mandible is dicondylic, its musculature is strongly reminiscent of the monocondylic musculature in apterygote insects, myriapods, and lower Crustacea.

The endoskeleton of the mandibles, mentioned above, is a thick tendon situated between the mandibles and upon which the heavy ventral adductor and abductor muscles insert (figs. 37, 38). The substance of the endoskeleton is extremely tough connective tissue, not sclerotized. Such cuticular components of the structure as may exist are not hard. The mandibular endoskeleton of Crustacea Malacostraca has been variously interpreted. In forms having a well-developed endoskeletal system in the thorax, the mandibular element is considered to be a part of that system.

In *Astacus*, Schmidt (1915) refers to the structure as the endoskeleton, specifically, the head apodeme. Snodgrass (1935), referring to a similar structure in the mandibles of a diplopod, uses the term median ligament. Whether this worker attributes the median ligament to the endoskeleton is not clear. Berkeley (1928) designates the same material in *Pandalus* as the anterior fascia. She evidently considers it to be endoskeletal in nature, and the fusion product of the mandibular and first maxillary segments. Grobben (1917) apparently believes the mandibular tendon to be endoskeletal, naming it the median transverse mandibular tendon. Snodgrass (1952) refers to an intergnathal ligament in *Anaspides tasmaniae* Thomson and an endosternum in *Cambarus longulus* Girard, in speaking of the structure. In the course of a histological study of muscular and skeletal elements in various Crustacea, Debaisieux (1954) emphasizes that the mandibular endoskeleton is an endosternite, fully homologous in his opinion with that of Arachnida.

No further evidence is offered in the present study for the homology of the endosternite of Arachnida with the mandibular endoskeleton of Crustacea. However, from the work of Debaisieux (1954) on the structure in Crustacea, we can be fairly certain that the mandibular endoskeleton of all crustaceans mentioned above are homologous. In response to the plethora of names for the mandibular endoskeleton, the present writer sees no objection to the terms "endosternite" or "endosternum" given by Debaisieux (1954) and Snodgrass (1952). These names are used here as equivalent to one another and to the expression, "mandibular endoskeleton." Whether an endoskeleton and an endosternite are morphologically equal is not made clear in the literature.

As a final word on the composition of the endoskeleton, it will be recalled that Schmidt (1915) describes two small medial muscles between the mesophragms of the endosternite, the endophragmal compressor muscles. Grobben (1917) denies the existence of muscle fibers in this material in the crawfish and establishes that the area is composed of connective tissue.

MUSCLE ELEMENTS

MANDIBULAR ABDUCTOR MUSCLES

FIGURES 33, 37, 38

At least three mandibular abductor muscles (figs. 33, 37, 38) are found in *Penaeus*. The smallest is the most anterior. This muscle arises in connective tissue in the anterior region of the gnathothorax, lateral to the esophagus and dorsal to the circumesophageal connective, and runs posteriorly and ventrad to insert on the anteromedial part of the mandibular endoskeleton. Contractions of these slender muscles aid in opening the mandibles. No counterpart of the muscle is described for the other crustaceans to which reference has been made.

The large and important mandibular abductors originate in connective tissue on the laterotergal plates (fig. 33) and run posteromedially to insertion areas on the mandibular endoskeleton (figs. 37, 38). Their contractions serve to open the

gnathal elements of the mandibles. These two mandibular abductor muscles are fully homologous with the major and minor mandibular abductor muscles in *Astacus* and with the mandibular abductor muscle in *Pandalus*. Presumably the homology holds for the major and minor mandibular abductors of *Callinectes*.

DORSOVENTRAL MANDIBULAR TENSOR MUSCLE

FIGURE 37

The long tendon of the dorsoventral mandibular tensor muscle (fig. 37) originates in connective tissue on the dorsal carapace by an extremely thin band mesad of the origin of the antennal promotor muscle. The thin apodeme runs ventrad to the muscle body which inserts on the anterior part of the mandibular endoskeleton, slightly laterad of the small mandibular abductor muscle. The muscle pulls the mandibular endoskeleton dorsad, possibly as a minor adjustment of the mandible in feeding. The muscle was named by Grobben (1917), who described it in a number of crustaceans, including species of *Penaeus*, *Palaemon*, *Leander*, *Pandalus*, and *Nebalia*. The description by Berkeley (1928) of *Pandalus danae* does not include the dorsoventral mandibular tensor muscle, although it is almost certainly present in that species. The muscle is missing in *Astacus*.

ANTERIOR MANDIBULAR ADDUCTOR MUSCLES

FIGURES 33, 34, 37, 38

The anterior mandibular adductor muscles (figs. 33, 34, 37, 38) are the largest occupants of the subcylindrical mandibular body. At least three muscles are evident in *Penaeus*, although a study of the nerves may show that the muscle groups are actually parts of the same muscle. The adductors originate laterally throughout the body of the mandible and insert extensively over the tissues of the mandibular endosternite. Contractions of the anterior mandibular adductors draw the gnathal lobes of the mandibles together. The action is direct and efficient. The anterior mandibular adductor muscles of *Penaeus* are the homologs of the musculus adductor anterior mandibulae in *Astacus* and *Pandalus*.

DORSOVENTRAL MANDIBULAR LIGAMENT

FIGURES 33, 34, 35, 37

The dorsoventral mandibular ligament (figs. 33, 34, 35, 37) originates in the thick connective tissue of the dorsal carapace by a narrow, thin, apodeme between the dorsal edges of the protocephalon attractor muscle and the gastric mill (fig. 35). The apodeme runs anteroventrally to a thin, fan-shaped muscle inserting on the dorsal surface of the endosternite. It crosses over the tendon of the dorsoventral maxillary tensor muscle medially. The muscle is closely appressed to the fibers of the dorsoventral maxillary tensor, but may be separated readily from the latter in the sagittal plane. The dorsoventral mandibular ligament (or muscle) aids in retaining the endosternite in position.

The structure was found in a species of *Penaeus* and of *Palaemon* and named by Grobben (1917). Since the dorsoventral mandibular ligament actually ends in a small muscle, Grobben's name should be replaced with the name, "dorsoventral mandibular muscle." A muscle in *Pandalus*, designated by Berkeley (1928) as the musculus dorsoventralis anterior 2, is probably the dorsoventral mandibular ligament.

POSTERIOR MANDIBULAR ADDUCTOR MUSCLE

FIGURES 30, 33, 34, 35, 37, 38

Taking origin in an elongate ovoid on the dorsal carapace is a large, wedge-shaped muscle, the posterior mandibular adductor muscle (figs. 35, 37). Growing narrower as it passes ventrad, the posterior adductor attaches to a broad apodeme (figs. 29, *B*; 30, apodeme, mandibular adductor muscle). The adductor apodeme arises from the posterior margin of the semitubular mandibular body. The apodeme is so placed that a dorsal pull of the powerful muscle brings the gnathal lobe to the midline. The posterior mandibular adductor muscles are widely represented in the Arthropoda.

MANDIBULAR PALP FLEXOR MUSCLE

FIGURE 29

The muscles operating the mandibular palp are situated either in the gnathal lobe of the mandible or in the basal segment of the palp. The distal lobe of the palp contains no muscles. The mandibular palp flexor muscle (fig. 29) originates in the proximal region of the basal palp segment near the foramen between the gnathal lobe and the palp base. The muscle runs distally, becoming broad and flat, and inserts on the posteroventrad margin of the distal palp lobe. In action, the mandibular palp flexor turns the distal lobe ventrad. An ap-

parently similar muscle in the palp of *Astacus* is called by Schmidt (1915) a palp flexor also. Berkeley (1928) describes both a palp flexor and a palp extensor in the body of the mandible of *Pandalus*.

MANDIBULAR PALP ADDUCTOR MUSCLES

FIGURE 29

The proximal, and larger, mandibular palp adductor muscle originates on the posterior wall of the gnathal lobe of the mandible and inserts on the medial margin of the basal palp foramen. The smaller palp adductor originates dorsad of the insertion of the larger palp adductor on the medial margin of the gnathal lobe foramen. Contractions of these muscles turn the palp segments toward the midline. The proximal mandibular palp adductor muscle is probably homologous with the musculus flexor *a* mandibulae of *Astacus* and either the palp flexor or extensor of *Pandalus*.

2. PARAGNATHA

The paragnatha (figs. 29, 39) are two rounded lobes suspended from small foramina in the ventral skeleton immediately posterior to the gnathal lobes of the mandibles. Their cuticle is very thin, except for a slightly thickened ridge along the posterior surface of each paragnath. No intrinsic muscles are found in the body of the paragnath in *Penaeus*; however, a small muscle, the paragnathal muscle (fig. 39), inserts on the lateral margin of the paragnath. The paragnathal muscle moves the paragnath laterally and anteriorly against the gnathal lobe of the mandible.

Classically, the paragnatha have been interpreted as a secondary development of the mandibular segment, on grounds of their embryonic development and because of their innervation by mandibular nerves. Also, the view that they belong to the maxillae has been expressed. The idea that the paragnatha are reduced true appendages has in general been discounted, despite the presence of movable terminal lobes in the paragnatha of Tanaidacea (Crustacea). Snodgrass (1935) mentions the similarity of the insectan superlinguae to the crustacean paragnatha. This worker feels, apparently, that there is no evidence that the paragnatha are appendicular or that the superlinguae and paragnatha are homologous structures. He does indicated (Snodgrass 1952) in a study of *Cambarus*, that the paragnatha are

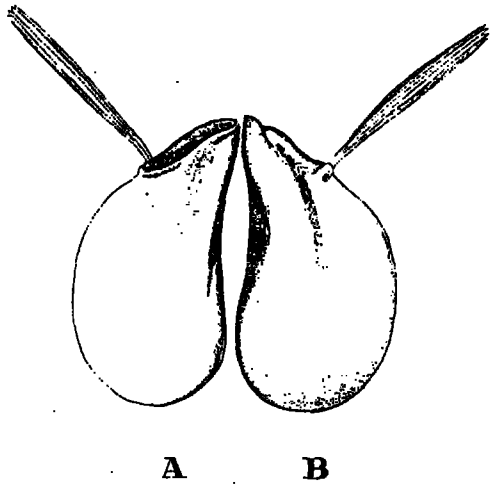

FIGURE 39.—Paragnatha. *A*. Anterior view. *B*. Posterior view.

mandibular entities. In a comparative study of arthropod nerves, Henry (1948a) assigns the paragnatha to the mandibular segment by virtue of their innervations. She invariably places the paragnathal nerves in a position posterior to those of the mandibles.

Recently, Chaudonneret (1955, 1956), in a detailed study of the gnathal nerves of *Orconectes limosus* (Rafinesque) (=*Cambarus affinis* Say), takes issue with Henry (1948a) and advances the idea that the paragnathal nerves are in fact anterior to those of the mandibles and entirely distinct from the mandibular nerves. On other grounds, furthermore, this worker suggests that the paragnathal foramina are anterior to the mandibular foramina and holds that their relative positions with respect to the mouth are constant in the Malacostraca. In the opinion of Chaudonneret (1956), the facts make difficult the interpretation of the paragnatha as either epithelial lobes or parts of the mandibles. Instead, this investigator thinks that the paragnatha may belong to a reduced premandibular, paragnathal segment homologous to the insectan superlingual segment.

If the paragnatha are indeed premandibular and homologous to the superlinguae, an interpretation which Snodgrass (1935) seems to consider possible, certain aspects of the morphology of the insect hypopharynx will need review. Careful study of the paragnathal nerves in *Penaeus* tends to support the view of Chaudonneret (1956) that this nerve is slightly anterior to the mandibular nerve. However, the gross anatomy will have to

be verified by histological work before a decision on this interesting point can be made.

3. MAXILLAE

3a. First Maxillae

SKELETAL ELEMENTS

The first maxillae articulate with the ventral gnathal skeleton at relatively large foramina slightly caudad and laterad of the paragnathal foramina (fig. 28, *A*). The medial lobes of these accessory feeding organs fit closely to the posterior surfaces of the paragnatha (fig. 30), and thus project anteroventrally over the mouth from the gnathal framework.

Although the first maxillae is true appendages, they are much modified for functional ends. The body of the first maxilla is produced into several lobes and a flagellum (figs. 29, 40). The flat medial lobes are the proximal coxopodite and the distal basipodite. The medial edges of these lobes are covered with stiff hairs or spines, those on the basipodite margin being especially strong. The spines function to hold food particles. Laterally, the coxopodite is produced into a rounded lobe from which a tuft of large, plumose, sensory setae project. Endites of the basipodite, including an anterior three-jointed flagellum, extend anterolaterally from the basipodite. Schmidt (1915) considers the endites the endopodite. Various lobes of the basipodite endites bear sensorial hairs. A single large seta projects anteriorly from the base of the flagellum.

MUSCLE ELEMENTS

The musculature of the first maxilla in *Penaeus* appears substantially similar to that of other Decapoda. Groups of muscles function to bring the spinous gnathal margins of the appendage to the midline in feeding. Other muscles open the opposing gnathal parts and make various position adjustments. *Peneaus* appears to have at least 10 muscles and muscle groups in the first maxilla, against 9 each for *Pandalus*, *Astacus*, and *Callinectes*.

COXOPODITE PROMOTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

The first maxilla coxopodite promotor muscle (fig. 40) originates on a large sternal apodeme arising from the brachia between the first and second maxillary foramina. This apodeme penetrates the substance of the endosternite. The promotor muscle runs ventrolaterally to insert in the lateral lobe of the coxopodite. Upon contraction, the muscle turns the first maxilla forward and upward. The first maxilla coxopodite promotor muscle in *Penaeus* is homologous with the musculus promotor I maxillae of *Pandalus*, *Astacus*, and *Callinectes*. Berkeley, Schmidt, and Cochran state that the promotor muscle originates on the head apodeme, or endosternite, in the above three crustaceans, whereas in *Penaeus* the area of origin of the promotor and other lateral muscles is not directly on the endosternite.

COXOPODITE REMOTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

Taking origin on the sternal apodeme some distance ventrad of the origin of the coxopodite promotor muscle, the first maxilla coxopodite remotor muscle (fig. 40) passes laterad to the lateral lobe of the coxopodite. Contractions of the muscle draw the first maxilla posteroventrad. The coxopodite remotor in *Penaeus* is the homolog of the musculus remotor *a* or *b* I maxillae of *Pandalus*, *Astatcus*, and *Callinectes*. In the latter three forms, two remotor muscles are described.

LATERAL COXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

The first maxilla lateral coxopodite adductor muscle (fig. 40) is a long, slender muscle originating on the laterotergal wall and running anteroventrally to a point of insertion on the medial region of the coxopodite. Contractions of the muscle raise the first maxilla and turn the gnathal lobes towards the midline. Berkeley and Schmidt maintain that the lateral coxopodite adductors in *Pandalus* and *Astacus* originate on the lateral carapace. Despite this difference, the lateral coxopodite adductors in the latter forms are homologous with those of *Penaeus*. Cochran (1935) finds in *Callinectes* a muscle termed by her the posterior adductor muscle. This muscle is a possible homolog of the lateral coxopodite adductors in *Penaeus*.

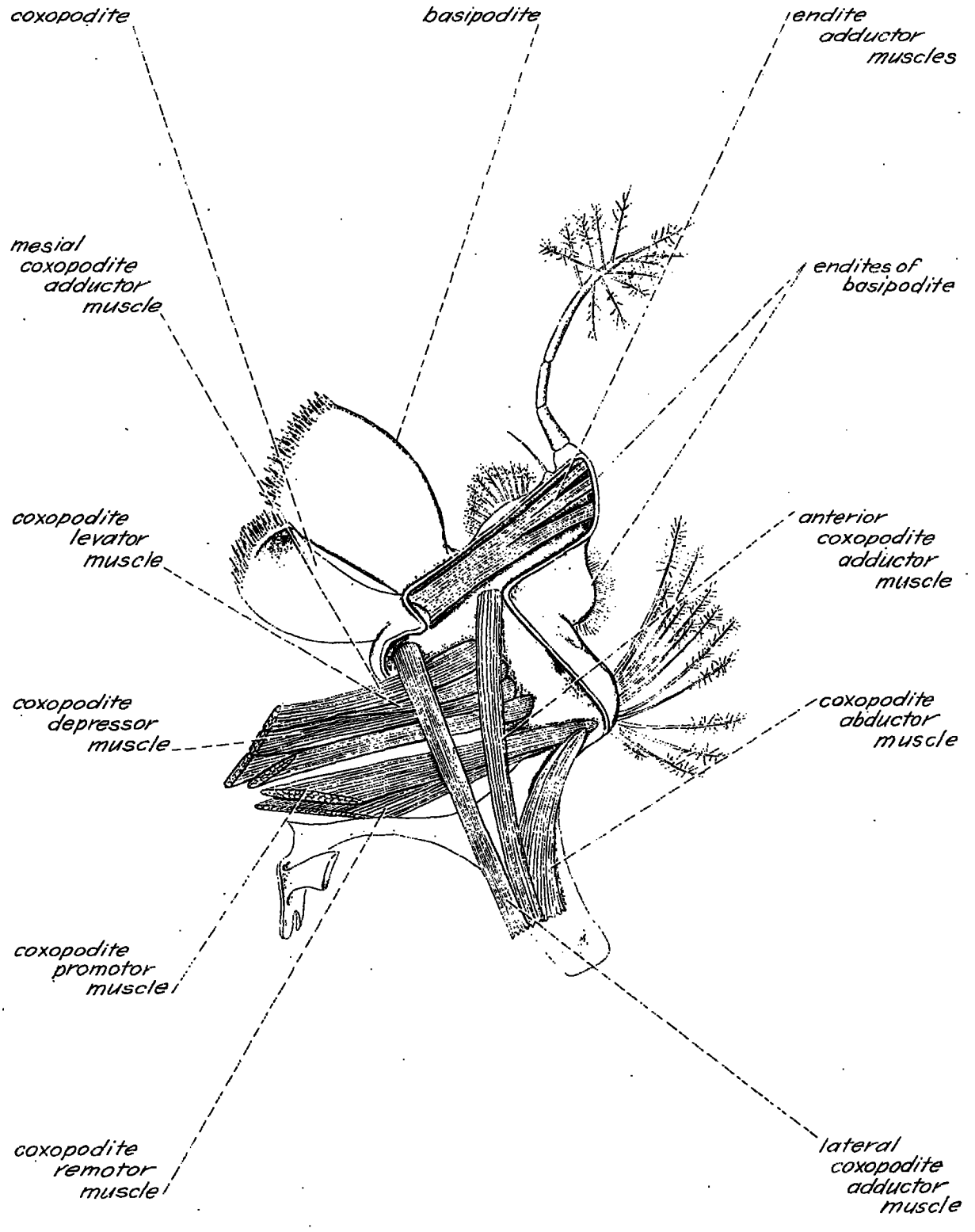

FIGURE 40.—Dorsal view of right first maxilla. Dorsal cuticle removed to show muscles.

MESIAL COXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

Arising from the large sternal apodeme of the coxopodite promotor muscle, the first maxilla mesial (=medial) coxopodite adductor muscle (fig. 40) inserts in the coxopodite. The muscle functions to turn the first maxilla to the midline, thus bringing the opposing gnathal lobes together. The first maxilla mesial coxopodite adductor muscle in *Penaeus* is the same muscle as the musculus adductor medialis coxopoditis I maxillae in *Astacus* and *Pandalus*. *Callinectes* does not appear to have this muscle.

ANTERIOR COXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

The first maxilla anterior coxopodite adductor muscle (fig. 40) originates on the laterotergal plate adjacent to the origin of the lateral coxopodite adductor muscle. The muscle passes anteroventrally, diverging from the lateral adductor, and inserts somewhat anteriorly of the insertion of the lateral adductor. Together with the medial and lateral coxopodite muscles, the anterior adductor closes the gnathal lobes of the first maxilla. The anterior adductor is not evident in *Astacus* or *Pandalus*, but does appear in *Callinectes*.

COXOPODITE ABDUCTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

The first maxilla coxopodite abductor muscle (fig. 40) originates with the anterior and lateral adductor muscles on the laterotergal wall. The muscle runs anteriorly and inserts in the lateral lobe of the coxopodite. Upon contraction, the muscle pulls the first maxilla away from the midline, opening the gnathal lobes. The coxopodite abductor muscle is found in *Pandalus*, *Astacus*, and *Callinectes*.

COXOPODITE LEVATOR MUSCLE OF FIRST MAXILLA

FIGURE 40

The first maxilla coxopodite levator muscle (fig. 40) is attached to the sternal apodeme upon which the medial adductor and the promotor and remotor muscles originate. It inserts on the coxopodite. The angle of the muscle attachment is such that its contractions raise the first maxilla. The same muscle as the coxopodite levator in *Penaeus* appears in *Astacus*, *Pandalus*, and *Callinectes*.

COXOPODITE DEPRESSOR MUSCLE OF FIRST MAXILLA

FIGURE 40

The first maxilla coxopodite depressor muscle (fig. 40) originates on the base of the sternal apodeme mentioned above. The muscle runs to its insertion on the coxopodite so that its contractions draw the first maxilla ventrad, thereby lowering the gnathal lobes away from the mandibles and paragnatha. The coxopodite depressor muscle exists in the other crustaceans referred to above.

ENDITE ADDUCTOR MUSCLE OF FIRST MAXILLA

FIGURE 40

Intrinsic to the endite of the basipodite is a group of muscles, the first maxilla endite adductor muscle (fig. 40), which pass across the proximal neck of the gnathal lobe of the basipodite to the base of the endite flagellum. The muscle bends the flagellum mesad. The endite adductor muscle is common to the first maxilla of *Penaeus*, *Pandalus*, *Astacus*, and *Callinectes*.

DORSOVENTRAL MAXILLARY TENSOR MUSCLE

FIGURES 33, 34, 35, 37

This muscle originates by a broad, fan-shaped apodeme in the connective tissue of the dorsal carapace just laterad of the gastric mill (fig. 35). The apodeme runs ventromedially to the small dorsoventral maxillary tensor muscle (fig. 37) lying laterad of the muscle of the dorsoventral mandibular ligament and closely applied to it. Schmidt (1915) described the muscle as the anterior dorsoventral muscle in *Astacus* and Berkeley (1928) has followed this terminologly in her work on *Pandalus danae*. Grobben (1917) studied the muscle in species of *Penaeus*, *Palaemon*, *Leander*, and *Pandalus*, and concluded that, on grounds of its innervation by nerves of the first maxilla, the muscle should be renamed the "dorsoventral maxillary tensor muscle." The name given by Grobben is adopted here.

3b. The Second Maxillae

The second maxilla is one of the most extensively modified appendages of higher Crustacea. The structure serves a double function. The medial lobes participate in feeding while the large lateral part pumps water over the gills. Despite its complexity, the second maxilla is so remarkably uniform in structure and musculature throughout a broad phyletic spectrum of higher Crustacea that, as Calman (1909) has shown, the appendage is of limited value in the study of crustacean evolution.

SKELETAL ELEMENTS

The second maxilla projects laterally and ventrally from its attachment point on the ventral skeleton. The large foramen enters a deeply sculptured coxopodite from which two small, medial gnathal lobes arises (figs. 29, *D;* 41). Distal to the coxopodite lies the complex basipodite bearing two larger, medial gnathal lobes and an anterior endite (figs. 29, *D;* 41). Spines on the gnathal lobes aid in holding food. Lateral to the basipodite lies the flat, indented scaphognathite, or gill pump (fig. 41). The folds and grooves of the scaphognathite represent areas of muscle attachment and of articulation.

Many different interpretations of the components of the second maxilla are encountered in the literature. In *Astacus*, Schmidt describes the gnathal lobes as partly coxal and partly basal, as had been done in the present study of *Penaeus*. However, the former considers the basipodite endite the endopodite, and is followed by Berkeley in *Pandalus*. Calman (1909) refers to the endite as a palp. The position of Cochran (1935) in her study of *Callinectes* is rather inconsistent. When describing the second maxilla of the blue crab, this worker calls all of the gnathal lobes endites of the coxopodite, and terms the basipodite endite the endopodite. By contrast, in a description of the mouthparts of a number of crustaceans included as a subsection of the study of the blue crab musculature, Cochran labels the median gnathal lobes as basal and the anterior lobe as an endite of the basipodite, as has been done by the present writer in *Penaeus*, even though the second maxillae of *Callinectes* and *Penaeus* are very similar. To say the least, the composition of the second maxilla needs clarification.

MUSCLE ELEMENTS

The principle function of the muscles of the second maxilla is the operation of the scaphognathite as a gill pump. As mentioned above, the gill pump lies in a narrow channel through which the water is moved that passes over the gills. If the body processes of a shrimp are reduced by chilling, and the branchiostegite is cut away, the gill pump may be observed in slow action. Two functionally interrelated but distinct oscillations of the scaphognathite occur. The more obvious is that taking place about the horizontal, lateral axis through the gill pump, and by which the scaphognathite is tipped back and forth, or rotated on its axis. The less obvious oscillation is the dorsoventral movement of the lateral margin of the scaphognathite about the long axis of the structure. The marginal undulation tends to ramify the former oscillation with respect to water pumping.

Water is drawn into the pumping chamber by a forward tipping of the anterior end of the gill pump to the floor of the chamber. At the same time the posterolateral margins of the pump are raised to the top of the chamber. The posterolateral margins of the pump are now brought ventrad at which time the anterior end rises, and the whole organ rolls anteriorly along the floor of the chamber, forcing water out of the cephalic aperture of the pumping chamber.

Conflicting opinions about the skeletal nomenclature of the second maxilla have given rise to some confusion in the naming of the muscles. In addition, small but important differences in the number, arrangement, and in particular the functions of the second maxillary muscles of *Penaeus* are apparent when the second maxilla of the white shrimp is compared to that of *Astacus*, *Pandalus*, and *Callinectes*. The differences are of sufficient magnitude to make difficult the homology of all the muscles in *Penaeus* with those in the three crustaceans mentioned without knowing the details of comparative innervations. Under pain of causing further confusion of names in the literature, the present writer renames the muscles of the second maxillae of *Penaeus* in accordance with their functions.

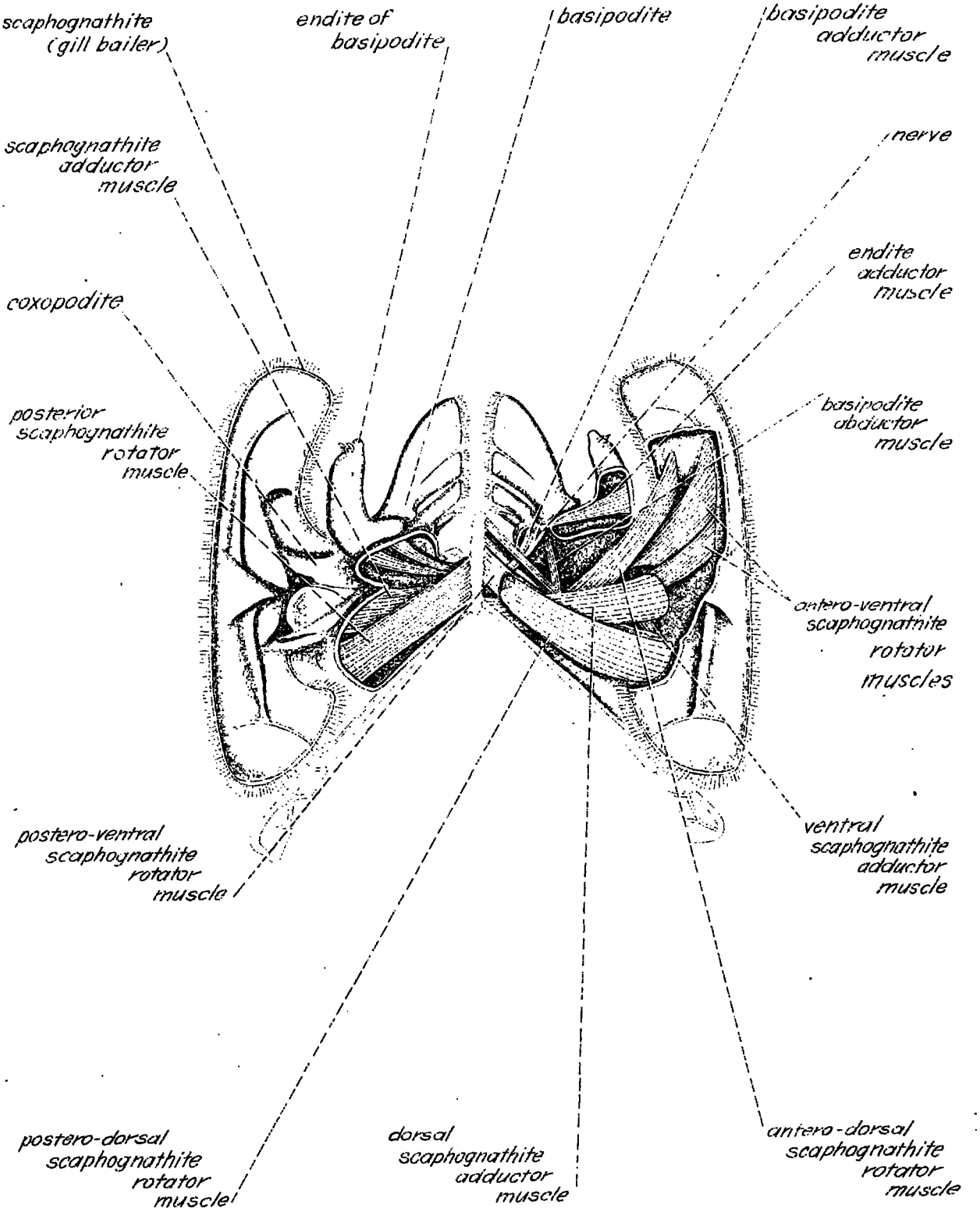

FIGURE 41.—Dorsal view of second maxilla. Left side, intact appendage. Right side, dorsal cuticle removed to show muscles.

BASIPODITE ADDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

This small muscle originates on the medial margin of the coxopodite and runs to the proximal region of the gnathal lobe of the basipodite. The second maxilla basipodite adductor muscle turns the basipodite lobes toward the midline. The only muscle in *Astacus* in a similar position is part of the musculus depressor II maxillae.

BASIPODITE ABDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

The basipodite abductor muscle runs from the posterior rim of the coxopodite to the proximal region of the basipodite gnathal lobes, laterad of the insertion of the basipodite adductor. Contractions of the basipodite abductor open the gnathal lobes. Like the basipodite adductor, the basipodite abductor may be the same muscle as part of Schmidt's musculus depressor II maxillae in *Astacus*.

ENDITE ADDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

The endite adductor muscles (fig. 41) arises in the proximal region of the basipodite gnathal lobes and passes laterad to insert on the lateral margin of the basipodite endite. Its contractions turn the endite mesad. The endite adductor of *Penaeus* is fully homologous with the endopodite adductor muscle of *Astacus*, *Pandalus*, and *Callinectes*.

POSTEROVENTRAL SCAPHOGNATHITE ROTATOR MUSCLE OF SECOND MAXILLA

FIGURE 41

The posteroventral scaphognathite rotator muscle, in company with several of the so-called respiratory muscles, originates on a large, sternal apodeme arising from the sternal brachia between the second maxilla and the first maxilliped. The dorsal, or distal, portion of this apodeme lies close to the dorsal end of the large sternal apodeme upon which muscles of the first maxilla are attached, but the second maxillary apodeme is not deeply embedded in the substance of the endosternite as is the first maxillary apodeme. The posteroventral scaphognathite rotator runs posterolaterally to a point of insertion on the ventral surface of the scaphognathite. This muscle brings the posterior tip of the gill pump ventrad and remotes the whole structure. The muscle is evidently the homolog of the musculus respiratorius *e* II maxillae in *Astacus* and the other forms referred to.

DORSAL SCAPHOGNATHITE ADDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

This muscle originates on the apodeme of the second maxilla and runs ventrolaterally to insert on the dorsal surface of the scaphognathite. The dorsal scaphognathite adductor muscle turns the posterolateral margin of the gill pump dorsad. Although far from clear, the muscle may be the same muscle as Schmidt's musculus respiratorius *b* II maxillae in *Astacus*.

POSTERODORSAL SCAPHOGNATHITE ROTATOR MUSCLE OF SECOND MAXILLA

FIGURE 41

The posterodorsal scaphognathite rotator muscle originates on the dorsal part of the sternal apodeme of the second maxilla and passes laterally to the dorsal surface of the scaphognathite. In action, the muscle aids the posteroventral rotator muscle in remoting the whole scaphognathite, but opposes the posteroventral rotator by lifting the posterior tip of the gill pump. The posterodorsal rotator in *Penaeus* is almost certainly the homolog of the musculus respiratorius *d* II maxillae of *Pandalus*, *Astacus*, and *Callinectes*.

VENTRAL SCAPHOGNATHITE ADDUCTOR MUSCLE OF SECOND MAXILLA

FIGURE 41

The ventral scaphognathite adductor muscle originates in the ventral region of the coxopodite and inserts on the scaphognathite ventrad of the insertion of the posteroventral rotator muscle. The muscle turns the lateral margin of the gill pump ventrad, in opposition to the action of the dorsal adductor.

ANTERODORSAL SCAPHOGNATHITE ROTATOR MUSCLES OF SECOND MAXILLA

FIGURE 41

The anteroventral scaphognathite rotator muscles have separate origins and may well be two different entities. The posteriormost of the two is a long muscle extending from the ventral apodeme to an area well out in the anterior region of the scaphognathite. The more anterior rotator originates in the coxopodite and passes to a broad area of insertion in the anterolateral region of the gill pump. This muscle may be the counterpart in *Penaeus* of the scaphognathite flexor muscle of *Astacus*, *Pandalus*, and *Callinectes*. The posteriormost rotator of this pair in *Penaeus* apparently is not homologous with any of the muscles in the other crustaceans referred to. These muscles bring the anterior tip of the scaphognathite dorsad and promote the whole structure.

ANTERODORSAL SCAPHOGNATHITE ROTATOR MUSCLE OF SECOND MAXILLA

FIGURE 41

The anterodorsal scaphognathite rotator muscle takes origin on the endosternal apodeme of the second maxilla and runs anteroventrally to an area of insertion mesad of the anteroventral rotator muscles. The muscle reinforces the action of the anteroventral rotators in raising the anterior tip of the scaphognathite and promoting the structure. As nearly as can be determined, the anterodorsal rotator in *Penaeus* is the musculus respiratorius *a* II maxillae in *Astacus*, *Pandalus*, and *Callinectes*.

4. MAXILLIPEDS

4a. First Maxilliped

Like the second maxilla, the first maxilliped is a highly modified appendage having a dual function. Its strong gnathal lobes and sensory flagellum participate in feeding, while its flat, lateral lobes and small arthrobranchia play a part in breathing. Superficially, the first maxilliped appears to be as widely modified from the plan of the typical appendage as is the second maxilla, but the muscles indicate otherwise. And whereas the second maxilla is a relatively stable phylogenetic entity in the Crustacea, the form of the first maxilliped is variable.

SKELETAL ELEMENTS

The skeleton of the first maxilliped is comprised of a series of lightly sclerotized lobes or plates. The appendage articulates with the ventral skeleton by a transversely elongate foramen. The foramen enters the fused coxopodite and basipodite (protopodite, fig. 42). Projecting anteroventrally from the protopodite is a set of three gnathal lobes, the large, thick distal lobe being the endite of the coxopodite (fig. 42). Together, the endites of the maxillipeds are cupped against the anterior mouthparts. Heavy spines directed mesad from the edge of the endites help to hold food. Laterad of the coxopodite endite and extending anteriorly is a slender lobe bearing on its medial surface the rudiment of the endopodite and the jointed flagellum of the exopodite. The exites of the coxopodite, lying laterally, are two large, flat sheets that close the gill pump chamber on the ventral surface. Posteriorly, a small, flattened gill may be seen. This gill is said to be an arthobranchia, but on embryological grounds it might be as easily a podobranch.

The components of the first maxilliped are interpreted in different ways by different authors. The structure called the protopodite in *Penaeus* is termed the coxopodite in *Astacus* by Schmidt. Also, Schmidt considers the coxopodite endite the basipodite, and refers to the coxopodite exites as epipodites. If, as has been discussed earlier, the coxopodite exites develop from podobranch primordia, then no objection to the term "epipodite" can be offered. In passing, we may note that the first maxilliped of *Penaeus* bears two coxopodite endites compared to one in the first maxilliped of *Pandalus*, *Astacus*, and *Callinectes*.

MUSCLE ELEMENTS

Compared to the musculature of the second maxilla, that of the first maxilliped is very light. The muscles function almost entirely in feeding, since the part played by the exites in breathing is mostly passive. Wider variation in the functions of the muscles of the first maxilliped in different crustaceans makes necessary a variety of muscle names, but most of them can be homologized. The first maxilliped of *Penaeus* has 12 muscles, against 9 for *Astacus*, 13 for *Pandalus*, and 11 in *Callinectes*.

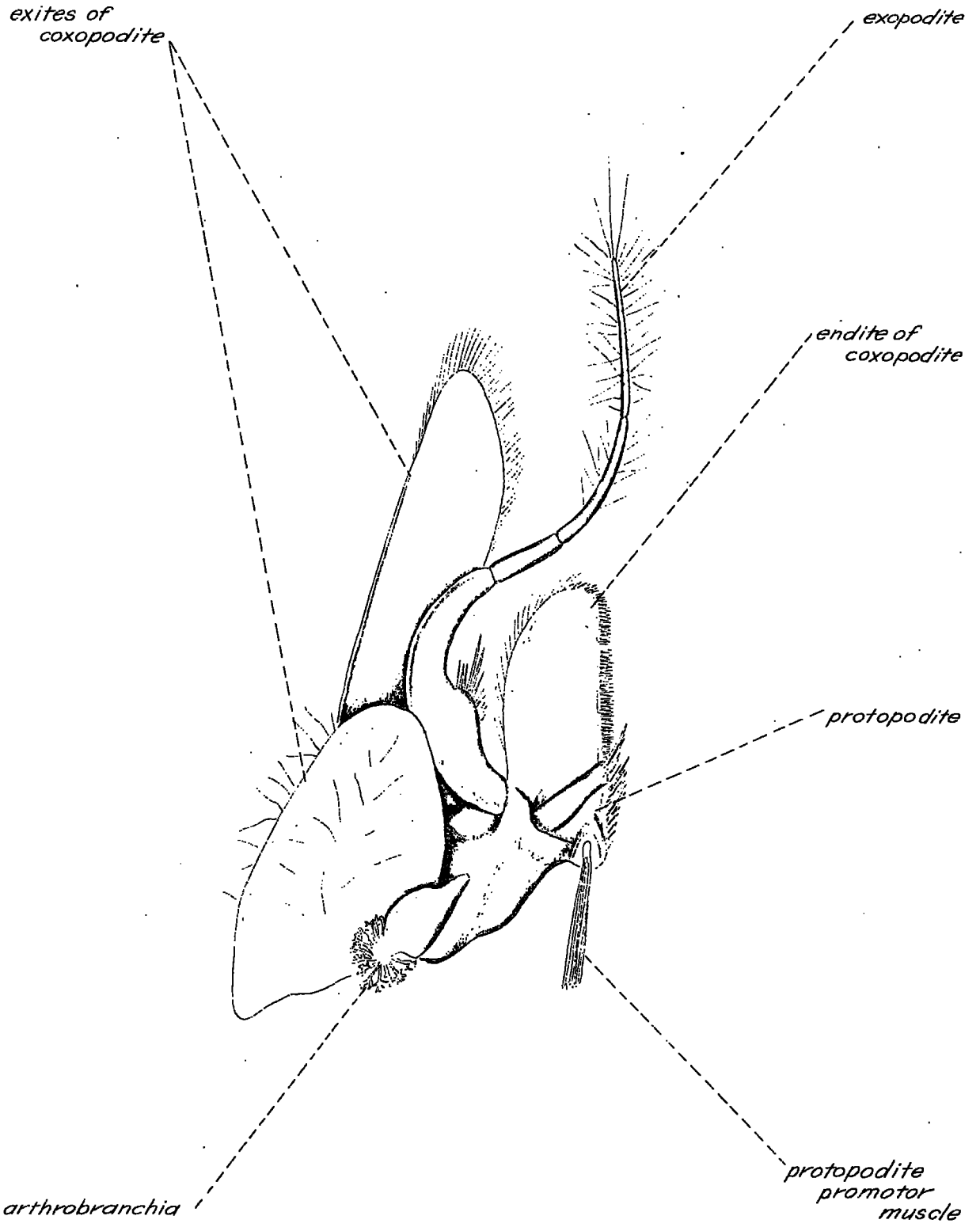

FIGURE 42.—Dorsal view of left first maxilliped.

PROTOPODITE PROMOTOR MUSCLES OF FIRST MAXILLIPED

FIGURES 42, 43

The protopodite promotor muscles (fig. 43) originate on the small sternal apodemes (paraphragms) arising from the sternal brachia between the first and second maxillipeds. The longer, medial promotor inserts on an apodeme on the anterior wall of the protopodite and the lateral promotor inserts in connective tissue ventrad of the medial promotor. Contractions of the promotors turn the first maxilliped forward and dorsad about a transverse axis. The protopodite promotors of *Penaeus* are very likely homologous with the lateral and medial promotor muscles of *Astacus*, *Callinectes*, and *Pandalus*.

PROTOPODITE LEVATOR MUSCLES OF FIRST MAXILLIPED

FIGURE 43

Penaeus has at least three protopodite levator muscles. All of them take origin on a small sternal apodeme overhanging the medial margin of the maxillipedal foramen. They fan out as they pass laterally to insert in connective tissue in the lateral part of the coxopodite. Contractions of the protopodite levators lift the dorsal edges of the coxopodite exites dorsad. At least a part of this muscle group is homologous with the levator muscle of *Pandalus*, *Astacus*, and *Callinectes*.

COXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLIPED

FIGURE 43

Taking origin in the proximal region of the coxopodite, the coxopodite adductor muscle passes ventrad along the medial wall of the coxopodite to insert on the coxopodite endite. Upon contraction, the muscle turns the endite mesad. The coxopodite adductor in *Penaeus* appears to be the maxillipedal depressor muscle of *Astacus* and *Pandalus*, and possibly one of the small unknown muscles in the coxopodite of *Callinectes*.

COXOPODITE ABDUCTOR MUSCLES OF FIRST MAXILLIPED

FIGURE 43

Two coxopodite abductor muscles exist in the first maxilliped of *Penaeus*. The muscles originate in the lateral part of the coxopodite, near the posterior exite, and run ventromedially to a point of insertion on the lateral margin of the coxopodite endite. Their contractions draw the endite laterad, in opposition to the coxopodite adductors. The endopodite reductor muscle of *Astacus* is a possible homolog of the coxopodite abductor in *Penaeus*.

EXITE ATTRACTOR MUSCLES OF FIRST MAXILLIPED

FIGURE 43

The first maxilliped of *Penaeus* contains at least two exite attractor muscles which pull the coxopodite exites caudad. The muscles originate on apodemes of the sternal brachia and insert on the medial margin of the posterior coxopodite exite. The epipodite attractor muscle in *Astacus* is very likely the homolog of the exite attractors of *Penaeus*.

EXOPODITE ADDUCTOR MUSCLE OF FIRST MAXILLIPED

FIGURE 43

The flagellum, or exopodite, of the first maxilliped is moved towards the midline by means of a short muscle, the exopodite adductor muscle, which originates at the base of the exopodite and runs distally within the structure. The homolog in *Astacus* is the exopodite adductor muscle.

EXOPODITE ABDUCTOR MUSCLE OF FIRST MAXILLIPED

FIGURE 43

The exopodite abductor muscle originates at the distal end of the exopodite adductor and runs distally in the flagellum. Its contractions tend to straighten the flagellum, thus turning the structure laterad. The muscle in *Penaeus* is in all probability the flagellum muscle of *Astacus*.

4b. Second Maxilliped

The structure of the second maxilliped is much more like that of the typical arthroappendage than the anterior gnathal appendages already treated. The typical number of appendage articles are found, albeit those of the basipodite and ischiopodite are fused. A large, flagellar exopodite is developed. A notable difference is that some of the endopodite articulations of the second maxilliped permit far more extensive movements than do the hinges of the anterior gnathal limbs.

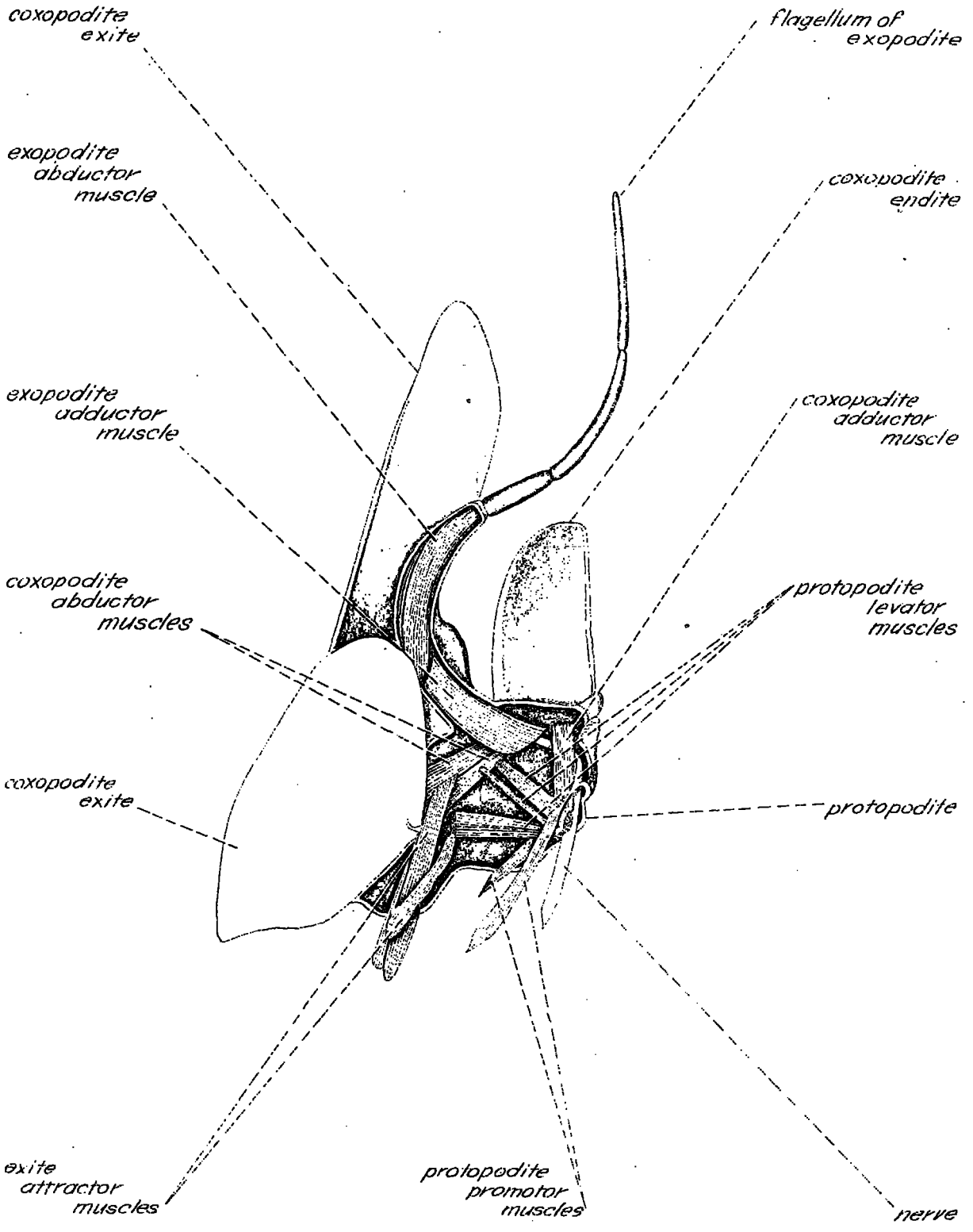

FIGURE 43.—Dorsal view of left first maxilliped, dorsal cuticle removed to show muscles.

The second maxilliped is an active participant in the process of feeding.

SKELETAL ELEMENTS

The coxopodite (fig. 44) of the second maxilliped projects ventrad from a region of the ventral skeleton thta is much more heavily sclerotized than are the corresponding areas anteriorly. The foramen of the second maxilliped is surrounded by several large sternal and laterotergal apodemes upon which muscles originate. The whole structure is distinctly heavier than is that of the anterior gnathal appendages, in keeping with the greater movability and strength of the second maxilliped compared to that of the anterior accessory mouth-parts. Projecting laterally from the coxopodite is a small gill, the podobranchia (fig. 44), and a mitten-shaped mastigobranchia, or epipodite. (See fig. 32.) The articular membrane dorsal to the coxopodite bears two arthrobranchiae.

The short, curved carpopodite is connected by dicondyles between the meropodite and the propodite placing the propodite laterad of the distal end of the meropodite. The propodite is a short, square article containing muscles operating the heart-shaped dactylopodite on its distal end. The dactylopodite lies laterad of the proximal part of the meropodite, its apex nearly touching the ischiopodite. The condyles between the carpopodite and propodite and between the propodite and dactylopodite are rotated 90° from the axis of the condyles between the meropodite and the carpopodite. Thus the movements of the distal segments are at right angles to those of the proximal segments.

The coxopodite articulates with the basipodite (fig. 44) by dorsoventral condyles which permit extensive lateral movements. The coxopodite and basipodite are said to be fused in *Pandalus* and *Astacus*. To the basipodite is articulated the exopodite, a long, annular, plumose flagellum (fig. 44) that extends anteriorly and then curves gracefully laterad. The ischiopodite (fig. 44) is immovably fused to the basipodite in *Penaeus*, as in *Callinectes*, but a fine line of light cuticle clearly distinguishes the two articles. The meropodite (fig. 44), the longest article of the endopodite, is attached to the ischiopodite so as to allow the distal segments limited movements from side to side as well as up and down. This article projects anteriorly from the ischiopodite to a position beneath the mandibles. Stiff spines on the medial side of the meropodite opposing those on the lateral side of the dactylopodite produce a functional chela or claw.

MUSCLE ELEMENTS

The musculature of the second maxilliped of *Penaeus* is substantially similar to that of *Pandalus*, *Astacus*, and *Callinectes*, although *Penaeus* has a larger number of discrete muscles. The second maxilliped of *Penaeus* contains 14 types of muscles including 23 muscles. *Astacus* has 15 muscle types with 17 muscles. The second maxilliped of *Pandalus* has 14 types of muscles and 16 discrete muscles, whereas *Callinectes* has 16 muscle types and 17 muscles. The classical muscle nomenclature has been changed slightly here as elsewhere to conform to the appendage article in which the muscles insert.

COXOPODITE PROMOTOR MUSCLE OF SECOND MAXILLIPED

FIGURES 44, 45

Taking origin on a paraphragmal apodeme on the lateral pleural wall, the coxopodite promotor muscle passes mesad to insert in connective tissue on the medial wall of the coxopodite. The muscle turns the coxopodite, and with it the distal segments, anterior and dorsad. The musculus promotor II pedis maxillaris of *Astacus*, *Pandalus*, and *Callinectes* is homologous with the coxopodite promotor muscle of *Penaeus*.

COXOPODITE REMOTOR MUSCLE OF SECOND MAXILLIPED

FIGURES 44, 45

The coxopodite remotor muscle originates on a paraphragmal apodeme above the posterolateral margin of the foramen and runs to an insertion in connective tissue on the posterior wall of the coxopodite. Its contractions turn the coxopodite caudad and the distal elements ventrad. The coxopodite remotor muscle in *Penaeus* is fully homologous to the second maxilliped remotor muscle in the other crustaceans mentioned.

BASIPODITE LEVATOR MUSCLES OF SECOND MAXILLIPED

FIGURES 44, 55

The basipodite levator muscles originate at two different points. The medial portion is attached

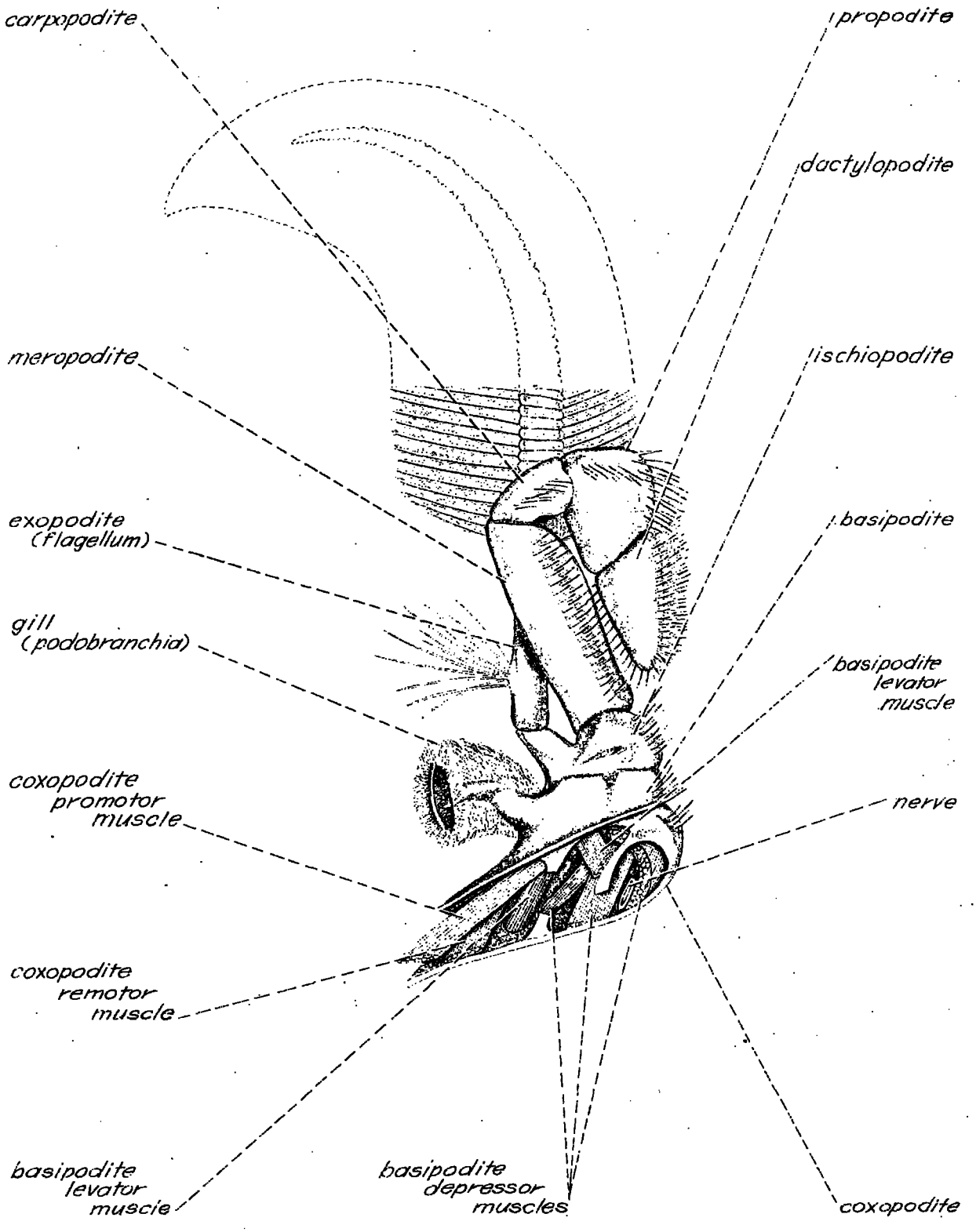

FIGURE 44.—Dorsal view of left second maxilliped.

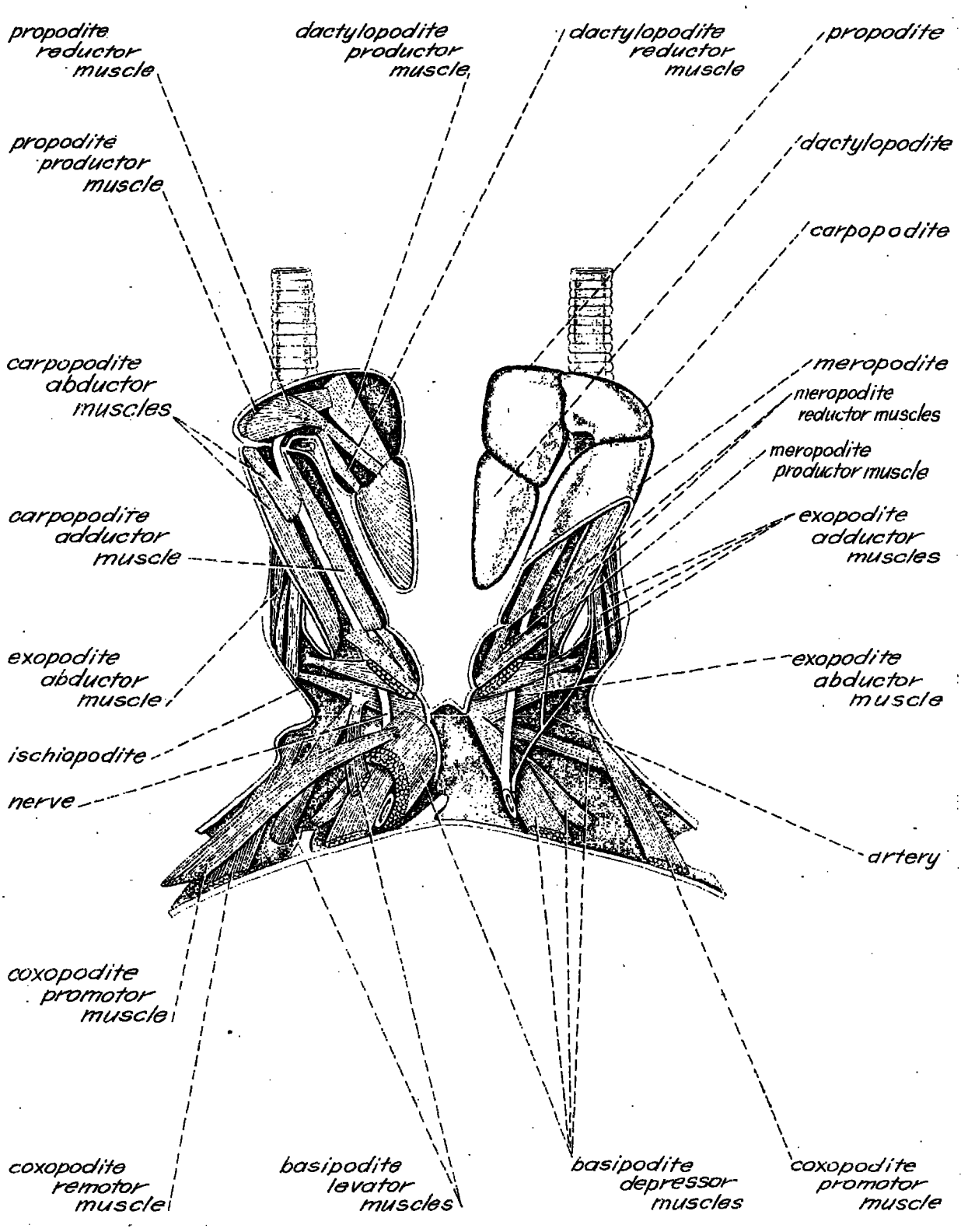

FIGURE 45.—Dorsal view of second maxilliped, cuticle removed to show muscles.

to a large sternal apodeme overhanging the anteromedial part of the foramen. The muscle runs beneath the coxopodite promotor and inserts together with the lateral basipodite levator on the anterior margin of the basipodite foramen, slightly laterad of the dorsal coxobasipodite condyle. The lateral levator muscle originates on the posterior wall of the coxopodite and runs ventrad to join the medial levator. The muscles raise the distal articles and also abduct them. The muscles are homologous with the levator muscles *a* and *b* of *Pandalus* and *Astacus*, and with the single levator in *Callinectes*.

BASIPODITE DEPRESSOR MUSCLES OF SECOND MAXILLIPED

FIGURES 44, 45

The second maxilliped of *Penaeus* contains four basipodite depressor muscles. The largest is the medial depressor, a short, strong, semicylindrical muscle which, in a manner of speaking, lines the medial curvature of the coxopodite. This muscle originates from the medial margin of the dorsal coxopodite foramen and inserts with the other depressors on the ventromedial margin of the coxopodite, mesad of the ventral condyle between the coxopodite and basipodite. Two other basipodite depressors arise, the larger from the posterior margin of the coxopodite foramen, the smaller from the posterior wall of the coxopodite. The fourth depressor muscle originates on the ventrolateral wall of the coxopodite, beneath the coxopodite remotor, and runs across the coxopodite to join the other basipodite depressors. The contractions of the depressor muscles turn the basipodite and thus the distal maxillipedal elements ventrad. In addition, as a consequence of their insertion mesad of the condylic axis, the depressor muscles turn the basipodite and the distal elements towards the midline.

In fact, from the arrangement of the basipodite levators and depressors with respect to the basipodite condyles, the true function of the muscles may be as abductors and adductors, rather than as levators and depressors. The latter names, of course, derive from *Astacus* in which the coxopodite and basipodite of the second maxilliped are fused. On functional grounds, then, Schmidt's names are at least partially incorrect when applied to *Penaeus*. The basipodite depressor muscles of *Penaeus* are nonetheless homologous with the depressor muscles *a* and *b* in *Pandalus*, *Astacus*, and *Callinectes*.

EXOPODITE ABDUCTOR MUSCLES OF SECOND MAXILLIPED

FIGURE 45

Two exopodite abductor muscles exist in the second maxilliped of *Penaeus*. The medial abductor is extrinsic, originating broadly on the medial wall of the basipodite and inserting on the posterior edge of the exopodite base. The extrinsic abductor turns the exopodite laterad. Intrinsic to the exopodite is a long abductor muscle which originates by a fine tendon on the base of the exopodite and extends distally for some distance in the exopodite flagellum. Its contractions bend the flagellum laterad. The intrinsic exopodite abductor muscle in *Penaeus* is homologus with the exopodite abductor muscle of *Astacus* and *Callinectes*, and the extrinsic abductor is probably the same muscle as the flagellum abductor in *Astacus*.

EXOPODITE ADDUCTOR MUSCLES OF SECOND MAXILLIPED

FIGURE 45

The second maxilliped of *Penaeus* has at least three exopodite adductor muscles. The extrinsic exopodite adductor originates in a broad fan across the dorsomedial wall of the basipodite and inserts on the anterior edge of the exopodite base. When it contracts, the exopodite is turned towards the midline. Within the exopodite are two exopodite adductors which function to straighten out the exopodite flagellum, in opposition to the action of the intrinsic exopodite abductor muscle. No homolog of the extrinsic exopodite adductor muscle is evident in *Astacus* or *Callinectes*. Berkeley (1928) illustrates an extrinsic adductor of the exopodite, but does not discuss the muscle. The intrinsic exopodite adductors of *Penaeus* apparently have no homologs in the crustaceans referred to here.

MEROPODITE PRODUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

The types and arrangement of the second maxilliped endopodite muscles are remarkably uniform in many higher Crustacea, in accordance

with the evolution of this versatile accessory feeding mechanism. The meropodite productor muscle originates on the medial side of the ischiopodite, near the exopodite adductor, and inserts on a small apodeme on the dorsal surface of the meropodite. The muscle lifts the meropodite and other distal elements towards the ventral surface of the mandibles. The same muscle appears in *Pandalus*, *Astacus*, and *Callinectes*.

MEROPODITE REDUCTOR MUSCLES OF SECOND MAXILLIPED

FIGURE 45

Penaeus has two meropodite reductor muscles. The medial reductor originates on the medial wall of the ischiopodite, ventrad of the meropodite productor, and inserts on an apodeme on the ventral margin of the meropodite. Another reductor muscle originates on the anterodorsal surface of the ischiopodite and passes to the same apodeme as the medial reductor. The muscles turn the meropodite ventrad. The meropodite reductors of *Penaeus* have partial counterparts in the second maxilliped of *Astacus*, *Pandalus*, and *Callinectes*, but in the latter only one reductor has been described.

CARPOPODITE ABDUCTOR MUSCLES OF SECOND MAXILLIPED

FIGURE 45

Two carpopodite abductor muscles are found in the second maxilliped of *Penaeus*. The smaller of these originates on the dorsal side of the meropodite and inserts on the common abductor apodeme on the lateral edge of the carpopodite. The larger abductor takes origin on the lateral side of the meropodite, proximally. The muscle runs out along the lateral side of the meropodite and attaches to the abductor apodeme on the carpopodite. The two muscles turn the small carpopodite laterad. However, with respect to the gnathal surface of the dactylopodite, the carpopodite abductors cause functional adduction, in consequence of the hooked shape of the endopodite. The large carpopodite abductor muscle is the same muscle as the carpopodite abductor in *Astacus*, *Pandalus*, and *Callinectes*. The small abductor in *Penaeus* is not described in any of the foregoing crustaceans.

CARPOPODITE ADDUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

The carpopodite adductor muscle runs from the proximal end of the meropodite to an adductor apodeme on the medial side of the carpopodite. The muscle is less powerful than the carpopodite abductors. The adductor turns the carpopodite mesad, but as a result of the distal hook, the gnathal surface of the dactylopodite is moved laterad. The carpopodite adductor of *Penaeus* is fully homologous with the carpopodite adductor in the other crustaceans to which reference has been made.

PROPODITE PRODUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

The propodite productor muscle is a short, thick structure originating on a proximal, ventral part of the carpopodite, and running to a broad apodeme on the ventrolateral side of the propodite. Its contractions turn the propodite and dactylopodite ventrad. The propodite productors in *Penaeus* are homologous with the propodite productor in *Astacus*, *Pandalus*, and *Callinectes*.

PROPODITE REDUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

The propodite reductor muscle occupies the dorsal part of the carpopodite in the shape of a fan. The broad portion originates in the proximal region of the carpopodite. The muscle becomes narrow as it inserts on a little apodeme on the dorsal side of the propodite. The muscle turns the propodite and dactylopodite dorsad, about the horizontal axis through the condyles. The propodite reductor muscle of *Penaeus* is represented in the second maxilliped of the three crustaceans to which frequent reference has been made.

DACTYLOPODITE PRODUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

The dactylopodite productor muscle is a small, fan-shaped muscle that originates proximally in the propodite and inserts on the ventral margin of the dactylopodite. It serves to straighten the

dactylopodite and turn the distal article ventrad, in opposition to the dactylopodite reductor. The same muscle as the dactylopodite productor in *Penaeus* is found in *Pandalus*, *Astacus*, and *Callinectes*.

DACTYLOPODITE REDUCTOR MUSCLE OF SECOND MAXILLIPED

FIGURE 45

Attached between the proximal part of the propodite and the dorsal edge of the dactylopodite is the small dactylopodite reductor muscle. Its function is to turn the dactylopodite dorsad, opposing the action of the productor. The muscle is homologous with the dactylopodite reductor of *Pandalus*, *Astacus*, and *Callinectes*.

4c. Third Maxilliped

The third maxilliped is the first accessory feeding appendage which lacks the jawlike characteristics of the anterior gnathal limbs. Far more than any of the other appendages, the third maxillipeds function to grasp large food particles passed up by the chelate legs and hold them next to the mouthparts for further reduction in size and for swallowing. Structurally, the third maxilliped is closely similar to the pereiopods.

SKELETAL ELEMENTS

The body hemocoel is confluent with that of the third maxilliped by means of a ventral skeletal foramen whose fringes are strongly sclerotized and from which phragmal apodemes project over the opening. The sternal plate between the foramina is wider at this point than that between the anterior mouthpart foramina. The heavily sclerotized coxopodite articulates with the ventral skeleton by a dorsal, laterotergal condyle and a ventral sternal condyle, the typical situation in the white shrimp limb. The axis through the condyles is about 45° from the vertical, with respect to the transverse plane. Since the distal elements are anterior, movements about these coxopodite condyles raise and lower the appendage, as well as promote and remote it. The basipodite articulates with the coxopodite by typical dicondylic connections, the axis of the condyles being horizontal. Thus the basipodite accounts for most of the depression and levation of the distal elements, an arrangement that is common to the third maxilliped and all of the walking legs. A large, tapering, annulated exopodite articulates with the basipodite laterally.

The ischiopodite is fused to the basipodite immovably, although the line of demarcation is clear. The ischiopodite is the longest article of the third maxilliped. The meropodite is connected to the distal end of the ischiopodite by two condyles whose axis permits both flexion of the distal articles towards the midline and reduction of the distal elements. The movements at this joint are extensive. Due to the bending at this joint the shrimp is able to grasp food with the third maxilliped. The carpopodite articulates with the distal end of the meropodite by two condyles. The axis of these dicondyles is vertical, permitting the carpopodite to flex on the meropodite.

The axis through the condyles of the joint between the carpopodite and the propodite is also vertical allowing the propodite to be flexed upon the carpopodite. The small dactylopodite is similarly articulated with the propodite.

The distal elements, beginning with the ischiopodite, bear rows of stout spines on their medial sides for holding food particles. The exopodite has long, plumose setae. The third maxilliped has a branchial arrangement similar to that of the first three walking legs. From the pleural plate arises a pleurobranchia. Two arthrobranchiae project from the dorsal articular membrane, and a bilobed mastigobranchia arises from the coxopodite.

MUSCLE ELEMENTS

The musculature of the third maxilliped of *Penaeus* is typical of that seen in the walking legs. Some variation, however, is evident when the third maxilliped of different crustaceans is compared, especially in the musculature of the exopodite and the distal articles of the endopodite. In *Penaeus*, most of the basipodite and coxopodite muscles originate on the laterotergal, pleural plates rather than on phragmal elements as in the anterior gnathal appendages. Pleural origins of these muscles are typical of all the posterior appendages, thoracic and abdominal alike.

The third maxilliped of *Penaeus* is operated by twenty muscles comprising 12 functional types. That of *Astacus* contains 17 muscles, including 14 types. The third maxilliped of *Pandalus* is somewhat modified, containing 13 muscles of 9 functional types, whereas the same appendage in

Callinectes has 16 muscles grouped into 15 muscle types.

COXOPODITE PROMOTER MUSCLE OF THIRD MAXILLIPED

FIGURES 46, 47, 48

The coxopodite promotor muscle is a strong, lozenge-shaped muscle (fig. 47, *B*) originating on the pleural plate along the anterodorsal margin of the muscle. The insertion is on the anterior margin of the coxopodite (fig. 46). The promotor turns the coxopodite forward and, since the distal parts extend directly anterior, the latter are raised against the other mouthparts. The promotor muscles of *Pandalus*, *Astacus*, and *Callinectes* are the counterparts of the coxopodite promotors in *Penaeus*.

COXOPODITE REMOTOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46, 47

The third maxilliped of *Penaeus* contains two coxopodite remotor muscles. They are much more powerful than the coxopodite promotor muscles which they oppose. The remotors originate on the the laterotergal plate dorsad (fig. 47) and insert on the posterior margin of the coxopodite. They turn the coxopodite caudad and thus the distal elements ventrad as well as laterally. The larger, lateral coxopodite remotor of *Penaeus* is fully homologous with the remotors in the three crustaceans to which we have referred.

BASIPODITE LEVATOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46, 47

The two basipodite levator muscles that have been found in *Penaeus* have different origins. The short, stout lateral levator takes origin on the anterolateral margin of the coxopodite and inserts on the anterior margin of the basipodite. The larger basipodite levator lies internal to the smaller muscle. The origin of the former is on the laterotergal plate and its insertion on the anterior rim of the coxopodite. The levators pull the anterior side of the basipodite upward and with it the distal maxillipedal elements. Three levators of the third maxilliped are described in *Pandalus*, *Astacus*, and *Callinectes*. Part of this group is very likely homologous with the levator pair in *Penaeus*.

BASIPODITE DEPRESSOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46, 47, 48

Considerable variation from the pattern of the depressor musculature of *Penaeus* is seen in the third maxillipeds of *Astacus*, *Pandalus*, and *Callinectes*. Schmidt and Berkeley describe two depressors of the third maxillipeds of *Astacus* and *Pandalus*, whereas Cochran shows one depressor in *Callinectes*. By contrast, *Penaeus* has at least four basipodite depressor muscles in the third maxilliped, just as in the second maxilliped.

The lateral basipodite depressor takes origin on the posterolateral margin of the coxopodite (fig. 47) and inserts, together with the other depressors, on the large apodeme on the posterior rim of the basipodite. Interior to the lateral basipodite depressor is a long, two-part depressor muscle (fig. 47, *B*) originating on the laterotergal plate mesad of the coxopodite remotor muscle. This depressor joins the short lateral depressor on the basipodite depressor apodeme. Immediately mesad of the long depressor lies a small, flat basipodite depressor muscle (figs. 46; 47, *A*) which originates on a medial apodeme of the maxillipedal foramen and inserts on the basipodite apodeme. The most internal basipodite depressor muscle (figs. 46, 48) is a semicylindrical structure originating on medial phragmal apodemes and inserting on the posteromedial edge of the basipodite.

The total action of the basipodite depressor muscles is relatively powerful. By their contractions the basipodite and distal elements of the third maxilliped are turned ventrad. The homologies of these muscles with those of *Astacus*, *Pandalus*, and *Callinectes* are not entirely clear. The depressor muscle *a* of *Astacus* and *Pandalus* is the same muscle as the innermost, medial basipodite depressor muscle in *Penaeus*. Undoubtedly, the depressor muscles a_1 and *b* in *Astacus*, and a_1, a_2 and *b* in *Pandalus* have counterparts in the third maxilliped of *Penaeus*, but their exact relationships are difficult to determine.

EXPODITE ABDUCTOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46, 47

Similar to the arrangement in the second maxilliped, the third maxilliped exopodite of *Penaeus* is moved by 2 exopodite abductor muscles, 1 ex-

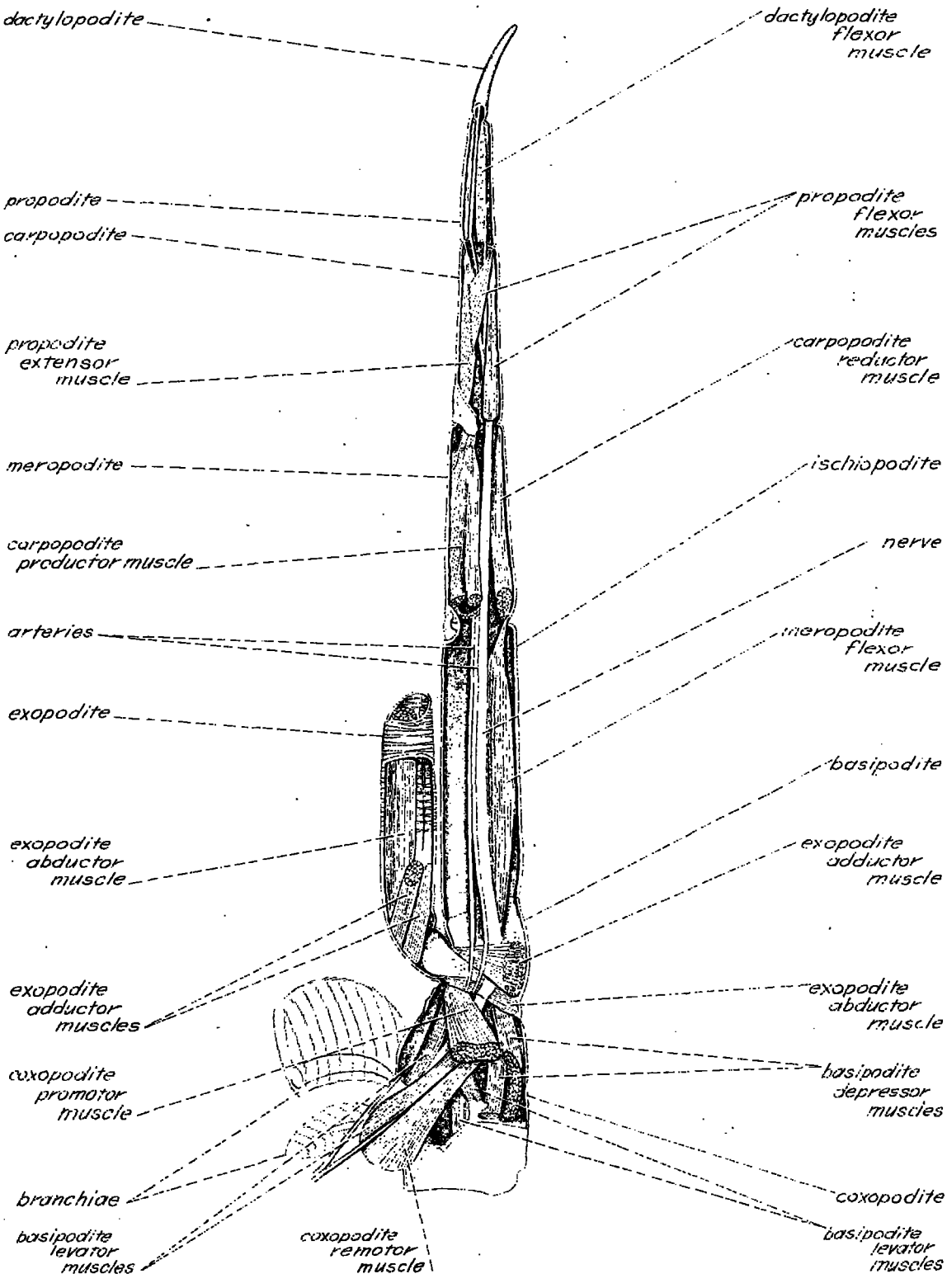

FIGURE 46.—Dorsal view of left third maxilliped, dorsal cuticle removed to show muscles.

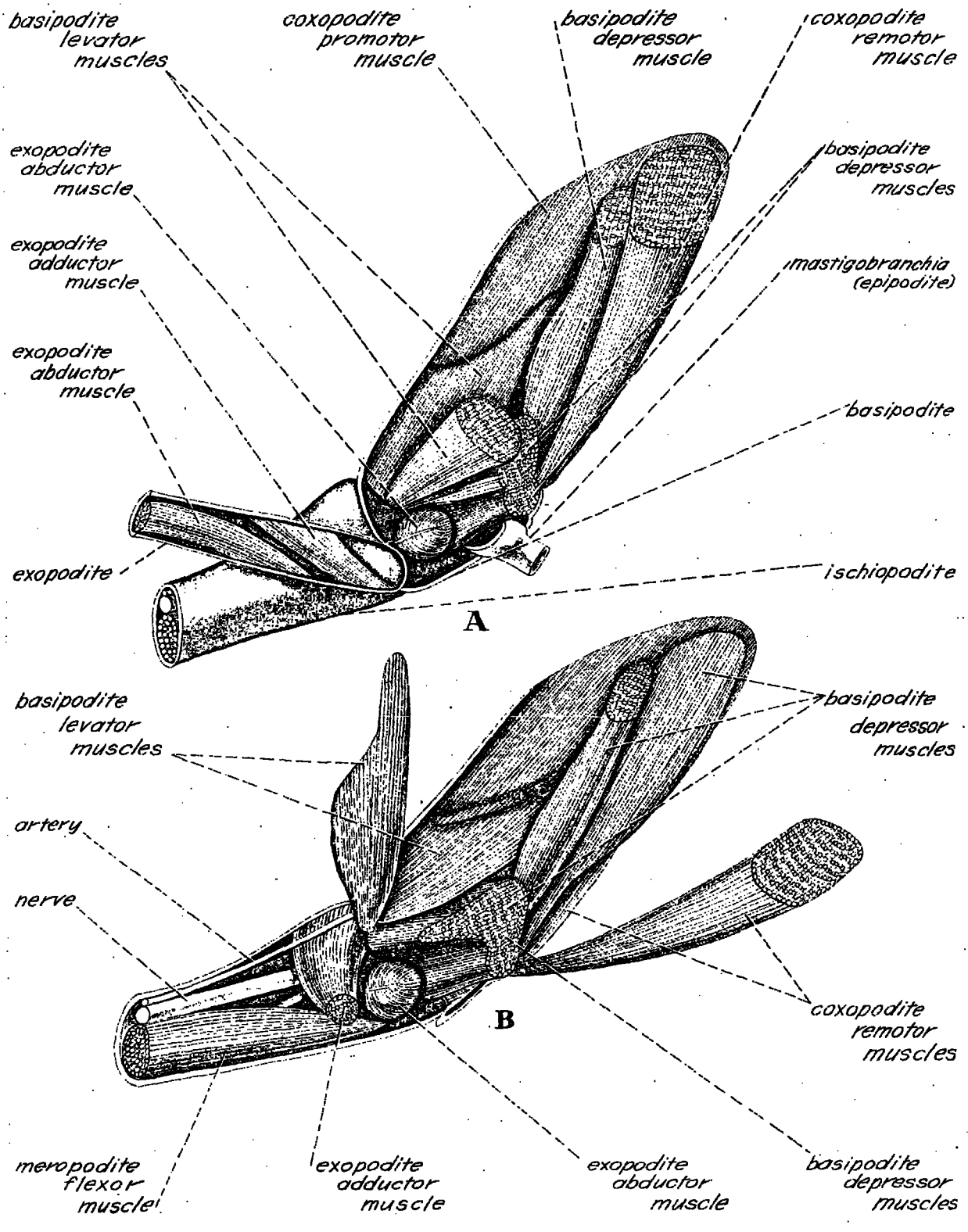

FIGURE 47.—Lateral view of leg base of left third maxilliped. Cuticle removed to show muscles. *A*. Superficial lateral and exopodite muscles. *B*. Lateral muscles, exopodite removed.

trinsic and 1 intrinsic to the structure. The wedge-shaped extrinsic abductor (figs. 46; 47, *B*) originates on the ventromedial wall of the basipodite. The muscle tapers to a point, laterally, inserting on the posterior margin of the exopodite foramen. Contractions of the exopodite abductor turn the exopodite laterad. Intrinsic to the flagellar exopodite is a long abductor muscle (fig. 46) which originates in the proximal region of the exopodite and runs distally along the lateral side of the flagellum. Its contractions increase the lateral curvature of the flagellum, thus turning it laterad. The extrinsic exopodite abductor muscle of *Penaeus* is represented under the same name in *Astacus* and *Callinectes*. The exopodite of *Pandalus* is extremely reduced. The intrinsic exopodite abductor probably appears as the exopodite flagellum muscle in *Astacus* and *Callinectes*.

EXPODITE ADDUCTOR MUSCLES OF THIRD MAXILLIPED

FIGURES 46; 47, *B*

Two exopodite adductor muscles in *Penaeus* turn the exopodite flagellum mesad. The conical extrinsic adductor originates on the dorsomedial wall of the basipodite, dorsad of the extrinsic exopodite abductor muscle (fig. 46), and inserts on the anterior rim of the exopodite foramen. The intrinsic exopodite adductor is comprised of a pair of small muscles originating on the posterolateral side of the flagellum base and attaching a short distance distally on the medial and dorsal wall of the flagellum. The extrinsic adductor has a counterpart in *Callinectes*, but not in *Astacus*. The little intrinsic adductor muscle in *Penaeus* possibly may be the exopodite flagellum abductor muscle of *Astacus* and *Callinectes*, although this is doubtful.

MEROPODITE FLEXOR MUSCLE OF THIRD MAXILLIPED

FIGURES 46, 47

The meropodite flexor muscle is a long, spindle-shaped muscle arising in the basipodite and passing distally along the lateral wall of the ischiopodite to an apodemal insertion on the proximal end of the meropodite. The apodeme of insertion is located ventromedially. When the meropodite flexor contracts, the meropodite and distal articles of the endopodite are turned sharply mesad and, due to the arrangement of the condyles, ventrad. The ischiopodite-meropodite junction is the major functional joint in the third maxilliped. The meropodite flexor muscle of *Penaeus* is fully homologous with the meropodite flexor muscle of *Astacus* and *Callinectes*. The third maxilliped endopodite of *Pandalus* has lost parts by fusion, making difficult the homologies of its muscles.

CARPOPODITE PRODUCTOR MUSCLE OF THIRD MAXILLIPED

FIGURE 46

The carpopodite productor muscle takes origin over an extensive area along the lateral side of the meropodite (fig. 46) and inserts on an apodeme of the carpopodite. Its contractions straighten the carpopodite with respect to the meropodite. The muscle is represented in the third maxilliped of *Astacus* and apparently in *Pandalus*. The productor muscle is referred to as an extensor by Cochran in *Callinectes* due to a difference in condylic orientation.

CARPOPODITE REDUCTOR MUSCLE OF THIRD MAXILLIPED

FIGURE 46

Opposing the action of the carpopodite productor muscle is the carpopodite reductor muscle. This muscle originates in the proximal region of the meropodite and passes distally along the medial side of the meropodite to insert on a ventromedial apodeme of the carpopodite. Upon contraction, the muscle turns the carpopodite and the distal articles ventrad. The carpopodite reductor muscle of *Penaeus* is the same muscle in *Astacus*, *Pandalus*, and *Callinectes*, although in the latter Cochran describes it as a flexor.

PROPODITE EXTENSOR MUSCLE OF THIRD MAXILLIPED

FIGURE 46

Originating for some length along the lateral margin of the carpopodite, the propodite extensor muscle inserts on a laterally located apodeme of the propodite. The muscle extends the propodite and dactylopodite directly anterior to the carpopodite. The same muscle is found in all the crustaceans to which reference has been made.

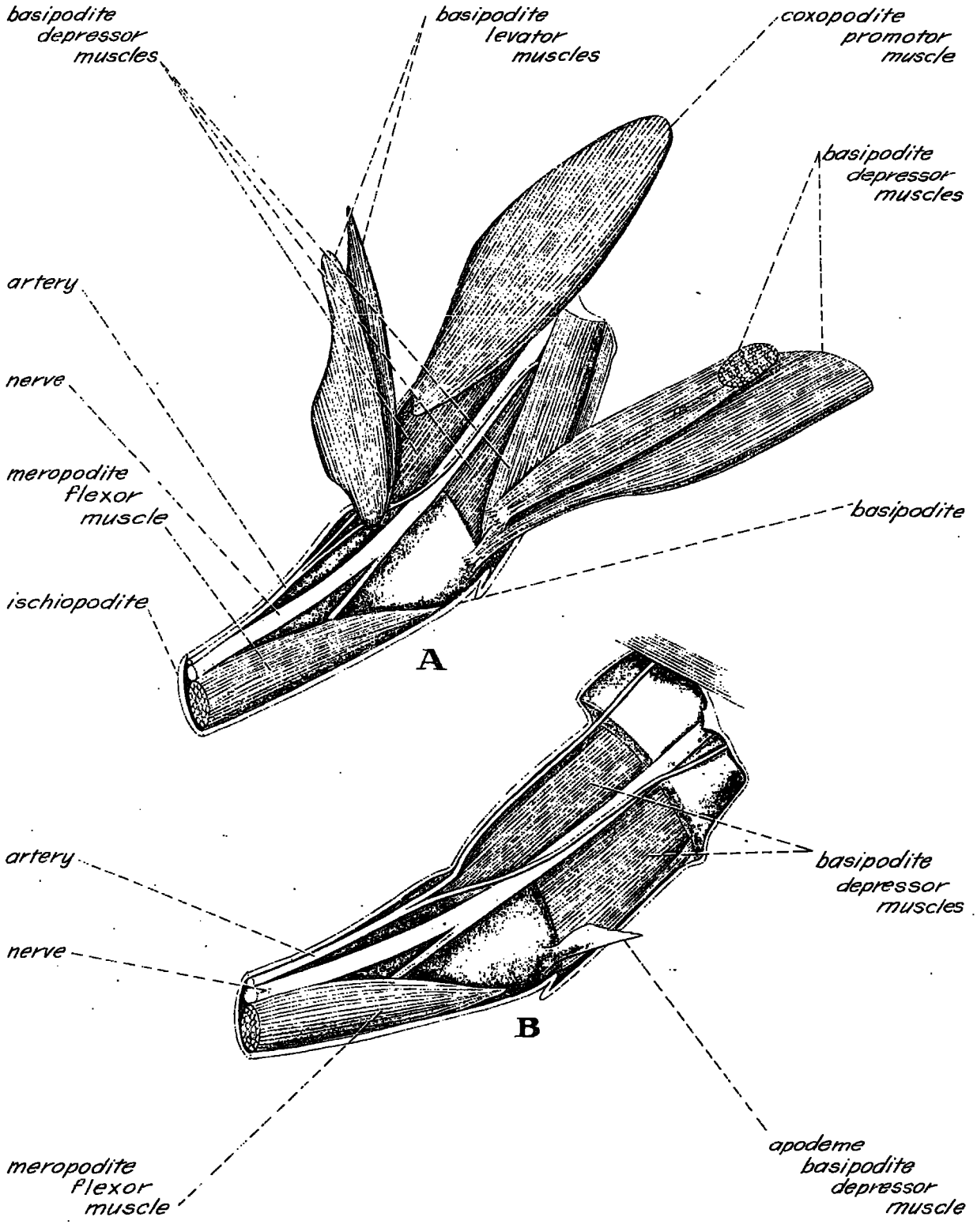

FIGURE 48.—Lateral view of leg base of left third maxilliped. *A*. Lateral and medial muscles. *B*. Medial muscles.

PROPODITE FLEXOR MUSCLES OF THIRD MAXILLIPED

FIGURE 46

The third maxilliped of *Penaeus* is unique by comparison with the same appendage of *Pandalus*, *Astacus*, and *Callinectes* in having two propodite flexor muscles. The larger originates in the carpopodite proximally and passes distally on the lateral side of the article to its insertion on an apodeme of the propodite. The smaller propodite flexor is a little triangular muscle (fig. 46) which has a common insertion with the larger flexor. The flexor muscles turn the propodite mesad on the carpopodite. The larger propodite flexor muscle is found in all the crustaceans referred to.

DACTYLOPODITE FLEXOR MUSCLE OF THIRD MAXILLIPED

FIGURE 46

The dactylopodite flexor muscle arises in the proximal portion of the propodite and is attached to an apodeme of the dactylopodite. The muscle turns the dactylopodite toward the midline. Dactylopodite flexors appear in the third maxilliped of *Astacus* and *Callinectes*. The distal articles are fused in *Pandalus* and the muscles thus lost. The third maxilliped of *Penaeus* has no dactylopodite extensor muscle, a structure described in *Astacus* and *Callinectes*.

5. PEREIOPODS

In the Crustacea Decapoda the last five pairs of thoracic appendages are usually referred to as walking legs, or pereiopods. Although their length, size, and functional modifications are variable in the group, the walking legs are all fundamentally alike in structure. Exopodites, usually small, are either present or absent. The large protopodite-endopodite is almost always composed of the typical seven appendage articles, although fusion of the basipodite with the ischiopodite has occurred in some groups. Some or all of the pereiopods may be chelate. Incidentally, Dougherty (Steinberg and Dougherty, 1957) objects to the spelling of the word "pereiopod" and offers good reasons for dropping the *i* in American usage. The common and perhaps incorrect spelling is used in the present work.

In *Penaeus*, the pereiopods are all relatively long and slender as befits a lightly sclerotized form whose body weight on the walking legs is not great. The first three pereiopods bear small chelae with sharp cutting edges. The last two walking legs are subchelate. Small exopodites are found on all five pairs of pereiopods. The joint between the basipodite and ischiopodite is movable in the walking legs of *Penaeus*. The coxopodite and basipodite comprise the protopodite to which an endopodite with the typical five articles is attached. Associated with the pereiopods are branchiae. With the third maxillipeds, the first, second, and third pereiopods have a bilobed mastigobranchia (epipodite) arising from the coxopodites, 2 arthrobranchiae on the dorsal articular membrane, and 1 pleurobranchia on the laterotergal plate. The mastigobranchia and one arthrobranchia is missing on the fourth pereiopod and the fifth pereiopod has only a pleurobranch.

Due to pronounced serial similarity of parts in the walking legs, only the first and fifth pereiopods will be considered in detail here.

5a. First Pereiopod

The first pereiopod is considered as an example of a chelate limb. It is ordinarily treated as the first walking leg. Whereas in the Reptantia the first pereiopods are modified into huge chelate chelipeds, those of the Penaeidae, while chelate, are similar in size to the remaining four pairs of walking legs. In point of fact, the first pereiopod of *Penaeus* is not a functional walking leg. That is to say, none of the body weight is supported on the appendage. The first pereiopods are carried horizontally, directed anteriorly, ventrad of the third maxillipeds, and function to pass food particles to the latter.

SKELETAL ELEMENTS

The strongly sclerotized coxopodite articulates with the ventral skeleton by dorsoventral dicondyles. The axis through the condyles is such that when the coxopodite swings forward it also approaches the midline. The rearward motion, on the other hand, turns the coxopodites away from the midline. The angular attitude of the dicondylic axis of the first pereiopod is thus raised laterally with respect to the frontal plane and rostrad with respect to the transverse plane. Proceeding caudad, the angular attitude of the axis through the coxopodite condyles rises laterally with respect to the frontal plane in conjunction with the shift dorsad of the dorsal condyle and the increased width between the ventral sternal

condyles. To the coxopodite is attached the strong, curving tube of the basipodite. The axis of the condyles between the coxopodite and basipodite is rotated 90° from the axis of the condyles connecting the coxopodite and the ventral skeleton. Primarily by means of the basipodite, the distal elements of the pereiopod are raised and lowered. A sharp process projects distally from the distomedial portion of the basipodite. A small, fingerlike exopodite bearing long setae projects laterad from the basipodite.

The ischiopodite is hinged to the basipodite to permit limited reduction of this article, and also some rotation of the distal elements due to the oblique angle of the condyles. Like the basipodite, the ischiopodite bears a sharp spine medially. The meropodite, one of the longer articles of the first pereiopod, articulates with the distal end of the ischiopodite, allowing some flexion and extension, together with a little reduction, of the distal segments. The most movable joint in the first walking leg is that connecting the meropodite and the carpopodite. The axis of the joint is horizontal, and the carpopodite is thereby capable of deep flexion on the meropodite. An antennal cleaning brush composed of comb-like setae resides in a distomedial depression of the carpopodite.

The chela is freely movable on the carpopodite. The propodite component is made up of a base element and a distal process (fig. 49). The dactylopodite articulates with the distal part of the base of the propodite, opposing the distal propodite process. Extremely fine calcareous teeth on the inner margins of the propodite process and dactylopodite enhance the cutting ability of the chela. Chemosensory pits from which project chemoreceptor tufts of fine setae are distributed in rows about the propodite process and dactylopodite surface.

MUSCLE ELEMENTS

The musculature of the first pereiopod is closely similar to that of the third maxilliped and the remaining walking legs. It is also similar to the pereiopod musculature of other decapods. The first pereiopod of *Penaeus* contains at least 21 discrete muscles arranged in 14 functional muscle types. *Astacus* has 19 muscles of 13 types, and *Callinectes* has 20 muscles functioning in 11 ways. The third pereiopod of *Pandalus* contains 16 muscles of 13 types.

COXOPODITE PROMOTOR MUSCLES OF FIRST PEREIOPOD

FIGS. 49, 50, 51

The first pereiopod of *Penaeus* possesses at least two coxopodite promotor muscles. They originate by broad regions along the anterodorsal margin of the pleural plate belonging to the segment and insert on the anterior rim of the coxopodite. Their contractions turn the coxopodite forward. The coxopodite promotors of *Penaeus* are represented in *Astacus*, *Pandalus*, and *Callinectes*.

COXOPODITE REMOTOR MUSCLE OF FIRST PEREIOPOD

FIGS. 49, 50, 51

The strong, spatulate coxopodite remotor muscle originates on the posterodorsal part of the laterotergal plate and attaches to a small apodeme on the posterior margin of the coxopodite foramen. The muscle turns the coxopodite rearward and in so doing brings the distal elements of the pereiopod ventrad, in opposition to the coxopodite promotors. The movement is evidently weaker than that of promotion, since the single remotor is much smaller than the promotor muscles. The homologies of the coxopodite remotor muscle of *Penaeus* with the remotor muscle of *Callinectes* are fairly obvious. *Astacus*, however, has three remotors. Which of these is homologous with the coxopodite remotor of *Penaeus* is not certain.

BASIPODITE LEVATOR MUSCLES OF FIRST PEREIOPOD

FIGURES 49, 50, 51

A characteristic of pereiopod musculature is the great weight and strength of the basipodite musculature, affording powerful levation and depression of that article and with it the distal elements of the leg. The situation in the Decapoda is reminiscent of the trochanteral musculature of the insects, except that the levators and depressors of the latter originate within the coxa, rather than on the pleural wall. Functionally, the basipodite depressors are the major support of the body between the walking legs.

The first walking leg of *Penaeus* has 4 basipodite levator muscles, of which 3 originate within the coxopodite and 1 dorsally on the pleural wall.

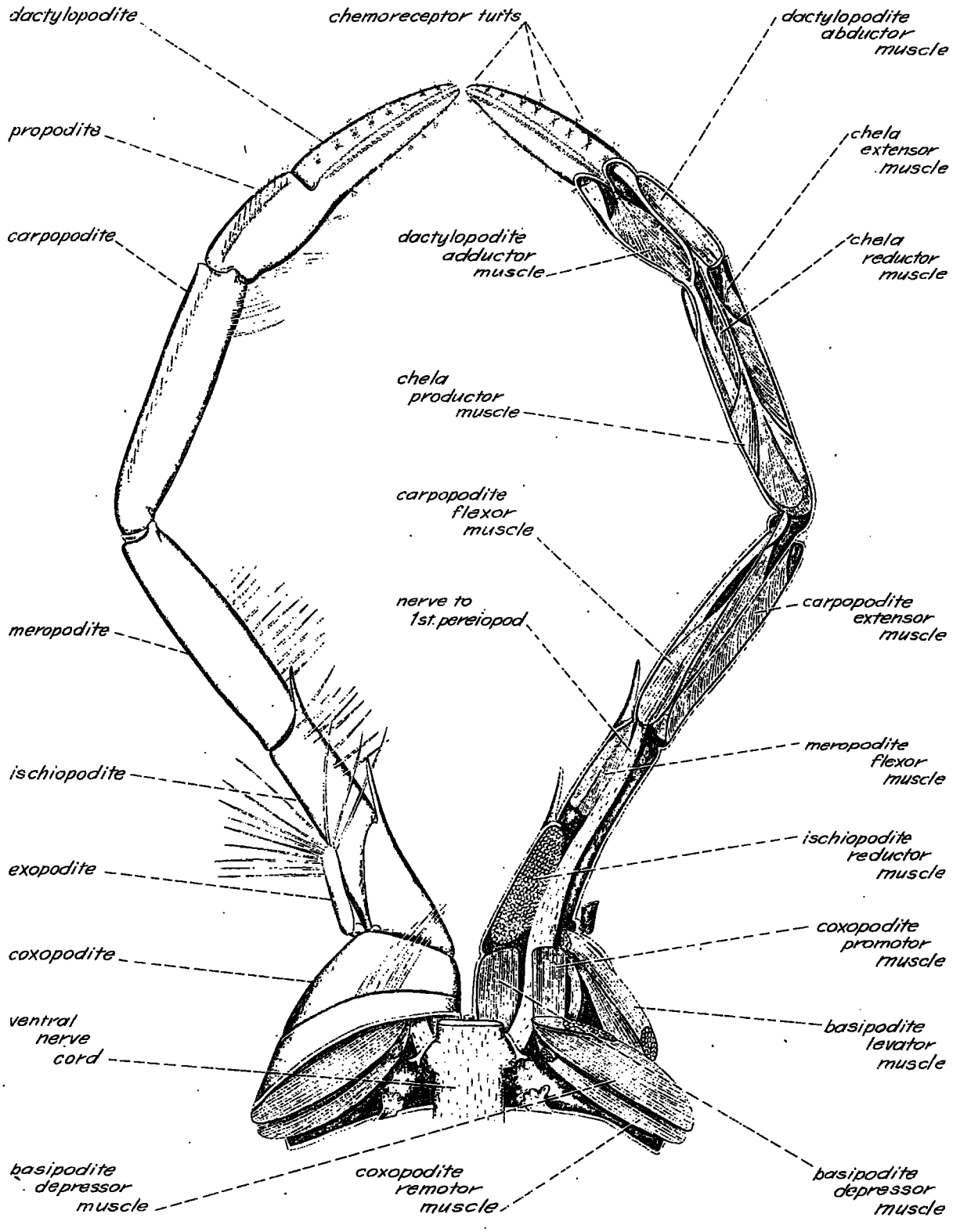

FIGURE 49.—Dorsal view of first pereiopod. Left side, intact appendage. Right side, dorsal cuticle removed to show muscles.

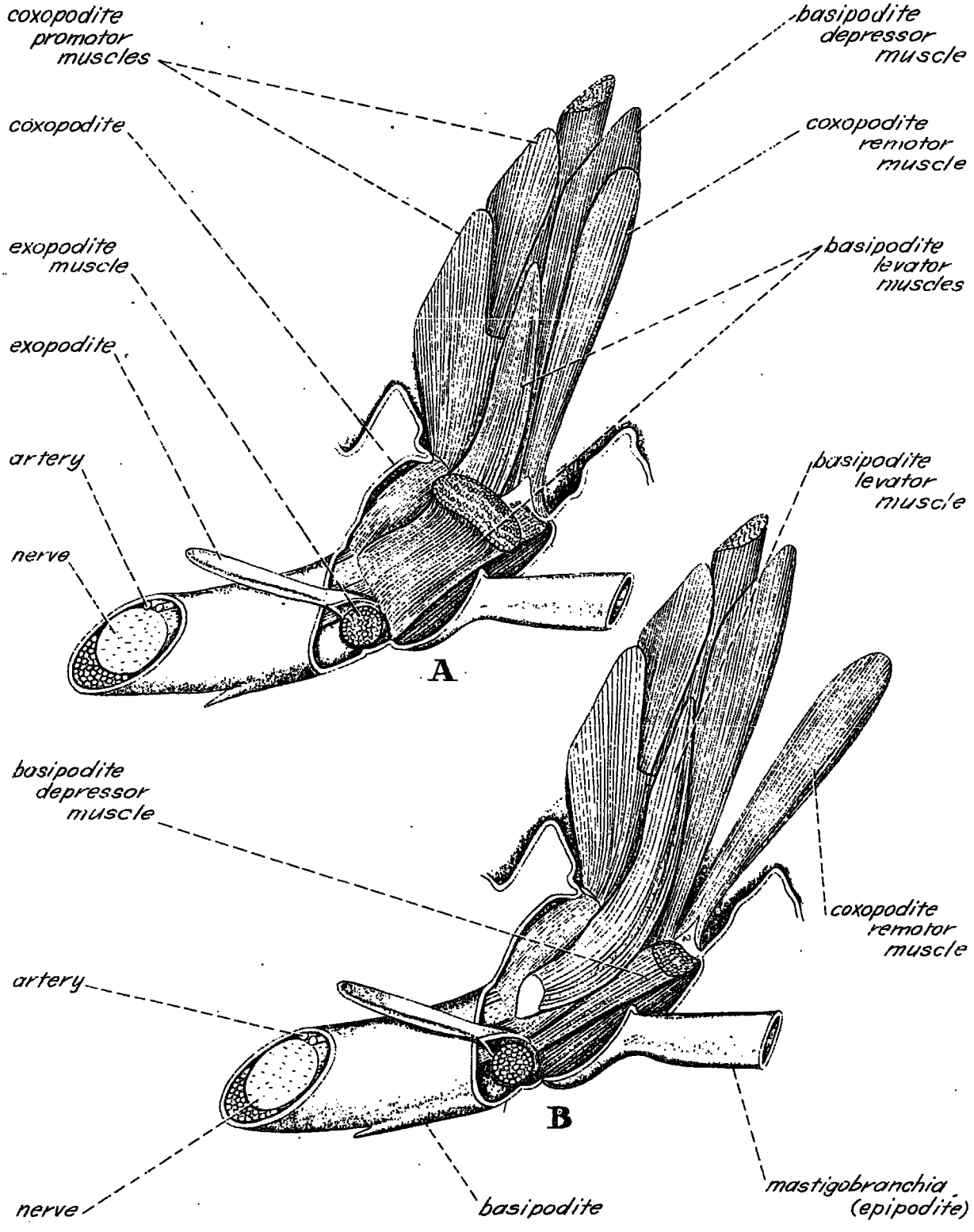

FIGURE 50.—Lateral view of leg base of left first pereiopod. *A*. Superficial lateral muscles. *B*. Some lateral muscles removed to show deeper muscles.

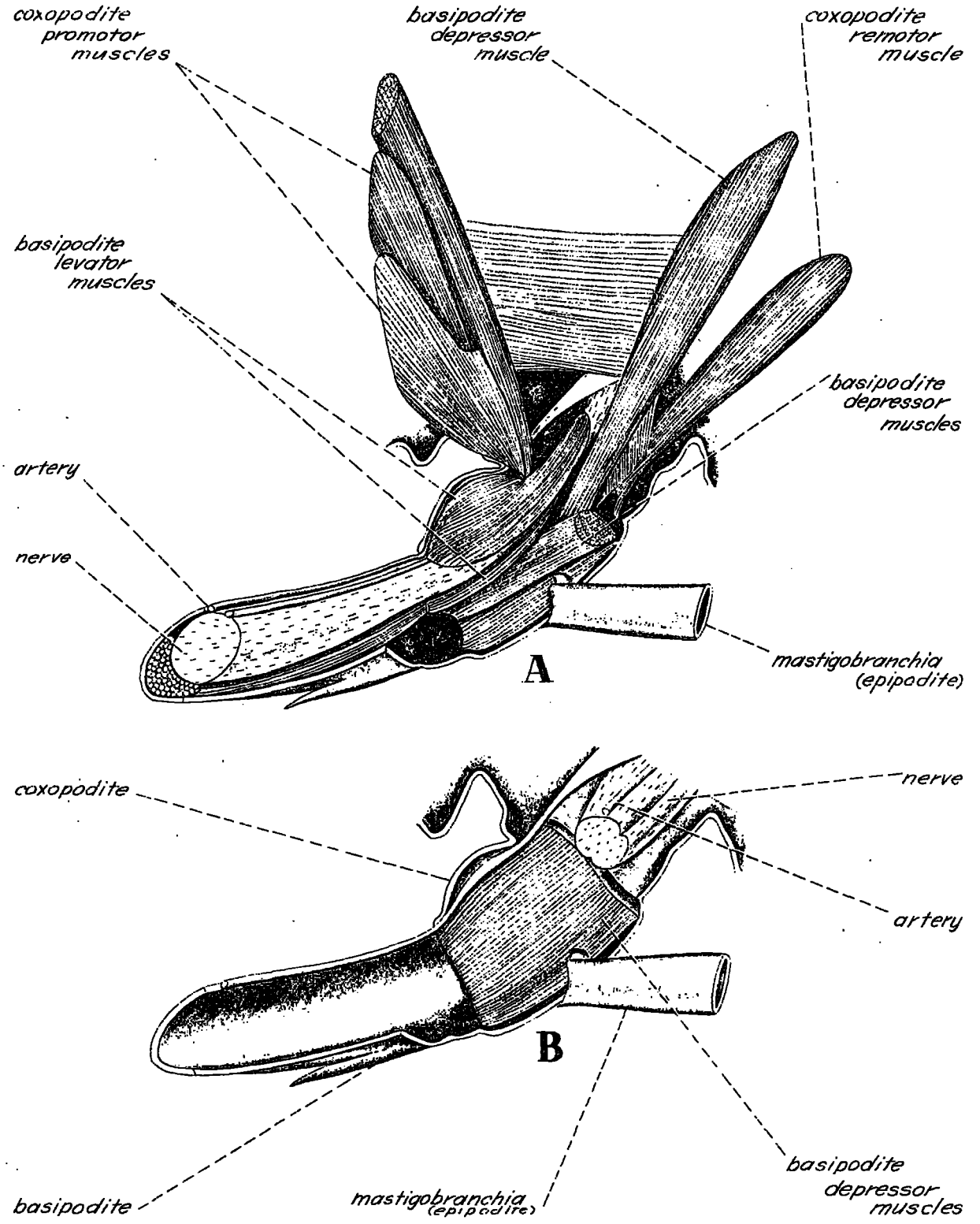

FIGURE 51.—Lateral view of leg base of left first perelopod. *A*. Lateral and medial muscles. *B*. Medial muscles.

The lateralmost levator (fig. 50, *A*) is a short, strong muscle taking origin on the lateral edge of the coxopodite and inserting on an anterolateral apodeme of the basipodite. Mesad of this levator lies a long, curving basipodite levator (fig. 50, *A*, *B*) which originates on the pleural plate and joins the former levator on the basipodite levator apodeme. The third basipodite levator is a short, rounded muscle situated mesad of the previously mentioned levators (fig. 50, *A*). The third levator originates in the coxopodite and inserts on the anterior rim of the basipodite. The medial, fourth levator, also originating on the coxopodite, inserts on the anteromedial edge of the basipodite (fig. 51, *A*). The basipodite levator muscles turn the basipodite and the distal leg article dorsad.

While the three walking leg levator muscles found in *Astacus* and *Callinectes* are undoubtedly homologous with some or all of the basipodite levators in *Penaeus*, the details of their relationships are uncertain.

BASIPODITE DEPRESSOR MUSCLES OF FIRST PEREIOPOD

FIGURES 49, 50, 51

The first walking leg of *Penaeus* has four basipodite depressor muscles. Two of the depressors originate in the coxopodite and two on the pleural wall. The lateralmost member of the group originates on the lateral side of the coxopodite (fig. 51, *A*) and passes ventromedially to insert on the common basipodite depressor apodeme. The longer, second depressor originates dorsad, on the pleural wall, and runs ventrad to the common apodeme. Mesad of the second basipodite depressor lies a short third depressor of the basipodite which is attached between the dorsomedial rim of the coxopodite and the basipodite apodeme. The fourth basipodite depressor muscle lines the medial side of the coxopodite. Unlike the other depressors, the fourth basipodite depressor inserts for some length along the posteromedial margin of the basipodite.

The basipodite depressor muscles turn the basipodite ventrad, thus accomplishing body support on the limbs. Considerable variation in basipodite musculature exists. The depressor muscle *a* of *Astacus* is very likely the homolog of the long, second basipodite depressor of *Penaeus*, whereas the depressor muscle *b* of *Astacus* is probably homologous to the lateral, first basipodite depressor muscle in *Penaeus*. The relationships in *Penaeus* to the seven depressor muscles of the blue crab are difficult to ascertain. The depressor muscle *b* in the third pereiopod of *Pandalus* looks much like the medial, fourth basipodite depressor muscle in the first pereiopod of *Penaeus*.

EXOPODITE MUSCLE OF FIRST PEREIOPOD

FIGURE 50

The little, spindle-shaped exopodite muscle originates on the wall of the basipodite, mesad, and passes across the basipodite to a point of insertion at the base of the exopodite. Presumably its contractions move the exopodite, which, while very reduced, is connected to the basipodite by an articular joint. Nothing similar to the exopodite muscle is described in the first pereiopod of the other crustaceans referred to. Berkeley describes an attractor of the mastigobranch in the pereiopods of *Pandalus*, but illustrates the muscle as a coxopodite component.

ISCHIOPODITE REDUCTOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

The ischiopodite reductor muscle originates over an extensive area on the dorsomedial surface of the basipodite. The muscle inserts on a proximal ischiopodite apodeme located on the ventromedial rim of the ischiopodite. The reductor pulls the ischiopodite and with it the distal articles ventrad. The ischiopodite reductor muscle of *Astacus* is the same as that of *Penaeus*. The muscle is missing in the blue crab, in which the basipodite and ischiopodite are fused.

MEROPODITE FLEXOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

The meropodite flexor muscle is a two-part structure whose short fibers insert at an angle on an elongate apodeme projecting from the ventromedial edge of the meropodite, proximally. The apodeme divides the muscle approximately in half on its long axis. The muscle fibers originate about a wide area of the ventral and medial surface of the ischiopodite. Their contractions turn the meropodite mesad and to a lesser extent ventrally. The meropodite flexor muscle apparently is subdivided into two parts in *Astacus*, in which

Schmidt describes them as reductors. A single meropodite reductor is shown in the study of *Callinectes*. The muscle is unopposed by an extensor or productor in *Penaeus* and the other forms considered here.

CARPOPODITE EXTENSOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

The fibers of the carpopodite extensor muscle take origin over very nearly the whole of the lateral side of the meropodite. The apodeme upon which they insert extends proximally from the lateral edge of the carpopodite and runs almost the length of the meropodite. The carpopodite extensor straightens the carpopodite on the meropodite in a horizontal plane. The muscle is represented in *Astacus* and *Callinectes* as the carpopodite abductor muscle.

CARPOPODITE FLEXOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

Somewhat like the carpopodite extensor, the carpopodite flexor muscle is a long muscle inserting on a long apodeme. The muscle origins occur about the medial and ventral surfaces of the meropodite. The carpopodite flexor apodeme arises from the proximal margin of the carpopodite, mesad of the dicondylic axis. A pull on this apodeme turns the carpopodite and chela deeply on the meropodite, for this joint is a free one. The same muscle is found in the first pereiopod of *Astacus* and *Callinectes*, but named the carpopodite adductor muscle.

CHELA PRODUCTOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

The fibers of the chela productor muscle arise from lateral, proximal, and medial regions of the dorsal part of the carpopodite and insert on the long productor apodeme of the propodite. Since the joint between the carpopodite and propodite is a free one, tension on the productor apodeme tends to straighten the chela with respect to the carpopodite and even to levate the chela. The propodite productor muscle of *Penaeus* is found in much the same form in *Astacus* and *Callinectes*, under the name of propodite productor muscle.

CHELA REDUCTOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

Directly ventrad of the chela productor muscle lies the chela reductor muscle, a structure also attaching by several slips to a long apodeme. The reductor apodeme arises from the ventral rim of the propodite. The chela reductor muscle turns the chela ventrad. The same muscle appears in the first pereiopod of *Astacus* and *Callinectes*, and in the second pereiopod of *Pandalus*, as the propodite reductor muscle.

CHELA EXTENSOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

As mentioned above, the joint between the carpopodite and propodite affords free movements of the latter on the former. The chela extensor muscle straightens the chela with respect to the carpopodite in the horizontal plane. The muscle originates in the distolateral part of the carpopodite and inserts on an apodeme projecting proximally from the lateral margin of the propodite. Exact counterparts of the chela extensor are missing in the first pereiopod of *Astacus* and *Callinectes*. Berkeley describes, however, 2 extensors and 2 flexors of the propodite in the second pereiopod of *Pandalus*. Homologies of these muscles without information about their innervations is not feasible.

DACTYLOPODITE ADDUCTOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

The dactylopodite adductor muscle originates throughout the medial part of the pod-shaped propodite and inserts on a heavy apodeme of the dactylopodite. Contractions of this large muscle close the dactylopodite on the distal gnathal process of the propodite. The dactylopodite adductor muscle is found in the first pereiopod of *Astacus* and *Callinectes*.

DACTYLOPODITE ABDUCTOR MUSCLE OF FIRST PEREIOPOD

FIGURE 49

Functioning in opposition to the dactylopodite adductor muscle, the fibers of the dactylopodite abductor muscle originate about the lateral surfaces of the propodite and insert on the abductor

468059 O—59——7

apodeme attached to the lateral margin of the dactylopodite. The muscle opens the jaws of the chela. The dactylopodite abductor muscle of *Penaeus* is fully homologous with the muscle of the same name in the first pereiopod of *Astacus* and *Callinectes*. The first pereiopod chela of *Pandalus* is reduced.

5b. Fifth Pereiopod

The fifth pereiopod has been chosen as an example of a nonchelate limb. It is truly ambulatory, slender and very long, much longer than the first pereiopod, mainly due to pronounced lengthening of the meropodite and carpopodite. Dorsad of the fifth pereiopod projects a single pleurobranchia.

SKELETAL ELEMENTS

The coxopodite (fig. 54) is a rounded box whose lateral corner projects dorsally to a point. This point makes contact with the dorsal condyle of the article. The ventral condyle is located on the sternal plate between the limbs. The arrangement of these coxopodite dicondyles permits this article great freedom of movement. A large region of thin cuticle, the articular cuticula (fig. 54), lying caudad of the coxopodite, presents little resistance to posterior movements of the segment. A second articular cuticula associated with basipodite movements is found on the lateral surface of the coxopodite.

The strong basipodite (fig. 54) is hinged to the ventral surface of the coxopodite in the typical way, allowing for extensive movements of this article and of the distal segments in the vertical plane. With the dorsolateral surface of the basipodite is articulated a small exopodite. The ischiopodite (fig. 52) makes an oblique connection with the basipodite. The joint is slightly movable. The ischiopodite may be bent ventrad on horizontally located condyles. The articulation point between the short ischiopodite and the long meropodite is a transverse one capable of limited motion. By means of the joint the meropodite may be turned ventrad.

The carpopodite articulates with the meropodite by means of a complex "knee" joint made up of a pair of heavy condyles so arranged that the joint has considerable freedom of action. Similarly oriented, but not so freely movable, is the articulation between the carpopodite and propodite. The propodite is not so long as the carpopodite. The slender, tapering dactylopodite makes contact with the propodite by a simple dicondylic joint. Chemoreceptor tufts and other sensory and mechanical setae are arranged in rows on the dactylopodite and to some extent on the propodite.

MUSCLE ELEMENTS

The arrangement of the muscles of the fifth pereiopod is typical of the true supporting limbs of the thorax. The ambulatory muscles are light by comparison with those of the heavy reptant crustaceans and the terrestrial arthropods. In response to the support function of this appendage, the depressor musculature of the basipodite is especially well developed. The only anatomical account of the fifth pereiopod of a crustacean known to the present writer is that of Cochran on *Callinectes*. However, the fifth leg of the blue crab is the swimming leg and hence its muscles, particularly the basal ones, have diverged from the typical pattern. A remarkable uniformity of endopodite musculature between *Penaeus* and *Callinectes* still remains, however. The fifth pereiopod of *Penaeus* is operated by 24 muscles grouped into 13 functional types.

COXOPODITE PROMOTOR MUSCLES OF FIFTH PEREIOPOD

FIGURES 52, 53, 55 to 57

Two coxopodite promotor muscles are found in the fifth pereiopod of *Penaeus*. The smaller lateral promotor originates by its broad, dorsal, fan-shaped portion on the laterotergal plate of the segment (figs. 55, 56) and inserts on the anterior rim of the coxopodite. Lying medial to the latter muscle is a larger promotor muscle mass originating somewhat dorsad of the smaller promotor on the pleural region. Contractions of these muscles turn the coxopodite forward on its condyles.

COXOPODITE REMOTOR MUSCLES OF FIFTH PEREIOPOD

FIGURES 52, 53, 55, 56

The fifth pereiopod of *Penaeus* has two coxopodite remotor muscles. These are large, flat muscles (fig. 55) situated beneath the thin material of the articular cuticula (fig. 54). Both originate by broad margins on the pleural plate and insert on the caudal margin of the coxopodite.

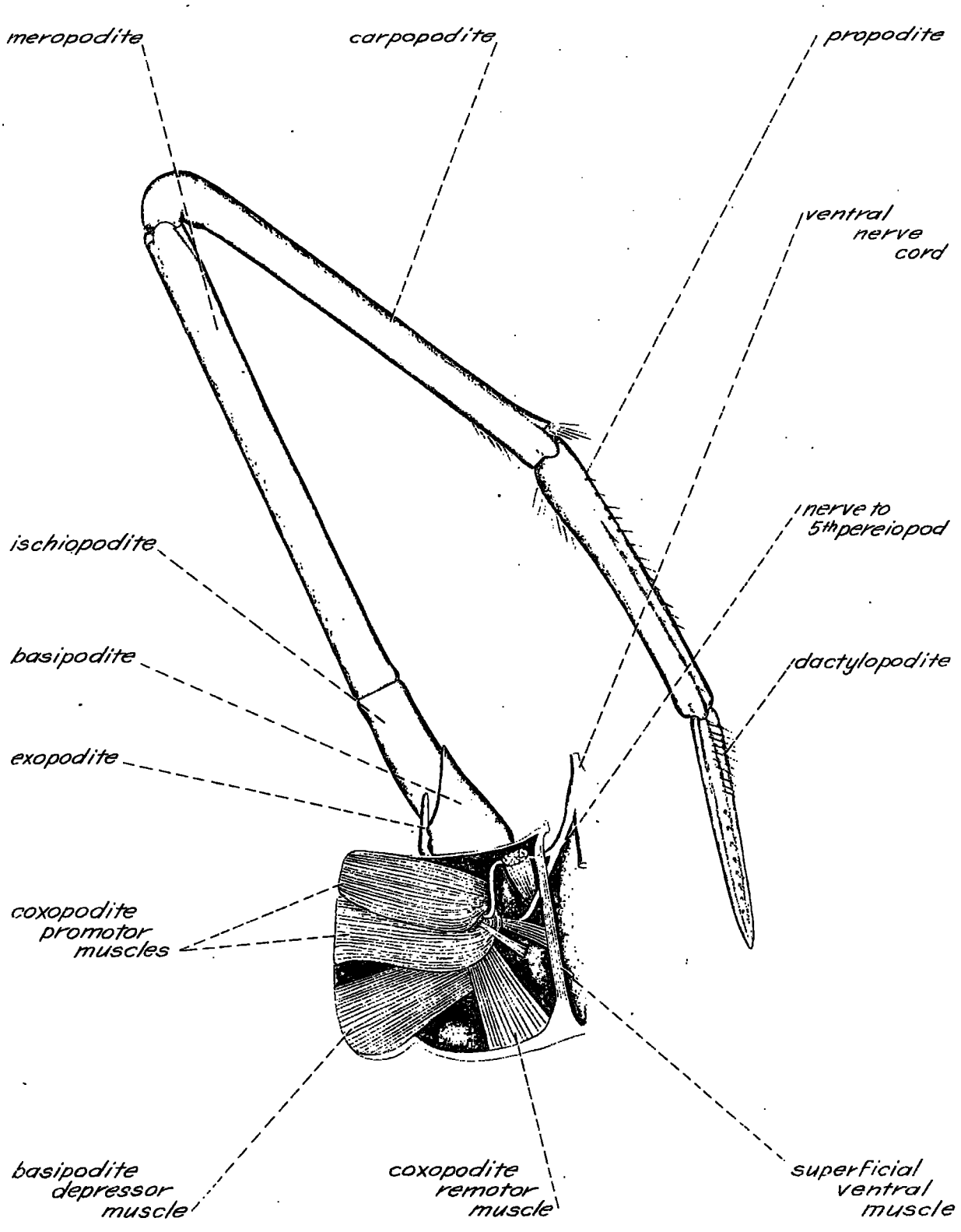

FIGURE 52.—Dorsal view of left fifth pereiopod showing protopodite muscles.

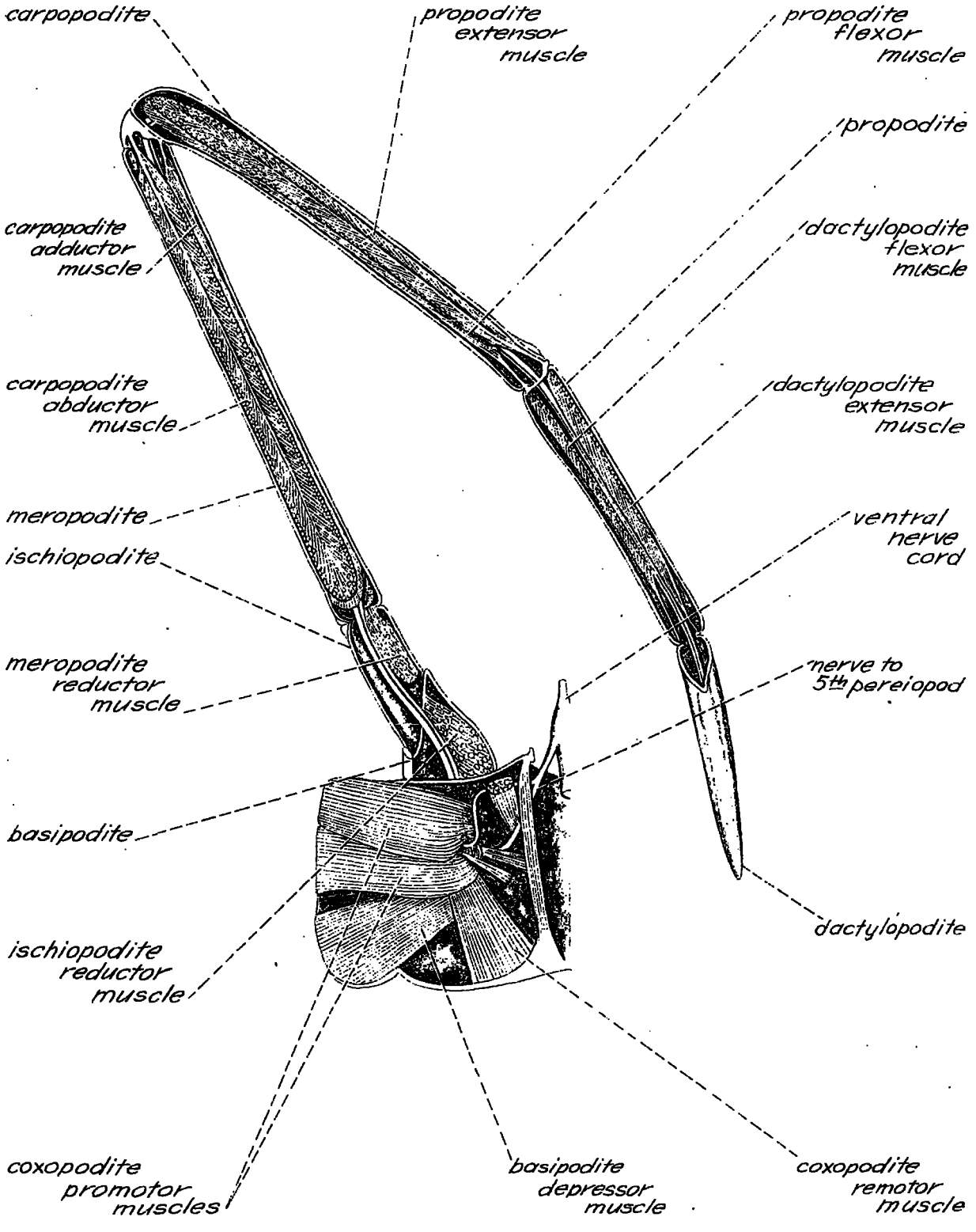

FIGURE 53.—Dorsal view of left fifth pereiopod. Dorsal cuticle removed to show muscles of protopodite and endopodite.

The coxopodite remotor muscles act with some power to turn the coxopodite rearward.

COXOPODITE DEPRESSOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 58

The coxopodite depressor muscle arises from phragmal material on the medial margin of the ventral skeletal foramen entering the coxopodite and runs to the medial margin of the coxopodite (fig. 58). Apparently the muscle is able to lift slightly the medial margin of the coxopodite, and for this reason the structure has been named the coxopodite depressor muscle.

BASIPODITE LEVATOR MUSCLES OF FIFTH PEREIOPOD

FIGURES 55, 56

Four basipodite levator muscles are seen in the fifth pereiopod of *Penaeus*. The two lateral levators constitute together a broad fan (fig. 55) originating along the caudal margin of the coxopodite. They become narrow as they run to their insertions on the lateral rim of the basipodite. Two longer levators lying mesad of the lateral levators originate in the dorsal apex of the coxopodite and run to heavy apodemal material common to the levator muscles. The basipodite levator muscles raise dorsally the basipodite and with it the distal elements of the limb.

BASIPODITE DEPRESSOR MUSCLES OF FIFTH PEREIOPOD

FIGURES 52, 53, 55 TO 58

The most important muscles of the fifth pereiopod of *Penaeus* are the depressors of the basipodite. Seven basipodite depressor muscles exist in the limb. The first and second depressor muscles are lateral (fig. 56). They take origins on areas of the caudal margin of the coxopodite and insert on the large common depressor apodeme of the basipodite. The third depressor (figs. 55, 56) is a large fan which originates broadly on the laterotergal plate of the body segment. The fourth basipodite depressor (fig. 57), also fan-shaped but narrower than the third, lies just mesad of the third depressor muscle. It, too, has a broad origin on the pleural area. The fifth depressor is a rather small muscle (fig. 58) which takes its origin on medial phragmal material of the ventral skeleton. All of the foregoing five muscles insert on the basipodite depressor apodeme. The sixth and seventh depressor muscles (fig. 58) arise on phragmal material on the medial side of the ventral skeletal foramen and insert for some length along the posteromedial rim of the basipodite. The function of the basipodite depressor muscles is to turn the fifth pereiopod ventrad, providing support for the body.

ISCHIOPODITE REDUCTOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

The ischiopodite reductor muscle has multiple origins over a substantial area on the dorsal and medial parts of the basipodite. It inserts on an apodeme projecting from the ventral surface of the ischiopodite. The muscle bends the ischiopodite ventrad slightly and to some extent rotates it, due to the oblique angle by which the basipodite and ischiopodite are connected (fig. 52). The muscle is not opposed by any other muscle.

MEROPODITE REDUCTOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

Arising by multiple origins on the dorsal and medial half of the ischiopodite, the meropodite reductor muscle fibers insert on a small apodeme on the ventral surface of the long meropodite, proximally. The meropodite reductor bends the meropodite ventrally a short distance.

CARPOPODITE ABDUCTOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

The fibers of the carpopodite abductor muscle originate over most of the dorsal half of the meropodite and insert on an extremely long apodeme running nearly the whole length of the meropodite along the midline. The length of pull of this muscle and of its opponent, the carpopodite adductor, is very great. The long apodeme to which it attaches arises from the proximal end of the carpopodite, lateral to the condylic axis. The muscle thus turns the carpopodite to a position in which the axes of the meropodite and carpopodite are in line. The carpopodite abductor muscle easily could be described as an extensor.

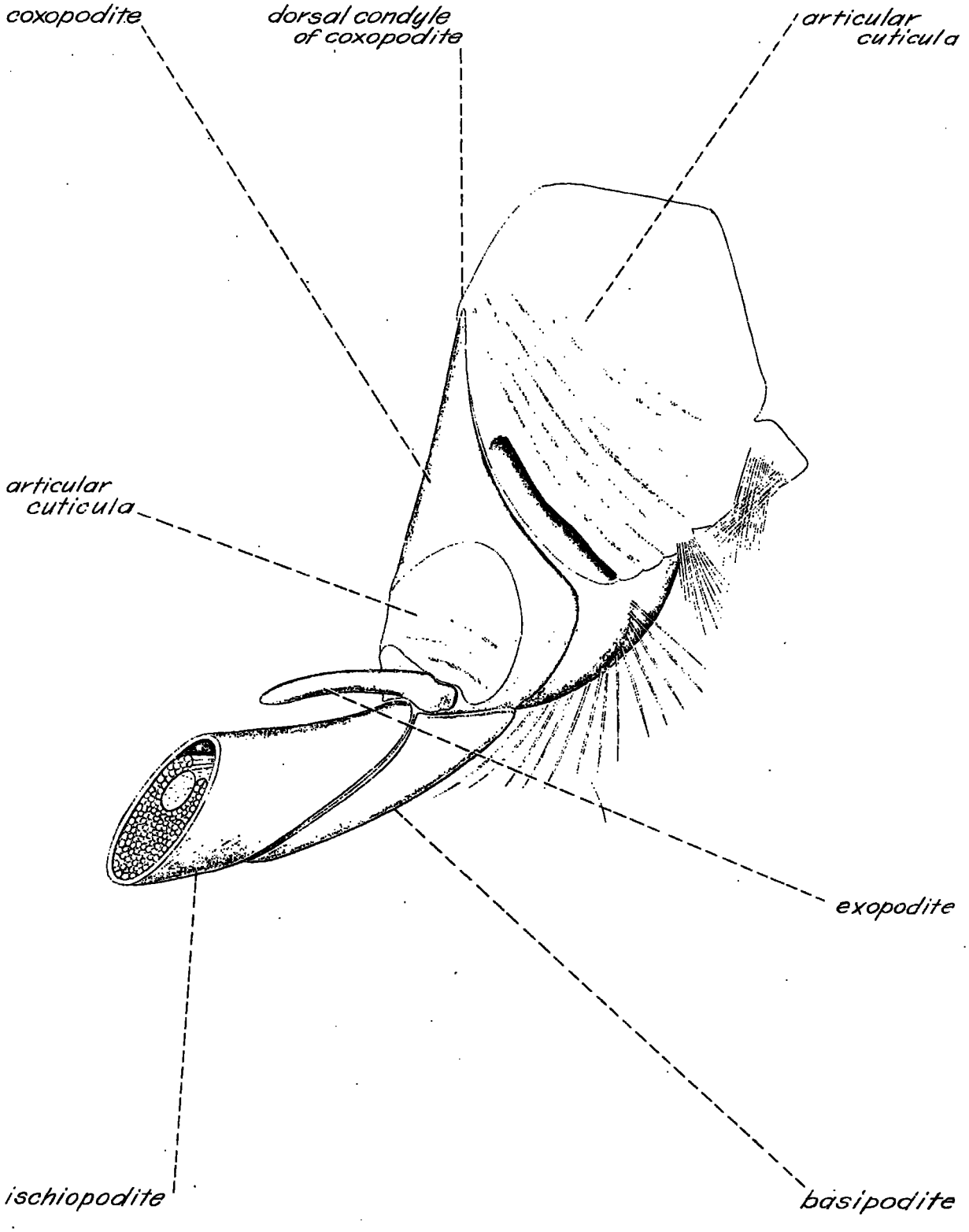

FIGURE 54.—Lateral view of leg base of left fifth pereiopod.

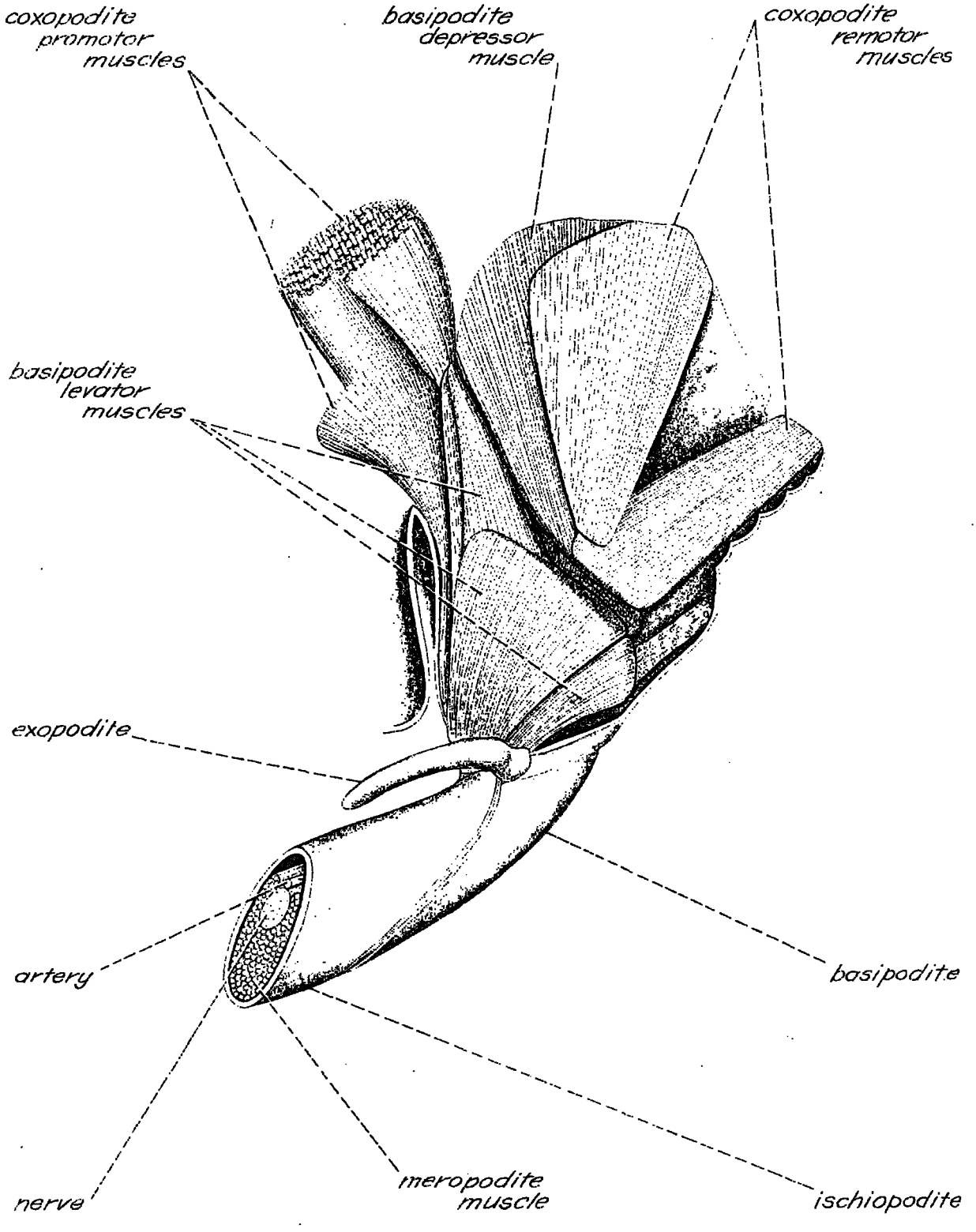

FIGURE 55.—Lateral view of leg base of left fifth pereiopod. Lateral cuticle removed to show superficial lateral muscles.

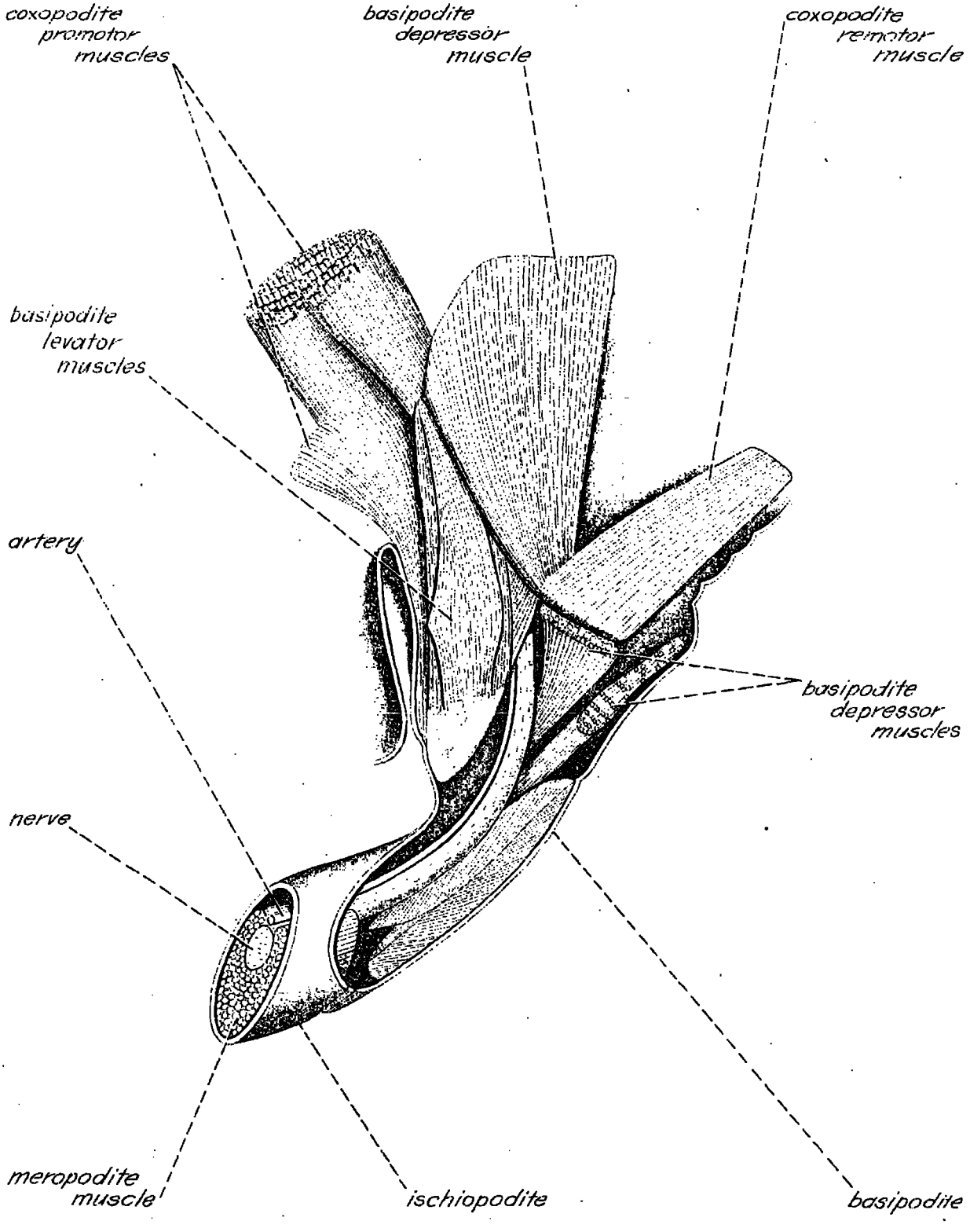

FIGURE 56.—Lateral view of leg base of left fifth pereiopod. Some superficial lateral muscles removed.

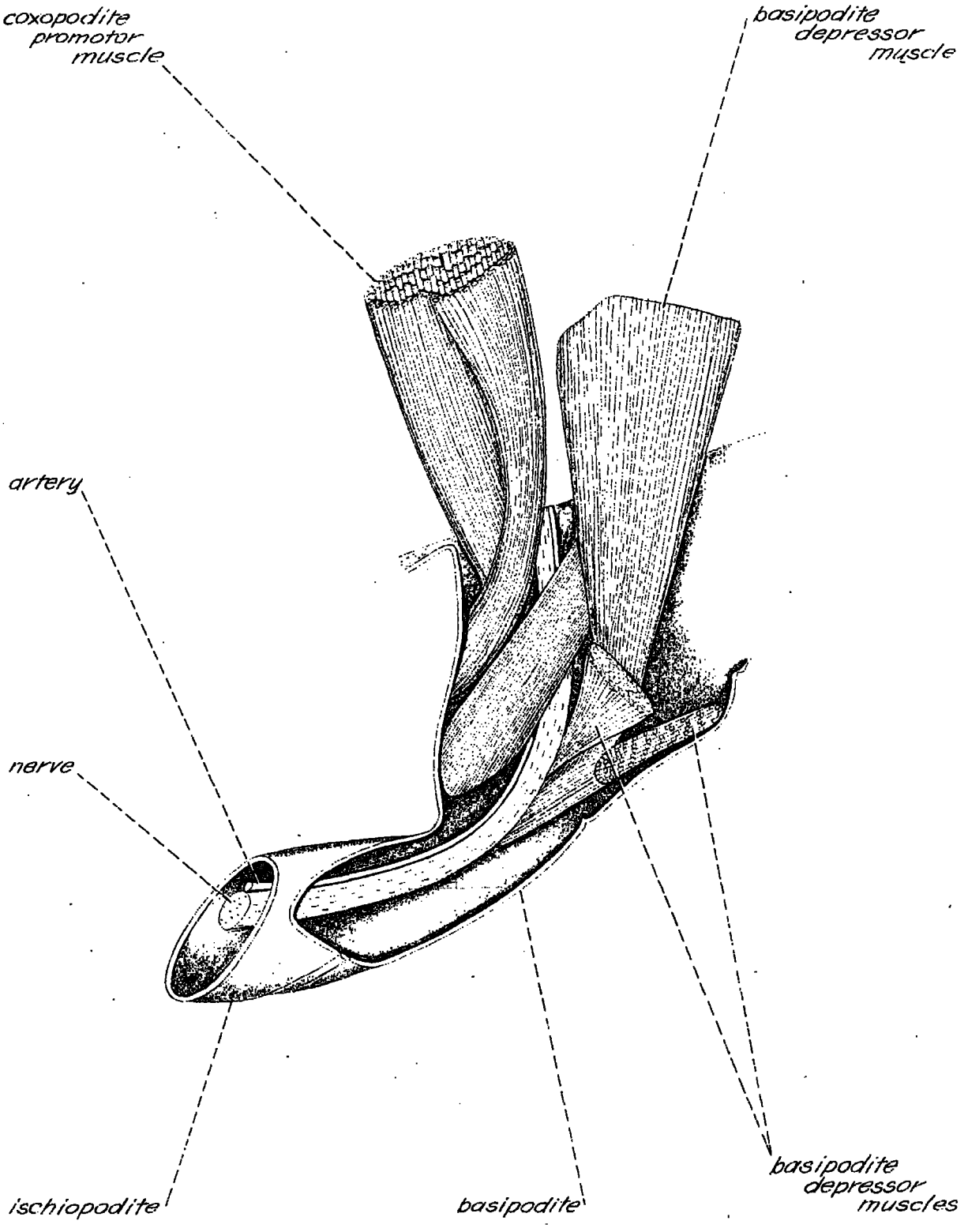

FIGURE 57.—Lateral view of leg base of left fifth pereiopod. Lateral muscles removed to show medial muscles.

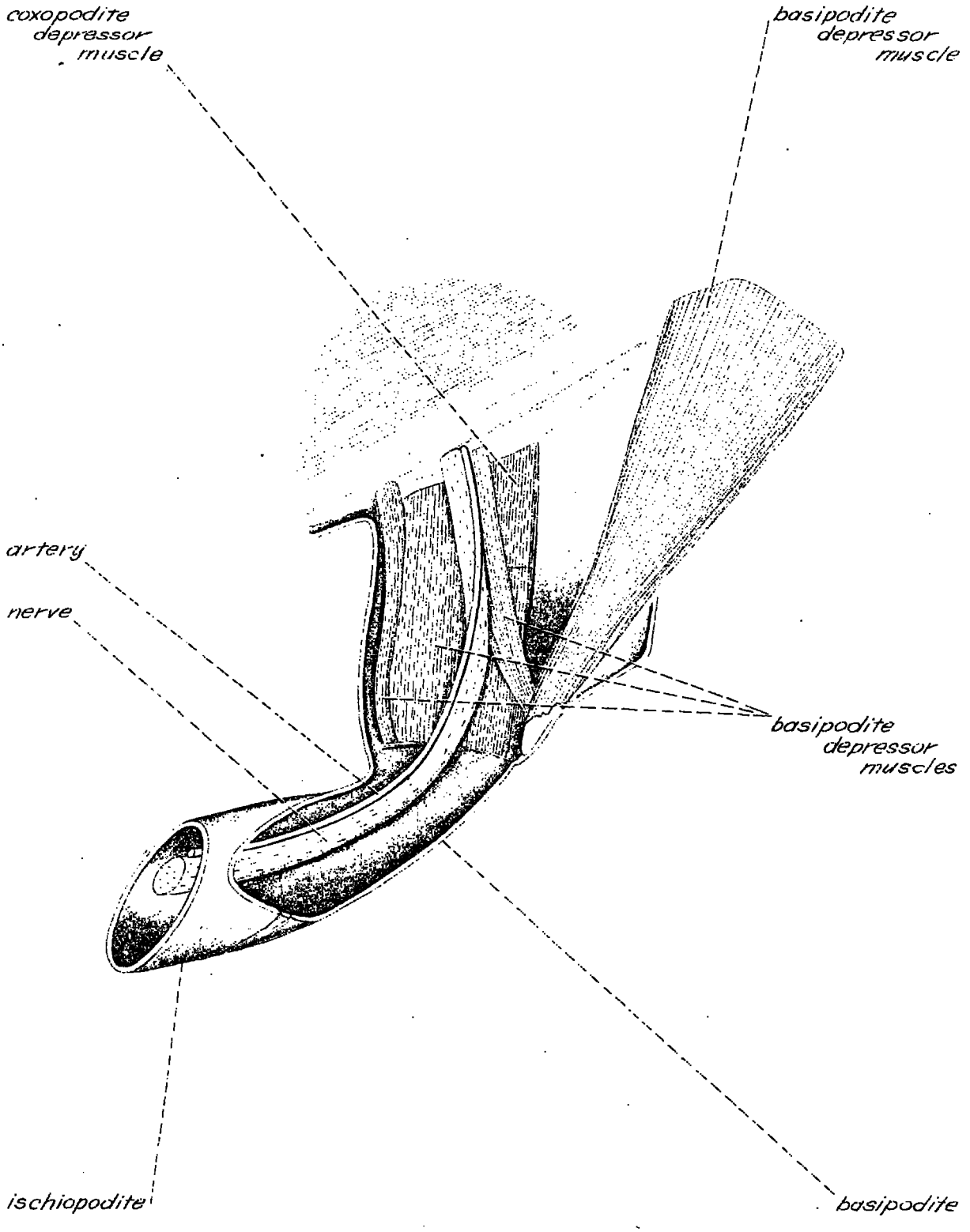

FIGURE 58.—Lateral view of leg base of left fifth pereiopod. Medial muscles.

CARPOPODITE ADDUCTOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

In like fashion to the carpopodite abductor, the carpopodite adductor muscle fibers originate on a large area of the meropodite, but on the ventral half of the article. The muscle inserts on a long apodeme arising from the proximal portion of the carpopodite, medial to the axis of the dicondyles. Carpopodite adductor muscle contractions serve to turn the carpopodite toward the body, and in fact deeply on the meropodite. The muscle might better be considered a flexor of the carpopodite.

PROPODITE EXTENSOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

The arrangement of the propodite muscles in the carpopodite is very similar to that of the carpopodite muscles within the meropodite. The propodite extensor muscle originates over much of the dorsal part of the carpopodite and inserts on a long apodeme projecting proximally from the base of the propodite. The apodeme is so connected to the propodite that a pull on it extends the propodite with respect to the carpopodite.

PROPODITE FLEXOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

The propodite flexor muscle opposes the action of the propodite extensor muscle. The fibers of the flexor muscle arise from the ventral surface of the carpopodite and, like those of the extensor, attach to a long apodeme of the propodite. This apodeme arises from a position opposite to that of the extensor apodeme. Contractions of the propodite flexor muscle flex the propodite upon the carpopodite.

DACTYLOPODITE EXTENSOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

The dactylopodite extensor muscle originates along the lateral side of the propodite and inserts on a long apodeme arising from the proximal end of the dactylopodite. The muscle straightens the dactylopodite on the propodite.

DACTYLOPODITE FLEXOR MUSCLE OF FIFTH PEREIOPOD

FIGURE 53

The dactylopodite flexor muscle bends the dactylopodite upon the propodite. Like the extensor muscle, the flexor has multiple origins upon the medial surface of the propodite. The muscle inserts on the long flexor apodeme of the dactylopodite.

C. Abdomen

Unlike the head and gnathothorax, the abdomen is almost entirely devoted to the propulsion of the white shrimp. Except for slender components of the gut, the gonads, and the nervous and circulatory systems, the space within the abdominal skeleton is filled with muscles, most of them concerned with the powerful flexion of which the animal is capable. The abdomen consists of six segments, all of which bear appendages, and a posterior telson which does not. The abdominal segments are attached to one another by deep folds of thin articular cuticle which allow each segment great freedom of movement with respect to its neighbors and with the thorax. Intersegmental connections in the abdomen are of several types. The simplest and perhaps most movable is that between the thorax and first abdominal segment (fig. 59). Here, cuticular folds of great depth reinforced by heavy muscles internally make ventral flexion possible between these body tagmata. The junction is without special, restrictive condyles, allowing extensive lateral movements of the abdomen on the thorax at this point.

The junctions of the first and second, and of the second with the third abdominal segments (fig. 59) are identical. Motion at these joints is limited to flexion and extension by lateral condyles of similar design. In contrast, the joint between the third and fourth adbominal segment differs from those between the first three segments. This connection is much simpler. The condyles are rather loosely connected, affording flexion and extension and a certain amount of lateral motion. The fourth, fifth, and sixth abdominal segments articulate with one another by means of two pairs of identical condyles similar in their rigidity to those between the first, second, and third segments, but different in structure (see enlargements of condylic structure, detail of articulation, fig. 59).

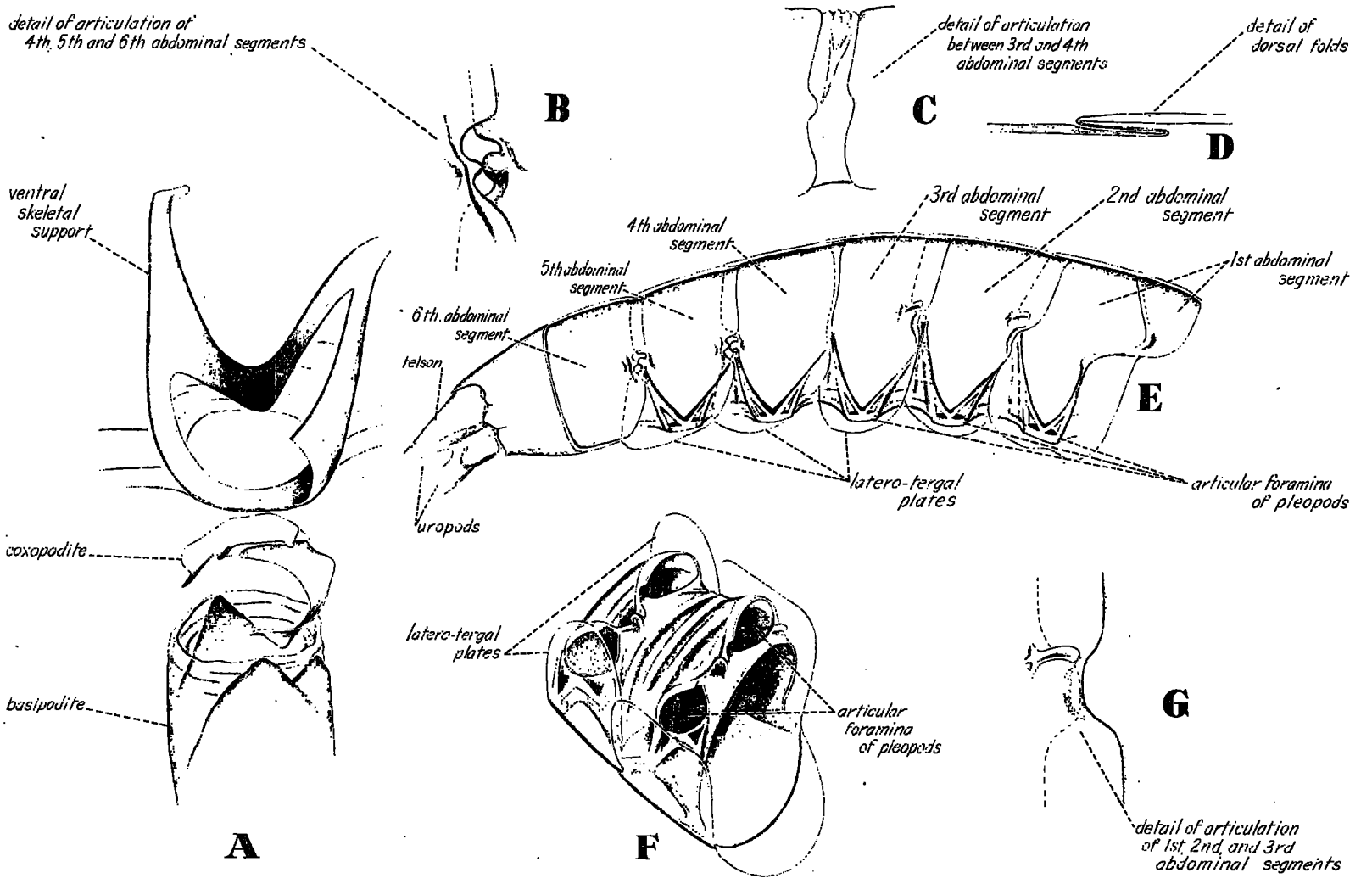

FIGURE 59.—Details of abdominal skeletal elements.

The posterior joints permit free extension and flexion, but probably resist lateral motion. We have, then, 4 kinds of intersegmental hinges functioning in 2 different ways. No reason for this multiplicity of structure in the hinges is readily apparent.

SKELETAL ELEMENTS

The abdominal segment of arthropods is comprised of a ring of cuticle. This ring, however, may be subdivided in parts. The abdominal somite in the Crustacea has usually been said to consist of an arched dorsal tergum and a flat, concave, or convex ventral sternum connected to the tergum by two lateral pleura, the latter often produced ventrad in a fold. The lateral pleuron has been variously interpreted. Snodgrass (1935) describes the pleural areas of arthropods as "typically membranous" to permit the movement of appendages arising from the pleuron. Pleural sclerites, when present, represent a contribution of the proximal parts of the appendages, according to this worker. He sets forth the fact also that the appendages articulate with the ventral margins of the pleural sclerites and with the lateral edges of the sternal sclerites. That this typical situation may not always obtain is shown by Hart (1952) who found that the first pleopod in *Cambarus longulus longulus* Girard, 1852, is connected to the abdominal venter entirely by sternal components.

Snodgrass (1935) apparently was of the opinion that the arthropod pleuron represented a distinct region of the segment. In a study of the Crustacea made at a later date, Snodgrass (1952) describes in *Anaspides tasmaniae* Thomson, 1892, a generalized malacostracan, a clearly demarked pleural sclerite with which the limb basis articulates. In the same study he refers to the pleural sclerite as a "laterotergal pleural plate" and states that the pleuron of the crustacean belongs to the tergum. Support of the more recent opinion of Snodgrass (1952) that the pleuron of crustaceans is tergal in origin may be found by a consideration of the abdominal segment of *Penaeus setiferus*.

The sternum and tergum are distinct regions in the white shrimp, but no line or suture can be seen which distinguishes a pleural component of the abdominal segment (fig. 59). From this we may conclude that the pleura are not needed in a morphological construct of the abdominal segment of the crustacean. That the term, "pleuron," for the laterotergal plates has become embedded ineradicably in the literature of crustacean systematics is therefore most regrettable.

Beyond what has been brought out about the general structure and articulation of the abdominal segments, little need be said further except for a brief mention of the modified posterior end of the sixth abdominal segment. Unlike the five anterior abdominal segments from which light appendages project, the sixth abdominal segment must be strong enough to bear the tail fan. For this reason the posterior end of the sixth segment is heavily sclerotized. In addition, the contents of the sixth segment are largely devoted to mediating the flexions of the tail fan which project caudad from the segment rather than ventrad as is the case with the preceding abdominal segments. The result is the visible difference in shape of the sixth segment compared to that of the typical abdominal segment. More will be said about the sixth abdominal segment when the tail fan is considered.

MUSCLE ELEMENTS

The characteristic of the abdominal muscles, apart from their great mass, is the unusual manner in which they are laid out. These muscle bodies are extraordinarily heavy and so intertwined with one another that their separation for study is difficult. In accordance with the system of Daniel (1931c), the abdominal muscles are divided into the following four functional muscle groups: (1) The superficial ventral muscles, (2) the lateral muscles, (3) the dorsal muscles, and (4) the main ventral muscles. They will be treated in that order.

SUPERFICIAL VENTRAL ABDOMINAL MUSCLES

FIGURES 61, 63

The superficial ventral abdominal muscles of *Penaeus* are attached between yokes of thin cuticle (fig. 63) lying transversely across the posterior portion of each abdominal segment beneath the ventral nerve cord. These yokes are associated with the folds of articular cuticle on the ventral surface, and they are so arranged that the superficial ventral muscles run from the posterior region of one abdominal segment to the posterior region of the next. The superficial ventral abdominal muscles are of course a continuous sys-

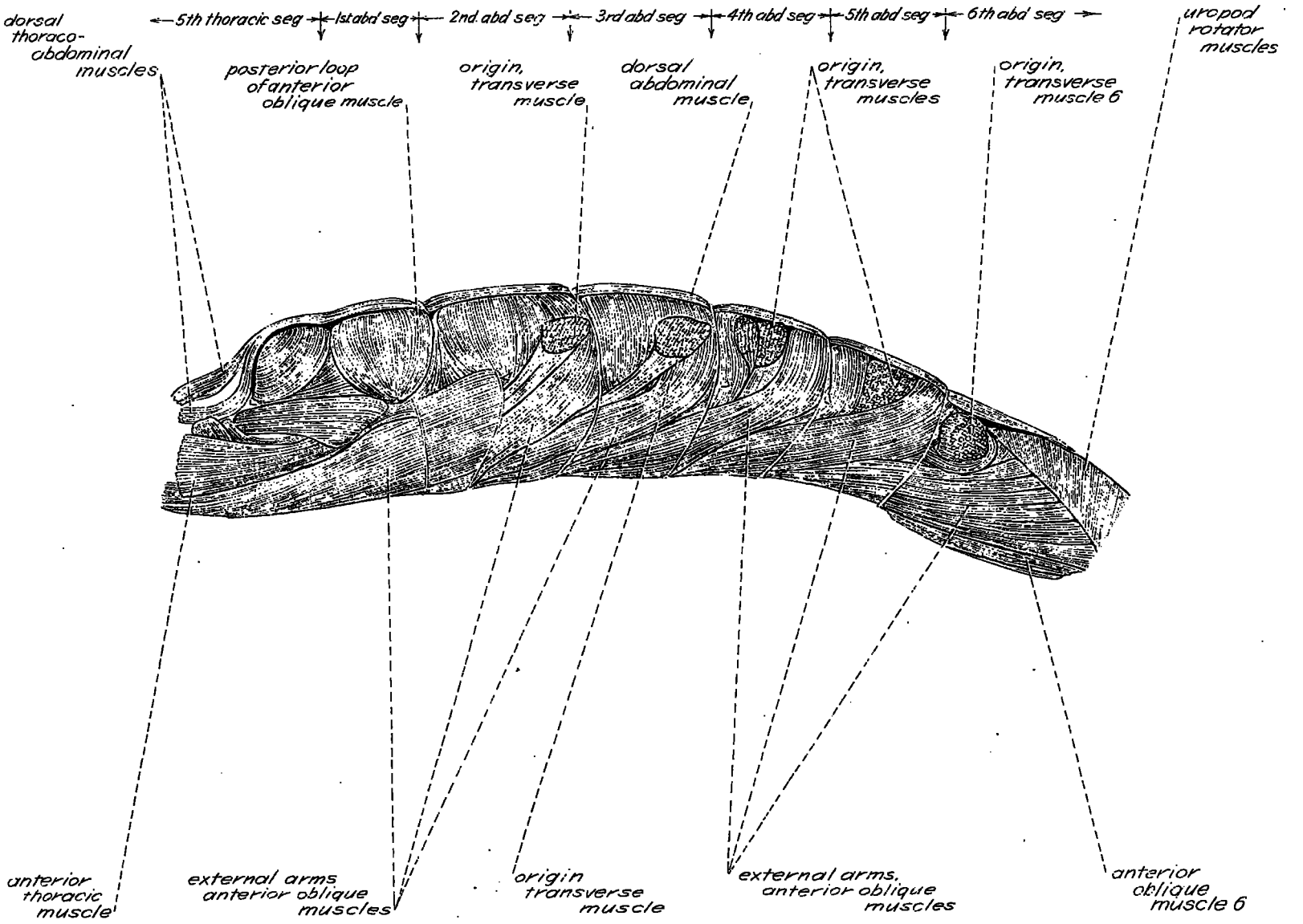

FIGURE 60.—Lateral view of left side of abdomen showing superficial abdominal muscles.

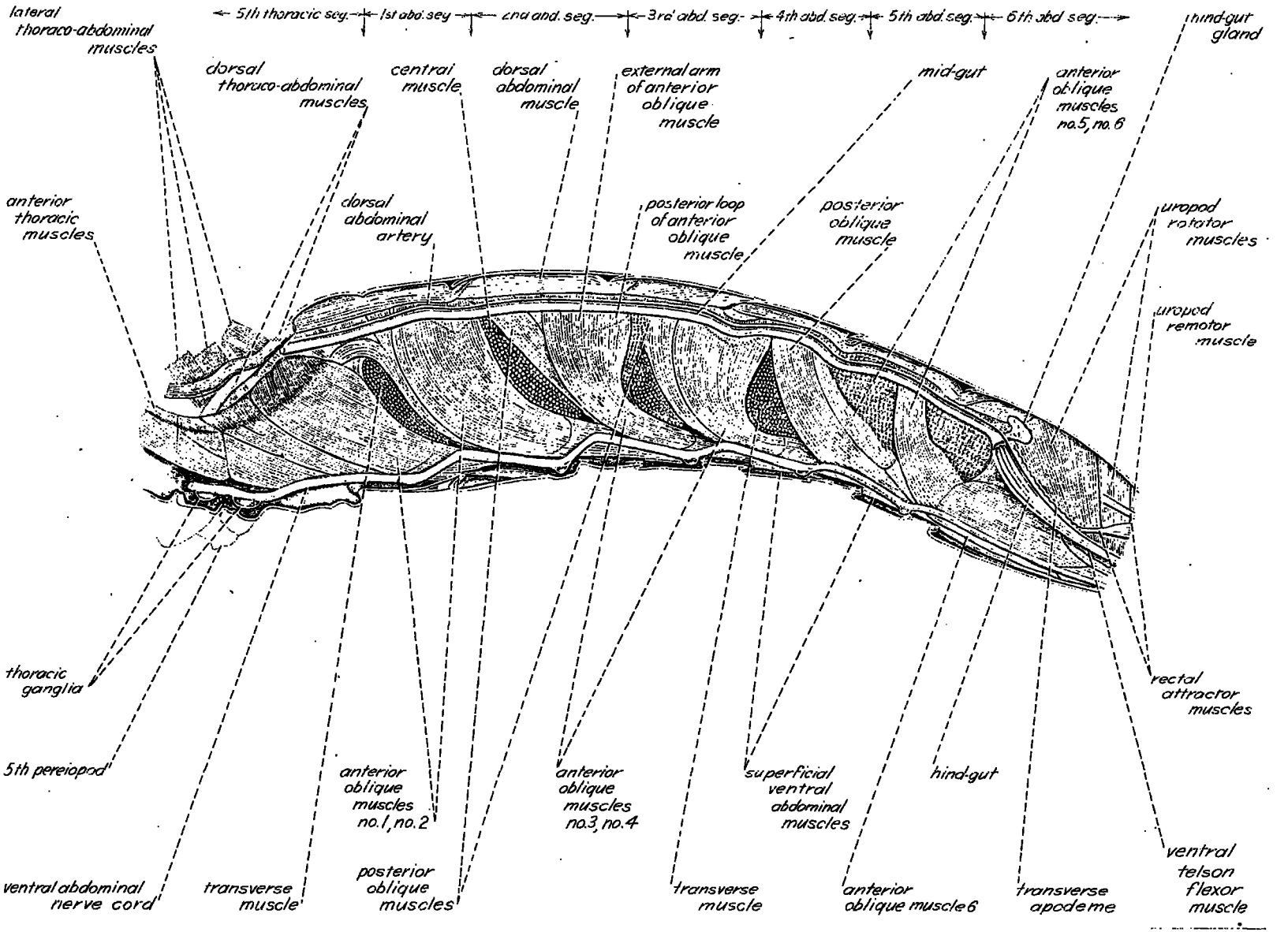

FIGURE 61.—Median sagittal cut through abdomen showing medial muscles.

tem with the superficial ventral thoracic and the superficial ventral thoracoabdominal muscles considered above in the section on the gnathothorax.

Like their thoracic counterparts, the superficial ventral abdominal muscles are very thin. Two of them are found on each side of the ventral nerve cord between the first and second and between the second and third abdominal segments. Only one is found on each side thereafter. Except for the ventral muscle that passes between the fifth and sixth abdominal segments, and which is ventrad of the nerve cord, all of them arise anterolaterally and run mesad. In this respect, the situation in *Pandalus* is much more like that of *Penaeus* than is *Astacus*. The superficial ventral muscles presumably function to hold the articular cuticle between the abdominal segments in place.

The superficial ventral muscles of *Pandalus*, *Astacus*, and *Callinectes* are probably homologous with the same muscles in *Penaeus*. Some differences exist. All of the superficial ventral muscles of the former crustaceans are single on a side, except for the last two abdominal segments of *Astacus* in which the muscles are double.

SUPERFICIAL LATERAL ABDOMINAL MUSCLES

Although these muscles are not illustrated here, their centers are indicated by small triangles on figure 60. The triangles represent apodemal depressions. Each superficial lateral abdominal muscle is attached to broad, tough apodemal material arising at the triangles. The muscles are very thin, fan-shaped structures, and apparently function to retain the position of the cuticle during movements of the white shrimp.

SUPERFICIAL DORSAL ABDOMINAL MUSCLES

FIGURE 62

Lateral to the midline on the dorsal surface of the abdomen lie the thin superficial dorsal abdominal muscles. The muscles arise in superficial connective tissue in the abdominal segments and pass to apodemal material at the anterior margins of the succeeding segments. Those inserting on the fourth, fifth, and sixth abdominal segments are square, flat muscles, situated laterad of the main dorsal abdominal muscles. The superficial dorsal abdominal muscle attached to the second abdominal somite is a long, thin muscle lying dorsad of the main dorsal muscles. Inserting on the third abdominal segment are two superficial dorsal abdominal muscles. The medial one is long and slender, while the lateral muscle is rectangular and has a lateral anterior projection. The superficial dorsal muscles probably hold the articular cuticle in position.

The superficial dorsal abdominal muscles have counterparts in *Pandalus* and *Astacus*. Those of *Pandalus*, however, are all single muscles on each side of the midline. In addition Berkeley illustrates a sixth superficial dorsal muscle in *Pandalus* inserting on the telson. In *Astacus*, 6 pairs of strong superficial dorsal muscles are found lateral to the midline and a single seventh muscle attached to the telson.

MAIN DORSAL ABDOMINAL MUSCLES

FIGURES 60, 61, 62

The main dorsal abdominal muscles function as abdominal extensor muscles in opposition to the action of the huge ventral abdominal muscle mass. The dorsal abdominal muscles make apodemal connection with the dorsal thoracoabdominal muscles (fig. 61) and as such represent a functional abdominal continuation of the latter. The dorsal abdominal muscles may be divided into two groups, the dorsolateral abdominal muscles, and the dorsomedial abdominal muscles. Both groups are easily distinguished from the underlying ventral muscles. Their removal exposes the midgut and various dorsal circulatory and nervous elements. The arrangement of the dorsolateral and dorsomedial muscles of *Astacus* appears to be similar to that of *Penaeus*, in that the two groups of muscles are distinct. In *Pandalus*, on the other hand, these muscle groups are so intertwined that Berkeley refers to the lateral and medial parts as slips of the same muscle.

In *Penaeus* the dorsolateral and dorsomedial abdominal muscles are markedly segmental and readily separable from one another, except for the dorsal abdominal muscle of the second segment (occupying the dorsum of the first abdominal segment (fig. 62)). Here, the muscles are fused. The medial portion is connected with the dorsal thoracoabdominal muscle and a lateral slip of fibers is attached to superficial connective tissue. The whole structure passes caudad to insert on the dorsal apodemal yoke dividing the first and second somites. The dorsolateral muscles occupying the second, third, fourth, fifth, and sixth abdominal segments all arise from the cuticular yokes

408629 O—59——8

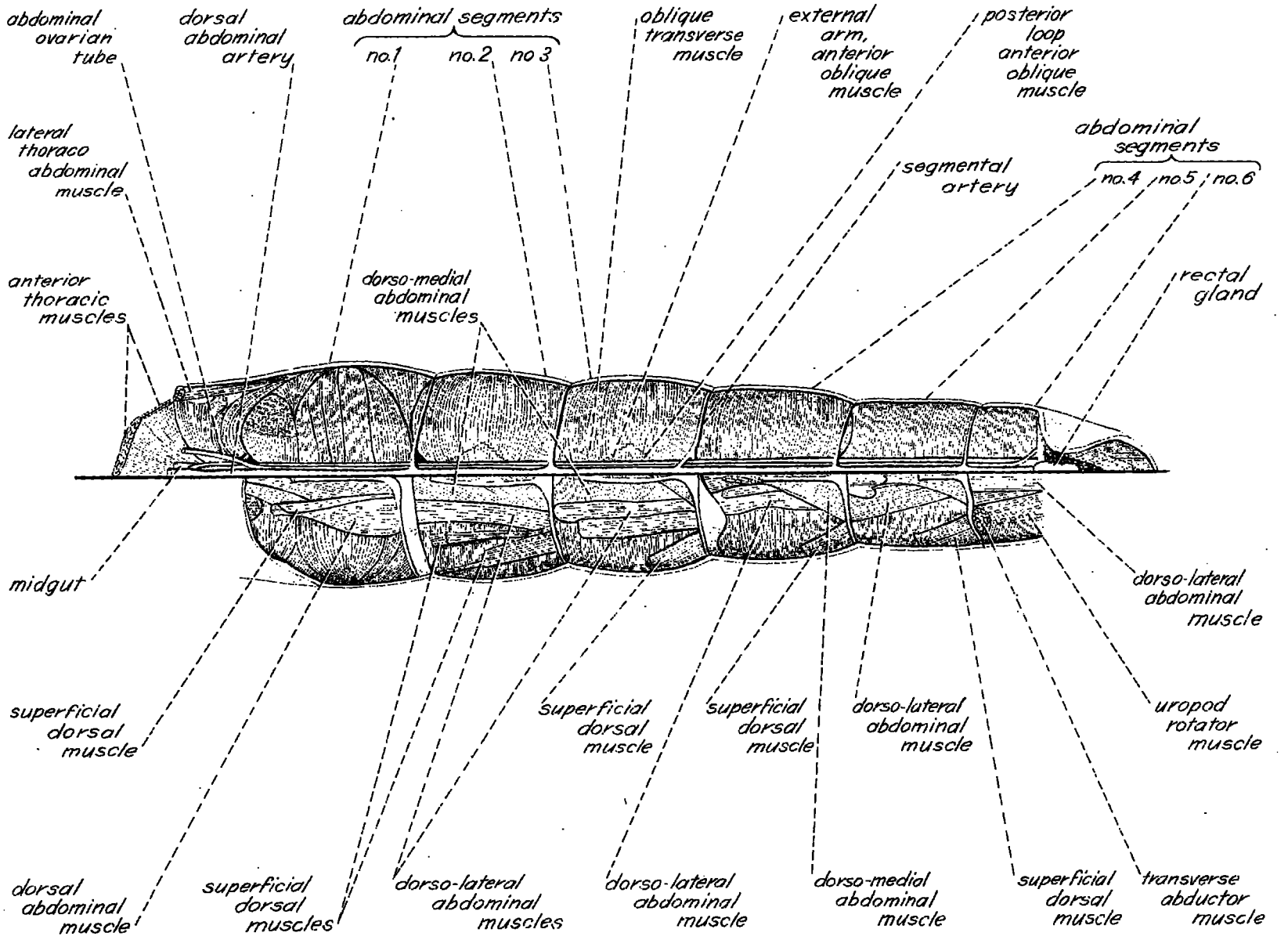

FIGURE 62.—Dorsal views of abdominal muscles. Lower section, intact musculature. Upper section, dorsal abdominal muscles removed.

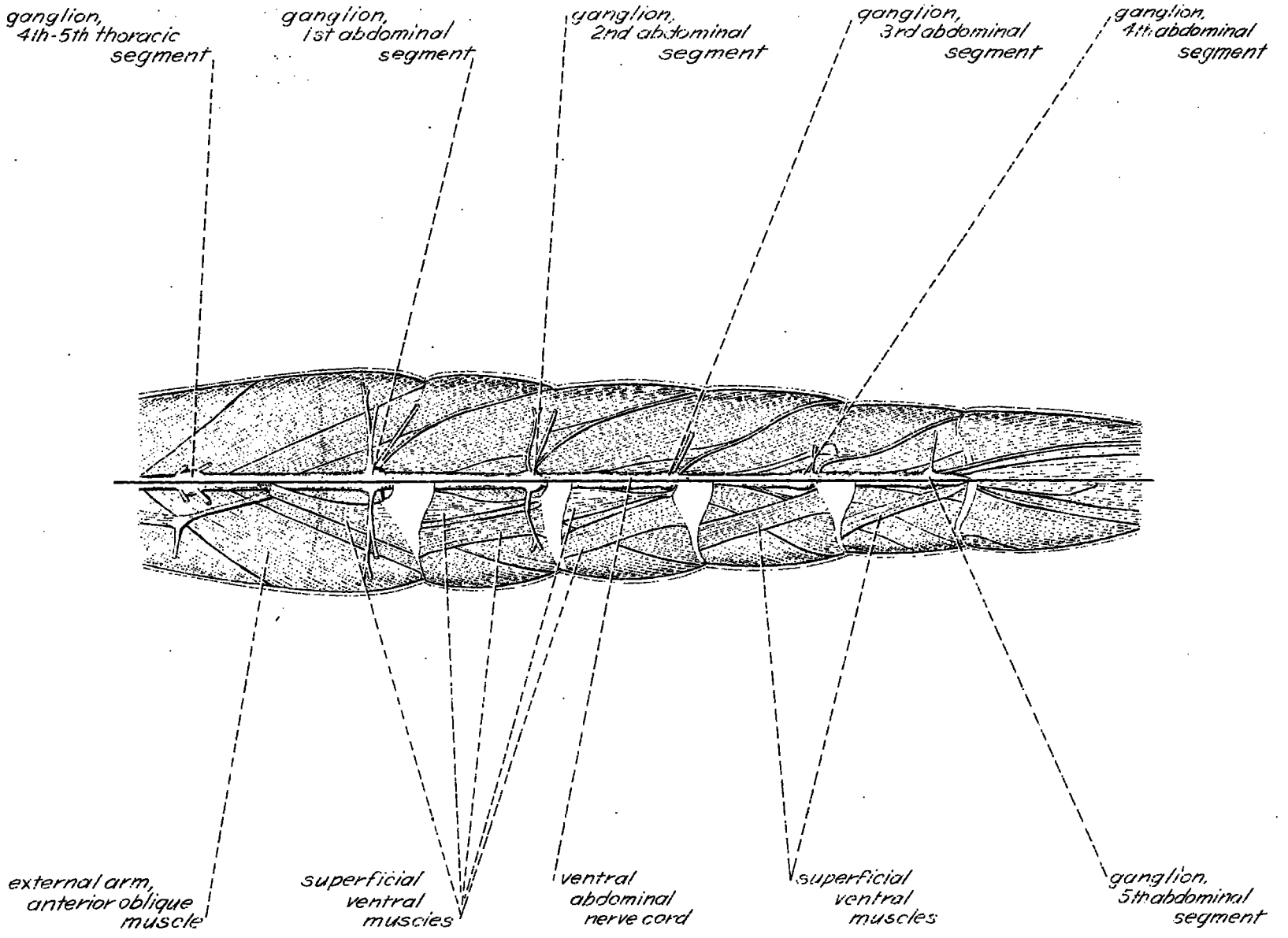

FIGURE 63.—Ventral views of abdominal muscles. Lower section, intact musculature. Upper section, superficial ventral muscles removed.

passing across the anterior part of each abdominal segment and from them run caudad to the next yoke. The axis of the fibers of the lateral muscles is approximately parallel with the long axis of the animal.

The fibers of the dorsomedial abdominal muscles are oblique to the long axis of the white shrimp. These muscles lie beneath the dorsolateral muscles. Each originates on a median sagittal apodeme within a segment and runs laterad to insert on an intersegmental apodeme, posteriorly. The arrangement in *Penaeus* is far simpler than that of the dorsal abdominal musculature of *Pandalus*.

Dorsad of the muscles under discussion, and very close to the middorsal line, are paired structures passing rostrad from the cuticular tissue dividing the abdominal segments (see lower half of fig. 62). The structures appear to be flattened tubes, soft and easily broken. They resemble vessels of the circulatory system more than anything else. Their function is unknown.

MAIN VENTRAL ABDOMINAL MUSCLES

The illustrations show that relatively few abdominal muscle types exist. However, the few that do are serially repeated and so extensively interwoven that their isolation is extremely difficult. Consequently no one should be surprised that an understanding of abdominal muscle function is of fairly recent derivation. Much of what we know is based upon the work of Daniel (1928, 1929, 1931a, 1931b, 1931c, 1931d, 1933) who first set forth the details of the comparative anatomy of abdominal muscles in higher Crustacea.

One of the most interesting features of abdominal anatomy is the contrast between the lightly sclerotized abdominal skeleton and the very heavy abdominal musculature. One would almost expect the light cuticle to be damaged by the powerful flexions of the abdomen. That such does not occur is explained by the unusual arrangement of the abdominal muscles. Some of them are attached to prevent extreme distortions that might otherwise take place. Some muscles, in a sense then, substitute for the skeleton. In addition, certain muscles act in the functional sense as great apodemes of other muscles, thereby freeing the abdominal skeleton of the requirement to produce all but the simplest apodemal material. These apodemal muscles, furthermore, act as fulcra to improve the mechanical advantage of long muscles, such as the anterior obliques, connected between two widely separated abdominal segments.

The terminology of the abdominal musculature of *Penaeus* has been adopted from the work of Daniel. For this reason, substantial differences in nomenclature will be found between the present study and the older morphological research. Daniel (1931c, 1932) has renamed some abdominal muscles and subdivided others. For the most part, however, he makes use of the classical abdominal muscle names.

CENTRAL MUSCLES OF ABDOMEN

FIGURE 61

The longitudinal central muscles are among the main fulcral muscles of the abdomen. They lie deep within the abdominal muscle mass. Six pairs of central muscles are found in the abdomen of *Penaeus*, joined together end to end in a wavy chain. Each central muscle takes origin on an apodeme of a dorsal branch of the preceding central muscle. These dorsal apodemes lie above the transverse muscles. As the central muscle passes caudad into the succeeding segment, it is first joined from above by the fibers of the oblique transverse muscle and then, in the neighborhood of the succeeding transverse muscle, the central muscle divides. The dorsal slip joins the apodeme of the next central muscle and the larger ventral part turns mesad along the anterior face of the transverse muscle. The central muscle apodemes dorsad of the transverse muscles also give rise to the posterior oblique muscles.

The counterparts of the central muscles of *Penaeus* in *Astacus* are not easy to determine. The only muscles in the European crawfish corresponding to the central muscles are the musculi ventrales profundi of Schmidt. The central muscles function to support the oblique muscles during the contractions of the latter.

TRANSVERSE ABDOMINAL MUSCLES

FIGURES 60, 61, 64

The large transverse abdominal muscles attach dorsolaterally on the abdominal tergum (fig. 60) and run across the abdomen in association with strong fasciae (the fasciae arise at points indicated by small triangles in fig. 60). The abdomen of *Penaeus* contains six transverse muscles. A midsagittal view of the abdomen (fig. 61) shows the

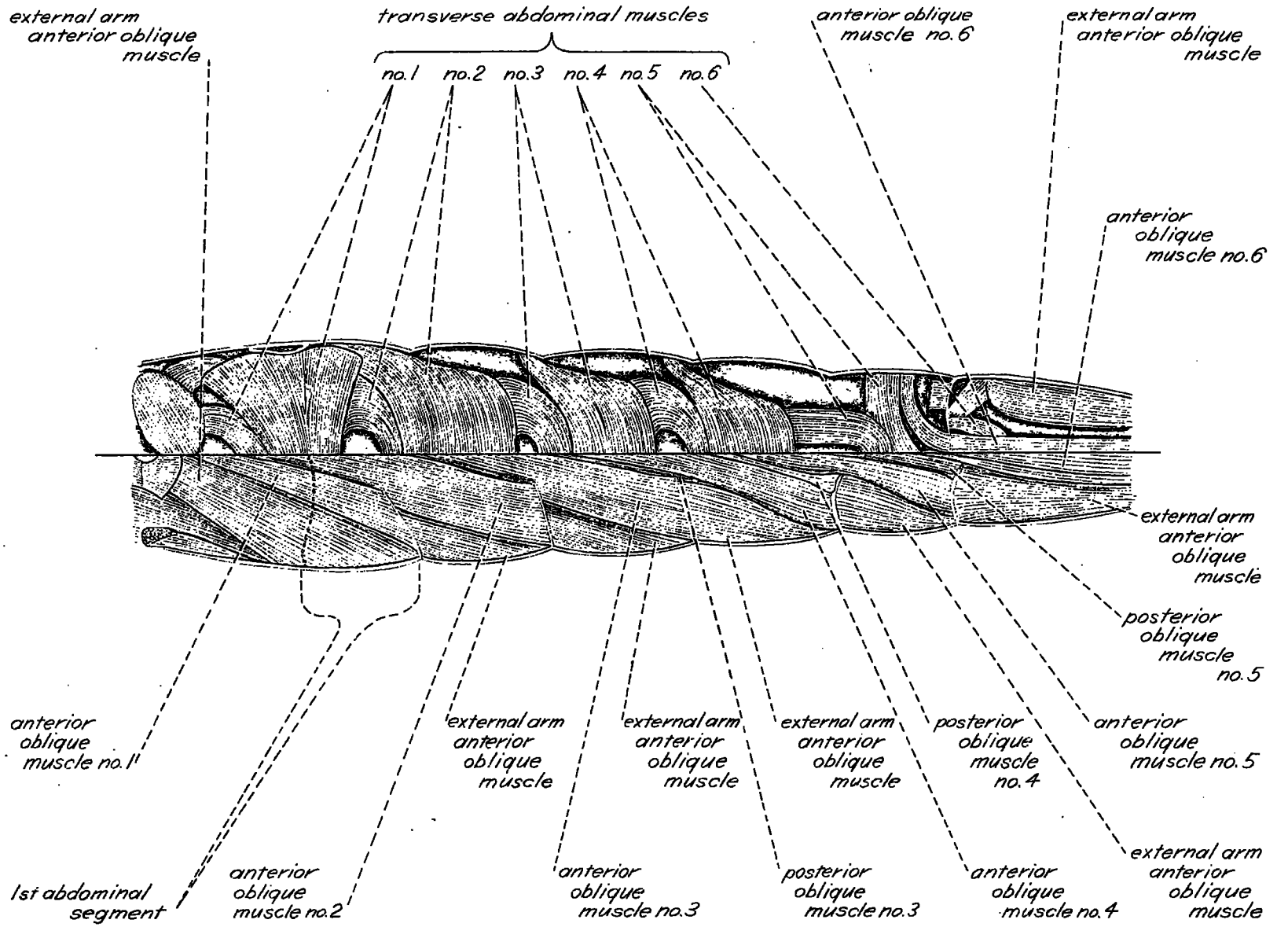

FIGURE 64.—Ventral view of abdominal muscles. The lower section shows the arrangement of the oblique muscles. The upper section shows the transverse abdominal muscles dorsad of the oblique muscles.

transverse muscles crossing the midline. Their great size at the midline is partly due to the addition of fibers of the posterior loop of the anterior oblique muscle, as well as those of the ventral slip of the central muscle, mentioned above. The muscles function in the fulcral support of the central muscles, together with lateral compression of the abdomen. The transverse abdominal muscles of *Penaeus* are fully homologous with those of *Pandalus* and *Astacus*. Both of the latter forms have six of these muscles.

ANTERIOR OBLIQUE MUSCLES OF ABDOMEN

FIGURES 60 TO 64

The anterior oblique muscles are directly responsible for the strong abdominal flexions of which the white shrimp is capable, and as such are on functional grounds the most important longitudinal muscles of the abdomen. Each anterior oblique muscle is made up of several parts. The thickest part runs mesad of the central muscle and is closely applied to its opposite number at the median sagittal line (fig. 61). From the midline, the main part of the anterior oblique turns ventrally and curves caudad to an insertion area two segments to the rear. The area of its insertion is on the posteroventral margin of the abdominal segment concerned. *Penaeus* has 6 anterior oblique muscles, compared with 7 each for *Pandalus* and *Astacus*.

FIRST ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

The first anterior oblique muscle arises in connective tissue in the fifth or last thoracic segment, mesad of the lateral thoracoabdominal muscle (fig. 61) and runs ventrocaudally through part of the last thoracic and all of the abdominal segment to an area of insertion on the posterior edge of the first abdominal segment (fig. 64). The muscle functions to pull the ventral surface of the first abdominal segment forwards about its hinges with the fifth thoracic segment. The muscle appears in the abdomen of *Pandalus* and *Astacus*.

SECOND ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

This muscle (fig. 61) traverses the first and second abdominal segments, inserting on the posteroventral portion of the second segment (fig. 64). By the contractions of the second anterior oblique muscle the ventral part of the second abdominal segment is brought rostrad. Homologs of this muscle have been described in *Astacus* and *Pandalus*.

THIRD ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

Beginning in the second abdominal segment (fig. 61), the third anterior oblique muscle sweeps posteroventrad and inserts on the posteroventral rim of the third abdominal segment. It pulls the ventral part of the third segment forward. The same muscle is found in the abdomen of *Pandalus* and *Astacus*.

FOURTH ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

From its origin in the third abdominal segment, the fourth anterior oblique runs directly ventrad, then turns sharply caudad and passes along the ventral surface of the abdomen to its insertion on the fourth segment (fig. 61). The muscle in *Penaeus* is represented in *Astacus* and *Pandalus*.

FIFTH ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

This muscle runs in a gentle curve from its dorsal origin in the fourth abdominal segment to its insertion in the rear of the fifth segment (fig. 61). The medial manifestation of the fifth anterior oblique is much slenderer than is that of the preceding anterior oblique muscles. Contractions of the muscle flex the fifth segment ventrad with respect to the fourth segment. Schmidt and Berkeley describe the muscle in *Astacus* and *Pandalus*.

SIXTH ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

Like the fifth anterior oblique, the sixth curves gently from the dorsal part of the fifth abdominal segment to its special insertions at the caudal end of the long sixth segment (fig. 61). The ventral part of the sixth anterior oblique muscle lying in the sixth segment may be seen to be very thick. Actually, its cross-sectional area is no greater than the caudal portions of the other anterior oblique muscles, but by virtue of its concentration along the midline, a median sagittal view reveals a large portion of the muscle. The muscle is functionally similar to the preceding anterior oblique muscles. However, its insertions upon the sixth segment and the parts of the tail fan are

substantially modified from the typical plan of the preceding anterior oblique muscles.

At the posterior end of the last segment, the sixth anterior oblique muscle has three areas of insertion. Moving caudad from the anterior end of the sixth segment, certain fibers of the sixth anterior oblique muscle insert in tough connective tissue over a large area on the ventral surface of the sixth somite (figs. 71, 72). These fibers are obviously associated with the flexion of the sixth abdominal segment on the fifth. The major portion of the ventral fibers of the sixth anterior oblique continue caudad beyond the sternal insertion area to insert on a strong tendon, or apodeme of anterior oblique muscle (figs. 71, 72). This apodeme is firmly connected to the uropod protopodite, the base element from which the uropods arise. Thus the sixth anterior oblique flexes the uropods as well as the sixth segment.

The third area of sixth anterior oblique insertion is slightly dorsad of the ventral anterior oblique apodeme. It, too, is apodemal, and, while lighter than the ventral apodeme, is a strong tendon. This dorsal anterior oblique apodeme is best seen in median sagittal aspect (figs. 61; 74, *B*). In contrast to the ventral anterior oblique apodeme, the dorsal tendon bifurcates anteriorly into two parts. Two large and distinct portions of the sixth anterior oblique muscle insert on the tendinous bifurcations. The two parts of the dorsal apodeme fuse and run caudad to a point on the ventrolateral surface of the telson. The sixth anterior oblique muscle clearly flexes the telson in addition to its previously mentioned activities.

The sixth anterior oblique muscle of *Penaeus* is undoubtedly homologous with that of *Pandalus* and *Astacus*. Berkeley and Schmidt indicate the presence in the latter forms of the ventral apodeme of the anterior oblique muscle. They do not mention the dorsal apodeme of this muscle.

POSTERIOR LOOP OF ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

FIGURES 60, 61

Arising from the posterior portion of the dorsomedial area of the anterior oblique muscle, where the bilateral pairs of the latter are fused at the midline, is the posterior loop of the anterior oblique muscle. The muscle runs ventrocaudally, laterad of the central muscle, and then passes mesad to join the transverse muscle. At the midline, the fibers of the posterior loop connect with those of its partner on the other side of the segment. Each anterior oblique muscle of *Penaeus* appears to have a posterior loop.

EXTERNAL ARM OF ANTERIOR OBLIQUE MUSCLE OF ABDOMEN

FIGURES 60, 63, 64

The external arm of anterior oblique muscle is much larger and more important than the posterior loop. The external arm connects with the broad dorsal end of the anterior oblique muscle at the midline (fig. 61). The muscle sweeps over the central muscle dorsally and then runs anteroventrad along the outside of the abdominal muscles to a ventrolateral point just inside the next anterior abdominal somite (fig. 60). Daniel (1931c) considers this point the origin of the external arm, and he notes that the area is the common insertion of the anterior and posterior obliques of an anterior segment. To summarize, each external arm originates on the posteroventral edge of an abdominal segment and traverses very nearly the whole of a segment to its insertion on the main body of the anterior oblique muscle. Taking the anterior oblique muscle as a whole, including its external arm, the muscle functionally traverses three segments from the ventral surface of one, over the central muscle of the second, dorsally, and hence to the ventral surface of the third segment.

As one would expect, the abdomen of *Penaeus* contains 6 external arms accompanying 6 anterior oblique muscles (fig. 60). Its counterparts in the abdomen of *Pandalus* and *Astacus* are not clear.

POSTERIOR OBLIQUE MUSCLES OF ABDOMEN

FIGURES 61, 64

The abdomen of *Penaeus* has five posterior oblique muscles, beginning with the first abdominal segment. The posterior obliques are associated with the anterior obliques and function with the latter in the flexion of the abdomen. Except for the first posterior oblique, the muscles arise dorsal to the transverse muscles in close association with the head or anterior end of the central muscles. The posterior oblique then runs ventrocaudally through two segments to insert ventrad in common with its accompanying anterior oblique muscle (fig. 61). The first posterior oblique originates in tendinous tissue dorsal to the anterior

thoracic muscles. No posterior oblique muscle has been identified in the highly modified sixth abdominal segment of *Penaeus*. The posterior oblique muscles of *Penaeus* are represented in the abdomen of *Astacus* and *Pandalus*. The latter forms also have five posterior obliques.

OBLIQUE TRANSVERSE MUSCLES OF ABDOMEN

FIGURE 61

The oblique transverse muscle splits off the anterior oblique muscle dorsomedially at the junction of the main anterior oblique muscle and the external arm. The fibers turn ventrad between the anterior oblique and the central muscle and there join the central muscle. The affinities of the oblique transverse muscles of *Penaeus* in *Astacus* and *Pandalus* are not known.

1. Pleopods

The pleopods or swimming legs in many natant Crustacea are well-developed swimming appendages that enable the animals to propel themselves forward rapidly for great distances. In *Penaeus setiferus* the pleopod is not only heavily muscled but so constructed that the muscles move the pleopod, and in particular the propellers, the exopodite and endopodite, through a long power stroke. Each pair of pleopods beats in unison. The beat of the pleopods is synchronized by volleys of nerve impulses passing along the ventral abdominal nerve cord so that a beat wave reminiscent of ciliary action passes down the abdomen from anterior to posterior. *P. setiferus* has five pairs of pleopods, typical of the Crustacea Natantia. The third set has been chosen for study here because of their unspecialized structure.

When feeding, the white shrimp creeps along the bottom on its long, slender walking legs, testing the substrate for food particles. The cephalic region of the shrimp is held high while the tail fan and telson rest on the bottom. As the animal moves about, the pleopods beat gently from time to time. The resulting flow of water aids in the animal's progress by slightly lifting the tail fan from the bottom. Close examination of the white shrimp on the bottom reveals that the main propulsive elements, the exopodites, beat in a lateral position, not brushing the substrate. The present writer assumed that when the shrimp, encountering an obstruction, rises free of the substrate, the pleopod exopodites would beat in a vertical plane, in a straight line with the proximal elements of the pleopods. Such is not the case, however. In *P. setiferus* the pleopod exopodites always beat in a horizontal plane at right angles to the proximal pleopod elements during the power stroke, no matter whether the animal is creeping along the bottom or swimming freely in the water above. Dr. Edward Peebles, Tulane Medical School, has suggested that the lateral position of the pleopod exopodites places these organs outside of the stream of turbulence created by the walking legs.

The return or recovery stroke, during which the pleopod exopodite must be feathered, is made in the vertical plane, or nearly so. This action might be thought to cause the long exopodite to drag on the bottom, but during the return stroke the organ is relaxed and bends before the pressure of the water passing over it. The distal tip of the exopodite describes an oval. The power stroke draws the tip in a flat arc lateral to the ventral plane of the abdomen. At the end of the power stroke, water pressure from the anterior causes the exopodite to bend caudally and, together with the contraction of rotator and flexor muscles, to rotate one-quarter of a turn about its longitudinal axis. Upon rotation of the exopodite, the inertial drift of the animal through the water helps extensor muscles bring the exopodite from the lateral position of the power stroke to a ventral position. Rotation of the exopodite also enables the organ to present to the flow of water its cross section of least resistance as it is brought forward in recovery.

SKELETAL ELEMENTS

The skeletal and muscular elements of the third pleopod of *Penaeus setiferus* are arranged to perform the functions described above. The skeletal parts are roughly similar to those of the third pleopod of the European crawfish *Astacus astacus*, to those of the first pleopod (the pleopod of the second abdominal segment) in the female of *Callinectes sapidus*, to those of the third pleopod of *Cambarus longulus longulus*, and to the parts of the third pleopod of *Pandalus danae*.

Where the third pleopod of *Penaeus setiferus* is attached to the abdominal venter, the region of articulation of the ventral skeleton is reinforced by two V-shaped structures comprised of sclerotized bars (fig. 59). The lateral V (fig. 65, ventral skeletal support), traditionally said to be a contribution of the pleuron, has its apex directed

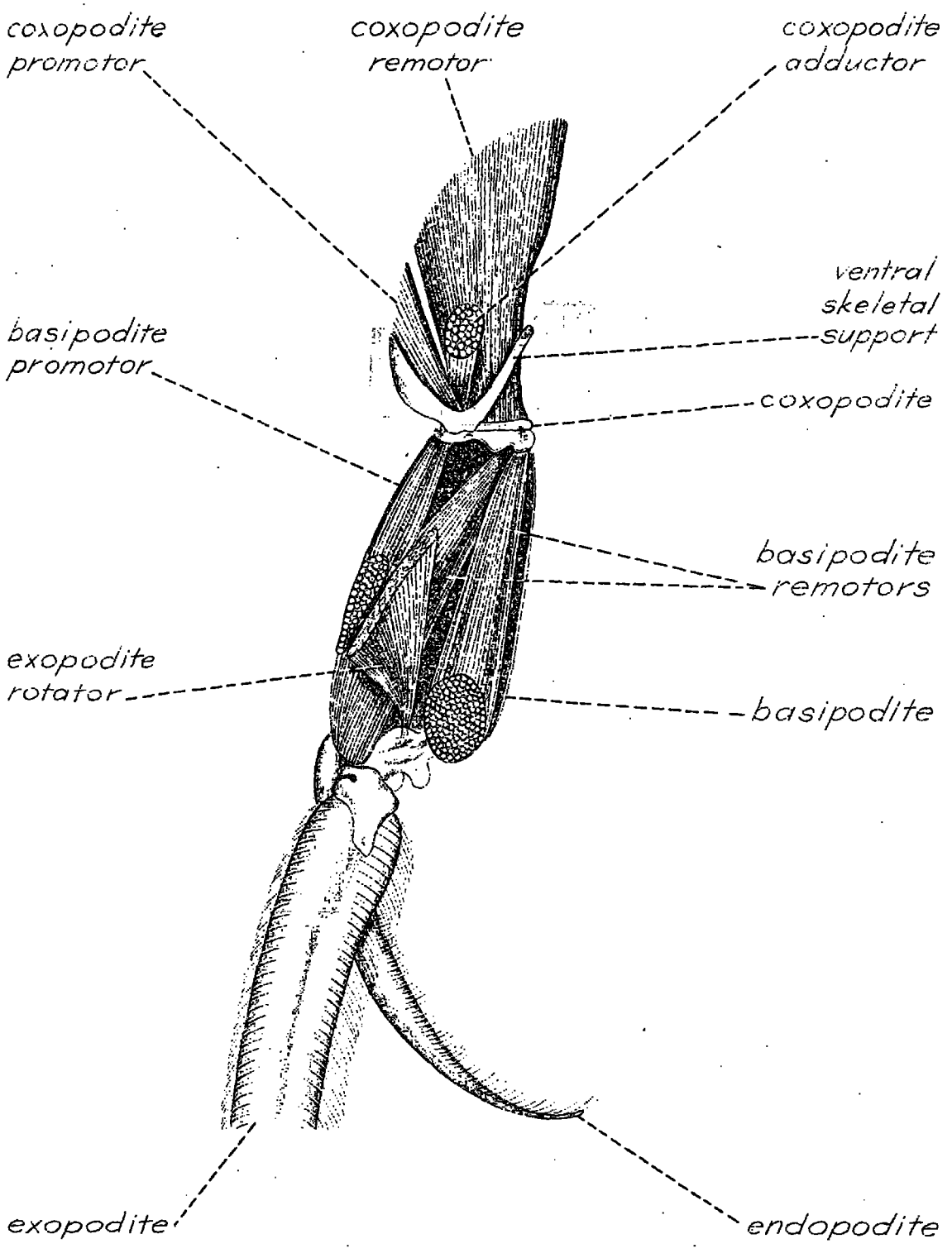

FIGURE 65.—Lateral view of left third pleopod showing basipodite and coxopodite musculature.

ventrad. At this point the structure articulates with the pleopod coxopodite. The mesial V, which also points ventrad, constitutes the support for the inner articulation of the pleopod coxopodite. The mesial V is a sternal element. The dorsal or free ends of the lateral and mesial arms of the V's are joined. The resulting ventral skeletal structure represents a set of combined triangles, if the coxopodite is included as a structural member, which can be described as a kind of Warren truss. The structural triangles provide support for the articular foramen to which the pleopod is attached. The ventral skeletal structure pertaining to the support of the pleopod is lighter in construction in *Penaeus* than in *Astacus* or *Cambarus*, although the pleopods of *Penaeus* are comparatively much larger and more powerful.

A further structural difference of note between the ventral skeletal pleopod support in *Penaeus* and that of the Astacura and the Brachyura is the position of the appendage relative to the ventral abdomen. In the Astacura particularly, the articular foramen of the pleopod is fully ventral, the ventral sternum and the so-called ventrolateral pleural plates being flat and lying horizontally. In *Penaeus* by contrast the sternum is convex and the lateral plates heretofore considered pleural are nearly vertical, placing the pleopod in a ventrolateral position exposed to the water in which the organ functions. Although Berkeley does not consider the subject, her illustrations indicate that the situation in *Pandalus* is similar to that in *Penaeus*.

The coxopodite (fig. 65) of the pleopod is a narrow, incomplete band or ring which articulates with the ventral skeletal elements dorsally and the basipodite ventrally. To the coxopodite are inserted muscles having their origins on the tergal plates of the abdominal skeleton and in the basipodite. The basipodite (fig. 65) is a broad and elongate structure, shaped like an inverted heart. The form of its cross section through the broad, distal portion is streamlined to reduce its resistance to the water during the recovery stroke. The basipodite articulates with the coxopodite proximally and with the endopodite and exopodite distally. By virtue of the arrangement of points of articulation and of its extensive musculature, the basipodite substantially reinforces the length and power of the propulsive stroke of the pleopod.

Distal to the basipodite, and visible only on the mesial side of the pleopod, lies a small, heavily sclerotized structure (fig. 68), the exopodite articular element, which articulates with the basipodite and the exopodite. Until more information is available, this structure will be considered an exopodite component. In *Penaeus*, several muscles insert in the structure. No trace of this appendage segment appears in the modified pleopods of *Astacus*, *Cambarus*, or *Callinectes*. Berkeley makes no reference to the structure in *Pandalus*.

The endopodite (fig. 68) articulates with the basipodite by a somewhat constricted area on the mesial side of the pleopod. Functionally the endopodite is simple, accompanying the exopodite in its movements. The exopodite (figs. 65 to 69) is a large, broad, oar-shaped organ, convex anteriorly and concave posteriorly. Like the endopodite, it is comprised of a long series of lightly sclerotized rings alternating with bands of thin cuticle. The skeleton of the exopodite is arranged thereby to bend when a stream of water strikes it from the anterior and to remain straight when water strikes it from the posterior. The exopodite functions like a curved, steel carpenter's rule which may be rolled on a spool in one direction, but which presents resistance to bending in the opposite direction. The functional surface of the endopodite and exopodite oar blades is greatly increased by long, plumose setae embedded in the margins. The pleopod endopodite and exopodite have been called flagella in *Astacus* and other reptant decapods in which the organs are extremely reduced by comparison with those of *Penaeus* and *Pandalus*. The term will not be used here, since the endopodites and exopodites of *Penaeus setiferus* are not flagella.

MUSCLE ELEMENTS

The third pleopod of *Penaeus setiferus* is operated by 17 or more muscles. The number of discrete muscles intrinsic to the pleopod endopodite in *Penaeus* is not clear, although the organ may contain two or more muscles. Schmidt in his account of *Astacus* describes 9 muscles for the third pleopod, Cochran lists 6 for the first pleopod of *Callinectes*, Hart (1952) describes 9 for the third pleopod of *Cambarus longulus longulus*, and Berkeley finds 11 in *Pandalus*.

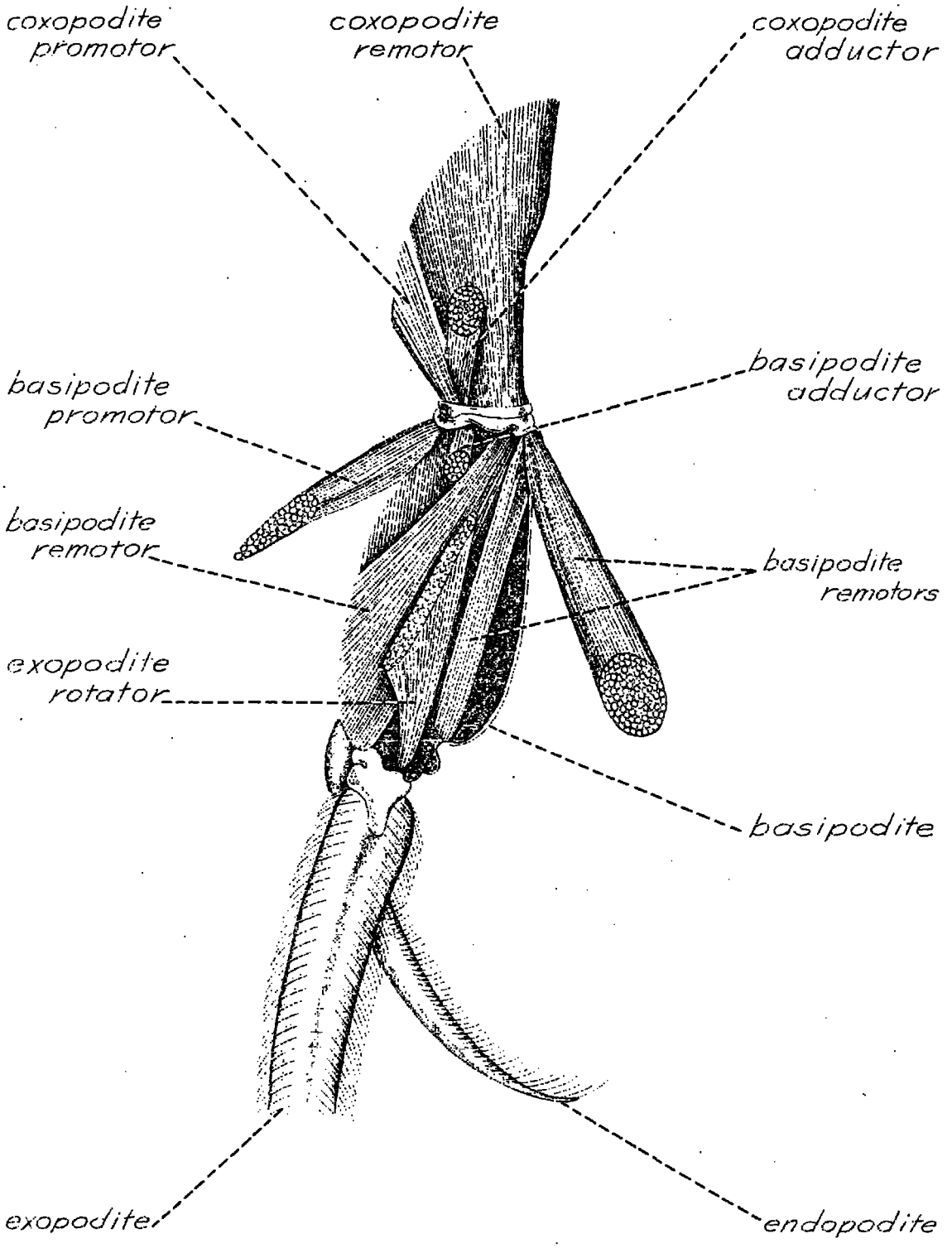

FIGURE 66.—Lateral view of left third pleopod showing basipodite and coxopodite musculature.

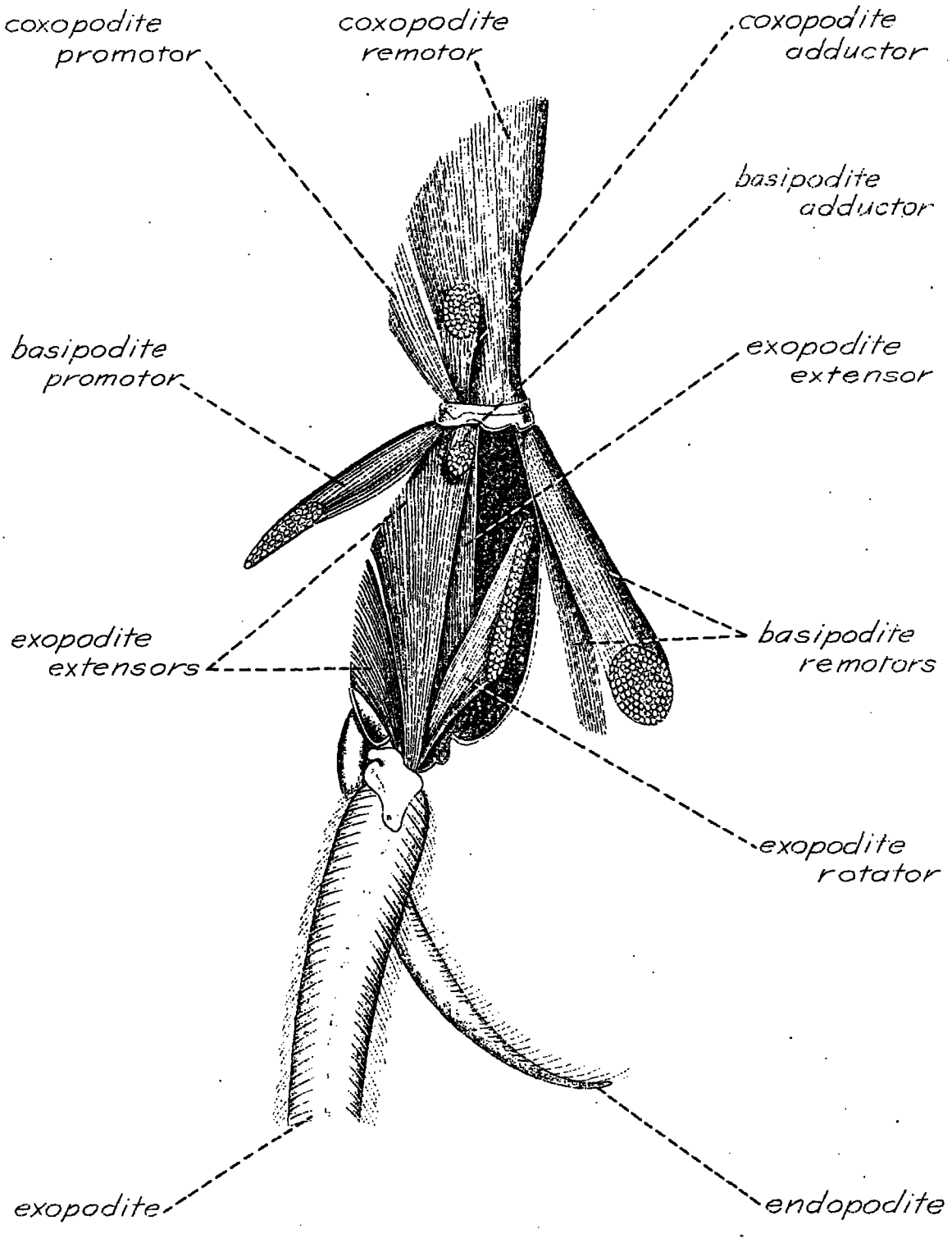

FIGURE 67.—Lateral view of left third pleopod showing basipodite and coxopodite musculature.

COXOPODITE REMOTOR MUSCLE

FIGURES 65 TO 69

The coxopodite remotor muscle, a broad upright fan, originates in fibrous connective tissue attached to the tergum, the arched dorsal plate of the abdominal skeleton, and inserts about an arc which represents approximately the posterior third of the coxopodite. The area of insertion of this muscle is located on the proximal margin of the coxopodite. Upon contraction the muscle draws the posterior edge of the coxopodite dorsad on the points of coxopodite articulation. The pull is an efficient one, since the coxopodite remotor contracts in an almost straight line. The contraction of the muscle thereby draws the distal pleopod elements through an anterior-to-posterior arc.

Berkeley illustrates the muscle in her work on *Pandalus*. Schmidt in *Astacus* and Hart (1952) in *Cambarus* describe a coxopodite remotor muscle (musculus remotor III pedis spurii) for each of these species of crawfishes. On the basis of information presently available, the coxopodite remotor muscle of *Penaeus* is homologous with the musculus remotor III pedis spurii of *Astacus*, *Cambarus*, and *Pandalus*, although proof must wait upon a comparative study of the nerves. Cochran does not find a coxopodite remotor in *Callinectes*.

COXOPODITE PROMOTOR MUSCLE

FIGURES 65 TO 69

The coxopodite promotor muscle originates on the abdominal tergum anteroventrally to the coxopodite remotor muscle and inserts on the proximal margin of the coxopodite anterior to a line through the lateral and mesial articulation points at which the coxopodite articulates with the ventral abdominal skeleton. Mechanically, the action of the coxopodite promotor is much weaker than are the contractions of the coxopodite remotor, since the coxopodite promotor is smaller than the remotor and its area of insertion is much closer to the proximal fulcral line of the coxopodite than is that of the remotor muscle.

The coxopodite promotor pulls the preaxial margin of the coxopodite dorsad. The distal pleopod elements thus are drawn through an arc anteriorly, in opposition to the action of the coxopodite remotor. The coxopodite promotor muscle has no exact functional counterpart in *Astacus* and *Cambarus*. The only muscle in the latter animals which could be homologous with the coxopodite promotor in *Penaeus* is the musculus rotator dorsalis basipoditis II pedis spurii described by Schmidt in *Astacus* and by Hart (1952) in *Cambarus*. The fact that the dorsal rotator muscle inserts on the basipodite in *Astacus* and *Cambarus* argues against this conclusion.

Berkeley describes a musculus rotator dorsalis basipoditis III pedis spurii in *Pandalus* that is very likely the homolog of the coxopodite promotor muscle in *Penaeus*, despite the difference in origin. However, her adoption of Schmidt's name for this muscle is unfortunate, since the musculus rotator dorsalis basipoditis in *Pandalus* actually promotes the basipodite, rather than rotates the pleopod. An appendage rotates about its long axis, not about an axis transverse to the appendage.

Cochran describes a coxopodite promotor muscle (musculus promotor coxopoditis I pedis spurii) in the pleopod of the second abdominal segment of *Callinectes*, and possibly the muscle is homologous with the coxopodite promotor in *Penaeus*. To remove from the realm of speculation a discussion of muscles having similar functions in two forms as distantly related as *Penaeus* and *Callinectes* will require careful study of the nerves.

COXOPODITE ADDUCTOR MUSCLES

FIGURES 65 to 67, 69

Two coxopodite adductor muscles are found in the pleopod of the white shrimp. The lateral coxopodite adductor muscle (figs. 65 to 67) is a small, short muscle originating on the lateral tergal surface and inserting on the dorsomedial rim of the coxopodite. The muscle pulls the mesial side of the coxopodite dorsally, and in so doing brings the distal pleopod elements mesad. The action of the lateral adductor muscle is reinforced by a second coxopodite adductor muscle (fig. 69) located on the mesial side of the ventral skeletal support. The mesial adductor originates on a phragmal fold of the postcoxal sternum and inserts on the dorsomedial margin of the coxopodite.

The lateral coxopodite adductor muscle has been lost in the Astacura to which reference has been made, but appears in *Callinectes* as the largest muscle in the blue crab pleopod. The

mesial coxopodite adductor muscle, which has disappeared in *Callinectes*, possibly exists in *Astacus*, *Cambarus*, and *Pandalus* as the ventral basipodite rotator muscle (musculus rotator ventralis basipoditis III pedis spurii). From Berkeley's account of the origin, insertion, and action of the muscle in *Pandalus*, the musculus rotator ventralis basipoditis is really an adductor muscle. Again, a study of the nerves is called for.

BASIPODITE ABDUCTOR MUSCLE

FIGURE 68

Opposing the action of the coxopodite adductor muscles which tend to draw the basipodite and other distal parts of the pleopod towards the abdomen is the basipodite abductor muscle. This fan-shaped muscle originates on the mesial surface of the basipodite. The area of origin is elongate in the long axis of the basipodite (fig. 68). The muscle becomes narrow as it courses dorsolaterally to insert on the ventrolateral margin of the coxopodite. When the basipodite abductor muscle contracts, the basipodite and the distal pleopod elements are drawn away from the abdomen. The muscle has been lost in *Callinectes* and in the Astacura referred to above. The basipodite abductor muscle of *Penaeus* may have a homolog in *Pandalus* as the musculus adductor basipodite II pedis spurii, a muscle that, according to the description of Berkeley, is evidently an abductor.

BASIPODITE PROMOTOR MUSCLE

FIGURES 65, 66, 67, 69

The basipodite promotor muscle originates on an area of the anterior margin of the basipodite about one-third of the distance from the distal end of the basipodite. The muscle inserts on the anteroventral margin of the coxopodite. Muscle contractions draw the basipodite, and the distal parts of the pleopod, cephalad with respect to the coxopodite. Together with the coxopodite promotor, the basipodite promotor muscle moves the pleopod in its recovery stroke. The basipodite promotor extends the length of the stroke. No homolog of the basipodite promotor muscle in *Penaeus* is evident in the pleopod of *Astacus*, *Cambarus*, or *Callinectes*.

The third pleopod of *Pandalus*, however, has a muscle, the musculus productor basipoditis III pedis spurii, that is similar in function and arrangement to the basipodite promotor muscle of *Penaeus*. The muscles in the two animals are almost certainly homologous, although proof must wait upon a study of nerve-muscle connections. Berkeley's use of the term "productor" for this muscle is questionable. She says, in part, that the musculus productor basipoditis ". . . moves the basipodite forward. . . ." In the opinion of the present writer, the action described by Berkeley for the muscle is not production, but promotion. Production, in the present context, is synonymous with the extension in length of a limb, and the musculus productor basipoditis of the third pleopod of *Pandalus* does not appear to be an extensor muscle.

BASIPODITE REMOTOR MUSCLES

FIGURES 65 to 69

The pleopod of the white shrimp contains 3 basipodite remotor muscles. Their contractions serve to increase greatly the length and power of the propulsive stroke initiated by the coxopodite remotor muscle. The anterior basipodite remotor muscle originates over a broad area in the anteroventral lobe of the basipodite (figs. 65, 66). From its origin the muscle runs diagonally across the interior of the basipodite to insert on the ventral edge of the coxopodite, posterior to a line through the points of articulation between the basipodite and the coxopodite. The posterior basipodite remotor muscles, of which there are two (figs. 65, 68), originate in the posteroventral lobe of the basipodite and extend dorsad to insert on the ventral margin of the coxopodite postaxially.

On the basis of arrangement and size, the anterior basipodite remotor muscle of *Penaeus* is evidently a homolog of the musculus reductor basipoditis III pedis spurii of *Pandalus*. The muscles are also functionally similar. Here again a question is raised over the use of terms. Berkeley describes the action of the musculus productor basipoditis as antagonistic to that of the musculus reductor basipoditis. If, as has been established above, the name "productor" for muscle function is synonymous with the term "extensor," then it follows that a reductor muscle is the same as a flexor muscle. Unfortunately, reduction has not in the anatomical sense the opposite meaning of production, but implies additional functions. For this reason the name "reductor" for muscle

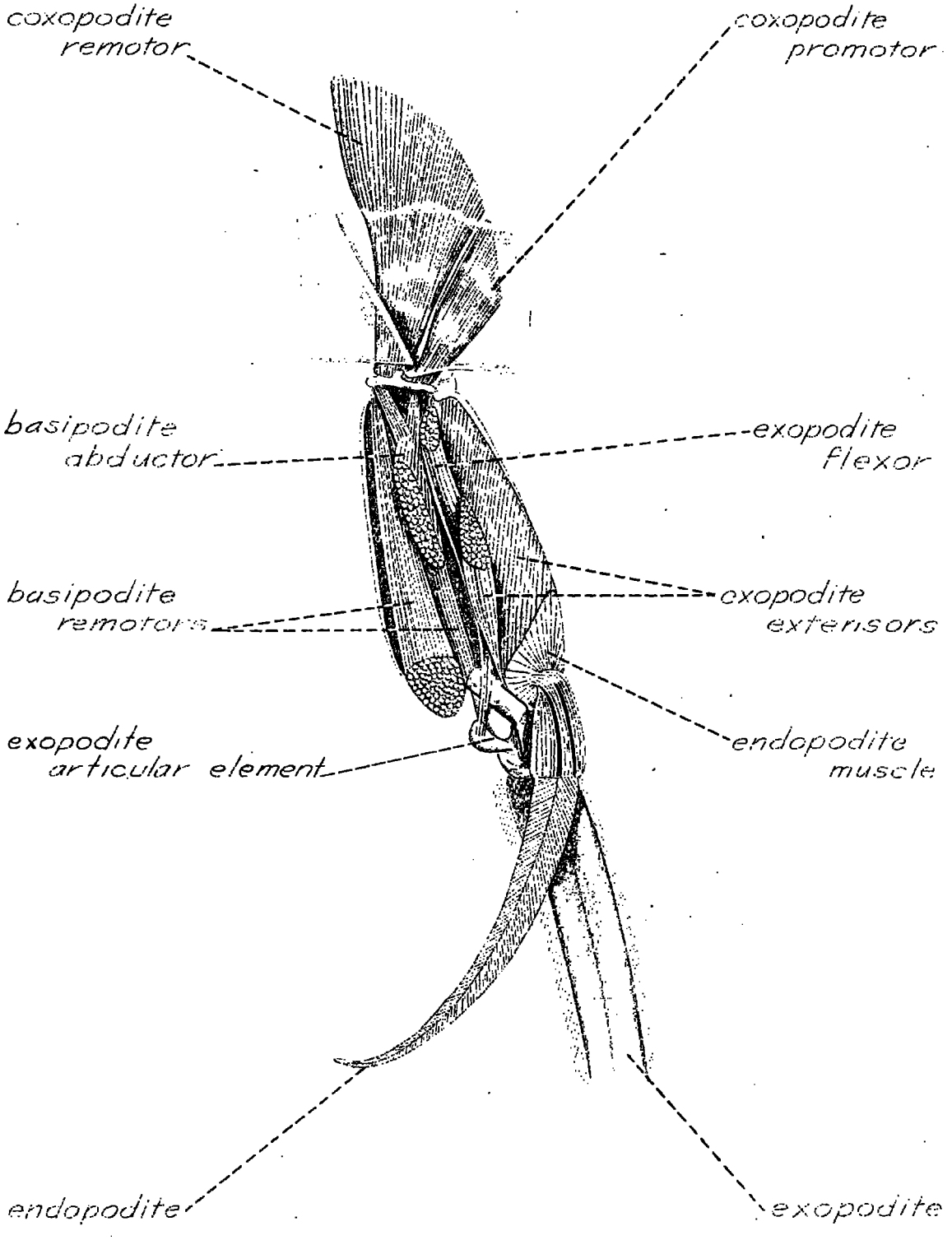

FIGURE 68.—Mesial view of left third pleopod showing coxopodite, basipodite, and endopodite musculature.

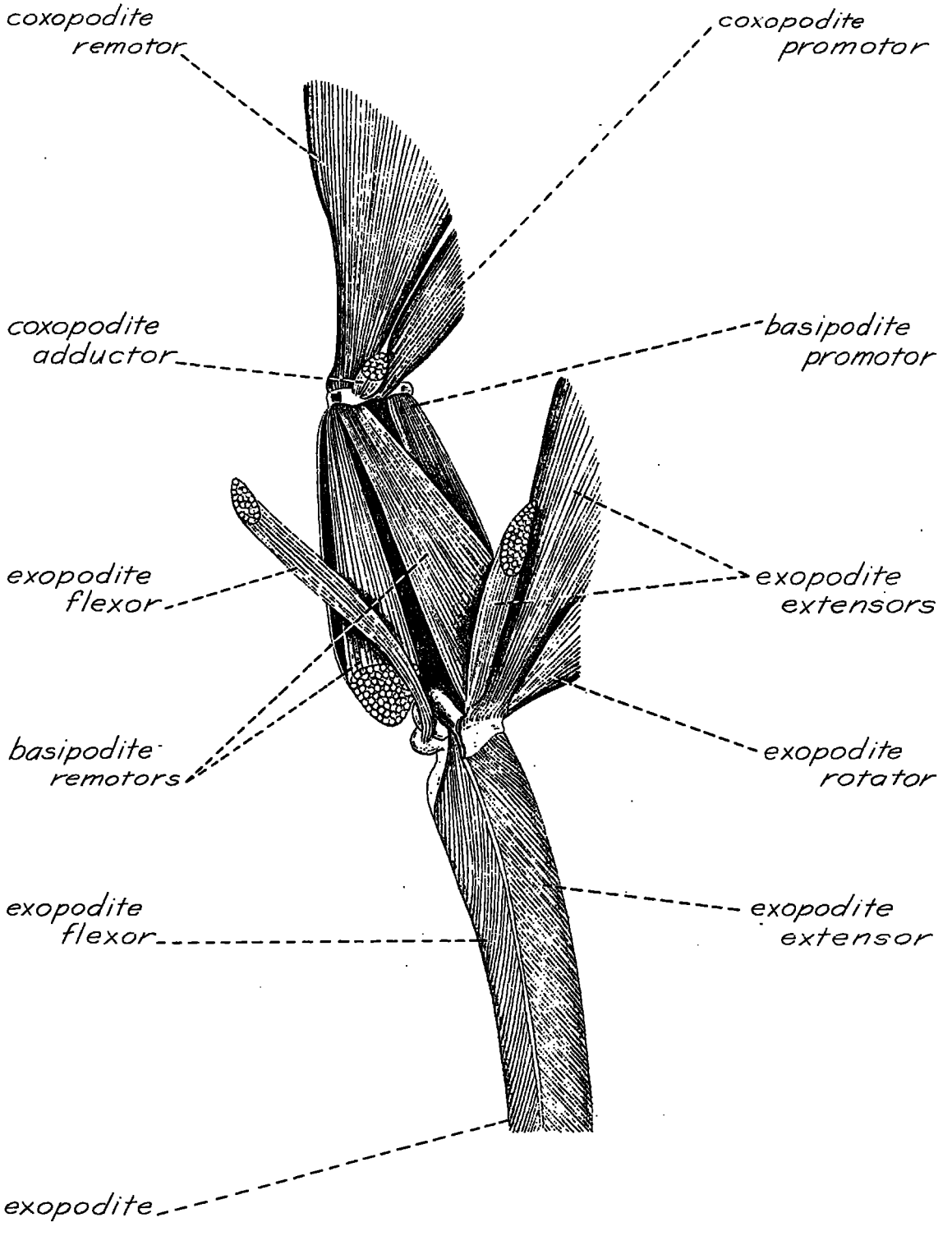

FIGURE 69.—Mesial view of left third pleopod showing muscles of coxopodite, basipodite, and exopodite. Endopodite removed.

action should be avoided. Moreover, the application of the term "reductor" to the musculus reductor basipoditis in *Pandalus* is questionable, since the muscle does not function as a flexor of the basipodite.

The basipodite remotor muscles apparently are not represented in the pleopod of *Astacus*, *Cambarus*, or *Callinectes*, although a trace of these important muscles in *Penaeus* may have remained during the evolution of the former animals as the basipodite reductor muscle (musculus reductor basipoditis).

EXPODITE ROTATOR MUSCLES

FIGURES 65, 66, 67, 69

The pleopod basipodite of *Penaeus setiferus* contains two muscles which rotate the exopodite. The elongate origin of the fan-shaped lateral exopodite rotator muscle is on the lateral surface of the basipodite and may be identified easily through the cuticle in preserved material (fig. 65). The muscle becomes narrow as it runs distomesially to insert on the mesial surface of the complex articular element joining the basipodite to the exopodite. The muscle functions to square the plane of the oar blade of the exopodite at the end of the recovery stroke for the catch of the following propulsive stroke. The mesial exopodite rotator muscle (fig. 69) is a small muscle located in the anterodistal lobe of the basipodite. Its contractions apparently aid in feathering the exopodite oar blade. These muscles do not appear in any of the crustaceans to which reference has been made, although the mesial exopodite rotator muscle may exist in *Pandalus* as the musculus adductor endopoditis.

EXOPODITE EXTENSOR MUSCLES

FIGURES 67 TO 69

The third pleopod of *Penaeus setiferus* is provided with 3 exopodite extensor muscles, 2 of which originate in the basipodite and 1 in the exopodite. The largest of these has its origins along the entire anterior margin of the basipodite (figs. 67, 68). It is one of the largest muscles in the pleopod. The muscle inserts on an apodeme of the exopodite articular element. Inserting on the same apodeme is a slender exopodite extensor muscle which is located just posterior to the anterior exopodite extensor muscle described above (figs. 68, 69). The posterior exopodite extensor has its origin on the mesial surface of the basipodite (fig. 68). When the two extensor muscles contract they draw the articular element of the exopodite dorsad. The plane of articulation of this element is such that the exopodite is swung down from its lateral position in the propulsive stroke to a fully extended position. At the same time the articular element rotates the exopodite on its longitudinal axis, with the aid of the mesial exopodite rotator muscle, to feather the exopodite oar blade.

That the two exopodite extensor muscles located in the pleopod basipodite of *Penaeus* are missing in *Astacus*, *Cambarus*, and *Callinectes* is not surprising in view of the extensive rearrangements in the swimming appendages of the latter form. The pleopod basipodite of *Pandalus* has retained at least the larger of the exopodite extensor muscles of *Penaeus*, as the musculus adductor exopoditis III pedis spurii.

The third exopodite extensor (fig. 69) lies along the mesial edge of the exopodite, attaching on the margin of the exopodite articular element. Its contractions serve to extend the exopodite and to straighten the leading edge of the exopodite during the recovery stroke. The muscle is homologous with the exopodite flagellum muscle described by Schmidt and Hart (1952) in Astacura, and by Berkeley in *Pandalus*. It is missing in *Callinectes*.

EXOPODITE FLEXOR MUSCLES

FIGURES 68, 69

Two exopodite flexor muscles appear in the third pleopod of *Penaeus setiferus*. One originates proximally on the medial surface of the basipodite (fig. 68), runs the length of the basipodite, and inserts on the posterior surface of the exopodite articular element (fig. 69). The muscle functions to flex the exopodite laterally to place the exopodite oar blade in position for the propulsive stroke. The proximal exopodite extensor muscle of *Penaeus* is in all likelihood the homolog of the musculus abductor exopoditis of the third pleopod of *Pandalus*.

The distal exopodite flexor muscle is intrinsic to the exopodite. The muscle is arranged along the lateral margin of the exopodite (fig. 69) and attaches to the posterior part of the exopodite articular element. The contractions of the muscle reinforce the flexing action of the proximal flexor

muscle. Like the distal exopodite extensor muscle, the distal exopodite flexor muscle is a homolog of the exopodite flagellum muscle (musculus flagellaris exopoditis III pedii spurii) in *Astacus*, *Cambarus*, and *Pandalus*.

ENDOPODITE MUSCLE

FIGURE 68

The endopodite muscle, or muscles, appears to be a multipart structure in *Penaeus setiferus*. A portion of the muscle lies mesially in the anterodistal lobe of the basipodite (fig. 68). Fibers of the muscle run through the constricted article connecting the basipodite with the endopodite and continue distally into the endopodite. Additional fibers that arise in the proximal end of the endopodite suggest that the endopodite contains more than one muscle body. The function of the endopodite musculature consists of stiffening the endopodite during the power stroke and, by their relaxation in the recovery stroke, of enabling the endopodite to bend before the flow of water.

The endopodite flagellum muscle of *Astacus*, *Cambarus*, and *Pandalus* is very likely the homolog of the muscle in the pleopod endopodite of *Penaeus*. The muscle has been lost in the blue crab.

2. Tail Fan

The tail fan is made up of the telson and uropods projecting from the posterior end of the sixth abdominal segment and intimately associated with it. Classically, the uropods have been treated as serially homologous appendages having the typical limb parts, however modified. The telson, on the other hand, has usually been considered an unsegmented posterior element bearing the anus, on grounds of the embryological addition of abdominal segments before the telson (Calman 1909). The whole tail fan is well adapted for the purpose of drawing the white shrimp backwards through the water as the great ventral abdominal muscles flex the abdomen.

SKELETAL ELEMENTS

The telson (figs. 70 to 74) is an apparently unpaired structure. Its broad, anterior portion articulates with the caudal end of the posterodorsal part of the sixth abdominal somite. Lateral condyles allow free movements in the vertical plane, but limit horizontal motion. The telson becomes narrow posteriorly, tapering to a sharp point. In section, the telson is roughly triangular. The thin sternum varies in shape from flat to slightly concave and the heavily sclerotized laterotergal plates are convex. Instead of having a mid-dorsal carina or ridge, the telson has a pair of ridges produced by a shallow groove in the dorsal midline (fig. 70). The structure lies above parts of the uropods and affords them some protection dorsally.

The uropods (figs. 70 to 74) arise from the posteroventral area of the sixth abdominal somite. Each is comprised of a strongly sclerotized basal element, the protopodite, from which the broad, flat uropods project. The large lateral uropod is the exopodite while the inner is the endopodite. The protopodite is supposed to be made up of the coxopodite and basipodite, but no skeletal trace of these articles is evident. A faint relic of segmentation in the exopodite remains on the dorsal surface (fig. 70) in the form of a transversely oriented groove. A portion of this groove sets off the tip of the lateral exopodite adductor muscle.

Due to the hinging of the uropodal elements, the uropods are capable of free motion. The articulation between the protopodite and the sixth abdominal segment, while strong, is relatively loose. The protopodite can move in the vertical and horizontal planes and also may rotate about its long axis. The points of articulation between the protopodite and the uropods are, on the other hand, condylic, and limit the exopodite and endopodite to the horizontal movements of spreading the uropods. Certain marginal areas of the telson and uropods are fringed with natatory hairs, much like the pleopods.

MUSCLE ELEMENTS

The muscles of the tail fan are all disposed to the function of these organs in the rapid backward swimming of the white shrimp. In plan the muscles are widely different from that of the typical limb. The most notable difference is the presence inside the sixth abdominal segment of several muscle groups which operate parts of the tail fan. This does not occur in the preceding abdominal segments. In comparing the muscles of the area in *Penaeus* with the tail fan muscles of *Astacus* and *Pandalus*, two kinds of differences are encountered. The first has to do with the number of functional muscle types, *Penaeus* having 16 compared with 18 muscle types in the crawfish.

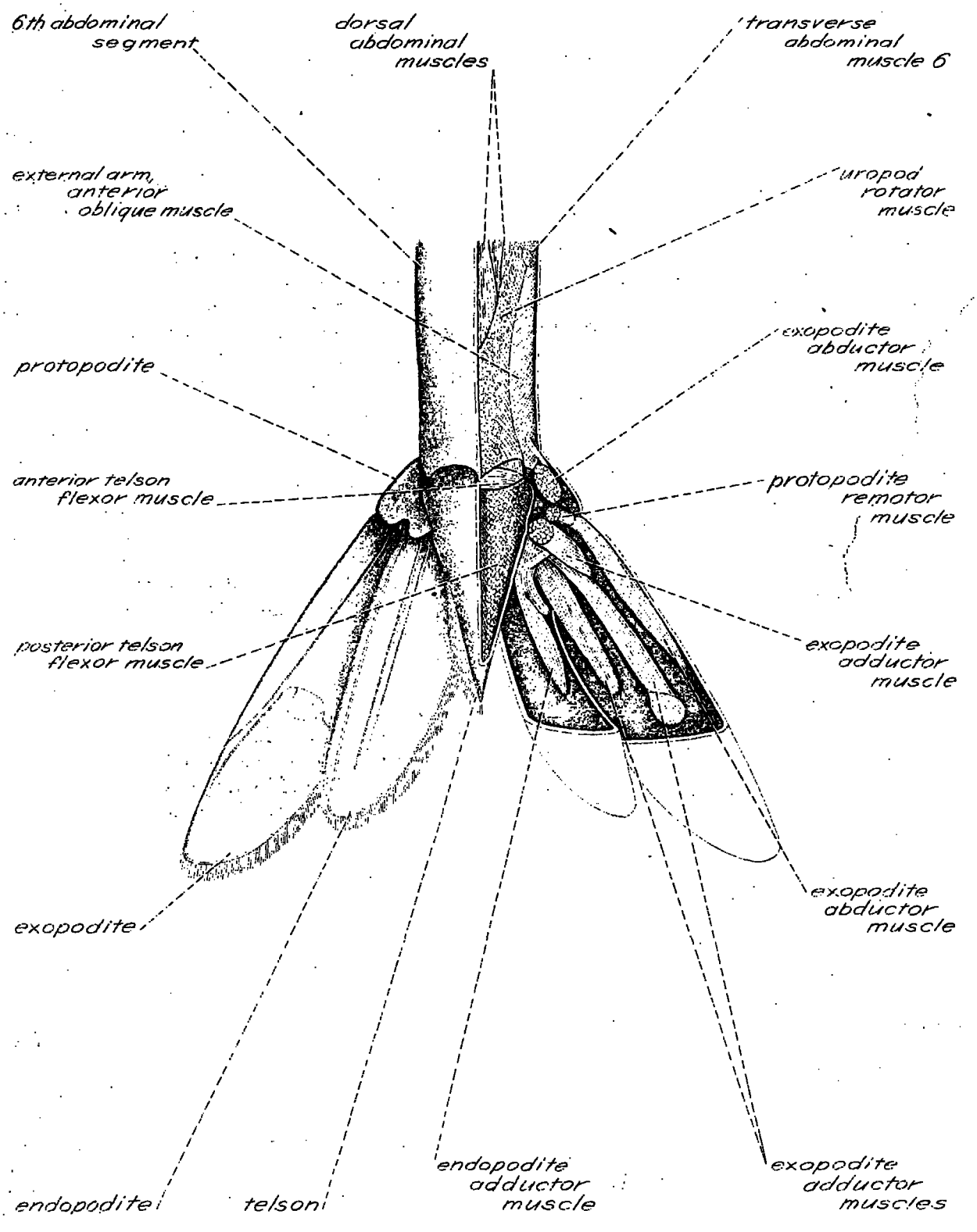

FIGURE 70.—Dorsal view of telson, uropods, and part of sixth abdominal segment. Left side intact. Dorsal cuticle of right side cut away to show muscles.

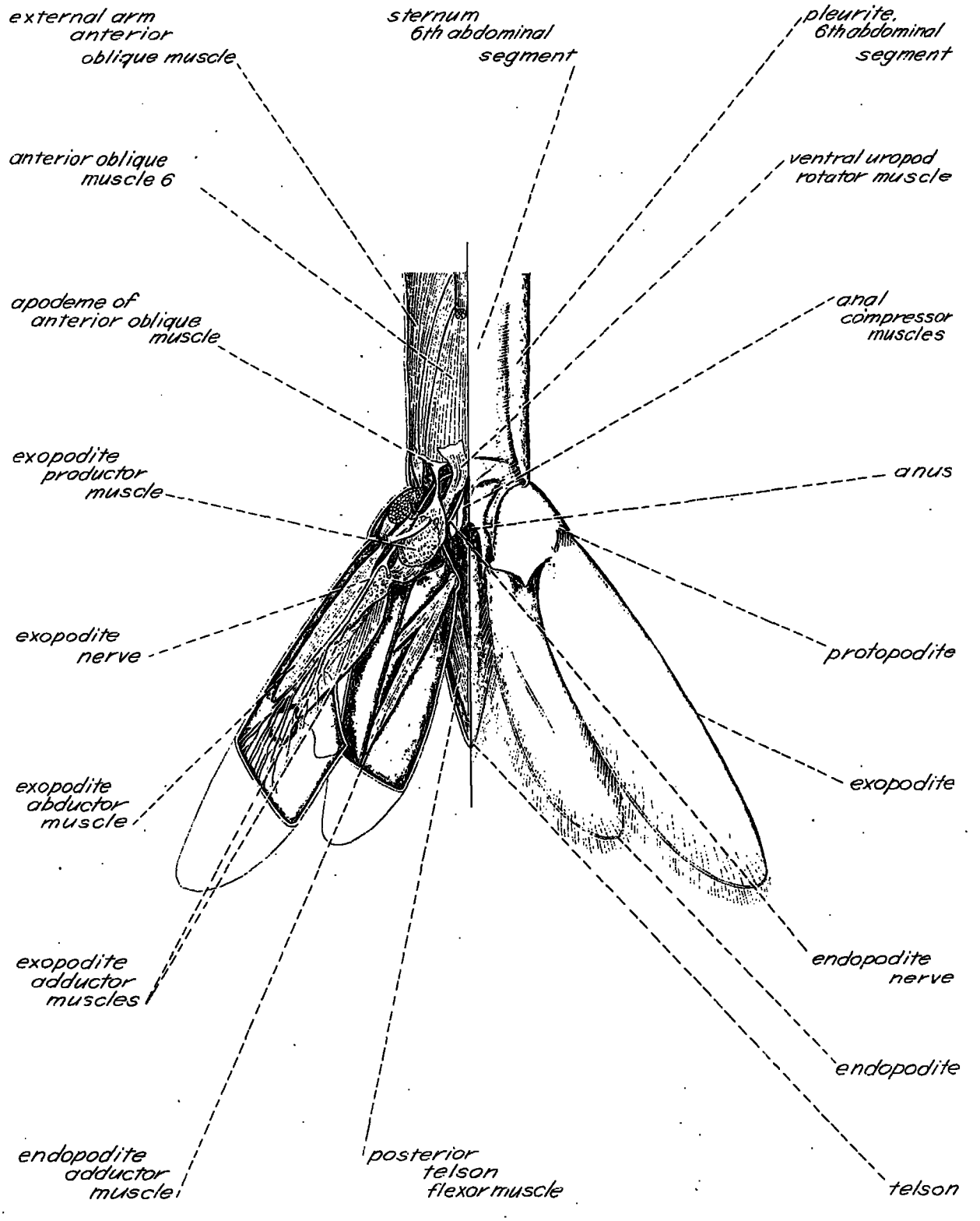

FIGURE 71.—Ventral view of telson, uropods, and part of sixth abdominal segment. Right side intact. Ventral cuticle of left side cut away to show muscles.

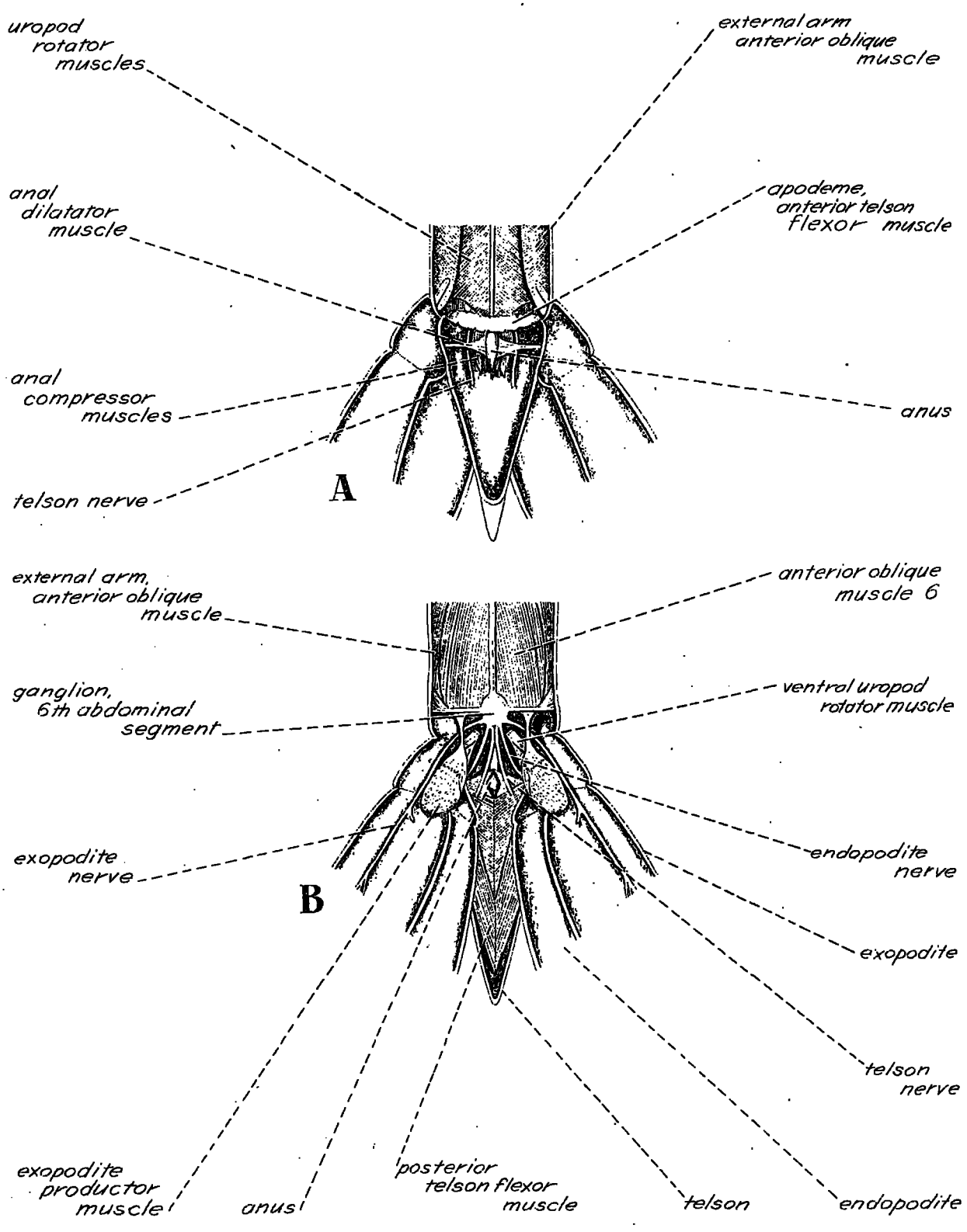

FIGURE 72.—Views of dissections of telson and uropods. *A*. Dorsal view. Muscles removed to show anus and posterior muscles of sixth abdominal segment. *B*. Ventral view. Muscles removed to show nerves.

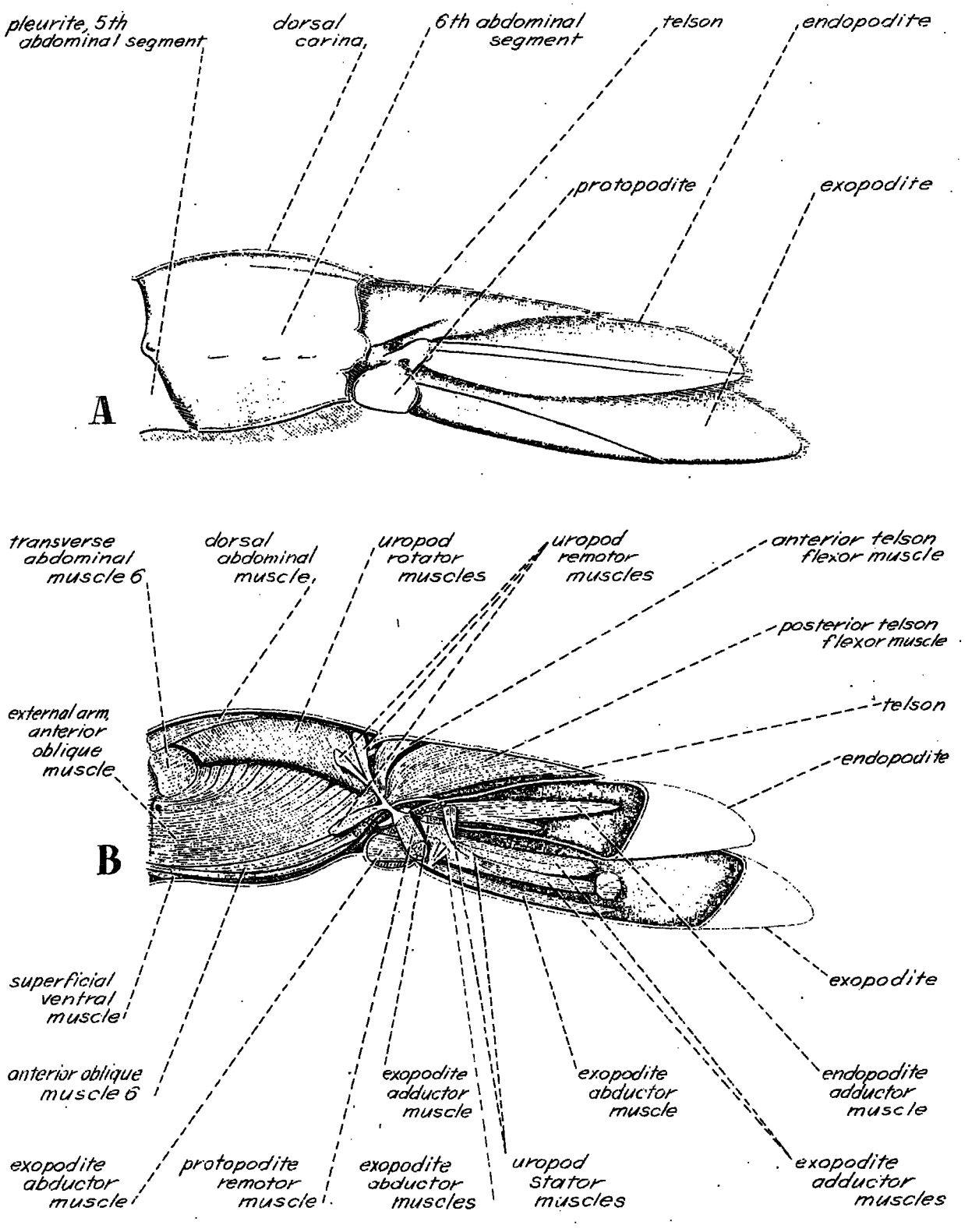

FIGURE 73.—Lateral view of left side of sixth abdominal segment, telson, and uropods. *A*. Intact structures. *B*. Lateral cuticle removed to show superficial lateral muscles.

The second difference follows from the first. We find muscles in the tail fan of *Penaeus*, similar to those in *Pandalus* and *Astacus*, that have quite dissimilar functions. These have been renamed in accordance with their presumed functions in *Penaeus*. The tail fan of the white shrimp appears to be operated by 27 muscles, including certain rectal muscles not found in *Astacus* or *Pandalus*. This compares with 18 muscles in *Astacus* and 13 in *Pandalus*.

UROPOD REMOTOR MUSCLES

FIGURE 73

Three uropod remotor muscles are found in the white shrimp. One originates dorsomedially in the posterodorsal corner of the sixth abdominal segment. The second arises slightly anterior to the first and runs posteroventrad to join the first on a common apodeme. The third originates lateroventrad of the first two and joins the common remotor apodeme at a point caudad of the first two remotor muscles. The common remotor apodeme now runs a short distance ventrocaudally to insert in heavy connective tissue beneath the dorsal rim of the uropod protopodite. Contractions of the muscles bring the uropods dorsad, in opposition to the action of the large abdominal muscles attached to the uropods. The two dorsal uropod remotor muscles are perhaps homologous to the medial uropod protopodite remotor muscle of *Pandalus* and *Astacus*, while the ventrolateral remotor is considered to be the homolog of the medial protopodite remotor muscle in the coon stripe shrimp and the crawfish.

PROTOPODITE REMOTOR MUSCLE OF UROPOD

FIGURES 70, 73

The protopodite remotor muscle is a short, thick structure originating in the same tendinous connective tissue upon which the uropod remotors insert. The protopodite remotor thus functionally prolongs the remotor muscle series to the caudal edge of the protopodite. The only muscle that looks similar to the protopodite remotor muscle of *Penaeus* is the exopodite reductor muscle of *Pandalus*, a muscle not found in *Penaeus*.

DORSAL UROPOD ROTATOR MUSCLES

FIGURES 70, 72, 73, 74

Due to the presence of transverse fasciae dividing them, three dorsal uropod rotator muscles are found in each half of the sixth abdominal segment of *Penaeus* (fig. 74, *A*). These large muscles originate over much of the dorsomedial and lateral areas of the sixth abdominal tergum to the margin of the external arm of the anterior oblique muscle (fig. 73, *B*). The dorsal uropod rotators pass ventrocaudally to insert upon three branches of a large apodemal tendon shared with the telson flexor muscles. The tendon arises from the ventral rim of the protopodite at its junction with the sixth abdominal segment. On contraction, the uropod rotators turn the lateral side of the protopodite downward, thereby maintaining the uropods in the most advantageous position for drawing the animal backwards through the water. The dorsal uropod rotator muscles of *Penaeus* appear to be homologous with those of *Astacus* and *Pandalus*.

VENTRAL UROPOD ROTATOR MUSCLE

FIGURES 71, 72

The small ventral uropod rotator muscle originates by a broad apodeme attached to the posteroventral sternum of the sixth abdominal segment (fig. 71). The muscle runs caudally and laterally to insert by a strong tendon into the medial edge of the protopodite. Contractions of the muscle rotate the protopodite about its long axis, thus bringing the lateral edge of the protopodite and exopodite downwards. The ventral uropod rotator muscle of *Penaeus* is not shown in the studies of *Pandalus*. A ventral uropod rotator is indicated by Schmidt in *Astacus*. The muscle in the crawfish is much larger than its counterpart in *Penaeus*.

PROTOPODITE ROTATOR MUSCLE

FIGURE 74

The protopodite rotator muscle is revealed by the removal of the thick exopodite abductor muscle located in the lateral part of the protopodite (fig. 73, *B*). The muscle takes origin in the same connective tissue providing insertions for the uropod remotors and the origin of the protopodite remotor muscle. The protopodite rotator passes laterally and ventrally to an area of insertion on the ventrolateral surface of the protopodite. The counterpart of the muscle in *Astacus* and *Pandalus* is not clear.

UROPOD STATOR MUSCLES

FIGURES 73, 74

The uropod stator muscles are 2 or 3 small muscles whose function appears to be the retention of the exopodite and endopodite in position with respect to one another. The affinities of these muscles in other crustaceans are not known.

EXOPODITE ABDUCTOR MUSCLES

FIGURES 70, 71, 73

The uropod of *Penaeus* contains 4 exopodite abductor muscles, all varying widely in shape and size. The anteriormost is a short, strong muscle occupying the lateral part of the protopodite (fig. 73, *B*). The muscle originates in the anterior curvature of the protopodite and inserts on the lateral margin of the exopodite. The muscle turns the exopodite laterally about its dorsoventral condyles. Also intrinsic to the protopodite are two smaller exopodite abductor muscles inserting in common with the first abductor. The small abductors lie beneath the protopodite remotor muscle and originate at two points on the ventromedial surface of the protopodite. The fourth and caudal exopodite abductor muscle, best seen in dorsal view (fig. 70), runs along the lateral margin of the exopodite. The muscle originates distally and inserts on a lateral apodeme of the protopodite. The function of the exopodite abductors is to spread the tail fan.

The first and fourth exopodite abductor muscles of *Penaeus* are homologous with the dorsal and lateral exopodite abductors of *Astacus* and with the lateral abductor muscle of *Pandalus*. The relationships of the two small abductors in *Penaeus* are not clear. The small ventral uropod exopodite abductor muscle shown by Schmidt in *Astacus* does not appear in *Penaeus*.

EXOPODITE ADDUCTOR MUSCLES

FIGURES 70, 71, 73, 74

The uropod exopodite of *Penaeus* is operated by three exopodite adductor muscles. The first exopodite adductor is rostral to the other two. It is a short, strong, twisted muscle originating on the posterodorsal surface of the protopodite (fig. 70). The first exopodite adductor passes ventrocaudally through other muscles to an area of insertion on the anteroventral surface of the exopodite (fig. 71). The second exopodite adductor muscle is the longest uropod muscle. The structure lies in the midline of the exopodite, inserting on the posterodorsal margin of the protopodite beneath the first adductor. The muscle takes origin in the distal region of the exopodite and on a little fascia dividing the main body of the muscle from a small, lenticular muscle (fig. 70). This little distal muscle is thought to be the vestige of a muscle operating the distal exopodite joint.

The third exopodite adductor lies along the medial margin of the exopodite. The muscle is made up of short fibers attaching to a long apodeme running through the middle of the structure. The apodeme arises from the posterodorsal margin of the protopodite. Contractions of the exopodite adductors turn the exopodite towards the midline of the animal, opposing the abductors.

The first exopodite adductor muscle of *Penaeus* appears in *Pandalus* as the anterior exopodite adductor. The second exopodite adductor found in the white shrimp is not represented in either *Pandalus* or *Astacus*. The third adductor of *Penaeus* is fully homologous with the muscle known as the posterior exopodite adductor in *Pandalus* and the uropod exopodite adductor muscle in the European crawfish.

EXOPODITE PRODUCTOR MUSCLE

FIGURES 71, 72, 74

The exopodite productor muscle of *Penaeus* is a broad, flat structure occupying the ventral part of the protopodite (figs. 71, 72). The productor originates in the heavy connective tissue of the large apodeme common to the dorsal uropod rotator muscles and the telson flexor muscles. The productor muscle passes caudad to a broad insertion on the ventral rim of the exopodite. The exopodite productor muscle is represented in the tail fan of *Pandalus*, but its relationships in the crawfish are not known. No reductor of the exopodite has been found in the tail fan of the white shrimp.

ENDOPODITE ADDUCTOR MUSCLE

FIGURES 70, 71, 73, 74

Originating in the distomedial part of the endopodite, the endopodite adductor muscle runs proximally in the endopodite to its point of in-

sertion on the ventromedial edge of the protopodite. The muscle turns the endopodite toward the midline, with the result that the endopodites are closed. The endopodite adductor of *Penaeus* is probably homologous with the same muscle in the tail fan of *Pandalus* and *Astacus*.

ANTERIOR TELSON FLEXOR MUSCLE

FIGURES 70, 72, 73, 74

The anterior telson flexor muscle originates over most of the anterodorsal portion of the telson (fig. 70). The muscle passes directly ventrad to insert on the apodeme shared by the dorsal rotators and the telson flexors. The muscle has almost exact counterparts in the telson of *Pandalus* and *Astacus*. The anterior telson flexor muscle pulls the telson downward upon the uropods in the vertical plane.

POSTERIOR TELSON FLEXOR MUSCLE

FIGURES 70, 71, 72, 73, 74

The posterior telson flexor muscle is much larger than the anterior telson flexor. The posterior telson flexor originates over all of the dorsal and lateral tergum of the telson not taken up by the small anterior flexor. The muscle fibers run anteroventrally, narrowing to their insertion on the common apodemal material to which the dorsal rotators and anterior telson flexor are attached (fig. 74, *A*). The posterior flexor reinforces the action of the anterior telson flexor in bringing the telson ventrad. The posterior telson flexor muscle of *Penaeus* is represented in similar form in *Astacus* and *Pandalus*.

VENTRAL TELSON FLEXOR MUSCLE

FIGURE 74, *B*

The ventral telson flexor muscle is located within the sixth abdominal segment dorsal to the anterior oblique muscle apodemes. The muscle occupies a scoop-shaped depression in the posterodorsal part of anterior oblique muscle 6 (fig. 74, *B*) where it takes its origin. The muscle passes directly caudad to insert on an apodeme arising from the anterior margin of the telson sternum. The muscle turns the telson ventrad in the vertical plane. A counterpart of the ventral telson flexor muscle of *Penaeus* is found in *Pandalus*. The muscle is missing in *Astacus*.

ANAL COMPRESSOR MUSCLES

FIGURES 71, 72

The anal compressor muscles lie ventral to the rectum and alongside of it and insert into the lateral side of the anal opening. Contractions of the muscles flatten the sides of the anal opening in the long axis and thereby tend to close it. A similar muscle is found in *Astacus*, but not, according to Berkeley, in *Pandalus*.

ANAL DILATATOR MUSCLE

FIGURE 72

The anal dilatator muscle runs at right angles to the anal compressor and slightly above it (fig. 72, *A*), connecting into the lateral tergum of the telson by a tendon. Contractions of the dilatator open the anal aperture. The same muscle is found in the other crustaceans to which we have made reference.

RECTAL ATTRACTOR MUSCLES

FIGURE 74, *B*

The rectal attractor muscles are two small muscles of doubtful affinity not described by Schmidt in *Astacus* or Berkeley in *Pandalus*. The muscles lie in the midline of the sixth abdominal segment, between the uropod rotators. Both are attached to the median dorsal edge of the telson. The small, dorsal attractor passes rostrad to a tendinous fascia associated with the uropod rotators. If this muscle were larger it might better be named a telson extensor, but its size argues against this interpretation. The larger, ventral attractor muscle inserts in connective tissue on the dorsal surface of the rectum and undoubtedly draws the rectum caudad in movements associated with defecation.

II. THE NERVOUS SYSTEM

To the comparative morphologist, the nervous system is of fundamental importance. Of all the systems—skeletal, muscle, alimentary, reproductive, etc.—the annulate nervous system has most nearly retained its generalized form during the evolution of the group. That is, the nervous systems of any two annulates are remarkably similar. Nervous systems of Annulata, then, as has been amply shown by Snodgrass (1938), Ferris (1953), and others, are singularly conservative of form in

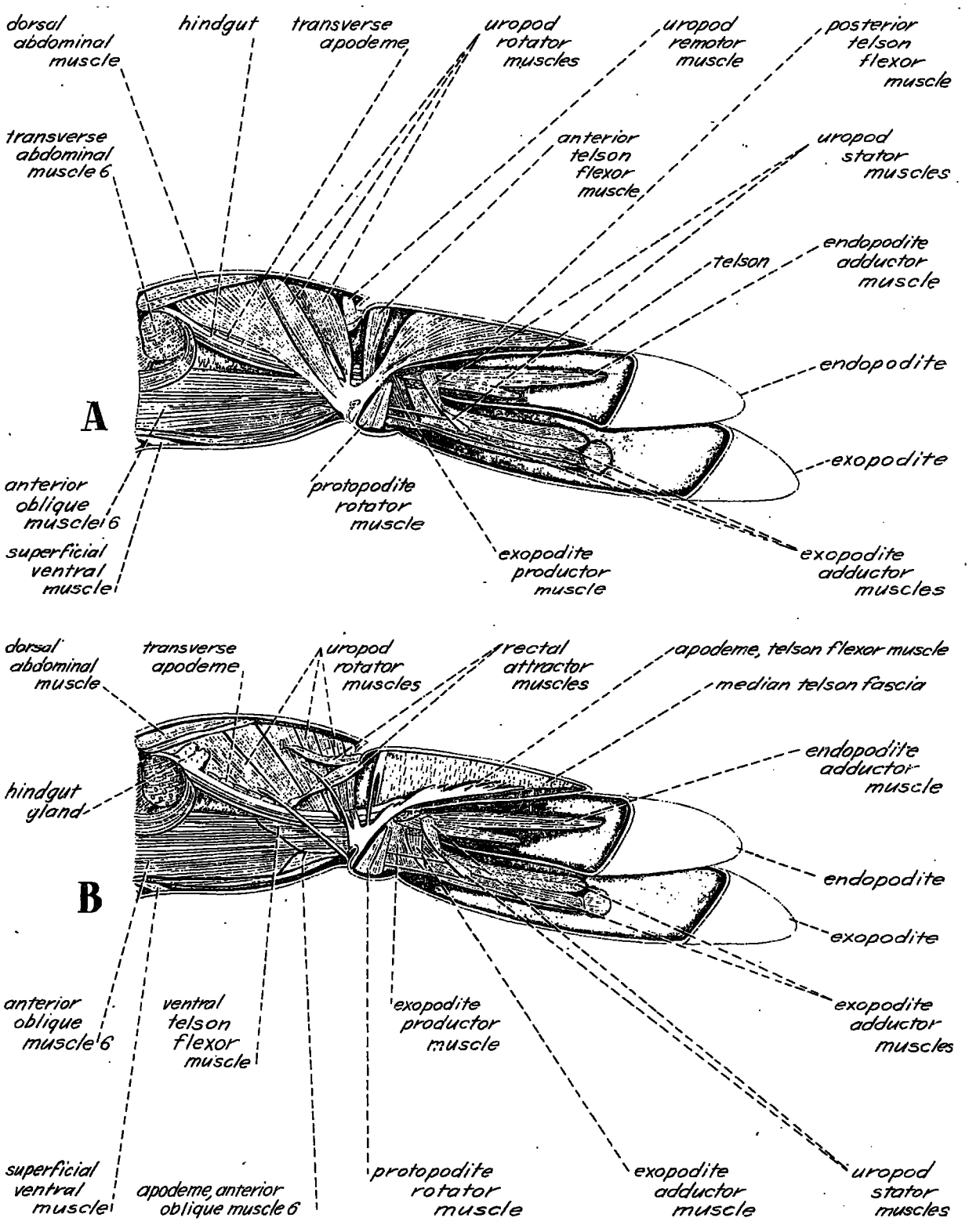

FIGURE 74.—Lateral view of left side of sixth abdominal segment, telson, and uropods. *A*. Lateral muscles removed. *B*. Median sagittal view.

time, and for this reason, may be used by the morphologist to bring order out of apparent phylogenetic chaos in the other organic systems. Gaps exist in our knowledge of decapod neuroanatomy, and frequent reference has been made to the lack of detailed information about innervations of muscles and other structures in morphological work.

The basis for an understanding of the history of muscles and other structures is the exact and full understanding of the details of the nervous system. The literature of arthropod morphology does not provide the facts, except in rare instances, nor are all the anatomical facts about the nerves of *Penaeus* made available in the present work. The reason for this is the high technical skill and great periods of time required to work out in detail the gross anatomy and histology of a nervous system. The 2 years devoted to the present research on white shrimp have not been sufficient for this purpose.

Despite present shortcomings, a number of important details of the central nervous system of *Penaeus* have been worked out. Typical of Annulata, the shrimp nervous system is comprised of a dorsal brain connected to the ganglionated ventral longitudinal nerve cord below the gut by two large tracts. The gut passes between these tracts. In general, the brain or supraesophageal ganglion, receives nerves from the special sense organs of the head and supplies nerves to the muscles operating them. The first ganglion of the ventral nerve cord, usually called the subesophageal ganglion, together with the following metameric ventral ganglia, receive impulses from sensory end organs of the body and appendages and send motor impulses to the muscles moving these structures.

The dorsal brain of annulates is variously composed. The arthropod brain is usually said to consist of an anterior protocerebrum containing the nerve centers of the eyes and other preantennal appendages supposed to have existed in primitive forms. The protocerebrum is joined to a second brain part, the deutocerebrum, an area associated with the antennules, or first antennae. In all insects and most Crustacea, a third brain region, the tritocerebrum, is added to the other parts. The tritocerebrum has traditionally been said to be the nerve center for the antennae (second antennae), although Ferris (1953) presents evidence opposing this view. Classically, the tritocerebrum has been considered the first ganglion of the ventral nerve cord due to the presence of a large postoral commissure between the lobes of the tritocerebrum. The tritocerebral lobes have thus moved around the mouth to join the dorsal brain in many arthropods.

In some crustaceans, however, including *Penaeus setiferus*, the tritocerebral lobes have not become part of the dorsal brain and instead remain ventrally located. Although clearly tritocerebral, the ganglia do not send nerves to the second antennae.

The ventral nerve cord is the fusion product of a "ladder" nervous system, wherein the paired ganglia of each segment have come together at the midline. Longitudinal segmental coalescence has frequently been followed by ganglionic coalescence in the ventral nerve cord with attendant obscuring of primitive metamerism.

In the following treatment, the nerves of the dorsal brain and tritocerebrum will be considered in the first section and those of the ventral nerve cord in the second.

A. Nerves of Supraesophageal Ganglion and Tritocerebrum

The supraesophageal ganglion, or dorsal brain (figs. 75, 76), lies within the head lobe in the dorsal part of the protocephalon. The head lobe is protected dorsally by the broadening base of the rostrum. The dorsal brain is made up of nerve cell bodies and tracts associated with the nerves running out of it.

TEGUMENTAL NERVES

FIGURES 75, 76

The tegumental nerves arise from slightly different points on the anterior face of the supraesophageal ganglion and run directly rostrad to the epidermis of the head lobe. Keim (1915) does not show similar structures in *Astacus*.

OPTIC TRACT

FIGURES 6 TO 10, 75, 76

The optic tract, a part of the brain, rises from the anterolateral region of the supraesophageal ganglion, runs distally in the eyestalk, increasing in diameter, and enters the calathus. Within the calathus, the optic tract enlarges to incorporate the various distal optic ganglia and makes contact with the nerves from the ommatidia (figs. 9, 10).

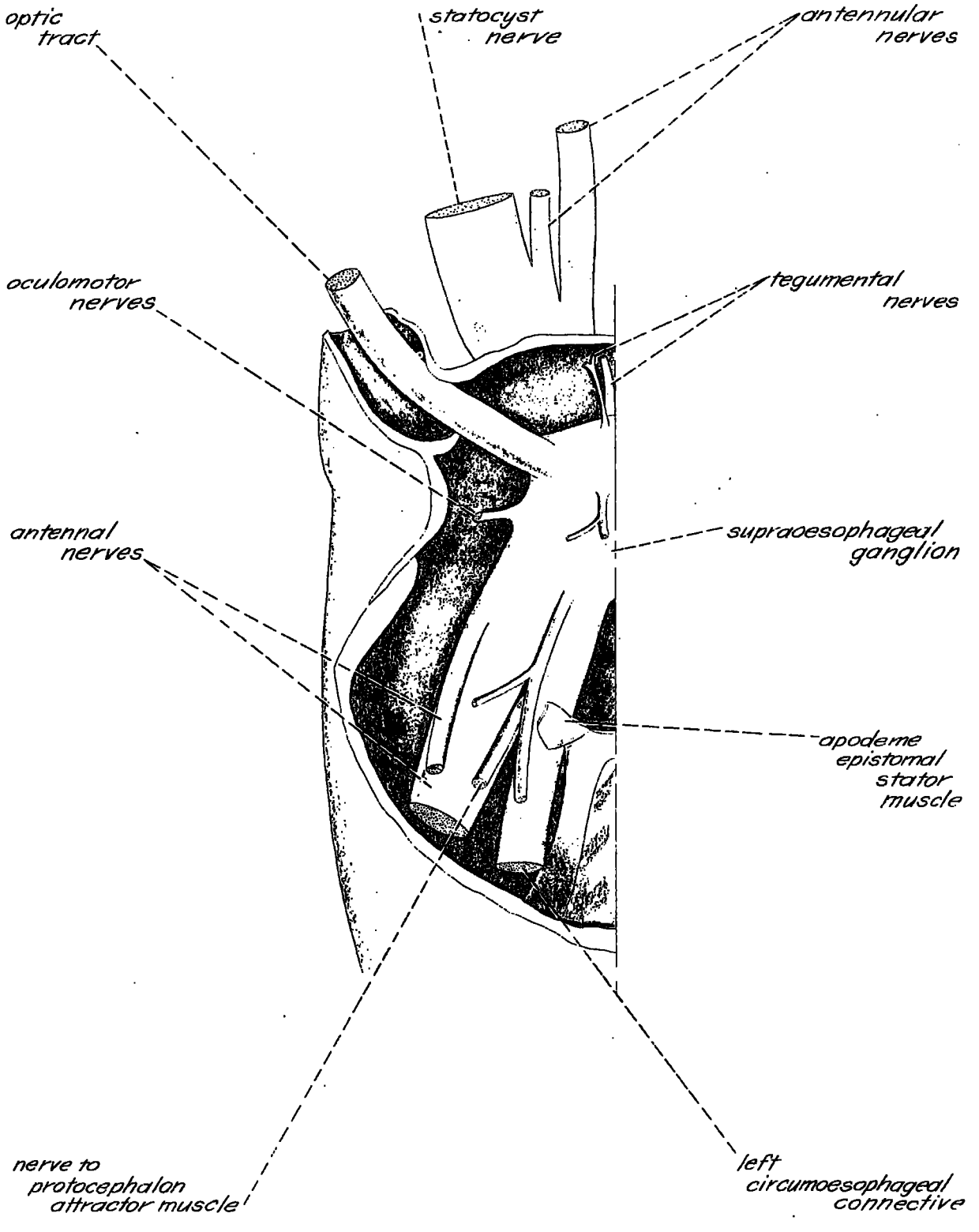

FIGURE 75.—Dorsal view of supraesophageal ganglion. Carapace and dorsal muscles removed.

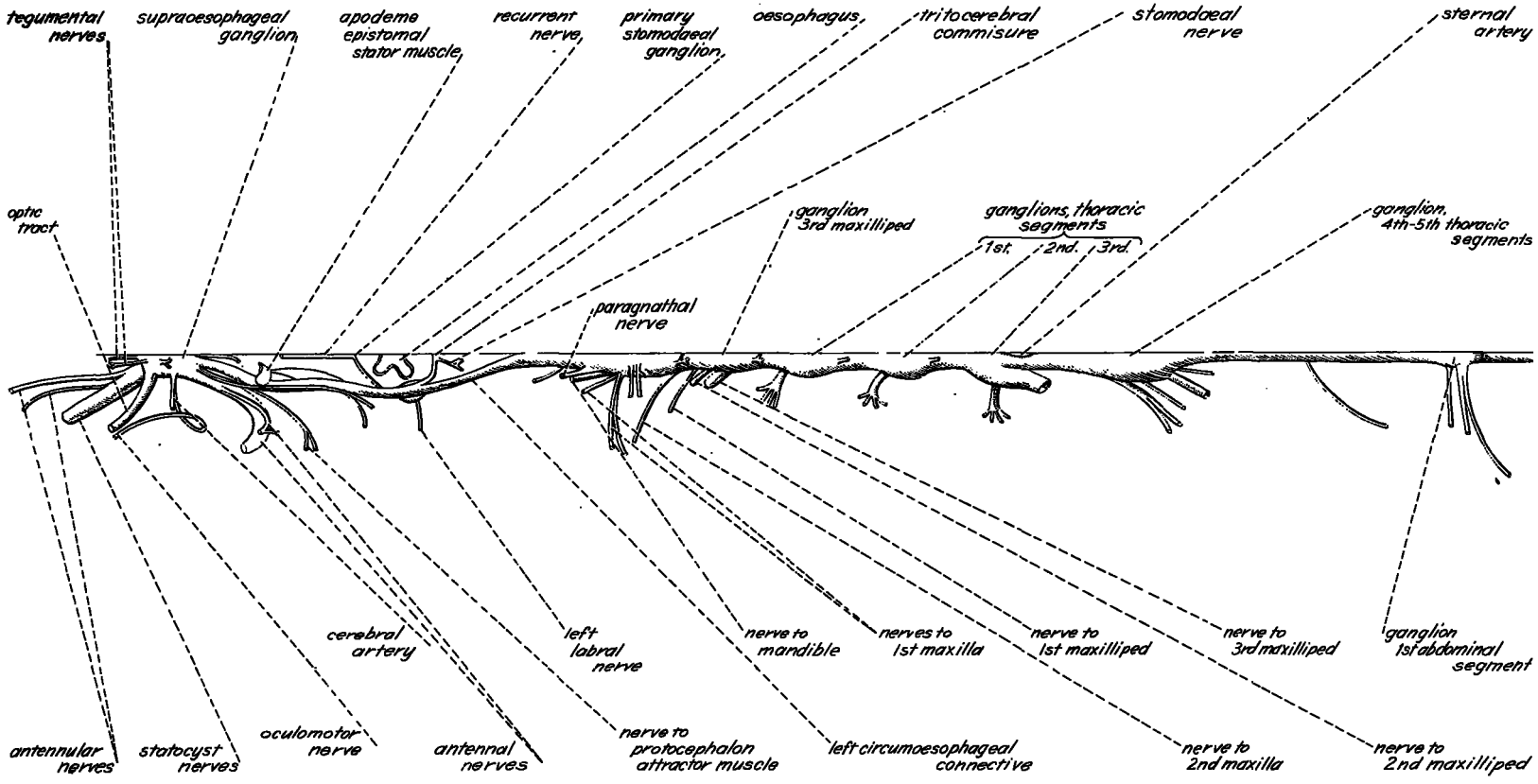

FIGURE 76.—Dorsal view of left half of brain and ventral nerve cord to ganglion of first abdominal segment.

These distal optic ganglia do not show superficially; however, longitudinal sections indicate very clearly the presence of a proximal, medial, and distal ganglion. If the distal optic ganglionic mass is pulled away from the dioptric elements of the eye, the tearing is confined to natural lines of weakness representing a deep concavity. Lining the concavity so produced is the capillary arbor (fig. 9), a structure which will be treated more fully in the section on the circulatory system.

NEUROHORMONAL ELEMENTS

FIGURE 10

Along the lateral side of the optic tract, and embedded in the perineurium in the proximal region of the optic tract, is a small nerve which branches out of the perineurium distal to the basal segment of the eyestalk. This nerve puts out several tiny branches to muscles and then enters a glandlike structure previously identified by Young (1956) as the X-Organ (fig. 10) of Hanström (1948), and which should be referred to as the pars ganglionaris X organi (Carlisle and Passano, 1953) rather than the X-Organ of Hanström.

From the pars ganglionaris X organi, a nerve continues along the optic tract distally to enter another, and larger, glandlike organ termed the "sinus gland" (fig. 10). The sinus gland lies against and sends branches into the optic ganglionic mass at the distal end of the optic tract. A second part of the X-Organ, that described by Hanström, is associated with the anterior eyestalk pore, or sensory pore (fig. 10). Knowles and Carlisle (1956) have proposed the term sensory pore X-Organ for the structure, to distinguish it from the ganglionic part. The identification of the parts of the X-Organ and of the sinus gland was made on doubtful grounds, since no supporting histological or experimental evidence was presented (Young 1956).

Confusion surrounding the identification of the X-Organ may be found in the literature of neurosecretory experiments (Knowles and Carlisle, 1956). Evidently the European and American workers have used the term "X-Organ" for different structures. The reason may lie in a weakness in communications, for the illustrations in some works of this literature are, to say the least, circumscribed (Passano 1953), however important the textual material may be to the experimental biologist. Welsh (1941), on the other hand, has taken pains to illustrate clearly his experiments on retinal pigment migrations in *Cambarus bartoni* (Fabricius 1798); unfortunately his identification of the X-Organ appears to be in error.

Keim (1915) in his account of the nerves in *Astacus* does not illustrate the sinus gland or the parts of the X-Organ.

OCULOMOTOR NERVE

FIGURES 8, 9, 10

The oculomotor nerve originates on the lateral side of the dorsal brain, slightly posterior to the optic tract, and, beginning ventrally, describes an almost complete loop around the protocephalon attractor muscles. It proceeds to the dorsolateral region of the protocephalon attractor, between the muscle and the outer epidermis. From the latter position the nerve turns sharply anterior and runs into the eyestalk, giving off branches to various of the eyestalk muscles. The nerve in *Penaeus* is the same as the eye muscle nerve described by Keim (1915) in *Astacus*.

Regrettably, very little can be said of homologies between the nerves serving the eyestalk of the various Crustacea, since so little information exists on the subject. Certainly, optic tracts, oculomotor nerves, and eyestalk neurohormonal elements in *Penaeus*, *Astacus*, and *Cambarus* are likely to be homologous structures. Further anatomical information on the nerves will have to be provided before the comparative morphology of this region of the brain and eyestalk will be in any way a satisfactory story.

ANTENNULAR NERVES

FIGURES 14, 15, 75, 76

The nerves of the antennule pass rostrad from the anteroventral region of the supraesophageal ganglion within a single perineurium. Inside the antennule the single tract divides into three nerves. The largest is the short, flat statocyst nerve which runs anterolaterally and spreads widely on the ventral surface of the first antennular segment beneath the statocyst. This nerve is presumably the sensory nerve of the statocyst. The smaller antennular nerves parallel the statocyst nerve in the proximal region of the anten-

nule, then turn anteriorly and run the length of the antennule including the flagella. This nerve is probably mixed, since it sends off branches to the muscles as well as to the sensory flagella.

Except for the work of Keim (1915) on the nerves of *Astacus*, little information exists on the innervation of the crustacean antennule. The situation in *Penaeus* appears to be roughly comparable to the arrangement of the antennular nerves in *Astacus*. The most striking difference is the size of the nerve innervating the statocyst. That of *Penaeus* is very much larger than the statocyst nerve of *Astacus*.

ANTENNAL NERVES

FIGURES 24, 75, 76

The antennal nerves pass out of the supraesophageal ganglion posteroventrally, from a point laterad of the circumesophageal connective. The antennal nerves proceed ventrocaudally for a short distance and then turn anteriorly to run into the antenna through its large foramen, or into the mass of the antennal muscles. Within the body of the antenna, the nerves give off branches to various muscles and sensory endings in the antenna and scale. One branch enters the antennal flagellum (fig. 24, *B*) and is extensively subdivided. Small groups of neurons are thus split off to each of the many sensory elements in the flagellum (fig. 25).

The antennal nerves of *Penaeus* appear to be similar to those described by Keim in *Astacus*.

NERVE TO PROTOCEPHALON ATTRACTOR MUSCLE

FIGURES 75, 76

This structure comes out of the dorsal brain between the antennal nerves and the circumesophageal connective and passes into the substance of the protocephalon attractor muscle. I have previously offered objections to assigning the protocephalon attractors to the "antennal" segment, on grounds of multiple insertions of the muscle. However, the position of the protocephalon attractor nerve origin on the brain tends to suggest that at least part of the muscle has affinities with the antenna.

LABRAL NERVE

FIGURES 27, 76

Each lateral half of the superficially unpaired labrum is supplied with a labral nerve descending from the tritocerebral ganglia (illustrated as the labral ganglion in fig. 27). Upon entering the labral sac, the nerve divides into parts which go to many labral muscles, to glands, and to sensory endings in the epidermis. From the work of Schmidt and Keim on the muscles and nerves of *Astacus* one receives the impression that this European crawfish does not posses a labrum, since no muscles or nerves are listed, nor in fact is the labrum mentioned. Henry (1948a) finds that the labral nerve of *Palaemon paucidens* de Haan and other Crustacea arises from the region of the primary stomodaeal ganglion, a stomatogastric ganglion connected to the tritocerebrum.

TRITOCEREBRAL GANGLIA AND NERVES

The tritocerebral ganglia or lobes represent the ganglia of the first ventral segment. As has been previously mentioned, the tritocerebral lobes are reflected into the dorsal brain in many arthropods, but not in *Penaeus*. In the latter the ganglia remain in the primitive, divided condition, connected by a transverse commissure, the tritocerebral (or stomodaeal) commissure (fig. 76), passing below the gut. The tritocerebral commissure sends a small nerve, the stomodaeal nerve, posteriorly from each side of the midline. The experimental workers evidently prefer the somewhat meaningless term, postcommissural nerve, for the structure (Knowles 1953). Keim makes no mention of the postcommissural, stomodaeal nerves in *Astacus*.

Associated with the tritocerebrum are the nerves of the stomodaeal system. So far as this system has been worked out in *Penaeus*, it appears to be simple. A primary stomodaeal ganglion lying on the anterior surface (primitive dorsal surface) of the esophagus is joined to each tritocerebral lobe by a nerve passing round the gut. From the primary stomodaeal ganglion another nerve, the recurrent nerve, passes dorsally along the dorsal surface of the esophagus to the gastric mill where it becomes subdivided. Keim finds a similar situation in *Astacus*. Henry (1948a) describes a secondary stomodaeal ganglion connected independently to the tritocerebrum, and from her work on lower Crustacea we may conclude that the presence of two stomodaeal ganglia is the more typical situation.

Posterior to the tritocerebral ganglia the circumesophageal connectives passing around the gut anastomose to form the ventral nerve cord.

Ventral Nerve Cord

FIGURES 36, 61, 63, 76

The ventral nerve cord of *Penaeus* is a longitudinal series of ganglia interconnected by fused pairs of intersegmental nerve tracts. A certain amount of longitudinal coalescence has taken place in the ventral cord, notably in the anterior, thoracic regions and less so in the abdomen. The ganglia of the gnathal appendages are conspicuously fused.

PARAGNATHAL NERVE

FIGURE 76

The element termed the nerve to paragnath arises from the ventral cord anterodorsad of the mandibular nerve. In *Penaeus* the paragnathal nerve is in no way posterior to the mandibular nerve as shown by Henry (1948a) for various crustaceans. However, whether the nerve is histologically anterior to the nerve to the mandible, as Chaudonneret (1956) holds, is not known. If Chaudonneret is correct in his claim that the paragnatha are anterior to the mandibles, then we are faced with the necessity of explaining the segmental interrelationships suggested by this view. Chaudonneret escapes from the dilemma by homologizing the paragnatha with the insectan superlinguae, a theory that has been advanced in the past (Snodgrass 1935). At the same time, Chaudonneret stoutly defends the morphological independence of the paragnathal nerve from that of the mandible. He thus arrives at a paradox, since the superlinguae arise from the hypopharynx and appear to belong to the mandibular segment (Snodgrass 1935). If, on the other hand, the superlinguae are not mandibular, and their homology with the paragnatha holds good, we must assign the paragnatha to some other segment, perhaps pre-mandibular and almost certainly postoral.

MANDIBULAR NERVE

FIGURES 36, 76

The large nerve to mandible is given off the ventrolateral surface of the anterior ventral nerve ganglion and runs into the heavy muscles of the mandibular segment. A branch of the nerve enters the mandibular palp.

MAXILLARY NERVES

FIGURES 36, 76

The nerves to the first and second maxillae depart from the ventral nerve cord and pass into the maxillae. The nerves to the first maxilla are much smaller than the one to the more active second maxilla. These nerves are very likely mixed since they separate into branches which run to muscles and to sensory end cells in the appendage extremities.

MAXILLIPEDAL NERVES

FIGURES 36, 43 TO 48, 76

The nerves to the first and second maxillipeds leave the anterior ventral nerve ganglion ventrolaterally from its caudal portion and run into the maxillipeds. The nerve to the third maxilliped arises from its own ganglion.

NERVES TO PEREIOPODS

FIGURES 36, 49, 51 TO 53, 56 TO 58

Beginning with the ganglion of the third maxillipeds, the thoracic ganglia are indicated for the most part by independent swellings in each segment. From the ventral surface of each ganglion a large nerve departs into each appendage. Between the ganglion of the third thoracic segment and the anterior portion of the coalesced fourth and fifth ganglia, the two longitudinal nerve tracts have been retained in the primitive divided condition to permit the sternal artery to pass through them. The thick ventral nerve cord of the thorax narrows posterior to the fused ganglia of the fourth and fifth thoracic segments and runs into the abdomen.

ABDOMINAL NERVES

FIGURES 61, 63, 71, 72, 76

The abdominal ganglia of the ventral nerve cord are all substantially similar, except for the terminal ganglion of the sixth abdominal segment. Two nerves arise from each of the first five abdominal ganglia. The anterior one enters the pleopod on that side and the posterior nerve sweeps laterally and dorsally to branch among the abdominal muscles of the segment.

The sixth abdominal ganglion lies in the posteroventral portion of the sixth segment (fig. 72, *B*). Four pairs of major nerves arise from it.

The first nerve is dorsolateral and runs beneath the apodeme of anterior oblique muscle 6 on its way to the muscles of the sixth abdominal segment. The second nerve serves the uropod exopodite, the third the endopodite, and the fourth, which arises posterodorsally, runs near the anal canal and enters the telson. These nerves are apparently mixed. The exopodite nerve (fig. 72, *B*) is easily observed. After giving off branches to the exopodite muscles, this nerve undergoes extensive subdivision to form a kind of sensory "cauda equina" in the distal regions of the exopodite.

III. CIRCULATORY SYSTEM

The typical blood circulatory system of Crustacea Decapoda is a closed arterial-open venous system. It consists of a heart and arteries by which blood is transported to arterial capillary beds throughout the body. Venous blood returns to the heart through conjoint blood sinuses in the appendages and body into which the capillaries empty. In general, the gills are served by the venous system. Although the circulatory systems of all decapods have marked similarities, the arteries display greater differences in detail than the nervous system or the muscle system. Furthermore, the circulatory elements are variable within the individual animal. The blood vascular system will be treated in two parts, the heart and pericardium and the blood vessels.

A. Heart and Pericardium

FIGURES 79, 80

The pericardium is a thin, contractile membrane surrounding the heart. The membrane is penetrated by passageways by which venous blood may enter the pericardial chamber. Slender muscle bundles inserted on the surface of the pericardium aid in its rhythmic contractions.

The heart of *Penaeus setiferus* is a many-sided structure lying within the muscular pericardium in the posterodorsal region of the carapace. Three pairs of valvular afferent ostia may be seen on the surface of the heart, two pairs dorsally and one pair placed laterally. By means of the valves in these pores, pericardial blood enters the heart during diastole and is prevented from escaping in the systolic beat. Structurally, the heart is more than a tubular expansion, and is, instead, comprised of a system of connected sinusoids. Microscopical sections indicate that the outer and intersinusoidal walls are made up of muscle fibers interspersed with connective tissue of a type strikingly reminiscent of the wavy elastic fibers in the tunica media of a vertebrate artery.

Although the details of cardiac innervation have not been worked out in the present study of *Penaeus*, the work of Alexandrowicz (1932) shows that considerable uniformity in the heart nerves of decapod crustaceans exists. Alexandrowicz has found that the decapod heart is well supplied with nerves. Restricted to the internal heart structures is a local system of heart neurons interspersed among the muscles of the sinusoidal septa. Alexandrowicz considers the local system inherently automatic.

The heart neurons are connected to the central nervous system by a pair of dorsal cardiac nerves which arise from the subesophageal ganglion. The dorsal nerves Alexandrowicz believes to be regulatory and he subdivides them functionally into two groups of inhibitory and one of accelerator fibers. Distinct from the heart neurons and dorsal nerves is a third system serving the muscles of the pericardium and heart valves. The pericardial nerves are ventral and the ostial valve nerves are situated dorsally, and the two are interconnected with one another. Inexplicably, the pericardium-ostial valve system is not tied to either the heart neurons or the dorsal cardiac nerves. Consequently, Alexandrowicz states, the pericardium has its own rhythm.

B. Blood Vessels of the Body

LATERAL ANTERIOR ARTERY

FIGURES 79, 80

The narrow, apical end of the heart points rostrally. From this point in the midline a very small vessel extends a short distance anteriorly (fig. 80). This little artery may be the vestige of the ophthalmic artery (Huxley 1906), or the median aorta (Baumann 1919) found in *Astacus* and other crustaceans. In the opinion of Professor Mayrat (letter, May 3, 1957), ophthalmic (or median aortic) vascular function has apparently been taken over by a pair of lateral anterior arteries (figs. 79, 80) arising from the anterior end of the heart, laterad of the midline.

As the lateral anterior arteries run forward, they give off a number of branches, the first of which leaves just anterior to the heart. The

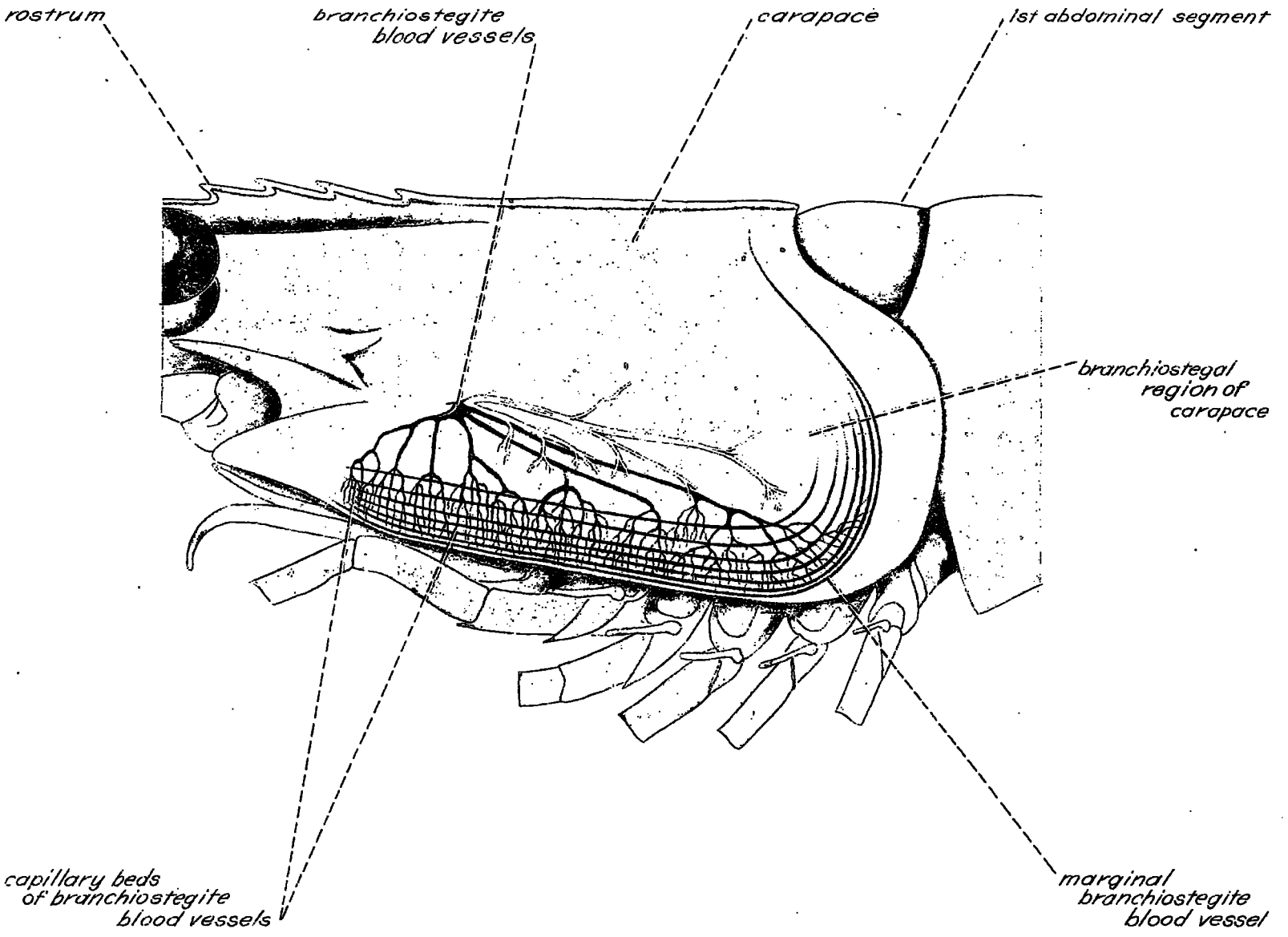

FIGURE 77.—Lateral view of gnathothorax showing blood vessels of branchiostegite epithelium.

468059 O—59——10

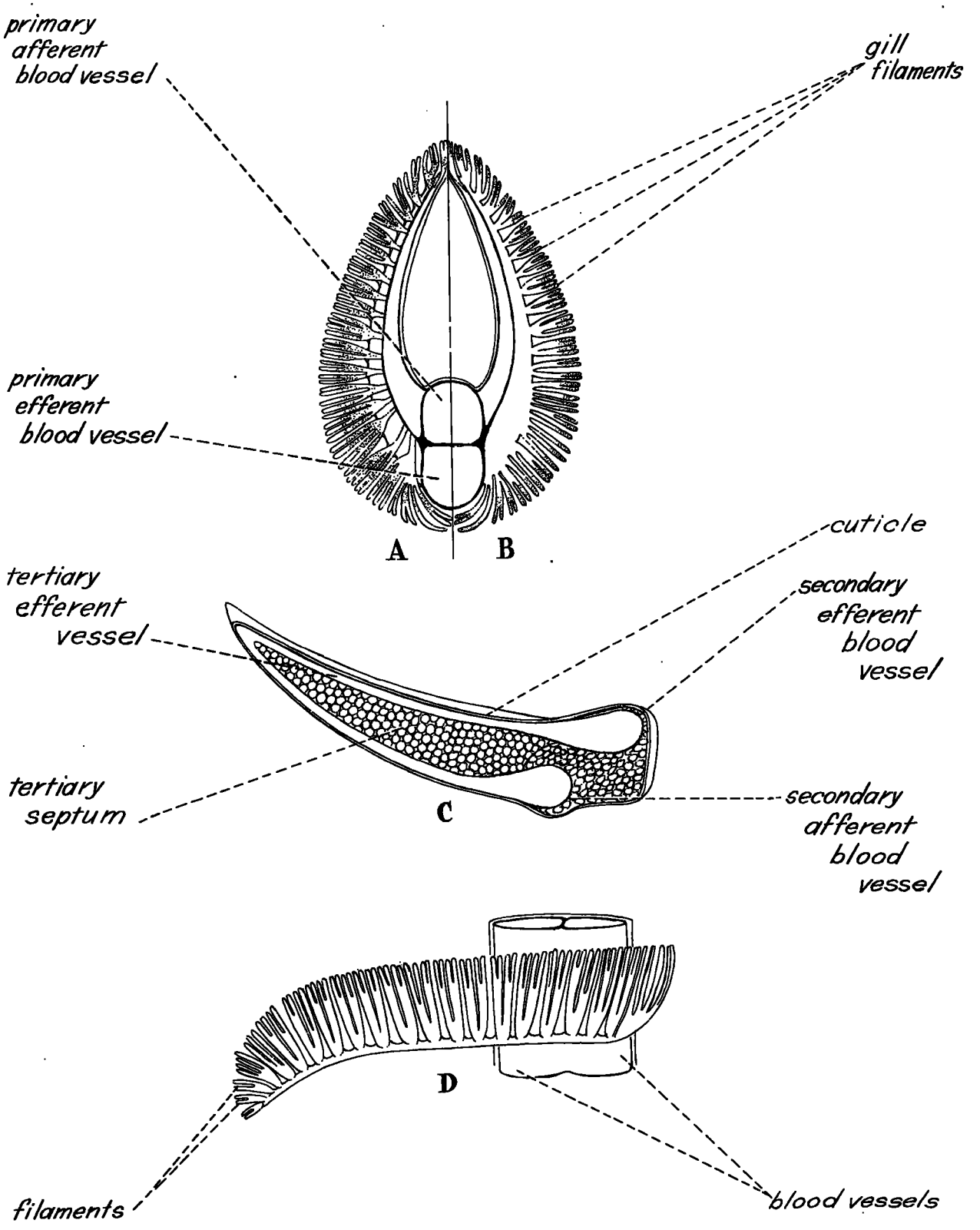

FIGURE 78.—Blood circulation of gills. *A*. Dorsal, and *B*. ventral views of single gill lamina. *C*. Lateral view of single gill filament showing circulation. *D*. Lateral view of single gill lamina.

branch is the subgastric artery (fig. 79) and it runs around the posterior end of the gastric mill to a curious glandlike organ lying beneath the gastric mill. The subgastric artery is similar to the internal ramus of the lateral anterior artery described by Baumann (1919) in *Astacus*. Rostrad of the subgastric branch, the lateral anterior artery puts out the dorsal gastric artery (figs. 79, 80) which serves the dorsal regions of the gastric mill. The gastric artery, too, divides into at least three major divisions (fig. 80), one running some distance rostrally, another caudad into a glandlike structure of unknown function (see fig. 79, dorsal gland, and a third passing around the gastric mill ventrally.

The lateral anterior artery now turns to the midline to join its counterpart from the opposite side. The optic artery continues anteriorly to the eyestalk from this turn, giving off a branch, the cerebral artery, to the supraesophageal ganglion. At the midline, the two lateral anterior arteries form a median longitudinal vessel. The anterior portion extends into the rostrum while the posterior part, the recurrent artery, runs caudad to the dorsal surface of the gastric mill. At the junction of the optic artery with the oculomotor, a small branch is given off which runs beneath the optic tract and thence to the midline to meet its opposite number from the other side (fig. 80) slightly rostrad of the dorsal brain. No evidence of the frontal heart so prominent in this region in other decapods (Baumann 1917) has been found in *Penaeus*.

The next major branch of the lateral anterior artery anterior to the gastric branch is the mandibular artery. Upon leaving the lateral anterior artery this branch passes between the lateral mandibular condyle and the origin of the lateral anterior thoracic muscle 1 (fig. 80) into the substance of the mandibular muscles where the vessel undergoes further subdivision.

Rostrad of the mandibular artery, the lateral anterior artery gives off the large antennal artery whose subdivisions include a branch to the antennule. The major portion of the antennal artery leads to the muscles and other organs of the antenna.

HEPATIC ARTERY

Running from the heart is another pair of arteries, the hepatic arteries (fig. 79). These project from the anteroventral surface of the heart and run into the hepatopancreas. They are difficult to follow within the gland in preserved material because of postmortem effects.

DORSAL ABDOMINAL ARTERY

The largest artery passing from the broad, posterior end of the heart is the unpaired dorsal abdominal artery (figs. 61, 62, 79, 80). This vessel runs the length of the abdomen between the dorsal abdominal muscles and the gut. As it proceeds caudad, the dorsal abdominal artery gives off pairs of segmental arteries at each segmental junction (fig. 62). In addition, numerous small vessels from the dorsal abdominal artery irrigate the gut throughout its length. Posteriorly, the dorsal abdominal artery bifurcates around the hindgut gland (fig. 82) and runs alongside the rectum as a paired vessel. In the neighborhood of the rectum the paired vessels turn ventrad, after giving several branches to various structures of the region, including the telson, and anastomose beneath the posterior part of the rectum. Having fused, the vessel passes caudad of the ganglion of the sixth abdominal segment and then turns anteriorly as the posterior subneural artery (figs. 81, 82). So far as can be determined, the posterior subneural artery extends no further rostrad than the anteroventral part of the sixth abdominal segment.

On the dorsal surface, the segmental arteries give off branches adjacent to the dorsal abdominal artery (fig. 62). These branches enter the large ventral abdominal muscles. The remainder of the segmental arteries now pass ventrally along the lateral surface of the abdomen at the intersegmental lines. A substantial branch splits off internally and runs across the external arm of the anterior oblique muscle in each segment (fig. 60). The segmental artery (see lateral artery, fig. 81) continues ventrad between the abdominal muscles and the promoter-remotor muscle mass of the pleopod and sends a branch, the pleopod artery, into the pleopod (fig. 81). A second branch proceeds into the substance of the abdominal ganglion. This branch also divides again to form the postganglionic loop (fig. 81) which provides a vascular connection between the segmental arteries of both sides.

STERNAL ARTERY

In general, the ventral vascular supply is less distinctly laid out than are the dorsal circulatory

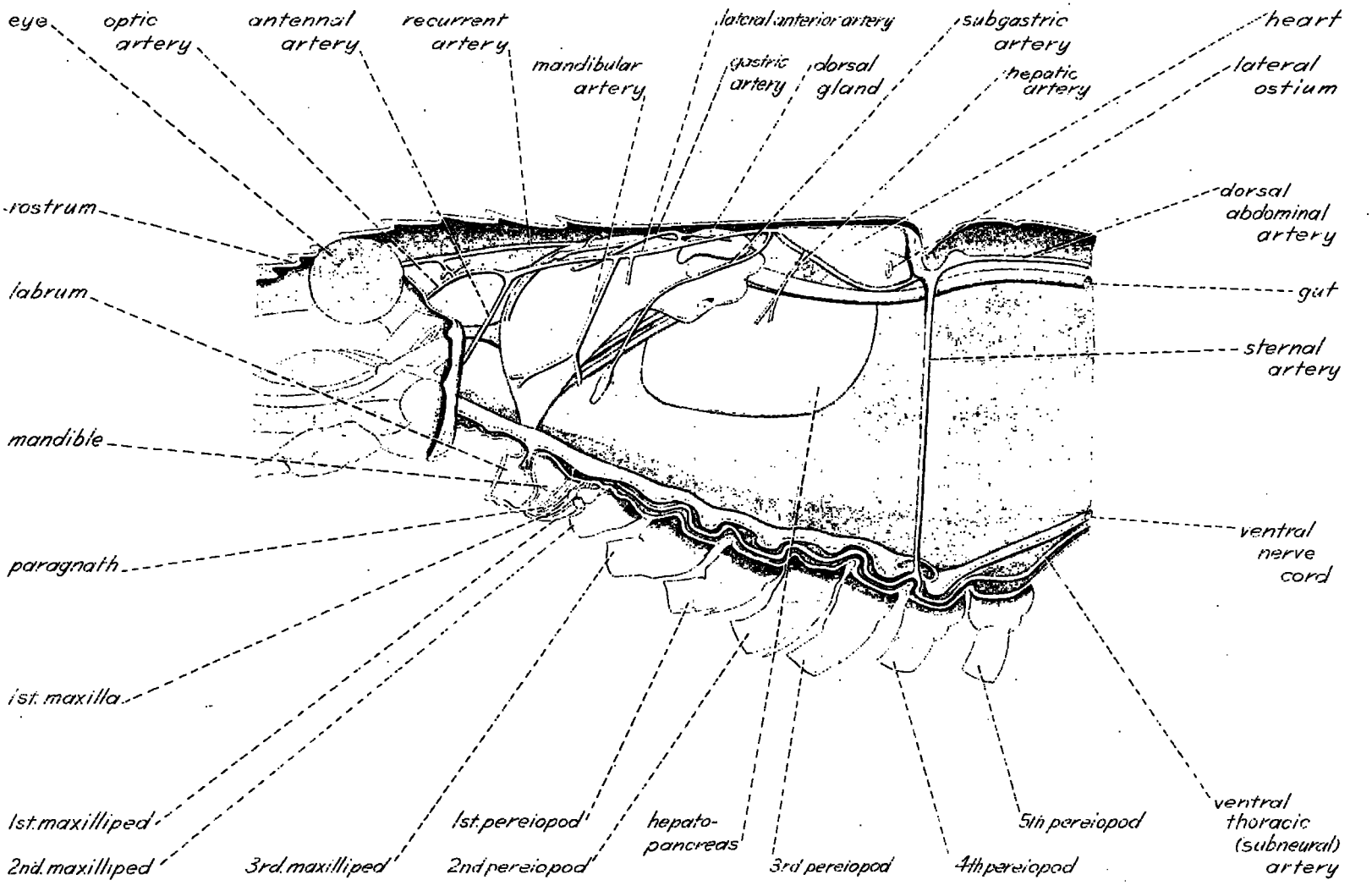

FIGURE 79.—Lateral view of gnathothorax showing circulatory elements.

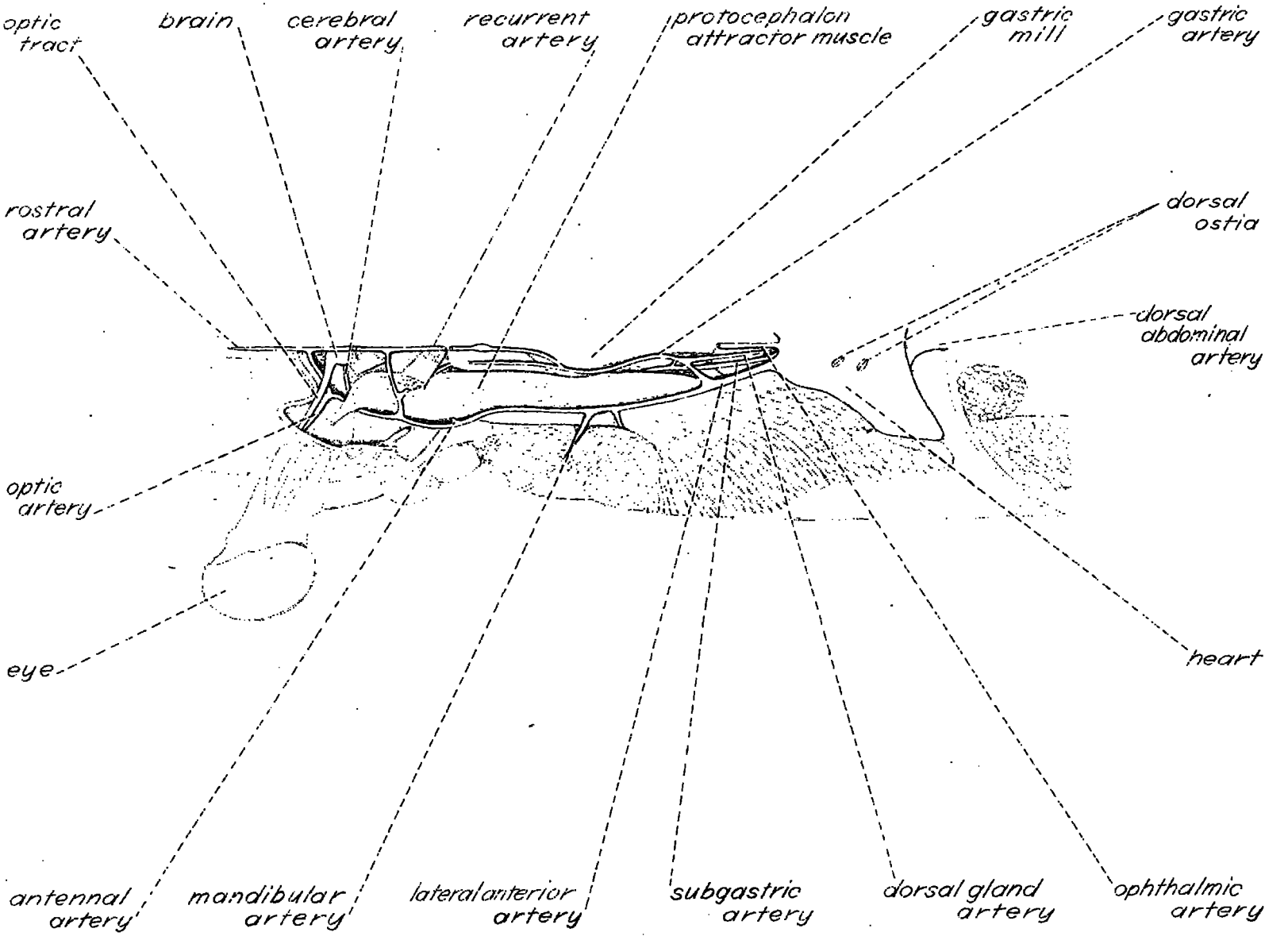

FIGURE 80.—Dorsal view of gnathothorax showing circulatory elements.

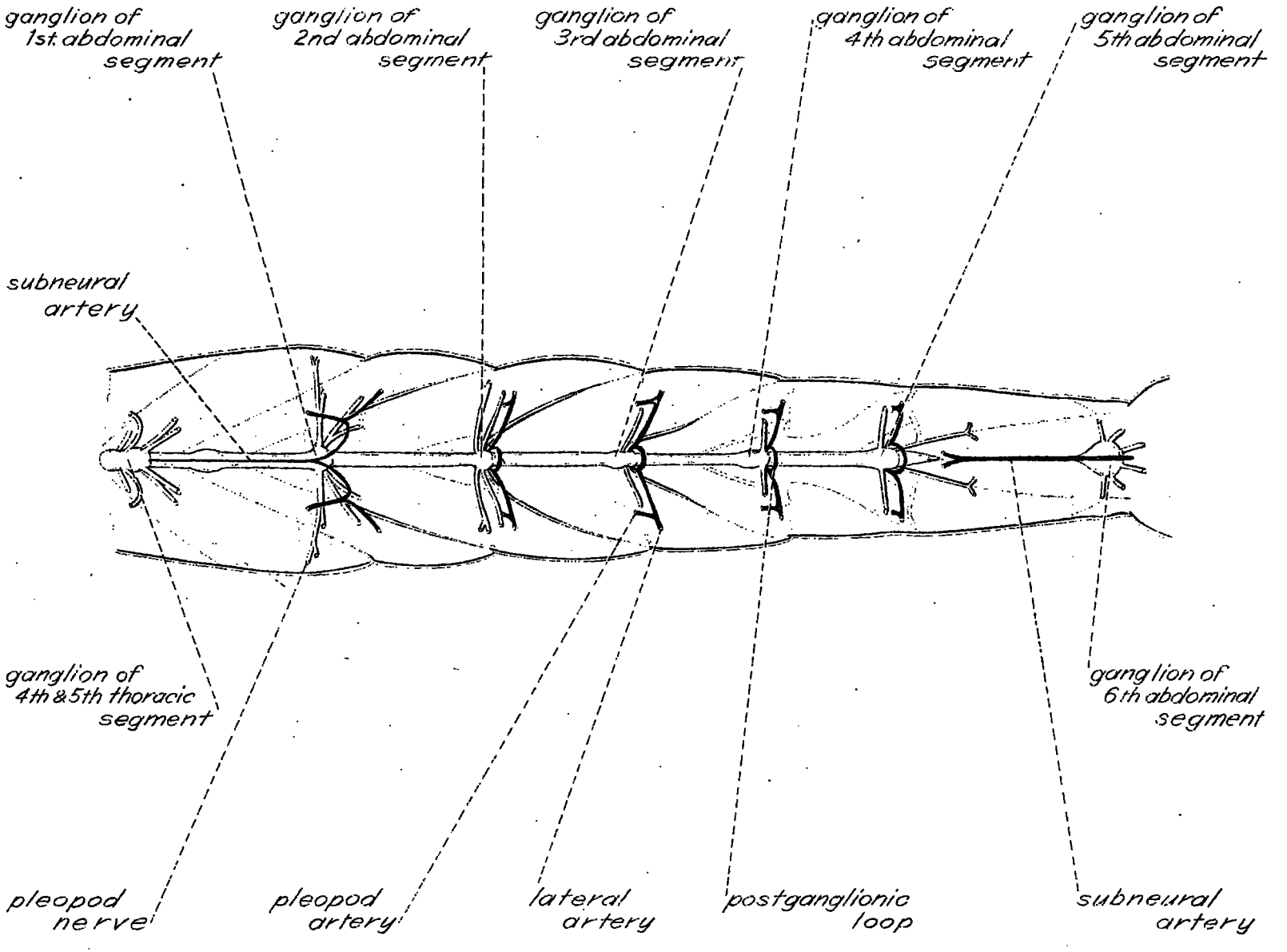

FIGURE 81.—Ventral view of abdomen showing neural and circulatory elements.

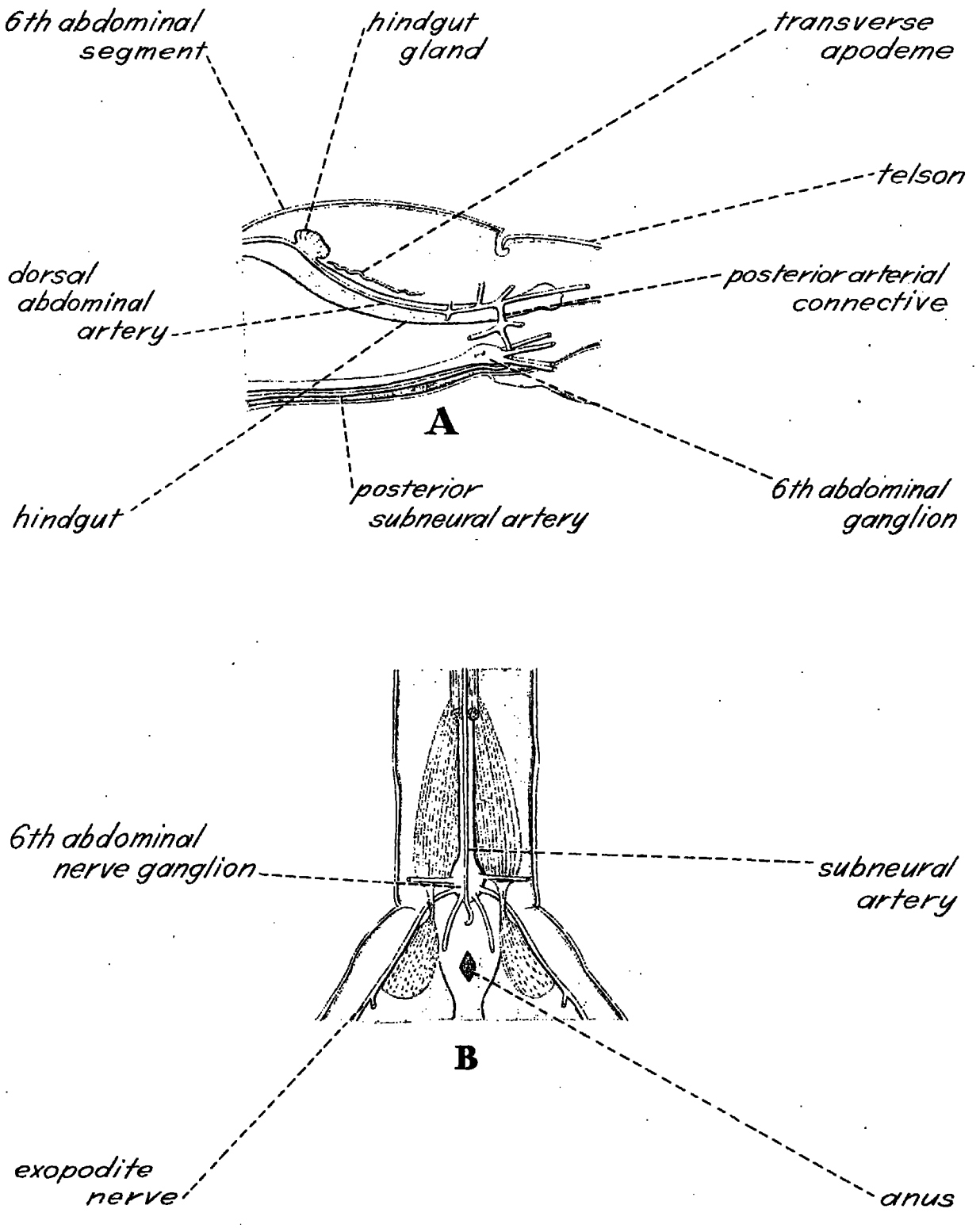

FIGURE 82.—Neural, circulatory, and digestive structures in posterior abdominal segments. *A*. Lateral view of sixth abdominal segment and part of telson. *B*. Ventral view of sixth abdominal segment, and parts of uropods and telson.

elements. The principal vessel supplying blood to the ventral regions is the sternal artery (fig. 79) which in some Malacostraca arises from the posteroventral surface of the heart, but in *Penaeus* is a branch of the very rostral portion of the dorsal abdominal artery. The sternal artery descends directly ventrad past the gut and through the ventral nerve cord between the ganglia of the third and fourth ambulatory legs (figs. 76, 79). Here, the artery divides into an anterior portion running forward beneath the nerve cord in the gnathothorax and a posterior piece which eventually enters the abdomen (figs. 36, 79, 81).

VENTRAL THORACIC ARTERY

The ventral thoracic (subneural) artery (figs. 36, 79) supplies blood to the gnathothoracic appendages (fig. 36) as it passes anteriorly. Slightly rostrad of the nerve to the second maxilla, the ventral thoracic artery bifurcates. The two branches turn sharply laterad, sending branches into the nerve cord in the region of the mandibular nerve and also into the anterior structures of the ventral thorax. No connection between the anterior branches of the ventral thoracic artery and the lateral anterior artery has been found in *Penaeus*.

The portion of the ventral thoracic artery posterior to the sternal junction gives off large branches to the fourth and fifth walking legs and the anterior ends of the anterior oblique muscles (fig. 36). A small branch continues subneurally to join other vessels beneath the first abdominal ganglion.

B. Appendicular Blood Vessels

EYESTALK VASCULAR SUPPLY

FIGURES 7 TO 10

Blood is pumped to the eyestalk through the optic branch of the lateral anterior artery. Once in the eyestalk the vessel, now known as the oculomotor artery, runs medially along the optic tract and divides into several branches at the distal end of the eyestalk. The most proximal branch bifurcates on the dorsal surface of the optic tract (figs. 7, 8), sending a short vessel to and apparently through a small gland on the optic tract here designated as the X-Organ of Hanström (1948) and about which something has been said in the section on the nervous system. A small part of the arterial branch to the gland continues proximally along the dorsal surface of the optic tract and has not been traced beyond the connective tissue of the basal segment of the eyestalk. The larger part of the proximal oculomotor branch runs distally into the distal optic ganglionic mass (figs. 7, 8).

Distally, the oculomotor artery divides into two large branches, one of which (figs. 8, 9) carries blood into a highly branched, dendritic structure embedded deeply among the optic ganglion cells (fig. 9). The organ has been named the capillary arbor (Young 1956), since it appears to distribute blood to ganglionic cells. Nothing similar has been found in the literature of the arthropod eye. However, Professor Mayrat reminds me that he has described (Mayrat 1956) a similar structure in *Praunus flexuosus* (O. F. Müller).

The other, and most-distal oculomotor branch, repeatedly divides to form a vascular plexus on the medial surface of the eyestalk, just beneath a pore to the exterior (figs. 9, 10). The pore is designated as the anterior eyestalk pore. This structure was first described by Hanström (1948) as the eye papilla or sensory papilla and is shown by him as having some kind of structural and spatial relationships with the X-Organ in several crustaceans. Mayrat (1956) also finds the X-Organ near the eyestalk pore in *Praunus*. The function of the anterior eyestalk pore is unknown.

ANTENNULAR BLOOD SUPPLY

FIGURE 14

The blood vascular supply to the antennule is comprised of a large branch of the antennal artery, which is in turn a branch of the lateral anterior artery. The antennal branch enters the antennule in the mesial region near the point of entry of the antennular nerves. The antennular artery courses anteriorly along the mesial side of the antennule giving off small branches to muscles and other structures and finally dividing to supply the two flagella. The arterial branches are seen to subdivide to form capillary beds about the antennule.

ANTENNAL BLOOD SUPPLY

FIGURES 21, 79, 80

The antenna receives its blood from the antennal branch of the lateral anterior artery. The vessel gives off branches in the region of the large

antennal muscles and enters the antenna proper with the antennal nerves. Here it divides to supply the antennal scale and endopodite segments.

VENTRAL APPENDAGE BLOOD SUPPLY

The ventrally located appendages of the head and gnathothorax all appear to receive blood from branches of the ventral thoracic artery. Those of the abdomen, as has already been mentioned, receive fluid from the segmental branches of the dorsal abdominal artery.

D. Venous System

Arterial circulation consists of a closed afferent system subdivided into capillary beds in muscles and other organs. Venous return to the heart appears to be carried out in an open system, through sinuses in the appendages which empty into larger sinuses in the hemocoel. In general, the appendicular sinusoids are found on either one margin or the other of the appendage, rather than in the middle. The sinuses of the body which drain the venous blood from the appendages are located in particular places in the body. The sinus into which the eyestalks empty occupies the anterodorsal regions of the protocephalon. This sinus runs into a larger one anterior to the gastric mill into which blood from the other protocephalon appendages drain. The largest thoracic sinus lies along the sternum. It receives blood from the dorsal sinuses and the gnathothoracic appendages and supplies blood to the respiratory organs. From the sternal sinus the venous blood passes dorsolaterally to the pericardium.

In the abdomen, the sinus system is relatively simple. The dorsal regions are drained by a sinus or set of sinuses between the dorsal and ventral abdominal arteries. These appear to run directly rostrad into the heart. On the ventral surface segmentally arranged, conjoint sinuses pass venous blood rostrally to the sternal sinus of the thorax and thence to the heart. The sternal sinuses of the abdomen extend some distance dorsolaterally in conjunction with the sinuses of the pleonic appendages.

E. Respiratory System

The subject of gill formulae and arrangement in *Penaeus* and other crustaceans has been discussed previously in the general section on the gnathothorax. The details of the respiratory system will be taken up at this point, since the organs concerned with gas exchange are intimately associated with the circulation of body fluids.

The gills of *Penaeus* are of the dendrobranchiate type (Calman 1909). This type of gill is comprised of a primary axis or rachis from which pairs of secondary structures bearing gill filaments arise at right angles. The secondary structures and gill filaments thus appear to be laminar units. Proceeding distally, each succeeding layer of secondary structures and filaments nests within the preceding layer.

For the details of gill circulation we are indebted to Prof. Jerome E. Stein, Texas Agriculture and Mechanical College, Galveston, Tex. He finds that blood enters the primary rachis of the gill by means of a primary afferent blood vessel (fig. 78, *A*, *B*) which is separated from the primary efferent blood vessel by a longitudinal septum. Primary afferent blood is directed into the secondary afferent blood vessels (fig. 78, *C*) by a secondary septum. Blood now passes out into the secondary structures to the gill filaments, into which it runs due to the arrangement of a tertiary septum dividing the tertiary afferent and efferent blood vessels in each filament. Blood thus flows around the tip of the filament and returns to the sternal sinus through the efferent vessels of the gill. The gill filament cuticle and epidermis appear to be very thin to allow for gas exchange.

An important accessory organ of respiration is the branchiostegite. The inner cuticle adjacent to the gills is thin and the underlying epidermal layers are heavily vascularized. Specimens preserved in Zenker's fluid display with great clarity the branchiostegal vessels (fig. 77) and fine nerves. The vessels appear to be of two types. One set represents the subdivisions of a large vessel seen at the dorsal margin of the branchiostegite a short distance caudad of the hepatic spine. The capillaries of the vessel approach the periphery of the branchiostegite at right angles to its margin. A second set of vessels run parallel to the margin of the branchiostegite (fig. 77), and are reminiscent of growth rings, since the larger shrimps in general have more rows of these vessels than do the younger animals. Whether the marginal vessels reflect the age of the white shrimp in terms of the number of molts is not known.

IV. DIGESTIVE SYSTEM

The digestive system is made up of those structures concerned with the enzymatic and mechanical reduction of food particles, the absorption of their products, and the evacuation of particulate wastes. The digestive systems of Crustacea Decapoda are all relatively uniform, being comprised of a stomodaeum, or foregut, which includes the esophagus and gastric mill, and probably the hepatopancreas; the midgut, or mesenteron, which in *Penaeus* appears to run from the gastric mill to the hindgut gland on the anterior end of the sixth abdominal segment; and the hindgut, or proctodaeum, which includes the rectal gland, rectum, and anal canal. The alimentary structures will be treated according to these three regions. The subdivisions of the gut are based upon the presence of a cuticular lining of the fore- and hindgut. That section not lined with cuticle is supposed to be the midgut. This criterion is here adopted for whatever it is worth.

A. Foregut

ESOPHAGUS

FIGURES 83 TO 85

The esophagus is a vertical tube which receives food particles thrust into the mouth by the labrum and postoral mouthparts. The tube is lined with cuticle, yet is so constructed that extensive contraction and expansion is possible. A cross-sectional view of the esophagus (fig. 85, *A*) indicates how these movements come about. The cuticular lining is folded inwards between the corners. Esophageal constrictor muscles (fig. 83), short fibers running transversely, draw the corners together and thereby close the lumen of the tube. Expansion of the lumen is accomplished by anterior and posterior esophageal dilatator muscles (fig. 83) which are inserted into the inward folds. Their contractions pull the folds outwards. The esophagus is constricted at its junction with the gastric mill preventing backflow of the food particles from the latter.

GASTRIC MILL

FIGURES 83 TO 85

The gastric mill is a bulbous, folded structure occupying the dorsomedial region of the thorax. As decapod gastric mill structure goes, that of *Penaeus* is relatively simple. Its surface is invested with thin sheets of constrictor muscles. Numerous dilatator muscles attach about the outside of the structure. The gastric mill, like the esophagus, is lined with cuticle, but here the latter substance is reflected into deep folds and toothlike structures (fig. 84) for the grinding of food. Transverse sections through the mill (fig. 85) indicate that the theoretical tubular form of the gastric mill is much modified. In general, the walls have been thrown into three pairs of folds. The uppermost fold (fig. 85, *B*), which disappears caudally (figs. 85, C_1, et seq.), serves no other purpose than the expansion and contraction of the gastric mill in response to feeding and digestion.

The middle fold, in contrast, constitutes a movable ridge or shoulder upon which a row of increasingly large teeth, the lateral denticles (fig. 84; 85, *B*, C_1, C_2) are borne. These apparently play an important role in the reduction in size of the gastric mill contents. The lower, or ventral, fold (fig. 85) is separated from the dorsal folds by an extensive lateral fold. The inner margin of the ventral fold is setose. The setae tend to set apart a ventral channel, or channels, running the length of the gastric mill. This ventral channel broadens posteriorly (fig. 85, *D*) and in the posterior end of the gastric mill the lateral ends of the channel bend ventrad (fig. 85, *E*). Here, the channel enters a filter (fig. 84) which is made up of the closely appressed, setose walls of the ventral channel. The setae are arranged in regular rows. According to Calman (1909), the filter is very constant in the penaeids. At its posterior end, the filter has a pair of ducts through which the digestive fluids of the hepatopancreas enter the gastric mill (fig. 85, *E*). Presumably the filter prevents the entry of particulate matter into the main collecting ducts of the hepatopancreas.

The principal device for chewing in the gastric mill is the median tooth, situated in the midline at the dorsalmost point of the mill (figs. 84; 85, C_2, *D*). The median tooth is a heavily sclerotized structure, a proliferation of the gastric mill wall. The tooth rests on articular rods which enable its operating muscles to move it some distance into and out of the lumen of the mill and with considerable force.

Posterior to the regions of the median tooth and beyond the filter the terminal lappets of the gastric mill project into the lumen of the midgut

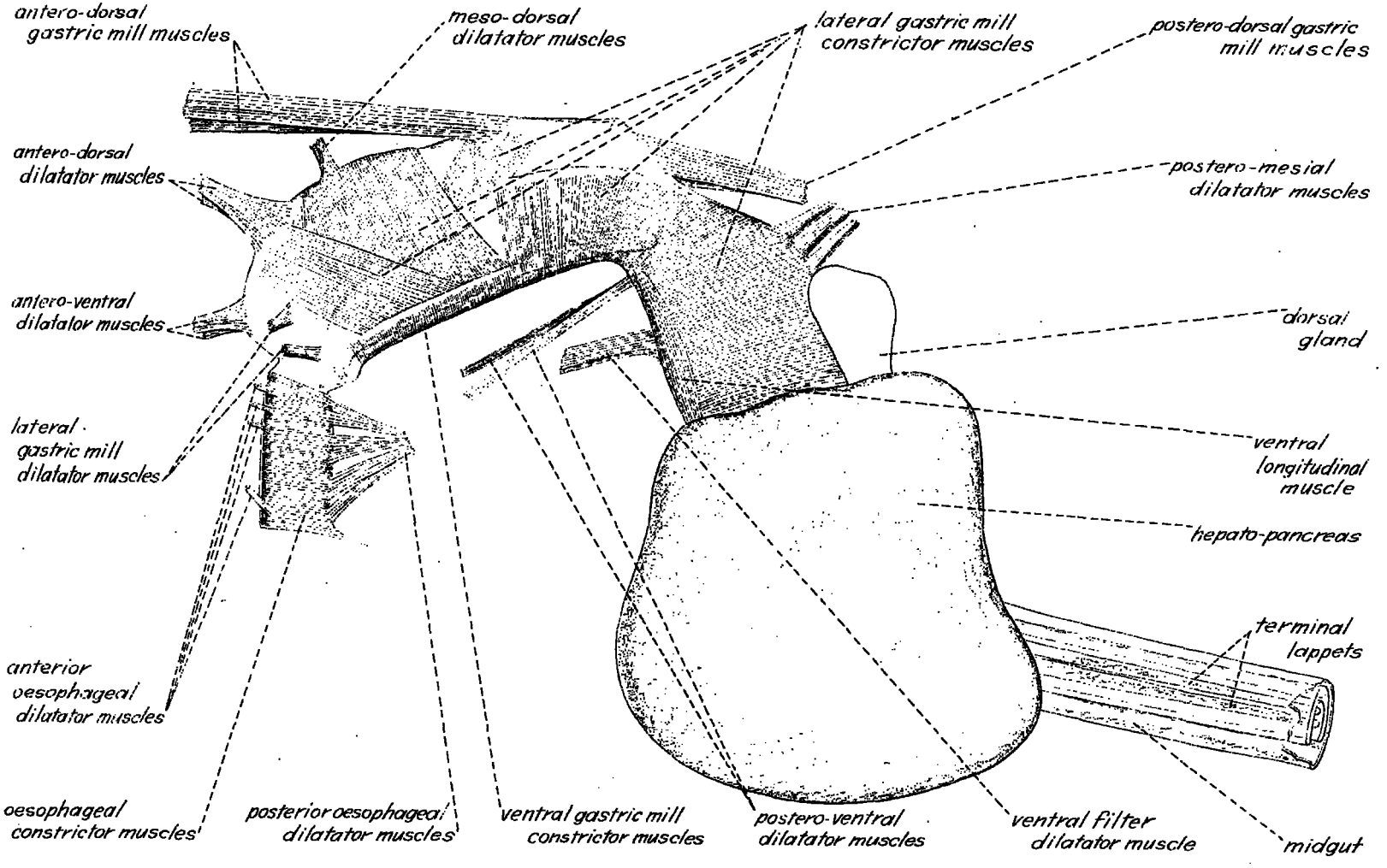

FIGURE 83.—Lateral view of left side of gastric mill and hepatopancreas.

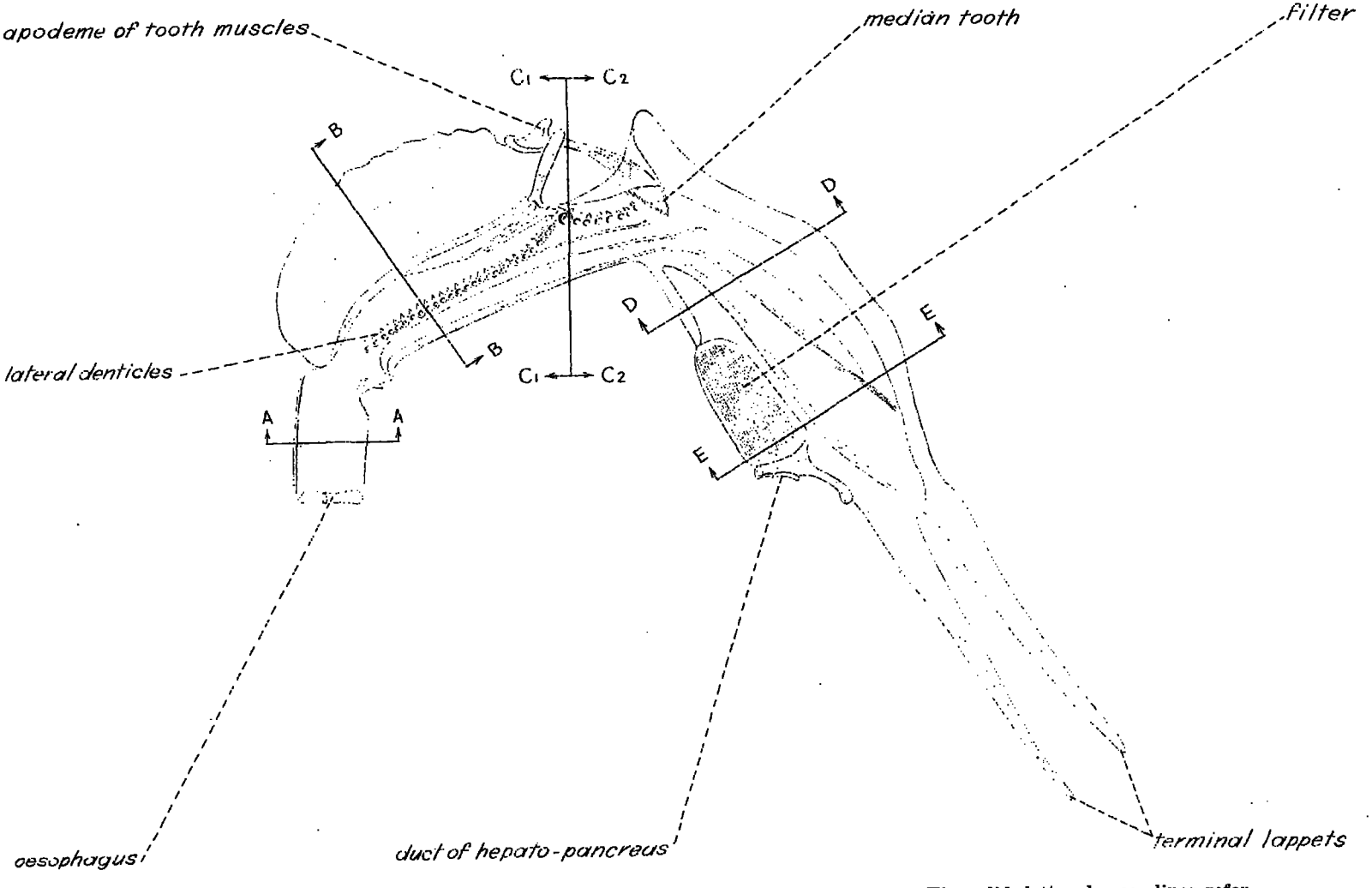

FIGURE 84.—Lateral view of cleared gastric mill showing sclerotized structures. The solid, lettered cross lines refer to the sections in figure 85. The arrows at the ends of the solid cross lines indicate the direction in which the viewer sees the sections in figure 85.

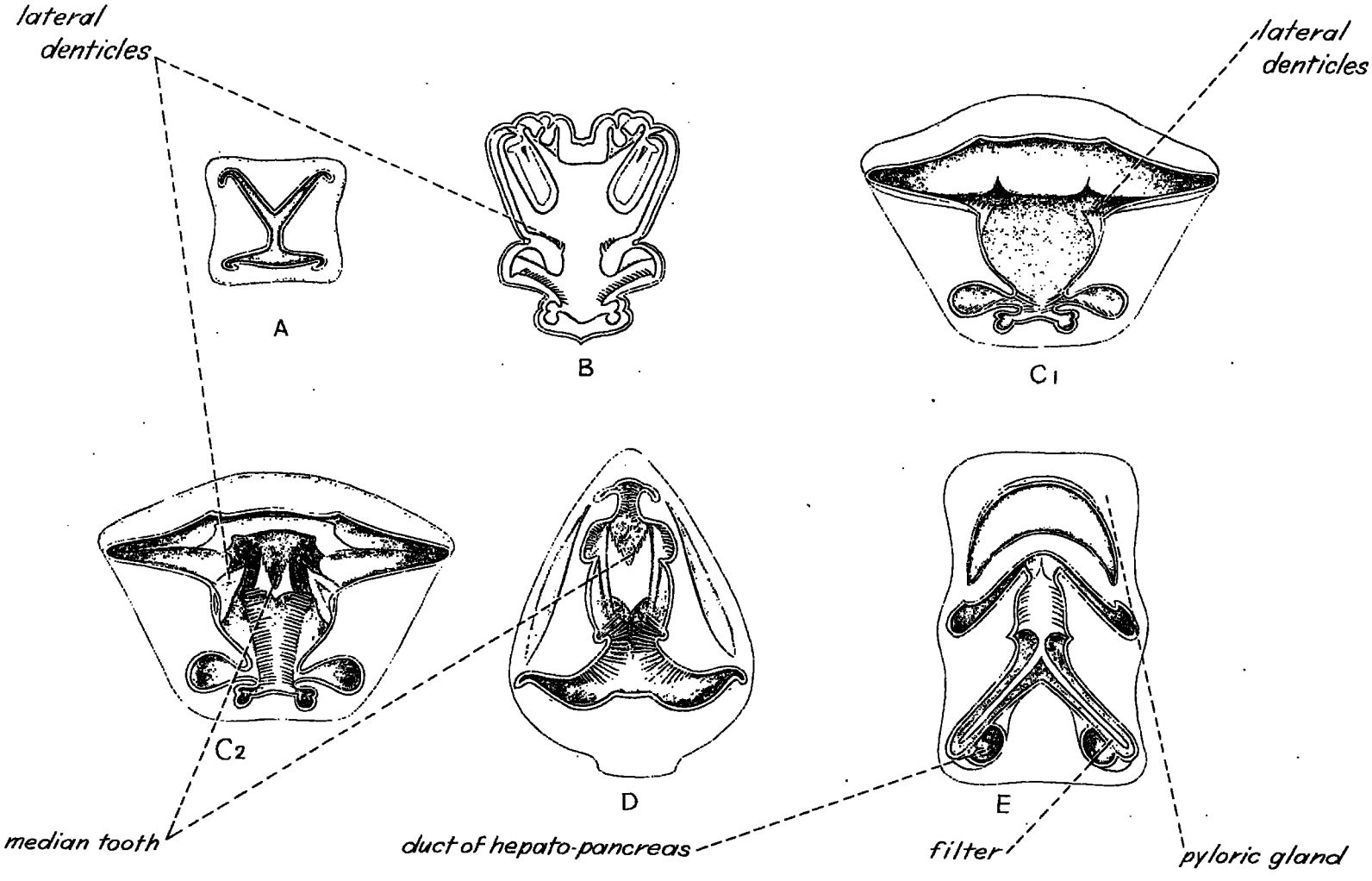

FIGURE 85.—Cross sections through the esophagus and gastric mill. The letters below the figures refer to the corresponding letters at the ends of the solid lines on figure 84.

(figs. 83, 84). In the posterior section of the gastric mill, dorsal to the filter, is a structure here designated as the dorsal (pyloric) gland (figs. 83; 85, *E*). The gland is mounted on the dorsal surface of the gastric mill. Its function is unknown.

The constrictor muscles of the gastric mill are arranged rather like those of the esophagus, in that the fibers are transverse to the long axis of the gut and are attached to lateral folds. The principal members of this group are the lateral gastric mill constrictor muscles (fig. 83). These attach between the long dorsolateral fold and the deep lateral fold dividing the inward ventral fold of the ventral channel. Contractions of the lateral constrictors reduce the diameter of the gut lumen and apply the lateral denticles to the gastric mill contents. Ventral gastric mill constrictor muscles (fig. 83) bring the setose margins of the ventral channel together. A third sheet of fibers, the ventral longitudinal muscle (fig. 83) runs between the lesser curvature of the gastric mill and the anterior end of the filter. Their function is not clear.

In general, the constrictor muscle systems is opposed by some 10 pairs of dilatator muscles. Just dorsad of the esophagus are two small lateral gastric mill dilatator muscles. Anterior to these is an anteroventral dilatator muscle, inserted hard by its mate on the other side. Next above is inserted the anterodorsal dilatator muscle, also close to its counterpart at the midline of the mill. On the anterodorsal surface of the gastric mill, caudad of the anterodorsal dilatators, is the mesodorsal dilatator muscle, inserting on the midline. Posteriorly, behind the curvature of the gastric mill, is inserted a group of perhaps three posteromedial dilatator muscles. Ventral to the gastric mill is found the long, thin posteroventral dilatator muscle which inserts with its counterpart into the ventral midline at the ventral curvature of the gastric mill. And lastly, a ventral filter dilatator muscle inserts into the ventral midline in the region of the filter.

Gross movements of the gastric mill, as well as operation of the median tooth, are accomplished by the large anterodorsal gastric mill muscle and the posterodorsal gastric mill muscle, both of which insert into the dorsal part of the mill, in the region of the median tooth. They are paired muscles. Some of the actions of these muscles may be observed in the living animal during feeding.

HEPATOPANCREAS

FIGURE 83

The main digestive gland of *Penaeus* appears to be the hepatopancreas. This large gland is situated in the posterior region of the thorax, anteroventrad of the heart. It surrounds the junction of the gastric mill with the midgut. In consistency, the hepatopancreas is a mass of closely packed secretory tubules whose products apparently are poured into the ducts of the hepatopancreas at the posterior end of the gastric mill filter.

B. Midgut

The extent of the midgut, or mesenteron, in Crustacea is evidently variable (Calman 1909). That part of the alimentary canal not sclerotized in *Penaeus* runs from some point near the posterior portion of the heptopancreas to the hindgut gland in, the reader will recall, the anterior end of the sixth abdominal segment. The midgut is a simple, straight tube throughout its length. Its association with the dorsal abdominal artery is intimate. Very many small vessels connect the two all the way from the heart to the hindgut gland. Transverse sections of the midgut at various points show that the gut lumen is lined with low columnar epithelium resting on a basement membrane. The outer layers appears to be connective tissue in which muscle fibers are distributed.

C. Hindgut

The proctodaeum, or hindgut, begins at the hindgut gland and includes the rectum and anus. Specimens cleared in strong alkali retain the cuticular lining of this region of the gut. The hindgut (rectal) gland (figs. 61, 62, 74) projects dorsad from the rectum. The gland is composed of tubules lined with large secretory cells. The tubules are blind dorsally and open into the dorsal surface of the rectum. The function of the gland is unknown. The rectum (figs. 61, 74, 83), too, is lined with secretory epithelium reflected into deep folds. The gland cells of the hindgut gland and rectum may play a part in osmotic balance. The anus (fig. 82) consists of a bulb of cuticle at the caudal end of the rectum and a large tube passing ventrad to the anal opening. As has been shown, the opening is controlled by muscles.

V. EXCRETORY SYSTEM

The details of the excretory system and antennal gland of *Penaeus* have not been worked out completely. Compared to the compact and easily visible green gland of the crawfishes, the excretory organs of the white shrimp are much more diffused. Attempts have been made to clarify the extent of the excretory glands of *Penaeus* by injecting dyes into the excretory pores, and such information as is here presented is based on these procedures.

The hemocoelic excretory gland of the white shrimp seems to be made up of two major portions. The smaller, dorsal portion lies above the supraesophageal ganglion (fig. 86). The gland is continuous with the larger, ventral part of the system by means of its lateral arms. The ventral gland lies beneath the dorsal brain on the midline (fig. 86) and extends into the body of the antennae. The dorsal and ventral glands are composed of soft, glandular walls and trabeculae enclosing myriads of sinusoids. The portion of the gland entering the antenna makes contact with a compact, nodular, antennal excretory gland (figs. 20, 21) in the basal segments of the antenna. If the surface of the antennal gland is removed, gland concretions or nodules are found embedded in the tissues. A short duct from the antennal gland leads to the exterior through the excretory pore (figs. 21, 23, 24). The median coxal location of the pore is a constant character of Decapoda.

VI. REPRODUCTIVE SYSTEM

The external sex organs of Crustacea Decapoda have been widely used as systematic characters in the groups and those of the Penaeidae are no exception. In the males the petasma (fig. 87), a modified endopodite of the first pleopod, and in the females the thelycum (fig. 89), the modified sternal plates of the fourth and fifth thoracic segments, have received attention. A system of descriptive nomenclature, largely meaningless, has grown up about the external sex characters, in particular the parts of the petasma. Of inferior taxonomic importance, but constant in the decapods, are the locations of the gonopores. Those of the male lie within folds of thin cuticle between the bases of the fifth walking legs (fig. 88), while the female gonoducts open to the exterior through labiate structures between the third walking legs (fig. 89). A modification of the second pleopods, the appendix masculina (fig. 3), varies in shape and size within the Tribe Penaeidae, that of some genera, as in *Penaeus*, being unspecialized compared to the complex appendix masculina in *Hymenopenaeus*.

The petasma of the male is a system of lightly sclerotized longitudinal rods connected to folds of thin cuticle which permit the petasma to inflate broadly. The structure is folded close to the basipodite of the first pleopod in young males. With the molt to sexual maturity, the medial margin of each half of the petasma becomes joined to its counterpart. Under the compound microscope one can see that the margins are invested with tiny, knobbed processes. Thrust together the knobs tend to form a lock, in the words of King (1948), "like a zipper." Although the copulatory act of penaeids has rarely been observed, apparently the spermatophore is extruded from the male gonopores and held on the posterior or ventral surface of the petasma and then thrust against the thelycum of the female where it is held in place by the setae and sculpturing of that region.

The thelycum of *Penaeus setiferus* (fig. 89) is made of a series of lobes and protuberances characteristic of the species (Burkenroad 1936). These presumably enable the animal to retain the spermatophore for a sufficient time to insure fertilization.

Enough research on the internal reproductive organs of *Penaeus setiferus* has been carried out in the present work to bear out the findings of King (1948), therefore no illustrations repeating his have been prepared on the subject.

The testes of the male are paired. They lie on the dorsal surface of the hepatopancreas ventral to the heart. Each testis is comprised of several lobes extending over the surface of the hepatopancreas. The vas deferens extends from the posterior end of the testis, makes a lateral loop and passes ventrad to the terminal ampoule, a vesicle situated above the male gonopore on the sternum. The ampoule is primarily a glandular structure that secretes the spermatophore.

The ovaries, like the testes, are paired. The ovary has a long, anterior projection which runs along the anterior portion of the esophagus and gastric mill and several lateral projections lying on the surface of the hepatopancreas. The heart is situated dorsal to the region with the lateral projections. Behind the heart a lobe of the ovary, the dorsal ovarian lobe (fig. 62), runs the length

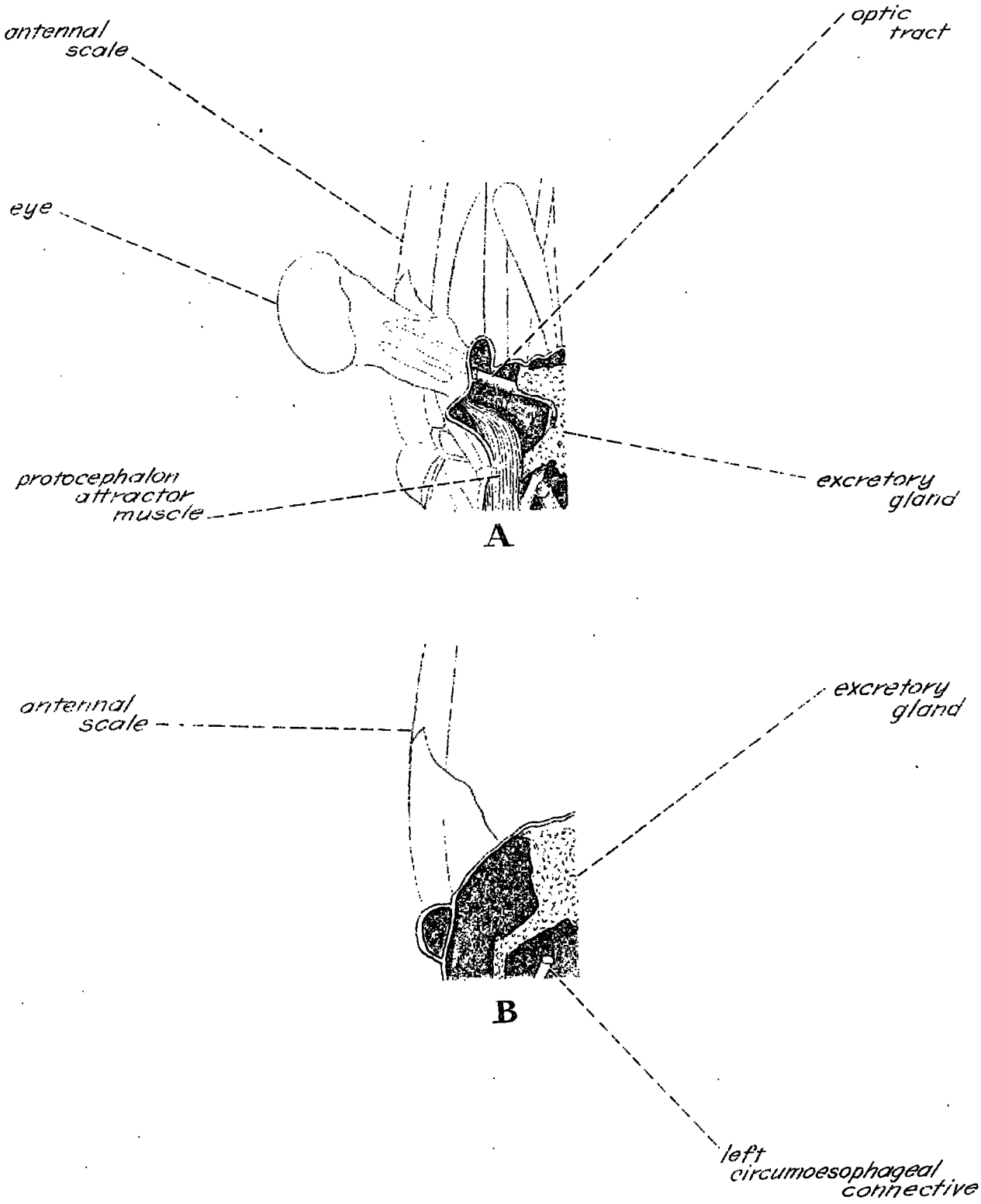

FIGURE 86.—Dorsal view of head region showing excretory gland. Carapace removed. *A*. Part of excretory gland dorsal to brain. *B*. Part of excretory gland ventral to brain.

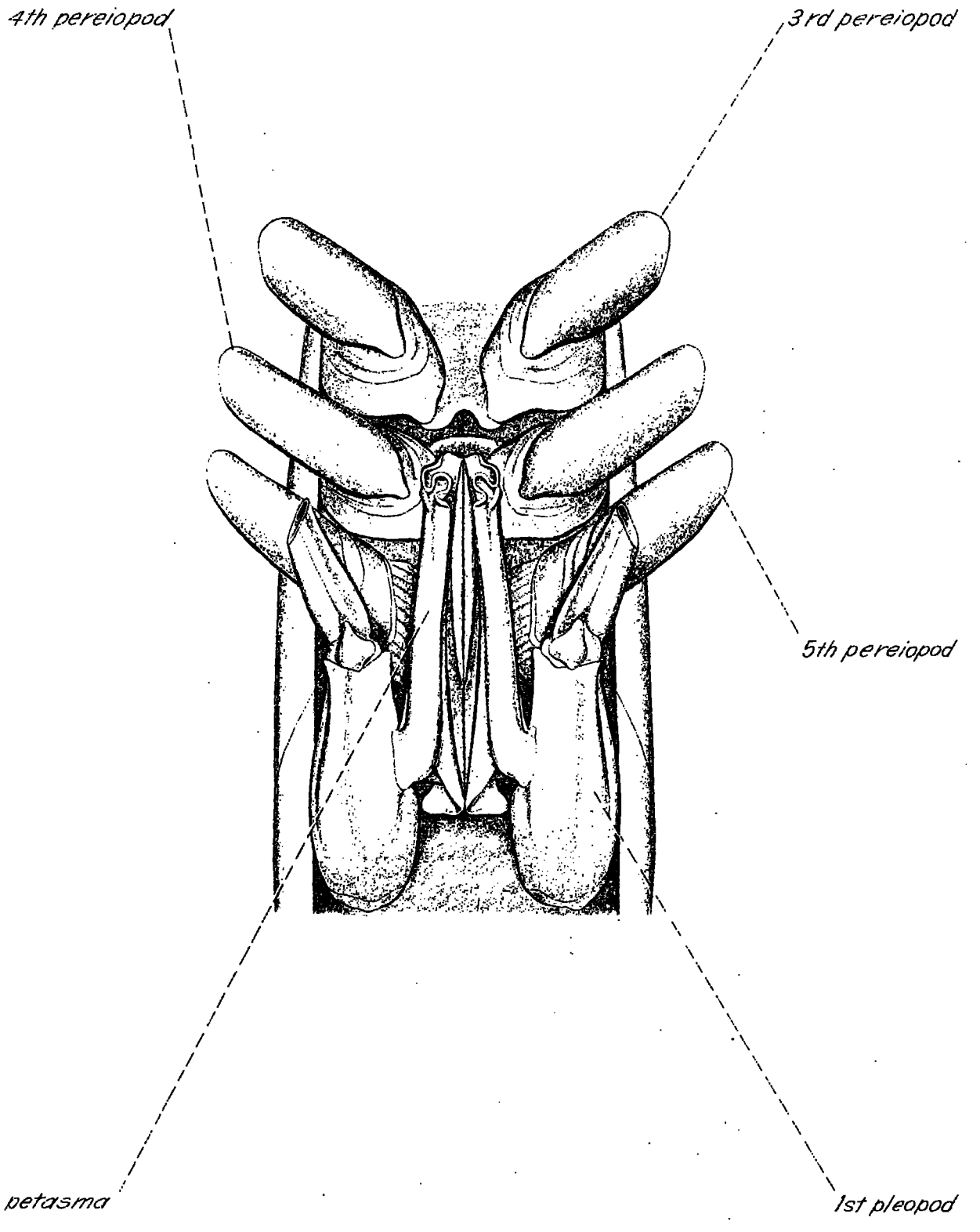

FIGURE 87.—Ventral view of parts of thorax and abdomen showing petasma of male.

468059 O - 59 - 11

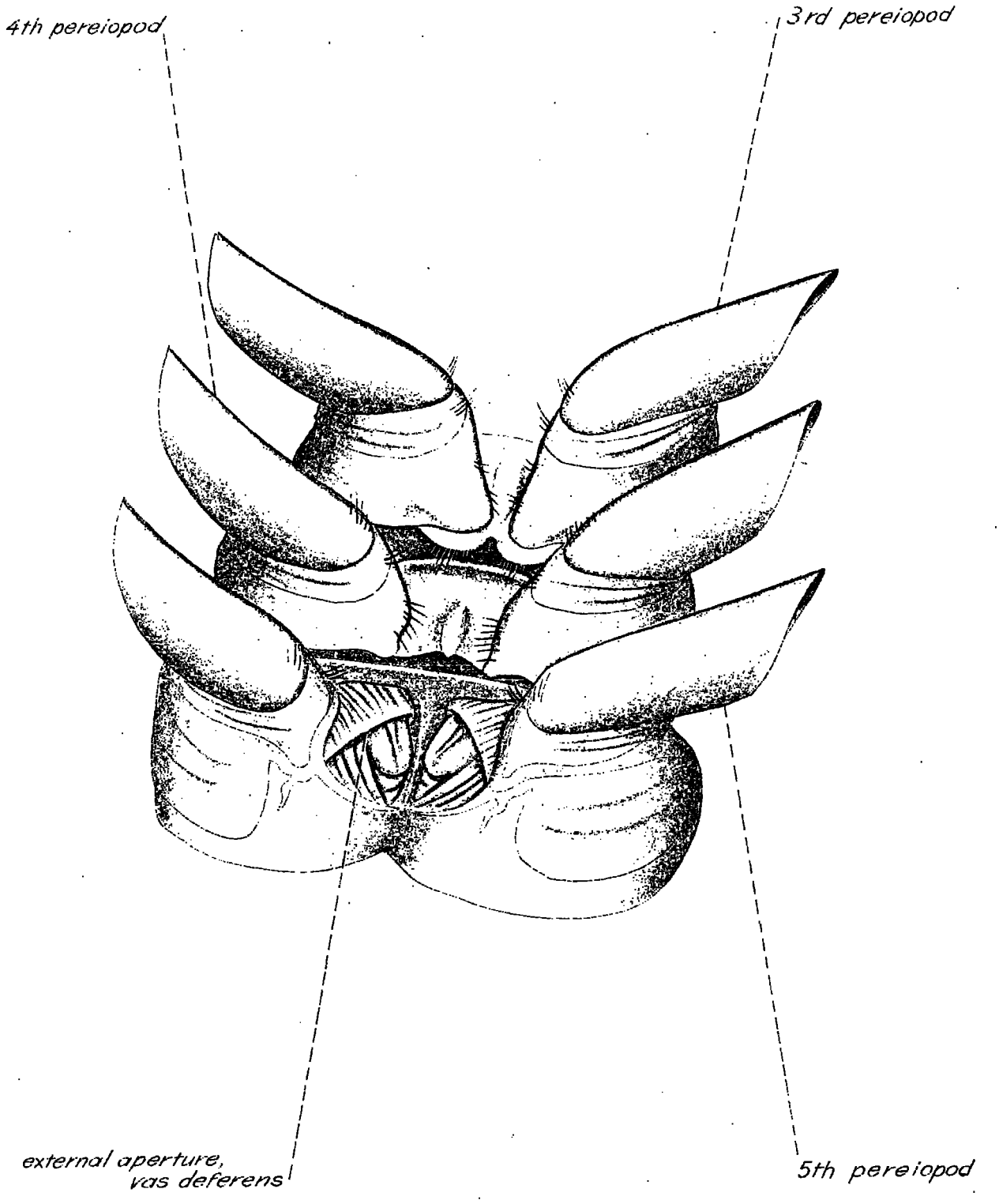

FIGURE 88.—Ventral view of parts of thorax in male. Petasma removed.

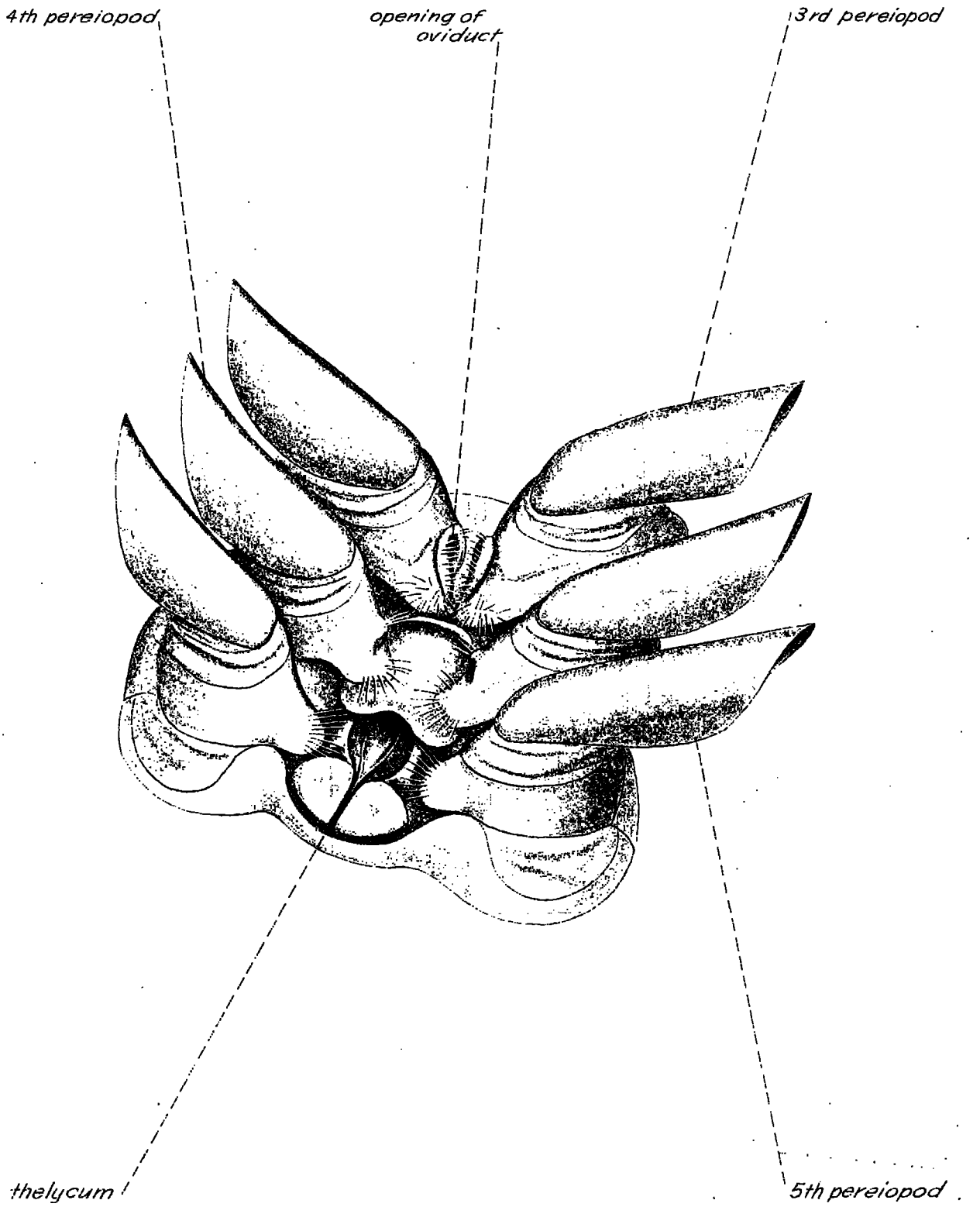

FIGURE 89.—Ventral view of parts of thorax in female.

of the abdomen dorsolateral to the midgut. The oviduct passes ventrad from the thoracic ovary to the female gonopore on the third thoracic leg.

LITERATURE CITED

ALEXANDROWICZ, J. S.
1932. The innervation of the heart in the Crustacea. I. Decapoda. Quarterly Journal of Microscopical Science, London, 75: 181-249.

BALSS, H.
1913. Ueber die Chemoreception bei Garneelen. Biologisches Zentralblatt, Leipzig, 33: 508–512.

BAUMANN, H.
1917. Das Cor frontale bei dekapoden Krebsen. Zoologischer Anzeiger, 49: 137-144.
1919. Das Gefäss-system von *Astacus fluviatilis* (*Potamobius astacus* L.). Ein Beitrag zur Morphologie der Dekapoden. Zeitschrift für Wissenschaftliche Zoologie, Leipzig, 118: 246-312.

BERKELEY, A. A.
1928. The musculature of *Pandalus danae* Stimpson. Transactions of the Royal Canadian Institute, Toronto, 16: 181-321.

BERNHARDS, H.
1916. Der Bau des Komplexauges von *Astacus fluviatilis*. Zeitschrift für Wissenschaftliche Zoologie, 116: 649-707.

BURKENROAD, MARTIN D.
1939. Further observations on Penaeidae of the northern Gulf of Mexico. Bulletin of the Bingham Oceanographic Collection, 6: 1-62.

CALMAN, W. T.
1909. Part VII, Appendiculata, Third Fascicle, Crustacea. In: A treatise on zoology, ed. by Sir Ray Lankester. London, Adam and Charles Black. 346 pp.

CARLISLE, D. B., and L. M. PASSANO.
1953. The X-organ of Crustacea. Nature, 171: 1070.

CHAUDONNERET, JEAN
1955. Le système nerveux de la région gnathale de l'écrevisse americaine (*Cambarus affinis* Say) et la question des paragnathes. (Note preliminaire) Travaux du Laboratoire de Zoologie et de la Station Aquicole Grimaldi de la Faculté des Sciences de Dijon, 12 1–6.
1956. Le système nerveux de la région gnathale de l'écrevisse *Cambarus affinis* (Say). Annales des Scieuces Naturelles: Zoologie et Biologie Animale, 11e Série, 18 (3): 33–61.

COCHRAN, DORIS M.
1935. The skeletal musculature of the blue crab, *Callinectes sapidus* Rathbun. Smithsonian Miscellaneous Collection, 92 (9): 1–76.

DANIEL, R. J.
1928. The abdominal muscular systems of *Praunus flexuosus* (Müller). Proceedings and Transactions of the Liverpool Biological Society (Appendix, 36 Lanc Sea Fish. Lab. Rept. for 1927), 42: 5–41.
1929. The abdominal muscular system of *Meganyctiphanes norvegica* (M. Sars). Proceedings and Transactions of the Liverpool Biological Society, 43: 149–180.

DANIEL, R. J.—Continued
1931a. The abdominal muscular systems of *Homarus vulgaris* (L.) and *Palinurus vulgaris* (Latr.). Proceedings and Transactions of the Liverpool Biological Society, 45: 3–49.
1931b. The abdominal muscles of the shore crab (*Carcinus moenas*) and of the Zoëa and Megalope stages. Proceedings and Transactions of the Liverpool Biological Society, 45: 50–56.
1931c. Comparative study of the abdominal musculature in Malacostraca. Part I. The main ventral muscles of the typical abdominal segments. Proceedings and Transactions of the Liverpool Biological Society, 45: 57–71.
1931d. The abdominal muscular systems of *Paranaspides lacustris* (Smith). Report of the Lancashire Sea-Fish. Laboratory for 1931, pages 26–45.
1933. The abdominal muscular systems of *Lophogaster typicus* M. Sars, and *Gnathophausia Zoëa* Suhm, and their relationships with the musculatures of other Malacostraca. Proceedings and Transactions of the Liverpool Biological Society, 47: 71–133.

DEBAISIEUX, P.
1954. Histogénèse des muscles et charpentes chez les Crustacés. La Cellule, Liége, T. 56, 3: 265–305.

DOFLEIN, Franz.
1911. Ueber den Geruchsinn bei Wassertieren. Biologisches Zentralblatt, Leipzig, 31: 706–707.

FERRIS, G. F.
1947. The contradictions of the insect head. Microentomology, 12 (3): 60–64.
1953. On the comparative morphology of the Annulata. A summing up. Microentomology, 18: 2–15.

GROBBEN, K.
1917. Der Schalenschliessmuskel der dekapoden Crustaceen, zugleich ein Beitrag zur Kenntnis ihrer Kopfmuskulatur. Sitzungsberichte der Kaiserliche Akademie der Wissenschaften, Wien, Abt. 1. 126: 473–494.
1919. Uber die Muskulatur des Vorderkopfes der Stomatopoden. Sitzungsberichte der Kaiserliche Akademie der Wissenschaften, Wien, Abt. 1, 128: 185–214.

HANSTRÖM, B.
1948. The brain, the sense organs, and the incretory organs of the head in the Crustacea Malacostraca. Bulletin Biologique de France et de Belgique, Supplement 33: 98–126.

HART, C. W., JR.
1952. The exoskeleton and musculature of the appendages of the first three abdominal segments of *Cambarus longulus longulus* Girard (Decapoda, Astacidae). Virginia Journal of Science, 3 (1): 39–48.

HENRY, L. M.
1948a. The nervous system and the segmentation of the head in the Annulata. Section IV, Arthropoda. Microentomology, 13 (1): 1–26.
1948b. The nervous system and the segmentation of the head in the Annulata. Section V, Onychophora. Microentomology, 13 (2): 27–48.

HUDINAGA, M.
1935. Studies on the development of *Penaeus japonicus* Bate. Report of the Hayatomo Fishery Institute, Tobata, Vol. 1, No. 1. Abstracted in: Japanese Journal of Zoology, 6 (4): 80, 1936.
1942. Reproduction, development and rearing of *Penaeus japonicus* Bate. Japanese Journal of Zoology, 10 (2): 305–393.

HUXLEY, T. H.
1906. The crayfish. 7th ed. Kegan Paul, Trench, Trübner & Co., Ltd., London. 371 pages.

JOHANNSEN, O. A., and F. H. BUTT.
1941. Embryology of insects and myriapods. McGraw-Hill Book Co., New York.

JOHNSON, M. C., and J. R. FIELDING.
1956. Propogation of the white shrimp, *Penaeus setiferus* (Linn.), in captivity. Tulane Studies in Zoology, 4 (6): 175–190.

KEIM, W.
1915. Das Nervensystem von *Astacus fluviatilis* (*Potamobius astacus* L.). Zeitschrift für Wissenschaftliche Zoologie, 113: 485–545.

KING, J. E.
1948. A study of the reproductive organs of the common marine shrimp, *Penaeus setiferus* (Linnaeus). Biological Bulletin, 94: 244–262.

KISHINOUYE, K.
1900. The nauplius stage of *Penaeus*. Zoologischer Anzeiger, Leipzig, 23 (607): 73–75.

KNOWLES, F. G. W.
1953. Endocrine activity in the crustacean nervous system. Proceedings of the Royal Society of London, Series B, Biological Sciences, 141: 248–267.

KNOWLES, F. G. W., and D. B. CARLISLE.
1956. Endocrine control in the Crustacea. Biological Reviews, 31: 396–473.

LISSMAN, H. W., and A. WOLSKY.
1935. Antennulen-Aussenast als Chemorezeptor. Erwiderung an Herrn Luther. Zoologischer Anzeiger, Leipzig, 110: 92–96.

MAYRAT, A.
1955. Mise en evidence de tendons chez les crustaces dans le muscle attracteur du synciput de *Praunus flexuosus* O. F. Müller. Bulletin de la Société Zoologique de France, 80 (2–3): 81–85.
1956a. Le système artériel de *Praunus flexuosus* et le prétendu coeur frontale des Malacostracés. Bulletin, Station Océanographique de Salammbô, Tunisia, 53: 44–49.
1956b. Oeil, centres optiques et glandes endocrines de *Praunus flexuosus* (O. F. Müller). Archives de Zoologie expérimentale et Générale, 93 (Fasc. 4): 319–363.

MEREDITH, S. S.
1954. The appendages of *Crangon vulgaris*, the brown shrimp. Proceedings of the Leeds Philosophical and Literary Society, Scientific Section, 6 (4): 228–242.

MÜLLER, F.
1863. Die Verwandlung der Garneelen. Arch. Naturgesch., 29: 8–23. (Translated in Annals and Magazine of Natural History, 14 (3): 104–115, 1864).

PASSANO, L. M.
1953. Neurosecretory control of molting in crabs by the X-organ sinus gland complex. Physiologia Comparata et Oecologia, 3 (2–3): 155–189.

PEARSON, J. C.
1939. The early life histories of some American Penaeidae, chiefly the commercial shrimp, *Penaeus setiferus* (Linn.). Bulletin of the Bureau of Fisheries, 49 (30): 1–73.

PERKINS, E. B.
1928. Color changes in crustacea, especially in *Palaemonetes*. Journal of Experimental Zoology, 50: 71–105.

RAMADAN, M. M.
1952. Contribution to our knowledge of the structure of the compound eyes of Decapoda Crustacea. Acta Universitatis Lundensis, N. S. 2, 48 (3): 1–20.

RICHARDS, A. GLENN.
1951. The integument of arthropods. University of Minnesota Press. 411 pages.

RIOJA, ENRIQUE
1939a. Estudios carcinologicos. I. Caracteres sexuales secundarios de los Penaeidae. El organo antennular de los machos. Anales del Instituto de Biologia, Mexico, 10 (3–4): 313–319.
1939b. Estudios carcinologicos. II. Caracteres sexuales secundarios de los Penaeidae. Los caracteres sexuales en algunas especies de Aristeinae: *Aristeus antennatus* (Risso), *Aristeomorpha foliacea* (Risso) y *Plesiopenaeus edwardsianus* (J. G. Johnson). Anales del Instituto de Biologia, Mexico, 10 (3–4): 322–333.
1940a. La morphologia de las cerdas de las piezas bucales de los Penaeidos (Crus. Decap.) y su valor diagnostico. Ciencia Mexico, 1: 116–117.
1940b. Estudios carcinologicos. III. Descripcion de un organo setiforme en el tercer maxilipedo de algunos Penaeidae. Anales del Instituto de Biologia, Mexico, 11 (1): 261–266.
1940c. Estudios carcinologicos. IV. Observaciones sobre las antenulas de algunas especies del genero *Penaeus*. Anales del Instituto de Biologia, Mexico, 11 (1): 267–273.
1941a. Estudios carcinologicos. VIII. Contribucion al la morfologia e interpretacion del petasma de los Penaeidae (Crust. Decapodos). Anales del Instituto de Biologia, Mexico, 12 (1): 199–221.
1941b. Estudios carcinologicos. IX. Descripcion del macho maduro de *Penaeus vannamei* Boone, hallado en las costas Pacifico de Mexico. Anales del Instituto de Biologia, Mexico, 12 (1): 223–229.
1942a. Estudios carcinologicos. XI. Observaciones acerca de algunos caracteres sexuales secundarios en el camaron de rostro largo (*Artemesia longinaris* Bate) y en el langostin (*Hymenopenaeus müllcri* Bate). Anales del Instituto de Biologia, Mexico, 13 (2): 659–674.
1942b. Estudios carcinologicos. XII. Contribucion al estudio de los caracteres sexuales secundarios de dos especies de los generos *Trachypeneus y Xiphopeneus* de las costas Mexicanas del Pacifico. Anales del Instituto de Biologia, Mexico, 13 (2): 675–684.

SCHMIDT, W.
1915. Die Muskulatur von *Astacus fluviatilis* (*Potamobius astacus* L.). Zeitschrift für Wissenschaftliche Zoologie, 113: 165–251.

SNODGRASS, R. E.
1935. Principles of insect morphology. McGraw-Hill Book Co., New York. 667 pages.
1938. Evolution of the Annelida, Onychophora, and Arthropoda. Smithsonian Miscellaneous Collections, 97 (6): 1–159.
1951a. Comparative studies on the head of mandibulate arthropods. Comstock Publishing Co., Ithaca, N. Y. 118 pages.
1951b. Comparative studies on the jaws of mandibulate arthropods. Smithsonian Miscellaneous Collections, 116: 1–85.
1952. A textbook of arthropod anatomy. Comstock Publishing Associates, Ithaca, N. Y.. 363 pages.

SPIEGEL, A.
1927. Uber die Chemorezeption von *Crangon vulgaris* Fabr. Zeitschrift für Wissenschaftliche Biologie, Abt. C. Zeitschrift für Vergleichende Physiologie, 6: 688–730.

STEINBERG, J. E., and E. C. DOUGHERTY.
1957. The skeleton shrimps (Crustacea: Caprellidae) of the Gulf of Mexico. Tulane Studies in Zoology, 5 (11): 267–288.

VOSS, G. L.
1955. A key to the commercial & potentially commercial shrimp of the Family Penaeidae of the Western North Atlantic and the Gulf of Mexico. Technical Series No. 14, The Marine Laboratory, University of Miami, pp. 1–23.

WELSH, J. H.
1941. The sinus gland and the 24-hour cycles of retinal pigment migration in the crayfish. Journal of Experimental Zoology, 86 (1): 35–49.

YOUNG, J. H.
1953. Embryology of the mouthparts of Anoplura. Microentomology, 18 (4): 85–133.
1956. Anatomy of the eyestalk of the white shrimp, *Penaeus setiferus* (Linn., 1758). Tulane Studies in Zoology, 10 (3): 169–190.

BIBLIOGRAPHY

ABRAHAM, A., and A. WOLSKY.
1930. Die Geruchsorgane der Landisopoden. Zeitschrift für Wissenschaftliche Biologie, Abt. für Anatomie, Morphologie, und Okologie der Tiere, 17: 441–463.

ABRAHAMCZIK-SCANZONI, H.
1942. Beiträge zur Kenntnis der Muckulatur und des Innenskeletts der Krabben. Zoologische Jahrbücher, Abt. 2 für Anatomie und Ontogenie der Tiere, Jena, 67: 293–380.

AIYER, R. P.
1953. On the female reproductive system of *Palaemon idae* Heller. Journal of the Zoological Society of India, 5 (2): 227–234.

ALEXANDROWICZ, J. S.
1933. Innervation des branchies de *Squilla mantis*. Archives de Zoologie Expérimentale et Générale, Paris, 75: 21–34.
1934. The innervation of the heart of Crustacea. II. Stomatopoda. Quarterly Journal of Microscopical Science, London, 76: 511–548.
1951. Muscle receptor organs in the abdomen of *Homarus vulgaris* and *Palinurus vulgaris*. Quarterly Journal of Microscopical Science, London, 92: 163–199.
1952a. Innervation of the heart of *Ligia oceanica*. Journal of the Marine Biological Association, U. K., 31: 85–95.
1952b. Receptor elements on the thoracic muscles of *Homarus vulgaris* and *Palinurus vulgaris*. Quarterly Journal of Microscopical Science, 93: 315–346.

ANDERSON, W. W., J. E. KING, and M. J. LINDNER.
1949. Early stages in the life history of the common marine shrimp. *Penaeus setiferus* (Linnaeus). Biological Bulletin, 96 (2): 168–172.

ANDERSON, W. W., and MILTON J. LINDNER.
1945. A provisional key to the shrimps of the family Penaeidae with especial reference to American forms. Transactions of the American Fisheries Society, 73 (for year of 1943): 284–319.

ANDREWS, E. A.
1911. Sperm transfer in certain decapods. Proceedings of the Smithsonian Institution, U. S. National Museum, 39: 419–434.

ARGILAS, A.
1929. Observations morpholgiques sur les espèces des côtes algériennes de la famille des Penaeidae (Macroures nageurs). Bulletin des Travaux Publiés par la Station d'Aquiculture et de Pêche de Castiglione, Nouvelle Serie, Algiers, fasc. 1, pp. 29–101.

ARVY, L., M. GABE, and J. LHOSTE.
1947. Etude mechanique du sang de *Ligia oceanica* L. Bulletin du Laboratoire Maritime du Muséum National d'Histoire Naturelle, Dinard, Fasc. 29, pp. 5–10.

BARTH, G.
1934. Untersuchungen über Myochordotonalorgane bei Dekapoden Crustaceen. Zeitschrift für Wissenschaftliche Zoologie, Leipzig, 145: 576–624.

BELL, J. C.
1906. The reactions of crayfish to chemical stimuli. Journal of Comparative Neurology, Philadelphia, 16: 299–326.

BERNARD, F.
1937. Recherches sur la morphogénèse des yeux composés d'Arthropodes. Développment, croissance, reduction. Bulletin Biologique de la France et de la Belgique, Supplement, 23: 1–162.

BLOCH, F.
1935. Contribution à l'etude des gamètes et de la fécondation chez les Crustacés Décapodes. Traveux de l'Institute Zoologique de Lille et de la Station Maritime de Wimereux (Pas-de-Calais), 12: 181–279.

BOAS, J. E. V.
1889. Kleinere carcinologische Mitteilungen. 2. Ueber den ungleichen Entwicklungagang der Salzwasser und der Süsswasser-Form von *Palaemonetes varians*. Zoologische Jahrbücher, Abt. 3 fur Systematik Ökologie und Geographie der Tiere, Jena, 4: 793–805.

BOCK, F.
1923. Die Blutcirculation in den Kiemen von Flusskrebs. Zoologischer Anzeiger, 56: 198–205.
1925. Die Respirationsorgane von *Potamobius astacus* Leach. Zeitschrift für Wissenschaftliche Zoologie, 124: 51–117.

BÖRNER, C.
1921. Die Gliedmassen der Arthropoden. *In* Arnold Lang's Handbuch der Morphologie der Wirbellosen Tiere, Jena, 4: 649–694.

BORRADAILE, L. A.
1907. On the classification of decapod crustaceans. Annals and Magazine of Natural History, Series 7. Vol. 19, p. 457.

BOUVIER, E. L.
1889. Le système nerveux des Crustacés Décapodes et ses rapports avec l'appareil circulatoire. Annales des Sciences Naturelles: Zoologie et Biologie Animale, 11e Série, Paris, (7): 73–106.
1891. Recherches anatomiques sur le système artériel des Crustacés Decapodes. Annales des Sciences Naturelles: Zoologie et Biologie Animale, 11e Série, Paris, (7), 9: 197–282.

BOUVIER, L.
1936a. Observations relatives à l'Ecrevisse sur le constitution des flancs chez les Crustacés. Comptes Rendus Hebdomadaires des Séances de L'Académie des Sciences, Paris, 203: 222–225.
1936b. Observations complémentaires sur les pattes des Crustacés decapodes apparenant à la section des Astacomorphes. Comptes Rendus Hebdomadaires des Séances de L'Académie des Sciences, Paris, 203: 1301–1305.

BOYDEN, A.
1943. Serology and animal systematics. American Naturalist, 77: 234–255.

BRIAN, A.
1938. L'armatura triturante dello stomaco di alcuni Peneidi meso-abissali a della *Pasiphaea multidentata* Esmark. Monitore Zoologica Italiano, Florence, 49: 153–165.

BROAD, CARTER.
1950. Results of shrimp research in North Carolina. Proceedings of the Gulf and Caribbean Fisheries Institute, Third Annual Session, 9 pages.

BROCK, F.
1948. Das Verhalten dekapoder Crustaceen beim Aufbau des Beutefeldes. Remane and others *in*: Verhandlungen der Deutsche Zoologischen Gesellschaft, Geest and Portig, Leipzig, 1949, pp. 416–426. (Published as Supplementband, Zoologischer Anzeiger.)

BROOKS, W. K.
1882. Lucifer: A study in morphology. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, 173: 57–137.
1883. The metamorphosis of *Penaeus*. Annals and Magazine of Natural History, 2 (19): 6.

BROOKS, W. K., and F. H. HERRICK.
1892. The embryology and metamorphosis of the Macroura. Memoirs of the National Academy of Science, 5: 323–463.

BURKENROAD, MARTIN D.
1934a. The Penaeidae of Louisiana with a discussion of their world relationships. Bulletin of the American Museum of Natural History, 68 (2): 61–143.
1934b. Littoral Penaeidae chiefly from the Bingham Oceanographic Collection. With a revision of *Penaeopsis* and descriptions of two new genera of eleven American species. Bulletin of the Bingham Oceanographic Collection, 4 (7): 1–109.
1936. A new species of *Penaeus* from the American Atlantic. Ann. Acad. Brasileira Sci., T. 8, No. 4.
1937. The Templeton Crocker Expedition. XII. Sergestidae (Crustacea Decapoda) from the lower Californian region, with descriptions of two new species and some remarks on the Organs of Pesta in *Sergestes*. Zoologica, New York, 22: 315–329.
1938. The Templeton Crocker Expedition. XIII. Penaeidae from the region of Lower California and Clarion Island, with descriptions of four new species. Zoologica, New York, 23 (1): 55–91.
1947. Reproductive activities of decapod Crustacea. American Naturalist, 81: 392–398.
1949. Occurrence and life histories of commercial shrimp. Science, 110 (2869: 688–689).
1950. Measurement of the natural growth rates of decapod crustaceans. Proceedings of the Gulf and Caribbean Fisheries Institute, Third Annual Session, 2 pp.

BRUNTZ, L.
1903. Contribution à l'étude de l'excrétion chez les Arthropodes. Archives de Biologie, Liége, 20: 217–422.

BUDDENBROCK, W. VON.
1914. Orientierung der Kresbse. Zoologische Jahrbücher, Abt. für Allgemeine Zoologie und Physiologie, 34: 479.

CALMAN, W. T.
1917. Notes on the morphology of *Bathynella* and some allied Crustacea. Quarterly Journal of Microscopical Science, 62: 489–514.

1920. The Cambridge natural history. Volume IV, ed. by S. F. Harmer and A. E. Shipley, p. 162.

CARLISLE, D. B., and P. F. R. DOHRN.
1953. Studies on *Lysmata seticaudata* Risso. VI. Notes on the structure of the neurosecretory system of the eyestalk. Publicazioni della Stazione Zoologica di Napoli, 24: 69–83.

CARLISLE, D. B., and C. G. BUTLER.
1956. The "queen-substance" of honeybees and the ovary-inhibiting hormone of crustaceans. Nature, 177: 276–277.

CHACE, F. A., JR.
1951. The number of species of decapod and stomatopod Crustacea. Journal of the Washington Academy of Sciences, 41: 370–372.

CHAPPUIS, P. A.
1915. *Bathynella natans* und ihre stellung in System. Zoologische Jahrbücher, Abt. für Systematik, Georgraphie und Biologie der Tiere, Jena, 40: 147–176.

CHIDESTER, F. E.
1912. The biology of the crayfish. American Naturalist, 46: 279–293.

CLARK, E., and F. M. BURNET.
1942. The application of serological methods to the study of Crustacea. Australian Journal of Experimental Biology and Medical Science, Adelaide, 20: 89–95.

CLAUS, C.
1891. Das Medianauge der Crustaceen. Arb. Zool. Inst. Univ. Wien, 9: 225–266.

CRAMPTON, G. C.
1928a. The evolution of insects, chilopods, diplopods, Crustacea, and other arthropods indicated by a study of the head capsule. Canadian Entomologist, 60: 284–301.
1928b. The evolution of the head region in lower arthropods and its bearing upon the origin and relationships of the arthropodan groups. Canadian Entomologist, 60: 284–301.

CRONIN, L. E.
1947. Anatomy and histology of the male reproductive system of *Callinectes sapidus* Rathbun. Journal of Morphology, 81: 209–239.

DAKIN, W. H.
1946. Life history of a species of *Metapenaeus* in Australian coastal lakes. Nature, 158 (4003): 99.

DANIEL, R. J.
1930. The abdominal muscular systems of the Zoëa and Mysis stages of the shrimp (*Crangon vulgaris* Fabr.) and their bearing on phylogeny. Proceedings and Transactions of the Liverpool Biological Society, 44: 95–109.
1932. Comparative study of the abdominal musculature in Malacostraca. Part II. The superficial and main ventral muscles and lateral muscles and their continuation into the thorax. Report of the Lancashire Sea-Fish. Laboratory for 1931, pp. 46–104.

DEBAISIEUX, P.
1948. Statocystes de *Praunus* et leurs poils sensoriels. Annales de la Société Royale Zoologique de Belgique, 78: 26–31.

DELAGE, Y.
1183. Circulation et respiration chez les Crustacés Schizopodes. Archives de Zoologie Expérimentale et Générale, Paris, S. 2, T. 1, pp. 105–130.

DEMAL, JEAN
1953. Genèse et différentiation d'hémocytes chez *Palaemon varians* Leach. La Cellule, Liége, 56: 85–102.

DESMARETS, A.
1929. Rapport entre la carapace des Crustacés et les organes internes. Bulletin de la Société d'Etude des Sciences Naturelles d'Elbeuf, 47: 65–74.

DUCHATEAU, G., ET AL.
1940. L'equipment enzymatique de l'hepatopancreas des Crustaces en ce que concerne le catabolisme des purines. Comptes Rendus des Séances de la Société de Biologie et de ses Filiales, Paris, 133: 274–276.

EINARSSON, H.
1942. On the systematic value of the spermatheca, on sexual dimorphism in *Nematoscelis*, and on the male in *Bentheuphausia*. Videnskabelige Medelelser Fra Dansk Naturhistorisk Forening I Kbenhavn, 106: 263–286.

ESCHALIER, G.
1954. Recherches expérimentales sur le rôle de "l'organ Y" dans la mue de *Carcinus moenas* (L.), Crustacé Décapode. Comptes Rendus Hebdomadaires des Séances de L'Académie des Sciences, Paris, 238: 523–524.

ESTEVE, MICHELINE.
1954. Présence simultanee d'un thelycum et d'un petasma chez *Parapenaeus longirostris* (Lucas) (Crustacé, Peneidae). Bulletin de la Société des Sciences Naturelles de Tunisie, Tome 8, pp. 89–92.

FAGE, L.
1944. Sur quelques caracteres sexuels secondaires des Cumacés du genre *Iphinoë*. Archives de Zoologie Expérimentale et Générale, Paris, Notes Rev., 83: 112–121.

FAXON, W.
1895. Reports . . . *Albatross*, 15: The stalk-eyed Crustacea. Memoirs of the Museum of Comparative Zoology, Harvard, 18: 292 pp.

FERRIS, G. F.
1944. On certain evolutionary tendencies in the heads of insects. Microentomology, 9: 78–84.

FESQUET, A. E. J.
1933. Anotaciones para una monografía sobre el Langostín (*Plcoticus müllcri* Bate). A. Kapelusz y Cia, Buenos Aires, pp. 1–35.
1941a. Estudio de la morphologia externa del Camaron de rostro largo (*Artemesia*). Anales de la Sociedad Cientifica Argentina, Buenos Aires, 131: 60–95.
1941b. Descriptión del mecanismo articular de los pedunculos oculares de *Artemesia longinaris* y de *Himenopenaeus müllcri* (Bate). Holmbergia: Revista del Centro de Estudiantes del Doctorado en Ciencias Naturales, Buenos Aires, 3 (6): 64–67.

FISCHBACH, E.
1951. Licht-, Schwere- und Geruchsinn bei Isopoden. Die Naturwissenschaften, 38 (17): 408.

GABE, M.
1953. Sur l'existence, chez quelques Crustacés Malacostracés d'un organ comparable à la glande de la mue des Insectes. Comptes Rendus Hebdomadaires des Séances de L'Académie des Sciences, Paris, 237 (18): 1111–1113.

GATES, W. H.
1910. Shrimp. Fifth Biennial Report, Director, Gulf Biologic Station, Cameron, Louisiana, pp. 8–12.
GEORGE, W. C. and J. NICHOLS.
1948. A study of the blood of some Crustacea. Journal of Morphology, 83: 425–440.
GERARD, P.
1937. Sur l'élimination rénale des colorants acides chez *Astacus fluviatilis*. Bulletin de la Classe des Sciences, Académie Royale de Belgique, 5e Serie, 23: 456–463.
GOWANLOCH, J. N.
1931. The probable cause of "iodine shrimp." Louisiana Conservation Review, 2: 31–32.
GRABER, V.
1888. Ueber die Empfindlichkeit einiger Meertiere gegen Riechstoffe. Biologisches Zentralblatt, Leipzig, 8: 743–754.
GROBBEN, K.
1881. Die Antennendrüse der Crustaceen. Arbeiten aus dem Zoologischen Institute der Universität Wien und der Zoologischen Station in Triest, 3: 93–110.
1892. Zur Kenntnis des Stammbaumes und des Systems der Crustaceen. Sitzungsberichte der Kaiserliche Akademie der Wissenschaften, Wein, Abt. 1, 101: 237–274.
GUILBEAU, B. H.
1908. Shrimp. Fourth Bienniel Report, Director, Gulf Biologic Station, Cameron, La., pp. 11–13.
GURNEY, R.
1924. Crustacea, Part 9. Decapod larvae. British Antarctic (Terra Nova) Expedition, 1910. Natural History Report, Zool., Volume 8, No. 2.
1926. The protozoeal stage in decapod development. Annals and Magazine of Natural History, 18 (Series 9, No. 103): 19–27.
1927. Report on the larvae of the Crustacea Decapoda. Cambridge Expedition, Suez Canal. Transactions of the Zoological Society of London, 22 (2) No. 15.
1942. Larvae of decapod Crustacea. The Ray Society, London. 306 pp.
1943. The larval development of two penaeid prawns from Bermuda of the genera *Sicyonia* and *Penaeopsis*. Proceeding of the Zoological Society of London, 113B: 1–16.
1950. A remarkable penaeid larva. Proceedings of the Zoological Society of London, 119: 803–806.
HANSON, H. J.
1893. Zur Morphologie der Gliedmassen und Mundtheile bei Crustaceen und Insecten. Zoologischer Anzeiger, 16: 193–198 and 201–212.
HANSTRÖM, B.
1929. Das Deutocerebrum der Crustaceen. Zoologische Jahrbücher, Jena, 51: 535–548.
HARMON, M.
1937. Les mechanismes produsant la dehiscence des spermatophores d'*Eupagarus prideauxi* Leach. Comptes Rendus Hebdomadaires des Séances de L'Académie des Sciences, Paris, 204: 1504–1506.
HART, C. W., JR.
1953. Serial homologies among three pairs of abdominal appendages of certain male crayfishes (Decapoda, Astacidae). Journal of Morphology, 93 (2): 285–299.
VAN HARREVELD, A.
1939a. The motor innervation of a triply innervated crustacean muscle. Journal of Experimental Biology, London, 16: 398–402.
1939b. The nerve supply to doubly and triply innervated crayfish muscles related to their function. Journal of Comparative Neurology, Philadelphia, 70: 267–284; 285–296.
VAN HARREVELD, A., and C. A. G. WIERSMA.
1939. The function of the quintuple innervation of a crustacean muscle. Journal of Experimental Biology, London, 16: 121–133.
HAY, W. P., and C. A. SHORE.
1918. The decapod crustaceans of Beaufort, N. C., and the surrounding region. Bulletin of the Bureau of Fisheries, 35: 371–475.
HEATH, J. P.
1941. The nervous system of the kelp crab, *Pugettia producta*. Journal of Morphology, 69: 481–500.
HEDGPETH, J. W.
1947. Interesting crustaceans about which little has been written. Progressive Fish Culturist, October 1947, pp. 181–184.
HEERGAARD, P.
1953. Observations of spawning and larval history of the shrimp *Penaeus setiferus* (L.). Publications of the Institute of Marine Science, University of Texas, 3: 73–105.
HELDT, J. H.
1931. Observations sur la ponte, la fécondation et les premiers stades du developpement de l'oeuf chez *Penaeus caramote* Risso. Comptes Rendus Hebdomadaires des Séances de L'Académie des Sciences, Paris, 193: 1039–1041.
1932a. Sur quelques differences sexuelles (coloration, taille, rostre) chez deux crevettes tunisiennes: *Penaeus caramote* Risso et *Parapenaeus longirostris* Lucas. Bulletin, Station Océanographique de Salammbô, Tunisia, 27: 1–20.
1932b. L'appareil génital mâle des crevettes nordafricanes de la famille des Penaeidae. Comptes Rendus Hebdomadaires des Séances de L'Académie des Sciences, Paris, 195: 1325–1327.
1938. La reproduction chez les Crustacés Décapodes de la famille des Pénéides. Annales de l'Institut Océanographique, Paris, 18: 31–206.
1948. Note sur des caracteres sexuels secondaire periodiques chez deux crevettes: *Processa canaliculata* Leach et *Periclemenes amethysteus* Risso. Bulletin de la Société des Sciences Naturelles du Tunisie, Fasc. 1. pp. 27–29.
HEMMING, F.
1952. Proposed correction of an erroneous entry on the "Official List of Generic Names in Zoology" relating to the name *Penaeus* Weber, 1795 (Class Crustacea, Order Decapoda) (corrections of an entry in Opinion 104). Bulletin of Zoological Nomenclature, 6: 318–319.

HENRY L. M.
1947a. The nervous system and the segmentation of the head in the Annulata. Microentomology, 12 (3) : 65–82.
1947b. The nervous system and the segmentation of the head in the Annulata. Section III. Polychaeta. Microentomology, 12 (4) : 83–110.

HERDMAN, W. A.
1904. An outline of the shrimp question. Proceedings and Transactions of the Liverpool Biological Society, 18: 157–167.

HERRICK, F. H.
1895. The American lobster: A study of its habits and development. Bulletin of the U. S. Fish Commission, 5: 1–252.
1909. Natural history of the American lobster. Bulletin of the U. S. Bureau of Fisheries, 29 (747), 408 pp.

HICKMAN, V. V.
1937. The embryology of the Syncarid crustacean, *Anaspides tasmaniae*. Papers and Proceedings of the Royal Society of Tasmania, for 1936, pp. 1–36.

HOLMES, S. J.
1901. Habits of *Amphithoe longimana* Smith. Biological Bulletin, 2: 165–193.

HOLMES, S. J., and E. S. HOMUTH.
1910. The seat of smell in the crayfish. Biological Bulletin, 18: 155–160.

HOLMES, W.
1942. The giant myelinated nerve fibers of the prawn. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, 213B: 293–311.
1943. Innervation of crustacean muscles. Nature, London, 151 : 531 :532.

IHLE, J. E. W., and M. E. IHLE-LANDENBERG.
1939. Die Segmentierung des Crustaceen-Kopfes und der Cephalothorax der Dekapoden. Bijdragen Tot De Dierkunde, Amsterdam, 27 : 27–30.

IKEMATSU, W.
1953. On the life history of *Acetes japonicus* Kishinouye, in Ariake Sea. Bulletin of the Japanese Society of Scientific Fisheries, 19 (6) : 771–780.
1955. On the life history of *Metapenaeus joyneri* (Miers) in Ariake Sea. Bulletin of the Japanese Society of Scientific Fisheries, 20 (11) : 969.

INGRAND, M.
1937. Morphologie des pinces et caracteres sexuels secondaires de *Munida bamffica*. Travaux de la Station Biologique de Roscoff, Nouvelle Serie, Roscoff, France, 15: 57–86.

JANCARÍK, A.
1951. Antenní chemoreceptory lasturnatky *Heterocypris incongruens* (Ostracoda). Sbornik Klubu Prirodovedeckeho V Brné, Brno, Czechoslovakia, 29 (1) : 21–28.

KISHINOUYE, K.
1900. Japanese species of the Genus *Penaeus*. Journal of the Fishery Bureau, Tokyo, 8 (1) : 1–29.
1928. On the branchial organs of the Sergestidae. Proceedings of the Imperial Academy of Tokyo, 4: 489–490.

KISHINOUYE, K.—Continued
1929. Penaeid crustaceans with the asymmetrical petasma. Proceedings of the Imperial Academy of Tokyo, 5: 280–283.

KORSCHELT, E., and K. HEIDER.
1890–1893. Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere. 8vo. Jena.

KREIDL, A.
1893. Weitere Beiträge zur Physiologie des Ohrlabyrinthes. II. Mittheilung. Versuche an Krebsen. Sitzungsberichte der Kaiserliche Akademie der Wissenschaften, Wien, Abt. 3, 101: 469–489; 102 : 149–174.

KUBO, I.
1955. On mass-growth of the prawn, *Penaeus japonicus* Bate. Bulletin of the Japanese Society of Scientific Fisheries, Tokyo, 20 (10) : 870–872.

LANG, D., and C. M. YONGE.
1935. The function of the tegumental glands in the statocyst of *Homarus vulgaris*. Journal of the Marine Biological Association, United Kingdom, 20: 333–339.

LAUBMANN, A. L.
1912. Untersuchungen über die Hautsinnesorgane bei dekapoden Krebsen auf der Gruppe der Carididen. Zoologische Jahrbücher, Abt. für Anatomie, Ontogenie, 35: 105–159.

LEBOUR, M. V.
1951. Notes on some larval decapods (Crustacea) from Bermuda. II. Proceedings of the Zoological Society of London, 120: 743–747.

LEONE, C. A., and C. W. PRYOR.
1952. Serological correspondence among three species of penaeid Crustacea. Journal of the Elisha Mitchell Science Society, 68: 27–31.

LERMA, B.
1951. Note originali e critiche sulla morfologia comparata degli organi frontali degli Artropodi. Annuario dell'Instituto e Museo di Zoologia dell'Universita di Napoli, 3 (1) : 1–25.

LOWNDES, A. G.
1937. Body orientation in the Crustacea. Nature, London, 140: 241–242.

MCRAE, E. D.
1952. The shrimp fishery. Bulletin of the Texas Game and Fishery Commission, 32: 1–21.

MENON, M. K.
1952. The life history and bionomics of an Indian penaeid prawn *Metapenaeus dobsoni* Miers. Proceedings of the Indo-Pacific Fishery Council for 1951, 3 : 80–93.
1937. Decapod larvae from the Madras plankton. Bulletin of the Madras Government Museum, New Series, 3 (5) : 1–55.

MENZEL, R. W.
1955. Marking of shrimp. Science, 121: 446.

MEREDITH, S. S.
1952. A study of *Crangon vulgaris* in the Liverpool Bay area. Proceedings and Transactions of the Liverpool Biological Society, 58: 75–109.

MOCQUARD, M. F.
1883. Recherches anatomiques sur l'estomac des Crustaces podophthalmaires. Annales des Sciences Naturelles, Zoologie et Biologie Animale, 11e Série, 16 (6): 1–311.

MOLLITOR, A.
1937. Beiträge zur Untersuchung des Exkretstoffwechsels und der Exkretion von *Eriocheir sinensis* H. Milne-Edwards. Zoologische Jahrbücher, Jena, Allgemeine Zoologie, 57: 323–354.

MONTICELLI, F. S., and S. LOBIANCO.
1900. Sullo sviluppo dei Peneidi del Golfo di Napoli. Monitore Zoologico Italiano, Florence, Suppl., 11: 23.
1901. Uova e larva di *Solenocera siphonocera* Phil. Monitore Zoologico Italiano, Volume 12.
1901. Sui Peneidi del Golfo di Napoli. Monitore Zoologico Italiano, 12: 798.

MORRIS, M. C., and I. BENNET.
1952. The life history of a penaeid prawn (*Metapenaeus*) breeding in a coastal lake (Tuggerah, New South Wales). Proceedings of the Linnean Society of New South Wales, Sydney, 76 (5–6): 164–182.

MOUCHET, S.
1932. Sur l'appareil génetal mâle de *Penaeus trisulcatus* Leach. Bulletin de la Société Zoologique de France, 57: 316–340.

MÜLLER, F.
1878. Ueber die Naupliusbrut der Garneelen. Zietschrift für Wissenschaftliche Zoologie, Leipzig, 30: 163–166.

OHSIMA, Y., and D. YASUDA.
1942. An ecological note on the prawn, *Penaeopsis affinis* (Milne-Edwards). Bulletin of the Japanese Society of Scientific Fisheries, 11: 135–145.

OKADA, Y. K.
1928. Note on the tail organs of *Acetes*. Annals and Magazine of Natural History, London, 1 (10): 308–310.

PANNING, A.
1926. Uber die Statocyste des *Astacus fluviatillis* L. (*Potamobius astacus* Leach). Mitteilungen auf dem Zoologischen Staatsinstitut und Zoologischen Museum in Hamburg, 42: 118–125.

PATWARDHAN, S. S.
1935. On the structure and mechanism of the gastric mill in Decapoda. VI. The structure of the gastric mill in Natantous Macrura—Penaeidae and Stenopidea, conclusion. Proceedings of the Indian Academy of Sciences, Section B, Bangalore, 2: 155–174.

PEARSON, J. C.
1935. Eggs of a peneid shrimp. Science, Vol. 82, No. 2121.

PEREZ, C.
1929. Sur quelques caractères sexuels des Crustacés Décapodes. International Congress of Zoology, Budapest, 10: 1142–1146.

PRENTISS, C. W.
1901. The otocyst of decapod Crustacea: its structure, development, and functions. Bulletin of the Museum of Comparative Zoology, 38 (7): 167–251.

PRESSWALLA, M. J.
1933. The nervous system of *Panulirus*. Current Science, Bangalore, Vol. 2.

RAMADAN, M. M.
1938. Crustaces: Penaeidae. The John Murray Expedition, 1933–34, Scientific Reports, British Museum (Natural History), 5 (5): 123–245.

REDDY, A. R.
1937. The physiology of digestion and absorption in the crab *Paratelphusa* (*Oziotelphusa*) *hydrodromus* (Herbst). Proceedings of the Indian Academy of Sciences, 6B: 170–193.

REYNOLDS, J. M.
1937. A further contribution to the problem of segmentation in the Arthropods. American Journal of Science, New Haven, 34: 30–63.

SAMUEL, N.
1945. Some aspects of the morphology and physiology of the antennary glands of three decapod crustaceans. Journal of the University of Bombay, Science Number, Section B: Biological Sciences Including Medicine, Bombay, N. S., 14B (3): 29–41.

SCHÄFER, W.
1954. Form und Funktion der Brachyuren-Schere. Abhandlungen der Senkenbergischen Naturforschenden Gesellschaft, Frankfurt am Main, 489: 1–65.

SCHLIEPER, C.
1933. Weitere Untersuchungen über die Beziehungen zwischen Bau und Funktion bei den Exkretionsorganen Dekapoden Crustaceen. Zeitschrift für Vergleichende Physiologie, 20: 255–257.

SCHMITT, WALDO L.
1934. The Macruran, Anomuran and Stomatopod Crustacea. Bijdragen tot de Kennis der Fauna von Curacae. Bijdragen Tot de Dierkunde, Amsterdam, Vol. 23.
1935. The West American species of the shrimps of the Genus *Penaeus*. Proceedings of the Biological Society of Washington, Vol. 48.

SCHÖNE, H.
1951. Die Arbeitsweise der Statocyste von *Astacus fluviatilis*. Die Naturwissenschaften, 38 (7): 157–158.

SCHORSTEIN, M. V.
1941. The sphincter valve of the antennal gland of *Marinogammarus marinus* (Leach) sens. str. Proceedings of the Royal Society of Edinburgh, Section B, Biology, 61B: 130–137.
1943. The larval maxillary glands of *Euphausia superba* Dana. Proceedings of the Royal Society of Edinburgh, Section B, Biology, 61B: 375–384.

SEIFERT, R.
1930. Sinnesphysiologische Untersuchungen am Keimfuss (*Triops cancriformis* Bosc.). Zeitschrift für Wissenschaftliche Biologie, Abt. C. Zeitschrift für Vergleichende Physiologie, 11: 386–436.

SENOO, HIDEMI.
1910. Growth rate of *Penaeus*. Magazine of Zoology, Tokyo, 22: 91–93.

SHEN, C. J.
1934. A comparative study of the statocysts of Eumalacostraca, with special reference to the Macrura. Proceedings of the Zoological Society of London, 104: 533–557.

SJOGREN, S.
1934. Die Blütdrüse und ihre Ausbildung bei den Dekapoden. Zoologische Jahrbücher, Jena, 58: 145–170.

SORDI, M.
1941. L'apparato digerente degli eufausiacei. Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano, 80: 5–12.

SPAULDING, M. H.
1908. Preliminary report on the life history and habits of the "lake shrimp" (*Penaeus setiferus*). Bulletin No. 11, Gulf Biologic Station, Cameron, La., pp. 1–29.

TAYLOR, G. L.
1941. The optical properties of the shrimp nerve fiber sheath. Journal of Cellular and Comparative Physiology, Philadelphia, 18: 233–242.

TEISSIER, G.
1938. Un procédé practique pour la conservation à sec des gros Crustacés. Bulletin de la Société Zoologique de France, 63: 152–154.

TISCHLER, W.
1935. Untersuchungen am Statozystemapparat bei *Sergestes edwardsii*. Zoologischer Anzeiger, Leipzig, 110: 14–16.

TONNER, F.
1933a. Das Problem der Krebsschere. Zeitschrift für Vergleichende Physiologie, 19: 762–784.
1933b. Ein Beitrag zur Anatomie und Physiologie des peripheren Nervensystems von *Astacus fluviatilis*. Zoologische Jahrbücher, Allgemeine Zoologie, Jena, 53: 101–152.
1934. Ueber chemorezeptoren in der Kiemenhöhle des Flusskrebses. Zeitschrift für Zellforschung und Mikroskopische Anatomie, Berlin, 20: 423–426.

TULIAN, E. A.
1923. The present status of the Louisiana shrimp industry. Transactions of the American Fisheries Society, 53d Annual Meeting.

UCHIDA, T.
1930. Observations sur le sens de la reconnaissance du sexe chez *Asellus*. Bulletin de la Société Zoologique de France, 55: 516–520.

VIEIRA, B. B.
1947. Observações sôbre a maturação de *Xiphopenaeus kroyeri* no litoral de São Paulo. Boletim do Museu Nacional, Zoologia, Rio de Janeiro, 74: 1–22.

VIOSCA, P.
1920. Report of the biologist. Fourth Biennial Report, Department of Conservation of Louisiana, pp. 120–130.
1953. Observations on the life history and habits of the lake shrimp. Louisiana Conservationist, 5 (4): 2–5, 18.

WELSH, J. H., and F. A. CHACE.
1938. Eyes of deep-sea crustaceans. II. Sergestidae. Biological Bulletin, 74: 364–375.

WEYMOUTH, F. W., M. J. LINDNER, and W. W. ANDERSON.
1932. Summary of the life history of the common shrimp (*Penaeus setiferus*) of the South Atlantic and Gulf Coasts of the United States. Transactions of the American Fisheries Society, Vol. 62.
1933. Preliminary report on the life history of the common shrimp *Penaeus setiferus* (Linn.). Bulletin of the Bureau of Fisheries, 48 (14): 1–26.

WIERSMA, C. A. G.
1949. The innervation of the legs of the coconut crab, *Birgus latro* L. Physiologia Comparata et Oecologia, 1: 68–75.
1951. On the innervation of the muscles in the leg of the lobster, *Homarus vulgaris* Milne-Edwards. Archives Neerlandaises de Zoologie, 8: 384–392.

WILKS, R. A. C.
1938. A new decalcification fluid. Nature, London, 142: 958–959.

WILLIAMSON, D. I.
1951. Studies in the biology of Talitridae (Crustacea, Amphipoda): visual orientation in *Talitrus saltator*. Journal of the Marine Biological Association, United Kingdom, 30: 91–99.

WILLIAMS, AUSTIN B.
1953. Identification of juvenile shrimp (Penaeidae) in North Carolina. Journal of the Elisha Mitchell Scientific Society, 69 (2): 156–160.
1955. A contribution to the life histories of commercial shrimps (Penaeidae) in North Carolina. Bulletin of Marine Science of the Gulf and Caribbean, University of Miami, 5 (2): 116–146.

YOKOYA, Y.
1941. On the classification of Penaeid shrimps by the structural features of the appendix masculina. Journal of the College of Agriculture, Tokyo Imperial University, 15 (1): 45–68.

YONGE, C. M.
1932. On the nature and permeability of chitin. I. The chitin lining of the foregut of decapod Crustacea and the function of the tegumental glands. Proceedings of the Royal Society of London, Series B, 111: 298–329.

YOSHIDA, H.
1949. On the life history of *Acetes japonicus* Kishinouye. Journal of the Shimonoseki College of Fisheries, 1: 51–55. (In Japanese with English summary)
1949. On the life history of the Korean shrimp, *Penaeus orientalis* Kishinouye. Bulletin of the Japanese Society of Scientific Fisheries, 15: 245–248. (In Japanese with English summary.)

YU, S. C.
1936. Contribution a l'etude anatomique et histologique d'une crevette chinoise (*Palaemon asperulus Mart*). Chinese Journal of Zoology, 2: 101–132.

ZILCH, A.
1936. Zur frage des Flimmerepithels bei Arthropoden. Zeitschrift für Wissenschaftliche Zoologie, Leipzig, 148: 89–132.

☆ U. S. GOVERNMENT PRINTING OFFICE : 1959 O -468059

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

DECLINE OF THE YELLOWTAIL FLOUNDER (*LIMANDA FERRUGINEA*) OFF NEW ENGLAND

By WILLIAM F. ROYCE, RAYMOND J. BULLER, AND ERNEST D. PREMETZ

FISHERY BULLETIN 146

From Fishery Bulletin of the Fish and Wildlife Service

VOLUME 59

UNITED STATES GOVERNMENT PRINTING OFFICE • WASHINGTON • 1959

For sale by the Superintendent of Documents, U. S. Government Printing Office, Washington 25, D. C.
Price 55 cents

Library of Congress catalog card for this bulletin:

Royce, William F

Decline of the yellowtail flounder (Limanda ferruginea) off New England, by William F. Royce, Raymond J. Buller, and Ernest D. Premetz. Washington, U. S. Govt. Print. Off., 1959.

iv, 169–267 p. illus., diagrs., tables. 26 cm. (U. S. Fish and Wildlife Service. Fishery bulletin 146)

"From Fishery bulletin of the Fish and Wildlife Service, volume 59."

Bibliography: p. 235–236.

1. Flounders. (Series: U. S. Fish and Wildlife Service. Fishery bulletin, v. 59, no. 146)

[SH11.A25 vol. 59, no. 146] Int 59–21

U. S. Dept. of the Interior. Library
for Library of Congress

Library of Congress catalog card for the series, Fishery Bulletin of the Fish and Wildlife Service:

U. S. *Fish and Wildlife Service.*

Fishery bulletin. v. 1–

Washington, U. S. Govt. Print. Off., 1881–19

v. in illus., maps (part fold.) 23–28 cm.

Some vols. issued in the congressional series as Senate or House documents.

Bulletins composing v. 47– also numbered 1–

Title varies: v. 1–49, Bulletin.

Vols. 1–49 issued by Bureau of Fisheries (called Fish Commission, v. 1–23)

1. Fisheries—U. S. 2. Fish-culture—U. S. I. Title.

SH11.A25 639.206173 9–35239 rev 2*

Library of Congress [r55e½]

CONTENTS

	Page
Introduction	169
Commercial production of yellowtail	170
Price trends	170
Landings	170
Producing areas	171
Migrations	175
Yellowtail stocks	183
The southern New England stock	184
Landings	184
Length composition of the catch	185
Length-weight relation	192
Calculating numbers of fish landed	195
Catch per unit of effort	195
Age determination	198
Rate of growth	202
Age composition of the landings	206
Survival, mortality, and availability	210
Immediate fishing mortality	210
Mortality from tag returns in successive years	210
Mortality and apparent abundance of age groups	212
Reproduction	215
Age and length at maturity	215
Spawning season	216
Distribution of eggs and larvae	217
Faunal changes on the yellowtail grounds	228
Effects of the fishery on yellowtail stocks, 1942–49	230
Management of the yellowtail flounder	231
Conclusions	232
Summary	233
Literature cited	235
Appendix	237
A. Sources of data on landings of yellowtail, 1940–49	237
B. Methods of estimating catch by statistical subarea	238
C. Length frequencies of yellowtail by statistical subarea, quarter, and sex, 1941–47	239
D. Length and age frequencies of yellowtail from the southern New England stock, by quarter and sex, 1942–47	246
E. Yellowtail larvae taken in 1932	256
F. Probit analysis	266

ABSTRACT

The yellowtail flounder fishery off New England was studied intensively from 1942 to 1949 to determine if changes in the yellowtail population were related to fishing pressure and whether regulation of the fishery was necessary to conserve the species.

Tagging and other evidence indicated the existence of five stocks, the most important of which to United States fishermen occurred off southern New England. The landings from the southern New England stock declined from 63,000,000 pounds in 1942 to 10,000,000 pounds in 1949, but the population did not exhibit the usual symptoms of heavy fishing: a declining average size, an increasing proportion of young fish, or an increasing growth rate. Estimates of mortality and recruitment indicated that the fishery was drawing gradually on a reserve which for unknown reasons was not replenished by young.

There is no clear evidence that greater total production could have been achieved by protecting fish at any size, in any area, or at any time of year.

DECLINE OF THE YELLOWTAIL FLOUNDER (*LIMANDA FERRUGINEA*) OFF NEW ENGLAND

By WILLIAM F. ROYCE, RAYMOND J. BULLER, AND ERNEST D. PREMETZ, *Fishery Research Biologists*

As recently as 1935, fishermen of New England found little value in the yellowtail flounder (*Limanda ferruginea*), which they caught incidentally in their trawls. This fish was considered too thin to compete with the winter, or blackback, flounder (*Pseudopleuronectes americanus*) for sale in the round, and it was not as well known as the dab, or American plaice (*Hippoglossoides platessoides*), or the gray sole or witch flounder (*Glyptocephalus cynoglossus*)—species commonly sold as fillet of sole. But two things occurred to change this. The winter flounder, mainstay of the fleet of small otter trawlers in southern New England, declined so severely in abundance in the middle thirties that fishermen and filleting concerns sought a substitute. The yellowtail, abundant, readily available, and fine-flavored, satisfied this need. Then from 1940 to 1942, the increasing demand for food that accompanied World War II was reflected in an expansion of the fisheries for almost any edible species wherever war restrictions would permit. Consequently, the catch of yellowtail rose from slightly less than 23 million pounds in 1938 to approximately 70 million pounds in 1942, at which time the fishery supported a fleet of 150 small otter trawlers.

These vessels fished from ports on Long Island, N. Y., and from Connecticut, Rhode Island, and southeastern Massachusetts ports as far north as Provincetown, Mass., and the yellowtail became the principal species of fish landed. Concurrent with the diversion of vessels to the yellowtail fishery was the development of the necessary handling and filleting facilities, chiefly at New Bedford, Mass., where about 20 filleting plants began operations.

NOTE.—Dr. William F. Royce is now director of the Fisheries Research Institute, University of Washington: Raymond J. Buller is central flyway representative, Bureau of Sport Fisheries and Wildlife, and Ernest D. Premetz commodity industry analyst, Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service.

Approved for publication, September 20, 1955. Fishery Bulletin 146.

The remarkable growth of the yellowtail fishery was followed by an almost equally remarkable decline. In 1944, the annual catch had been reduced by more than half and the following 9 years produced no sign of recovery. The decline and continuing scarcity of the yellowtail caused great concern, not only because this species closely paralleled the winter flounder in its decrease in the early and middle thirties (a decline from which the winter flounder had not recovered as late as 1951), but also because the fishermen who now depended on yellowtail fishing for their principal livelihood could expect to find no other abundant species of fish of similar value within the range of their small otter trawlers.

This pronounced reduction in the catch of a species of major importance to the New England fisheries was the impetus for a more concentrated study of the yellowtail. Prior to the peak of the yellowtail fishery, the question arose of how much expansion could be expected. Now, after its decline, fishermen and the general public alike want to know if they can expect a recurrence of the yellowtail's former abundance, if regulation of the fishery is needed, or if the sad history of other depleted species is to be repeated. To answer these questions we needed to know two things: First, what sizes and numbers of fish can be expected from a given fishing effort; and second, what measures would result in the greatest return from the fishery.

We have approached the answers to these basic questions through a study of the effect of fishing on the yellowtail. Determining the effects of fishing required a delineation of the stocks and a breakdown of the catch data according to the geographical units in which the stocks were homogeneous or in which the fishing pressure was uniform. (In either case, we may assume that the effect of fishing on the stock or stocks will be uniform.) After determining what fishing grounds should be considered to constitute a more

or less homogeneous unit, we assembled data aimed at determining the relative size of the stock, the mortality due to fishing and natural causes, the growth, and the recruitment of young fish.

A complete and accurate determination of these factors would permit a precise estimate of the effect of fishing on the species. The factors vary, however, and the best we can expect from our present knowledge is an approximation; consequently, our estimates will be subject to revision as additional data become available. Therefore, we anticipate further study of the yellowtail and are making the data fully available in this report even though some appear inconclusive or irrelevant to the major problem at this time.

Little information on the habits and life history of the yellowtail is available in the literature, although naturalists and taxonomists have known the species for many years as one of a considerable group of very similar flounders of the genus *Limanda*. Species of this genus occur off northwest Europe, in the Bering Sea, and off the west coast of Canada. In the northwest Atlantic, the yellowtail (*L. ferruginea*) occurs from the northern part of the Gulf of St. Lawrence south to the vicinity of Chesapeake Bay. Its habits have been summarized by Bigelow and Schroeder (1953, pp. 271–275) and by Hildebrand and Schroeder (1928, p. 168).

Our data are the result of many people's efforts. Milton J. Lobell was assigned in 1938 to investigate the several species of flounder. His principal task was the study of the winter flounder, but he made many observations on the yellowtail. Alfred Perlmutter, from 1939 to 1942, continued the study of the winter flounder, but, recognizing the growing commercial importance of the yellowtail, he began to tag that species and obtain samples of the commercial catch. In October 1942, a study of the yellowtail was begun by William F. Royce, who was detailed to the port of New Bedford, where most of the landings were being made. He sampled the catch and interviewed fishermen for information on place of fishing and amount of fishing effort. This work was continued by Raymond J. Buller from 1946 to 1949 and by Ernest D. Premetz from 1949 to 1951. O. E. Sette made available the data on eggs and larvae of yellowtail that he had collected in connection with his investigation of the mackerel in 1929 and 1932. We also acknowledge the interest and cooperation of many fishermen, especially Captains Albert Griek and R. E. Sutcliffe.

COMMERCIAL PRODUCTION OF YELLOWTAIL

PRICE TRENDS

Before considering any of the data that may have had a bearing on the decline of the yellowtail flounder, we considered the possibility that fluctuations in the catch may have been due to changes in demand. In table 1 we have assembled data from the statistical reports of the United States Fish and Wildlife Service on the average annual prices received for yellowtail by the fishermen. The data indicate that the greatly increased production from 1938 to 1942 was accompanied by an increase in price that may well have contributed to the increased production. However, the price rose further in 1943 when production declined markedly. In late 1943, in 1944, 1945, and part of 1946, prices were fixed under wartime price regulations, and we can note only that during this period production continued to be fairly small. After controls were removed in 1946, the average price rose to 8.1 cents a pound in 1947 and continued to rise in the following years, reaching 13 cents a pound in 1951—a price almost three times that of 1942, the peak production year. Despite this incentive the fishermen produced far less in 1951 than in 1942. Thus, the production of yellowtail has declined and remained low despite increases in price that reflect larger markets and greater demand. From this we have concluded that the decline in production was not due to a decrease in demand.

TABLE 1.—*Average price received by fishermen in New England for yellowtail, by years, 1938–51*

Year	Price per pound (cents)	Year	Price per pound (cents)
1938	[1] 2.0	1945	5.9
1939	[1] 2.0	1946	7.0
1940	[1] 3.2	1947	8.1
1941	[2] 2.4	1948	9.2
1942	4.5	1949	9.5
1943	7.0	1950	10.6
1944	6.4	1951	13.0

[1] Includes small quantities of sand dab (*Hippoglossoides platessoides*).
[2] Price at principal ports of Gloucester, Boston, and Portland only.

LANDINGS

Detailed records on the landings of most species of fish in the northeastern United States are

available from the published reports of the United States Fish and Wildlife Service. Since 1938, when the several species of flounders were separated in the statistics, these records show landings of yellowtail from Maine to New Jersey (table 2). From north to south, the ports of landing have included Gloucester, Boston, Plymouth, Provincetown, Chatham, Woods Hole, New Bedford, Point Judith, Stonington, Montauk, and New York City, with a few smaller ports receiving minor quantities. Since 1941, 50 percent or more of the yellowtail catch has been landed at New Bedford, Mass., with no other port even close in total volume.

TABLE 2.—*Annual United States landings of yellowtail, by ports and years, 1938–49*

[In thousands of pounds; see appendix A, p. 237, for source of the data]

Year	Maine	Massachusetts				Rhode Island	Connecticut	New York City	Long Island and New Jersey	Total [1]
		Gloucester	Boston	Cape Cod and Plymouth	New Bedford					
1938	301	108	3,012	7,794	6,071	364	1,781	2,041	1,343	22,815
1939	222	642	3,679	5,621	10,720	397	3,129	3,725	591	28,726
1940	827	2,380	4,587	3,866	17,519	1,059	4,090	4,183	2,361	40,872
1941	276	2,058	3,133	4,394	28,327	334	4,246	6,440	2,481	51,689
1942	26	3,277	2,328	5,605	36,722	2,420	6,193	8,568	3,439	68,578
1943	46	1,152	1,782	4,484	25,479	2,052	3,605	4,027	3,160	45,787
1944	127	901	964	2,999	14,354	3,027	3,187	1,428	4,090	31,077
1945	73	1,139	4,208	3,173	15,838	2,852	2,801	521	2,564	33,169
1946	37	486	3,268	2,680	17,128	2,240	3,171	394	1,917	31,321
1947	91	441	3,238	2,564	20,822	2,259	3,006	821	2,512	35,754
1948	118	635	3,258	2,320	25,214	3,293	1,352	1,201	1,577	38,968
1949	120	567	1,702	2,338	19,652	[2] 1,956	[2] 995	[2] 1,072	[2] 1,408	[2] 29,810

[1] Slight discrepancies occur due to rounding off of the figures.
[2] Includes some estimates.

PRODUCING AREAS

In order to determine the catch of yellowtail from each stock as defined on page 183, the locality fished was determined for each vessel landing at each port. Source of the catch has been obtained for all species of fish for many years at the principal ports of Boston, Gloucester, and Portland, and since 1942 at the port of New Bedford, where the collection of such information was commenced especially for the study of the yellowtail. At these ports the captain or mate of each vessel was interviewed to learn where he fished, how long he fished, and what he caught. His catch was then allocated to its statistical area (fig. 1), according to the system described by Rounsefell (1948).

At the smaller ports of Plymouth, Provincetown, Chatham, Stonington, Point Judith, and Montauk Point, the vessels were smaller and fished closer to port. Usually, after interviews with a few fishermen each year, the catch landed at these ports could be allocated satisfactorily to the one or two statistical areas concerned. At a few other ports, where the vessels were larger and interviews with the fishermen indicated that they fished with the New Bedford fleet, the landings were allocated among statistical areas in proportion to the New Bedford landings. The methods of allocation are listed in appendix B, page 238 and the resulting data are given in table 3.

Table 3 is the basis for many of the computations in this paper that concern the yellowtail populations, and it will be referred to repeatedly. At this point we note merely the following points: First, that the largest but also greatly fluctuating catches have come from the adjoining statistical subareas O, Q, S, and R, which are south of Massachusetts and Rhode Island; second, that moderate quantities of yellowtail have consistently been caught near Cape Cod in subareas E and G; and third, that the catches from Georges Bank, subareas H, J, M, and N, greatly increased from 1946 to 1949.

These statistical subareas, separated by major ecological and political boundaries, necessarily include a wide range of depth zones and bottom types, and thus give rather a poor idea of the ecological conditions preferred by the yellowtail. To provide more precise knowledge of the localities inhabited by this flounder, we have made a special study of the catch landed at New Bedford during 1943 and 1947 and allocated it to smaller

TABLE 3.—*United States landings of yellowtail, by month and fishing area, 1942–49*

[In thousands of pounds]

Date	Statistical area— Nova Scotian Banks (XXI)	New England Banks (XXII) B-C-D	E	G	H	J	M	N	O	Q-R	S	Off Long Island (XXIII)	Total [1]
1942													
January	8	3	261	16	371		21	16	74	3,986	571	250	
February		2	265		16		10	2	28	2,263	1,088	340	
March		4	320	28	50	1	69	3	3,419	918	1,836	583	
April	6	7	38	197	12	93	495	2	943	886	3,316	465	
May	17		25	115	11	65	144	12	374	1,129	1,210	134	
June			45	197	8	72	23	2	50	3,221	1,113	214	
July	9	1	61	163	2	27	14		645	4,618	479	240	
August			18	355	5	10	19		3,931	3,042	287	143	
September		1	36	629		7	24		4,632	471	190	96	
October			84	42		3	21		6,303	804	519	260	
November		8	168	3	8	6	77	20	1,841	1,690	525	252	
December			224	40	625		4	15	6	2,541	539	332	
Total	40	26	1,545	1,785	1,108	284	921	72	22,246	25,569	11,673	3,309	68,578
1943													
January	1	5	235	5	784		8	25	1,338	2,542	752	273	
February		24	257	14	208		5	2	1,613	1,289	674	279	
March		5	149	276	12		46	46	2,473	1,146	923	387	
April	11	12	68	69	8	89	398	26	360	1,677	627	329	
May	32		95	165	55	86	226	23	242	722	458	207	
June	38	6	55	83	25	69	124	26	230	1,601	301	100	
July	12	3	52	78	171	20	61		135	3,016	283	104	
August	40		56	138	2	3	27	8	1,739	3,496	355	180	
September	1	2	31	56	1	6	19		3,945	726	205	103	
October	2	5	157	54		11			1,885	106	94	81	
November	159	3	561	16	11	8	83	60	119	1,578	144	79	
December	25	10	160	1	2				100	186	339	236	
Total	321	74	1,876	955	1,279	292	997	216	14,179	18,085	5,155	2,358	45,78
1944													
January		10	298	51	1,480		73	42	55	2,190	1,015	441	
February	2	8	220	78	360		15	48	567	1,677	1,133	353	
March		8	212	172	691	9	69	15	1,003	786	1,252	415	
April	11	7	164	163	19	45	91	18	284	635	1,101	498	
May	69	11	133	236	62	24	28	35	41	341	514	246	
June	12	6	37	67	13	21	8	16	49	393	359	176	
July	60		56	244	9	8	3	14	49	1,630	682	280	
August	24		70	188	3	13	26	15	727	1,514	433	240	
September	2	2	121	100	2	5	10		92	41	12	6	
October	34		153	138	2	7	4	2	14	169	309	155	
November	148	3	262	14	11	8	40	8	52	243	328	206	
December	246	13	99	59	277		13	8	16	231	272	121	
Total	608	68	1,825	1,510	2,929	140	380	221	3,009	9,850	7,410	3,137	31,087
1945													
January	93		125	16	945		13	19	113	593	422	195	
February	30		333	30	507		3	3	361	706	347	159	
March	20	3	170	283	172	3	13	5	816	1,668	626	291	
April	57	2	105	299	21	26	61	22	133	207	224	88	
May	517	5	137	165	39	9	4	58	120	161	120	53	
June	532		38	79	46	33	3	47	130	167	56	28	
July	684	1	18	54	24	23	53	24	109	813	731	174	
August	564		23	59	31	23	461	8	148	2,052	126	60	
September	191	2	39	57	3	36	58	2	588	1,900	48	24	
October	1,037		69	109	11	11	12		2,373	635	142	71	
November	575	14	196	6	27		28	34	1,457	2,031	408	177	
December	434	3	128	16	41	4	2	22	188	296	364	162	
Total	4,734	30	1,381	1,173	1,867	168	711	244	6,536	11,229	3,615	1,482	33,169
1946													
January	13	3	222	54	385		1	32	445	419	862	397	
February	1		262	19	150	2	6	4	209	444	331	160	
March	1		82	334	26	7	32	25	980	1,143	809	367	
April	26		57	277	29	13	38	49	45	76	308	154	
May	110	5	59	180	25	35	84	79	49	67	263	132	
June	266		151	65	50	14	5	10	27	355	888	268	
July	759	1	103	108	16	5	17	25	95	1,730	260	77	
August	544	5	75	107	7	16	167	69	1,102	290	78	39	
September	29	2	72	112	3	25	2		1,248	292	104	52	
October	92	4	87	70	3	17	45	17	2,220	642	279	145	
November	560	3	131	12	45	38	159	2	1,422	753	445	145	
December	336	7	114	21	64	15	52	3	10	2,469	494	278	
Total	2,737	30	1,415	1,359	803	187	608	315	7,852	8,680	5,121	2,214	31,321

[1] Slight discrepancies occur due to rounding off of the figures.

TABLE 3.—*United States landings of yellowtail, by month and fishing area, 1942–49*—Continued

[In thousands of pounds]

Date	Statistical area—												Total [1]
	Nova Scotian Banks (XXI)	New England Banks (XXII)										Off Long Island (XXIII)	
		B-C-D	E	G	H	J	M	N	O	Q-R	S		
1947													
January	62	3	154	31	126	5	35	94	231	2,172	221	17	
February	22	2	13	29	42	22	132	71	199	453	69	16	
March	36	20	131	40	45	12	107	72	300	1,494	215	28	
April	82	15	165	70	55	80	270	94	286	846	240	29	
May	305	3	50	72	100	31	63	96	273	588	183	14	
June	428	.....	50	86	59	39	37	103	263	964	453	26	
July	323	2	110	444	40	18	26	124	189	1,792	541	381	
August	94	.....	47	178	40	14	29	47	1,278	401	53	18	
September	24	1	142	72	40	12	22	910	2,098	473	71	20	
October	39	1	134	50	57	14	79	745	2,446	1,391	101	23	
November	85	1	99	43	112	7	46	73	292	2,198	138	17	
December	136	1	122	55	616	7	39	69	241	2,395	524	45	
Total	1,636	49	1,217	1,170	1,332	261	885	2,498	8,096	15,167	2,809	634	35,754
1948													
January	40	2	108	40	285	9	48	190	190	1,102	595	122	
February	96	2	95	12	149	4	60	267	263	685	167	145	
March	34	2	84	8	19	2	58	191	276	650	400	378	
April	27	3	204	21	20	68	81	172	378	399	430	67	
May	754	.....	77	29	46	7	229	180	473	379	113	61	
June	1,133	2	86	30	95	10	61	165	258	555	336	600	
July	377	11	115	42	36	21	152	188	1,120	914	471	757	
August	102	.....	56	37	25	8	235	2,817	962	207	34	55	
September	59	.....	71	49	40	9	709	2,195	1,244	285	68	80	
October	76	.....	49	48	29	5	140	2,724	1,369	288	70	81	
November	192	1	64	26	49	20	118	220	2,376	550	40	59	
December	247	.....	83	30	52	13	65	186	264	1,431	59	66	
Total	3,137	23	1,092	372	845	176	1,956	9,495	9,173	7,445	2,783	2,471	38,968
1949													
January	14	4	176	85	265	11	209	107	225	887	48	2	
February	8	1	160	82	111	3	236	97	570	794	36	2	
March	9	5	108	145	162	6	417	104	585	280	17	2	
April	131	5	140	140	33	47	300	109	142	132	130	2	
May	49	2	61	136	146	17	164	113	111	64	40	1	
June	56	3	74	102	165	16	236	343	269	94	31	30	
July	44	1	67	115	59	12	272	928	156	131	179	11	
August	21	.....	34	103	37	6	2,523	1,021	392	117	16	2	
September	8	.....	49	153	45	46	2,304	95	848	93	13	2	
October	36	9	165	123	33	3	2,414	624	377	125	15	2	
November	228	13	144	124	42	5	1,043	338	964	343	16	2	
December	47	3	127	98	66	4	234	526	965	996	20	26	
Total	651	46	1,305	1,406	1,164	176	10,352	4,405	5,604	4,056	561	84	29,810

[1] Slight discrepancies occur due to rounding off of the figures.

areas, or unit areas, which are rectangles of 10 minutes of latitude or longitude to a side and enclose an area of about 70 square miles. Thus, for about 60 percent of the catch we have determined the actual unit areas fished. By assuming that this distribution of the catch was representative of the fishing from all ports during 1943 and 1947, the total catch for each subarea was allotted among the unit areas. Figure 2 shows the localities fished and the catches made during 1947. The fishing grounds of 1943 were almost identical with those of 1947 and therefore have not been shown.

Most of the catch came from near the 20-fathom contour from south of Montauk Point to south of Nantucket Shoals, with smaller quantities taken on Georges Bank, in the vicinity of Cape Cod, and farther north in the Gulf of Maine. Most of the catch was taken between 15 and 35 fathoms, although moderate quantities were taken out to a depth of 45 fathoms. This is the preferred depth range of the species if we assume that these fishing grounds represent the areas inhabited by most of the yellowtail. This assumption is reasonable, because there are very few localities too rough to trawl and most of the Continental Shelf is heavily fished for other species. The chance of yellowtail concentrations remaining undiscovered is extremely small.

The ocean bottom in the areas of yellowtail

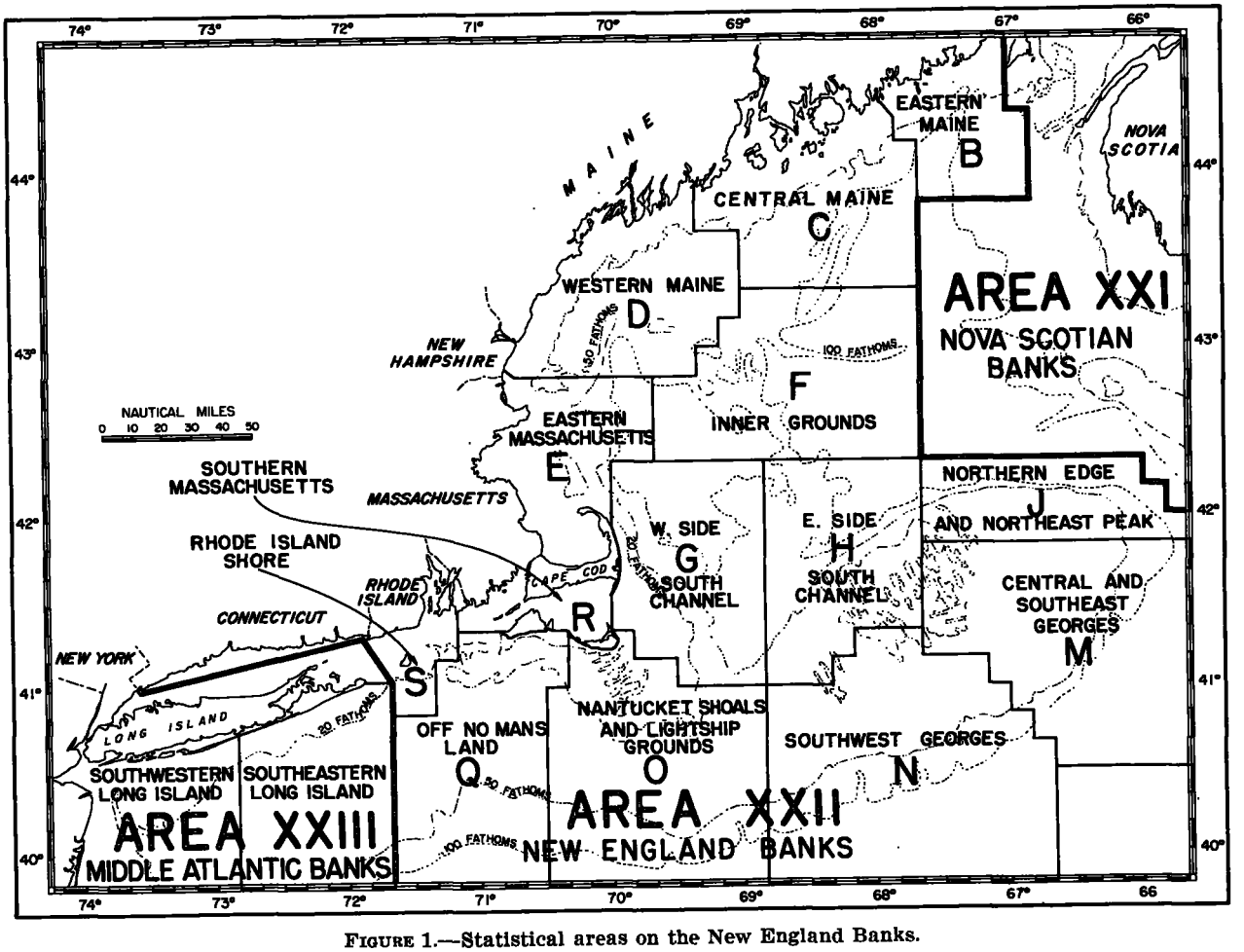

FIGURE 1.—Statistical areas on the New England Banks.

concentrations usually is indicated on the charts as sand, sand and gravel, gray sand, or sand and shell. Sand appears to be the constant ingredient, and it is significant that the distribution of the yellowtail corresponds closely to the location of the near-shore sand zone delineated by Stetson (1938). He describes the bottom sediments encountered in a section running approximately due south from Martha's Vineyard, and he states (p. 14)—

> At the six-mile mark, in 27.5 meters of water * * *. Relatively coarse sands are encountered, interspersed with finer, from this point seaward until 48 meters of water is reached 18 miles from shore. This belt of coarse material, flanked on either side by finer sediment, occurs in the other traverses in the same relative position * * *. The sand is heavily stained with limonite and is much redder than the beach material * * *. From the sixteen-mile point onward the red stain disappears * * * it seems probable that the sediments throughout this zone are being strongly worked upon by bottom currents which vary greatly in velocity from place to place.

Stetson further reports that this near-shore zone of coarse sand was found in 10 to 29 fathoms in a section running slightly east of south from Block Island.

Our method of recording yellowtail-catch areas does not permit a precise statement of their depths, but the unit areas south of the center of Martha's Vineyard that produced yellowtail include charted depths to 27 fathoms, with those south southeast of Block Island running to 37 fathoms. Furthermore, the fishermen reported that very few fish were caught in less than 15 fathoms. Thus, the zones of coarse reddish sand and of yellowtail catch are in fairly good agreement, but perhaps better evidence of such a relation is to be found in the coloration of this

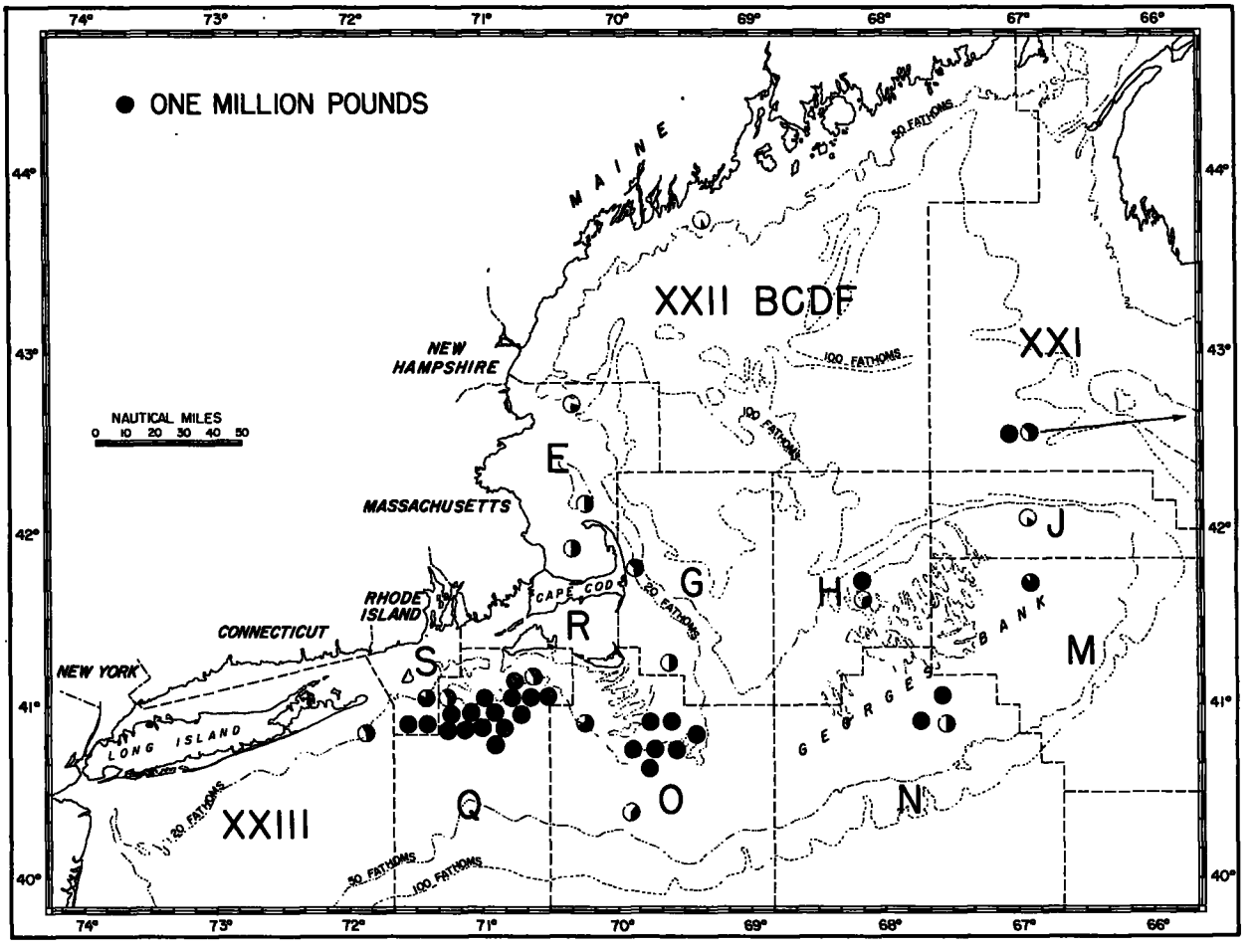

FIGURE 2.—Yellowtail flounder fishing areas and catch during 1947. Solid dots indicate 1 million pounds taken; partial dots represent fractions of 1 million pounds.

flounder which, like others of the group, adjusts its color quickly to the bottom type. Characteristically, on most grounds where it is taken, the yellowtail is speckled with rusty red spots from ½ to 1 centimeter in diameter; hence, its other common name, rusty dab.

With a preference for coarse, reddish sand in 15 to 35 fathoms of water, the yellowtail of commercial size on many of the grounds are surrounded by water depths and bottom types that may be a deterrent if not a bar to migration. The Fundian Channel, more than 100 fathoms deep, separates the Georges and Nova Scotian Banks; the South Channel with a minimum, central depth of 36 fathoms separates Georges Bank from the Nantucket Shoals region and only a narrow and tenuous strip of between 15 and 35 fathoms exists around Cape Cod and Nantucket Shoals. Thus it would appear that movement of yellowtail populations among these areas may be sparse or lacking.

MIGRATIONS

The yellowtail in northwest Atlantic waters has been described as a single species with a range from Labrador to Virginia. While morphological differences between populations of the yellowtail may exist,[1] we believe that they are slight in the fishing areas from Maine to New Jersey. Therefore, we have not attempted to show morphological differences, but we have relied on tagging to indicate the extent of intermingling and the heterogeneity of the populations.

[1] Scott (1954) has demonstrated differences in the relative size of the head, right pectoral fin, left otolith, and dorsal and anal fin-ray numbers between Nova Scotian and Cape Cod yellowtail.

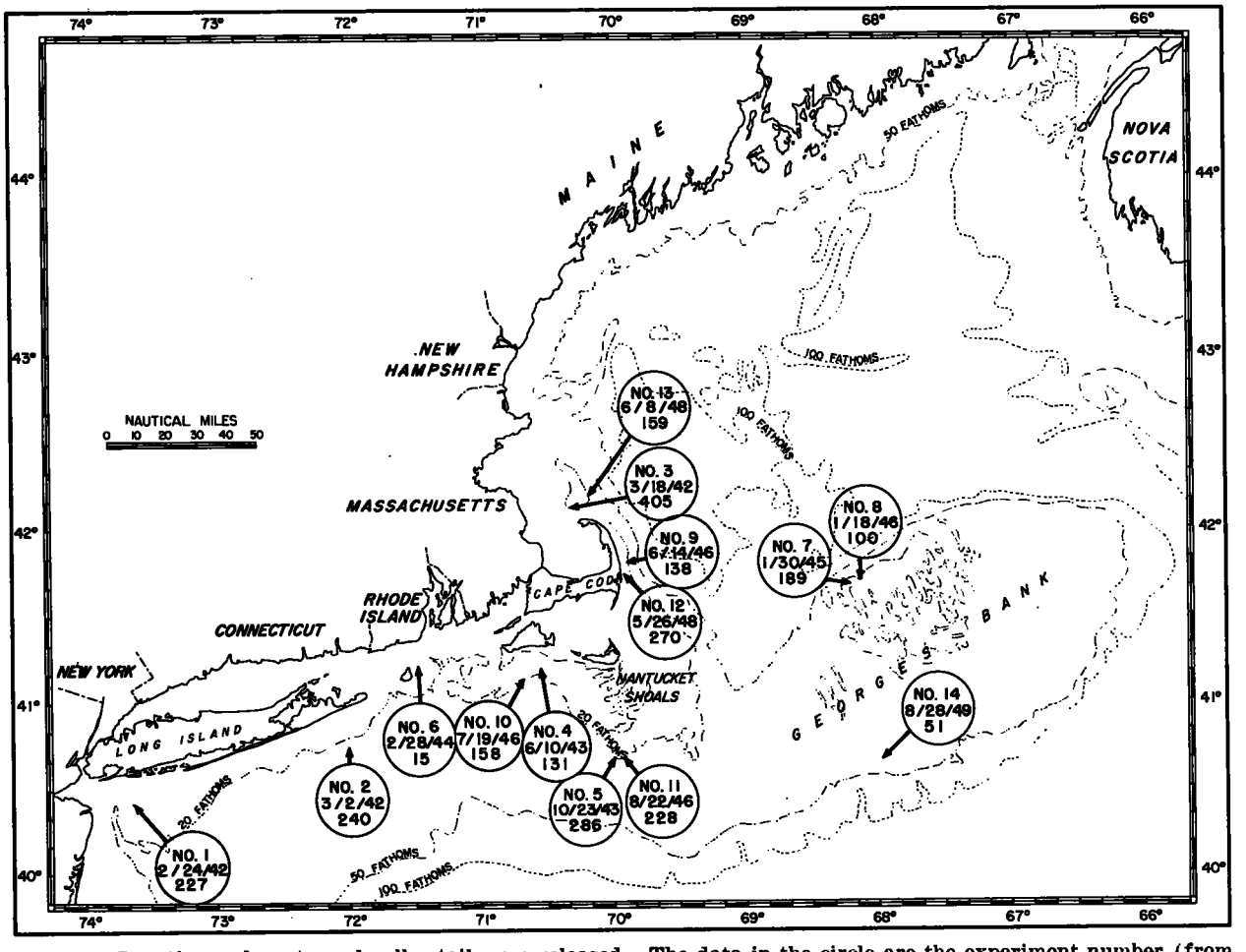

FIGURE 3.—Locations where tagged yellowtail were released. The data in the circle are the experiment number (from table 4), the date released, and the number released.

In discussing these groups of yellowtail we shall use the word "population" to mean an assemblage of yellowtail in a small area at a definite time. The time specification is important because it appears that different populations are found in an area at different times. We shall use the word "stock" to specify larger groups of yellowtail consisting of several intermingling populations all of which can be fished by a single fleet of vessels.

Between February 27, 1942, and August 31, 1949, a total of 2,597 yellowtail was tagged and released (table 4, fig. 3) on all of the major United States fishing grounds. Recaptured through December 1952 were 377, or 14.5 percent.

A tag consisting of two cellulose-nitrate disks joined by a pure nickel pin was placed on each fish selected for tagging. This tag had been successfully used with winter flounders (Perlmutter 1946), which are very similar to the yellowtail in body shape and habits. The disk was ½ inch in diameter and bore a serial number and instruction to the finder regarding return of the tag. The tag was attached by pushing the pin through the muscular part of the fish's body about 1½ inches behind the head and ¾ inch from the base of the dorsal fin. The pin was looped over with pliers leaving about ⅛ inch for growth between the disks and the body of the fish.

The finder was paid $1 for return of the tag, but this was not always enough to stimulate a busy fisherman to send in the tag. In the early part of the program a considerable proportion of the returns came from filleters and other handlers. By increasing our personal contact with the fishermen, however, we obtained more tags from them, as well as more complete information concerning the recapture.

TABLE 4.—*Returns from 2,597 tagged yellowtail flounder, by lot and locality, 1942–52*

[Roman numerals and letters refer to international areas and subdivisions as shown in figure 1]

Time of recapture	Number of fish recaptured in area—												Total
	XXIII		XXII									Unknown	
	Southwestern Long Island	Southeastern Long Island	S	Q	O	G	E	D	H	M	N		
Lot No. 1 (227 fish released 8 to 9 miles south of Jones Beach, N. Y., Feb. 24, 1942, in area XXIII, southwestern Long Island):													
Year 1942:													
February	3												3
March	9												9
April	3												3
June			4	1								3	8
July		1	1	9								1	12
August				5								4	9
September				4								1	5
October				1	3							2	6
November		1										1	2
December					1								1
Year 1943:													
January	1												1
February	1												1
April	1												1
July				3									3
August				4								1	5
September					1								1
October					1								1
Year 1944:													
January	1												1
March												1	1
May												1	1
November												1	1
Year 1945: September				1									1
Year 1946:													
January	1												1
June												1	1
Total	20	2	5	28	6							17	78
Lot No. 2 (240 fish released 16 to 20 miles southwest of Montauk Point, N. Y., Mar. 2, 1942, in area XXIII, southeastern Long Island):													
Year 1942:													
March		1	2									2	5
April		1	3									5	9
May		1	2	1								2	6
June			1	3								1	5
July				5								2	7
August				1								2	3
October				2	1							2	5
November				1									1
December												2	2
Year 1943:													
January		1		1									2
February		1	1										2
May			1										1
November												1	1
Year 1944:													
March		1											1
August												1	1
Total		6	10	14	1							20	51
Lot No. 3 (405 fish released 5 miles northwest of Race Point, Mass., Mar. 18, 1942, in area XXII, E):													
Year 1942:													
March							9					7	16
April							3					1	4
May							1					1	2
July							1						1
Year 1943: March							1						1
Total							15					9	24
Lot No. 4 (131 fish released 16 miles east southeast of No Mans Land, Mass., June 10, 1943, in area XXII, Q):													
Year 1943:													
June				1								1	2
August				2									2
September				1	1							1	3
Year 1944:													
January												1	1
April			1										1
Year 1945: August				1									1
Year 1946: January	1												1
Total	1		1	5	1							3	11

TABLE 4.—*Returns from 2,597 tagged yellowtail flounder, by lot and locality, 1942–52*—Continued

Time of recapture	Number of fish recaptured in area—												Total
	XXIII		XXII									Unknown	
	Southwestern Long Island	Southeastern Long Island	S	Q	O	G	E	D	H	M	N		
Lot No. 5 (286 fish released, off Nantucket Shoals 47 miles southeast by south of No Mans Land, Oct. 22–24, 1943, in area XXII, O):													
Year 1943: October					12							2	14
Year 1944:													
January												1	1
February												1	1
March					1								1
April			1	1									2
Year 1945:													
April												1	1
November												1	1
No date												1	1
Total			1	1	13							7	22
Lot No. 6 (15 fish released 8 miles south by east of Point Judith, Feb. 28–29, 1944, in area XXII, S):													
Year 1944:													
March			1										1
July												1	1
Total			1									1	2
Lot No. 7 (189 fish released 3 miles west of Cultivator Buoy, Georges Bank, Jan. 28–31, 1945, in area XXII, H):													
Year 1945:													
January									7				7
February									8			4	12
March									2				2
April												1	1
Year 1946: January									1				1
Year 1949: January									1				1
Total									19			5	24
Lot No. 8 (100 fish released 2 miles east of Cultivator Buoy, Georges Bank, Jan. 17–18, 1946, in area XXII, H):													
Year 1946:													
January									2			2	4
February									1				1
March									1				1
Year 1947: October									1				1
Total									5			2	7
Lot No. 9 (138 fish released 5 to 8 miles south southeast of Nauset Beach Light, June 14, 1946, in area XXII, G):													
Year 1946:													
June												2	2
July												2	2
August					1	3						1	5
September						1							1
November												1	1
December												1	1
Year 1947:													
January												1	1
March						2						2	4
April						1						3	4
May												1	1
June												1	1
August						1							1
September						1							1
October								1					1
November							1						1
Year 1948:													
January							1						1
February												1	1
April							1						1
June												2	2
December						1							1
Year 1949: April						1							1
Year 1951: March												1	1
Year 1952: May						1							1
Total					1	12	3	1				19	36

TABLE 4.—*Returns from 2,597 tagged yellowtail flounder, by lot and locality, 1942–52*—Continued

Time of recapture	Number of fish recaptured in area—											Total
	XXIII		XXII								Unknown	
	Southwestern Long Island	Southeastern Long Island	S	Q	O	G	E	D	H	M	N	
Lot No. 10 (158 fish released 14 miles southeast of No Mans Land, July 19, 1946, in area XXII, Q):												
Year 1946:												
July				7								7
August				4	3						2	9
September				3	2						2	7
October											1	1
November			1								1	2
Year 1947:												
January											1	1
August				1								1
October											1	1
Year 1948: August			1									1
Total			2	15	5						8	30
Lot No. 11 (228 fish released off Nantucket Shoals 50 miles southeast ½ mile south of No Mans Land, Aug. 21–23, 1946, in area XXII, O):												
Year 1946:												
August				16							5	21
September			1	5							7	13
October			1	4								5
November											1	1
December			2									2
Year 1947:												
January			1									1
July			3	1								4
August					1						1	2
September					1							1
December				1							1	2
Year 1948: March											1	1
Total			8	27	2					1	15	53
Lot No. 12 (270 fish released 3 miles southeast of Nauset Harbor, May 26–27, 1948, in area XXII, G):												
Year 1949:												
February						1					1	2
March											2	2
April						1					2	3
Year 1951: January							1					1
Total						2	1				5	8
Lot No. 13 (159 fish released 5 miles north 10 miles north northeast of Race Point, June 8, 1948, in area XXII, E):												
Year 1948:												
July							1					1
November											1	1
Year 1949:												
January											1	1
March							1					1
June											1	1
November							1					1
Year 1950:												
January							1					1
February											1	1
March											1	1
Year 1951: July							1					1
Total							5				5	10
Lot No. 14 (51 fish released 65 miles east and 105 miles east ¼ south of Nantucket Lightship, Aug. 28–31, 1949, in area XXII, N):												
Year 1949:												
August											2	1	3
September											1	1	2
October											1		1
November											2		2
Year 1950:													
January				1									1
February					1						1		2
March												1	1
April												1	1
June									1				1
July											1	1	2
August											1	2	3
October												1	1
Year 1952: December				1									1
Total				2	1				1		9	8	21

Fortunately, our difficulties with the tags and pins were not nearly as serious as those reported by Calhoun, Fry, and Hughes (1951, p. 310). They reported that at the end of 7 months in an aquarium "19 of the 20 tags in which the nickel pins had been used had fallen off as a direct result of pin corrosion." In our experiments with yellowtail we recovered 1 tagged specimen after it had been out 5 years and 11 months, and 58 of our 377 recaptures were made after a year at sea. Of 52 of the tags that had been out more than 1 year (all of which were available for examination), pin corrosion was evident in only 2, which were out 3 years and 5 months, and 2 years and 8 months. Of course, flounders that had lost their tags could not be distinguished in the commercial catch, but if corrosion had been a serious problem many more partly corroded pins should have been recovered. However, the finding of even 2 corroded pins indicates that some tags probably were lost and this probability must be considered in estimates of mortality from the tagging data.

The yellowtail collected for tagging were caught with otter-trawl nets from commercial vessels prior to June 1946, and subsequently from the Fish and Wildlife Service vessels *Skimmer* and *Albatross III* (except lot No. 11 released in August 1946). Naturally, only lively fish were selected for release, although with the Service vessels it was possible to make short tows and give the fish much better handling. Even when the fish were given the best of handling and appeared to be in good condition, many were slightly injured and probably some mortality occurred. Manzer (1952), who tagged Pacific coast flounder with the Petersen disk tag, found considerable mortality even under the best conditions.

Most of the yellowtail released from the Service vessels were classified in three groups according to the degree of visible injury (table 5): those with no injury apparent under casual examination (0); those with marks less severe than the following (1); those with more than three splits in fins, or with any part of a fin missing, or with red marks on the white side more than 2 millimeters wide, or with more than 2 square centimeters of scales missing from the dark side (2). All fish showing severe injury or any lethargy were rejected.

Large differences were found in the recovery rates of the three groups. Fish from the 0 group, not noticeably injured, were recovered at a rate of 19.7 percent, from the 1 group, 13.1 percent and the 2 group, only 3 percent. The chi-square value of the smaller difference between groups 0 and 1 is 4.32, a statistically significant value. In addition to such direct evidence, the low returns from one release off Cape Cod (lot No. 3, 5.9 percent), which was tagged under severe weather conditions in a heavily fished area, suggest that considerable mortality due to tagging occurred. Obviously, our methods of handling killed some of the tagged fish and, equally obvious, in future experiments only completely uninjured fish should be used even though others may be lively.

TABLE 5.—*Recaptured yellowtail classified by degree of injury at time of tagging*

[Based on lot Nos. 9, 10, 12, 13, and 14]

Degree of injury	Number tagged	Recaptured	
		Number	Percent
0	213	42	19.7
1	329	43	13.1
2	203	6	3
Total	745	91	

Evidence of a regular seasonal migration is provided by the recovery of yellowtail (lot No. 1) released off Jones Beach, N. Y., in February 1942 (table 4). These fish were recaptured on the principal fishing grounds off No Mans Land and Nantucket (fig. 4) in the summers of 1942, 1943, and 1945, and back near the point of their release in the winters of 1943, 1944, and 1946. These winter recaptures are especially significant because the majority of the landings in the winter fishery originated from the grounds off No Mans Land and Nantucket Shoals (table 3). This indicates that the fish tagged off Jones Beach are not a part of the stock found off Nantucket Shoals and No Mans Land in the winter, and suggests that the population found off Nantucket and No Mans Land in the summer differs from the winter population of the same place.

A similar pattern of migration is evident from the recaptures of yellowtail released off Montauk Point (fig. 4). These tagged fish were taken to the east of No Mans Land and Nantucket Shoals during the summer of 1942 and back off Montauk Point in the winters of 1943 and 1944. It may be significant that no fish released off Montauk Point were recaptured off Jones Beach. It appears

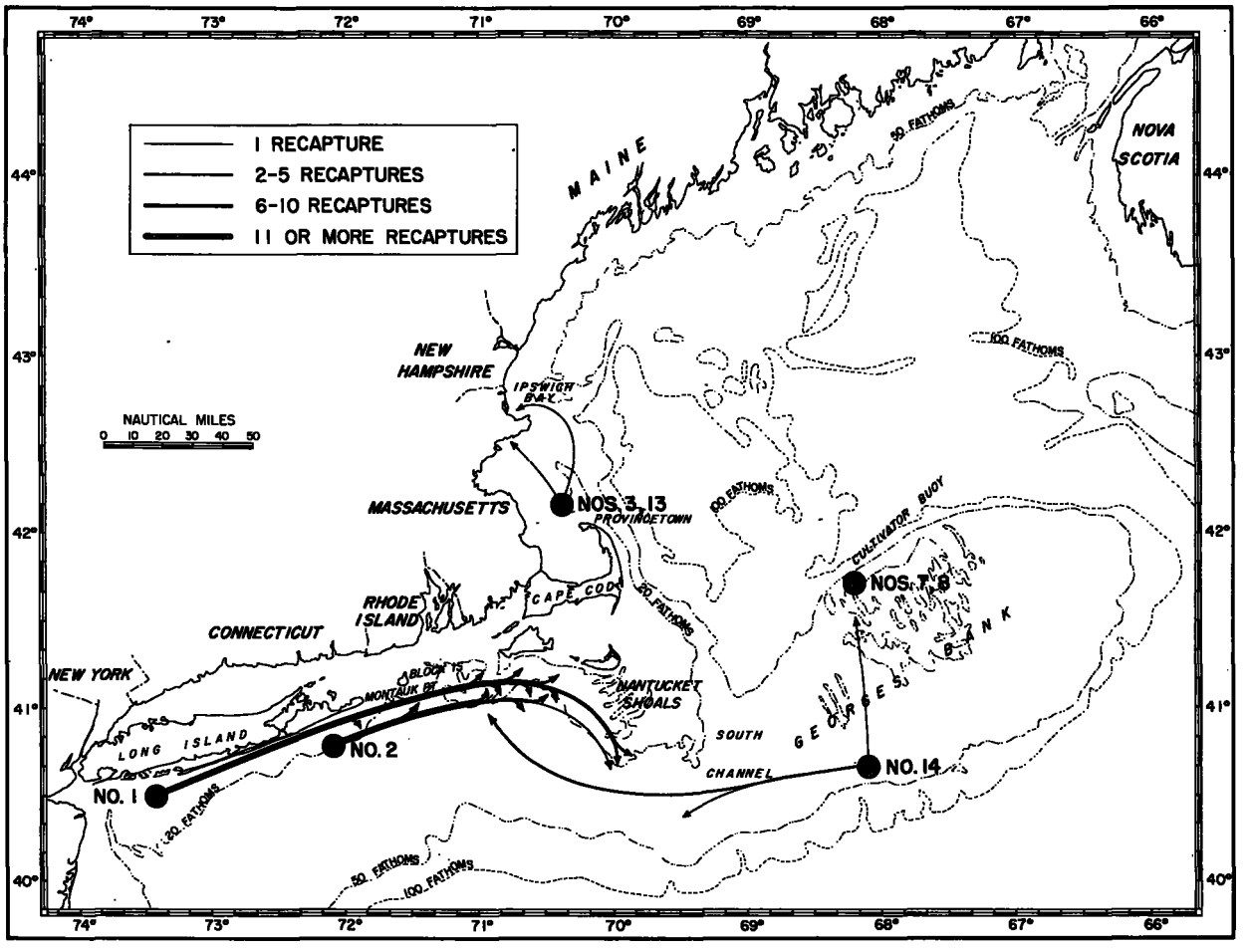

FIGURE 4.—Distant recaptures of yellowtail released off Jones Beach (No. 1), Montauk Point (No. 2), Provincetown (Nos. 3 and 13), and east of Nantucket Lightship (No. 14).

probable that the fish from Montauk Point mingled with those from Jones Beach on the grounds off southern Massachusetts during the summer and separated from them in the winter on the westward migration.

Recaptures from the yellowtail released off No Mans Land and Nantucket Shoals during the summer and fall months of 1943 and 1946 (fig. 5) were almost all made in the area where the fish had been released or in the areas between Block Island and Nantucket Shoals. Only one flounder was caught westward off Jones Beach and only one moved eastward to be caught on Georges Bank.

The yellowtail that were released off Race Point on the tip of Cape Cod (fig. 4) remained in the eastern Massachusetts area, although one was caught as far north as Ipswich Bay, just north of Gloucester. Those fish tagged off Nauset Beach ranged farther (fig. 5): one moved across Nantucket Shoals to be recaptured south of Nantucket, one was caught off Maine, and other yellowtail were taken in Cape Cod Bay near Plymouth, Mass.

Those released in the Cultivator Buoy region on Georges Bank (lot Nos. 7 and 8) were recaptured in the same area, one of them 4 years later. Thus, there was no evidence of migration from this area, even though we suspect that these fish must mix to some extent with those on the other parts of Georges Bank.

The yellowtail tagged on the southwestern part of Georges Bank, east of Nantucket Lightship (fig. 4), were mostly recaptured in the area of release, but one had migrated to the Cultivator Shoals area and three moved westward to cross South Channel and were taken south of Nantucket and off No Mans Land. These three fish

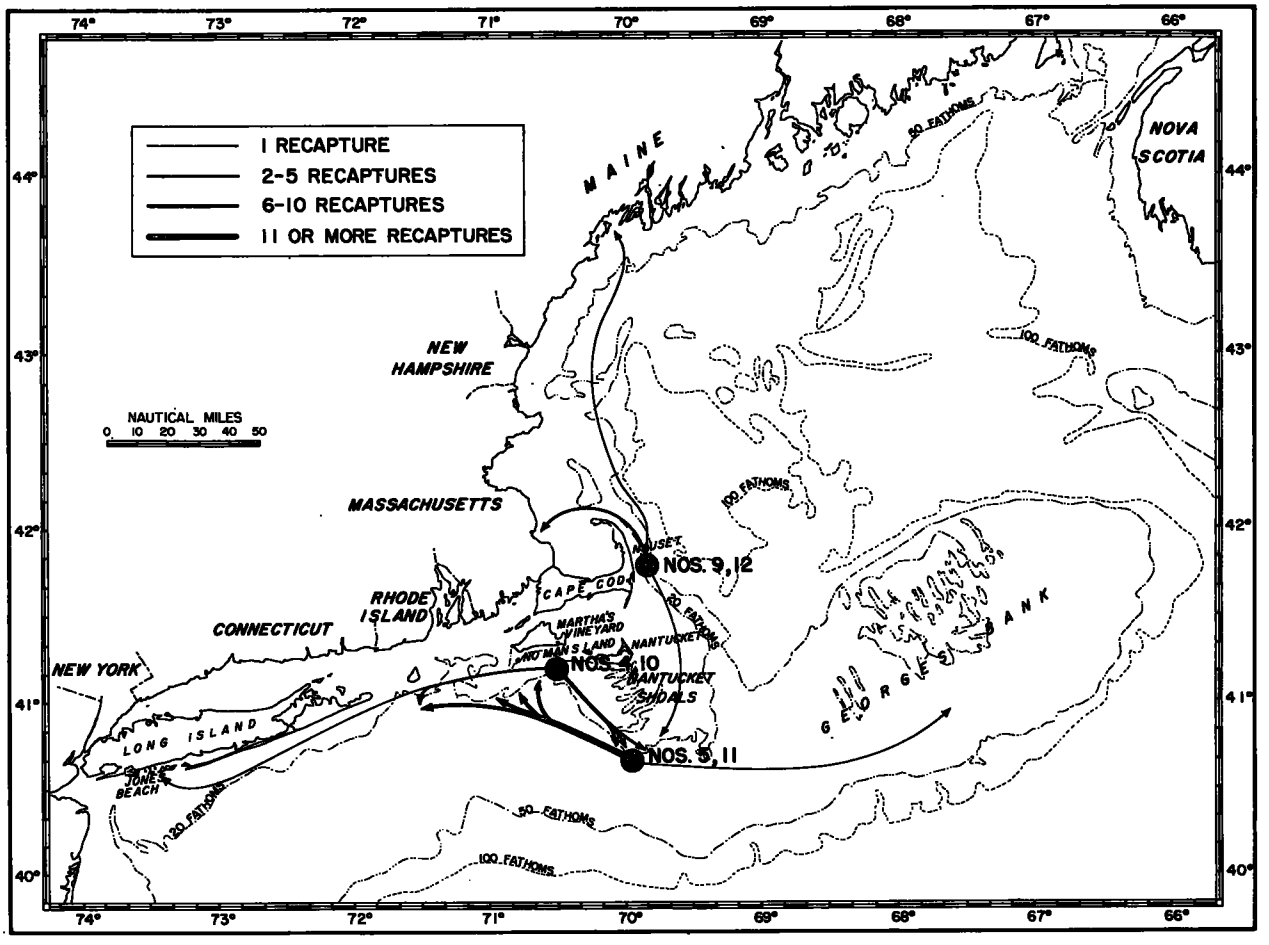

FIGURE 5.—Distant recaptures of yellowtail flounder released off No Mans Land (Nos. 4 and 10), Nantucket Shoals (Nos. 5 and 11) and off Nauset Beach (Nos. 9 and 12).

were winter returns from summer releases, and Clyde C. Taylor has suggested that they indicate a seasonal migration from Georges Bank to the southern New England grounds in the winter time. There was also one winter return from southwestern Georges Bank. It would be consistent with the returns from this one experiment to postulate a summer population on Georges Bank which moves westward to the southern New England grounds in the winter. Such an east-west migration would be similar to the seasonal movements already noted for the releases south of Long Island. It appears unlikely that such a seasonal migration involved many fish during the peak years of the fishery, because only minor quantities of yellowtail were taken on Georges Bank by the extensive otter-trawl fisheries prior to 1947.

These recaptures do indicate only a small amount of intermingling among the populations on the major fishing grounds. The Nantucket Shoals, which are shallower than the preferred depth of the yellowtail flounder, apparently limit migration across them. Considering only the tagged yellowtail released in adjacent areas, we noted that none of the 54 fish recaptured from the 514 released in subarea O were found across Nantucket Shoals, and only 1 of the 15 recaptures from the 408 fish tagged off the east side of Cape Cod was found south across the Shoals. South Channel appears to be somewhat less of a deterrent to movement because 1 fish tagged in subarea O west of the Channel was found east of it and 3 of 12 recaptures from the 51 tagged in subarea N just east of the Channel were found west of it.

In general, then, the yellowtail are to be found in relatively localized populations, which may make short, seasonal migrations. Our most dis-

tant recapture was only 170 miles from the point of release, and the majority of the recaptures were within 50 miles of their points of release. In this respect, movement of the yellowtail is not quite as localized as that of the winter flounder (Perlmutter 1946), but certainly it ranges far less than do such species as the cod, striped bass, and mackerel.

YELLOWTAIL STOCKS

The tagging data when considered together with the concentrations of fishing effort provide the basis for delineating the stock of yellowtail. A stock is defined here as the population or populations of yellowtail which occur in a fishing concentration during a year. In the following paragraphs we delineate the stocks and discuss for the minor stocks the trends in production and problems of intermingling. The discussion of the southern New England stock will be the subject of most of the rest of this report.

1. *Southern New England Stock.*—This stock is found between Nantucket Shoals and Long Island, chiefly in water 15 to 35 fathoms in depth. It appears to be limited on the southwest by unsuitable temperature conditions and on the east by the less-favorable shoal waters of Nantucket Shoals and the deep waters of South Channel. The populations intermingle to a large extent, but are not entirely homogeneous. The area is close enough to the scattered small fishing ports to enable the small trawlers to fish any concentration that they may find.

2. *Georges Bank Stock.*—This stock tends to be restricted to Georges Bank by the less-favored deep waters around the Bank. This area is accessible to medium and large trawlers, which fish the entire Bank except for a few small areas where the bottom is too rough. For many years the Georges Bank catch of yellowtail flounders was taken either in the winter in the Cultivator Shoals area by vessels seeking yellowtail or incidentally throughout the year on the rest of the Bank by vessels seeking other species of fish. Beginning in 1947, increasing quantities of yellowtail were found on southwestern Georges Bank, and in 1948 and 1949 much larger quantities were obtained on southeastern and southwestern Georges Bank (tables 3 and 6).

TABLE 6.—*Annual United States landings of yellowtail by stocks, 1942-49*

[In thousands of pounds]

Year	Southern New England	Georges Bank	Cape Cod	Northern Gulf of Maine	Nova Scotian Banks	Total[1]
1942	62,797	2,385	3,330	26	40	68,578
1943	39,777	2,784	2,831	74	321	45,787
1944	23,406	3,670	3,335	68	608	31,087
1945	22,861	2,989	2,554	30	4,734	33,169
1946	23,867	1,913	2,774	30	2,737	31,321
1947	26,706	4,976	2,387	49	1,636	35,754
1948	21,872	12,472	1,464	23	3,137	38,968
1949	10,305	16,097	2,711	46	651	29,810

[1] Slight discrepancies occur due to rounding off of the figures.

Naturally, with a catch increasing so phenomenally, the question arises as to whether it increased because the fish became more abundant in the area or because they had not been previously found. Distribution of the other trawl fisheries on Georges Bank appears to answer the question. The principal fishery here is for haddock, and according to Schuck (1951) the southeastern part of Georges Bank produced 24.4 percent of all the Georges Bank landings of haddock from 1936 to 1948, while the southwestern part produced but 6.8 percent. The haddock fishery is concentrated in somewhat deeper water than the yellowtail flounder prefers, but nevertheless enough haddock fishing occurs in almost all trawlable areas on Georges Bank that any important concentrations of yellowtail almost certainly would have been discovered. This view is further strengthened by Schuck's observation that the southwestern part of Georges Bank produced 14.7 percent of the haddock in 1944 and 18.9 percent in 1945. From the same investigator we learn that fishing effort on the southwestern part of Georges Bank fell off to 7 percent in 1946, 6.2 percent in 1947, and 4.9 percent in 1948. As the yellowtail catches did not increase until 1947, 1948, and 1949 (table 3), the increased yellowtail catches did not coincide with increased trawling for haddock, but followed it about 2 years later. Clearly the yellowtail became more abundant in the area after the haddock declined.

Since the increase in catches of yellowtail on Georges Bank coincided with a decrease in catches from the southern New England stock west of Nantucket Shoals and the tagging results show that migration may occur across the South Channel, part of the southern New England stock of yellowtail may have moved to Georges Bank. The

proportion is probably small, however, because 386 yellowtail were tagged in subareas Q and O to the west of Nantucket Shoals in 1946, the year before the big increase in catch, and only 1 of the 60 fish recaptured was taken on Georges Bank. However, the winter population in Q and O may have moved to Georges Bank to be caught mostly in the summer. (See p. 182).

3. *Cape Cod Stock.*—It occurs east and north of Cape Cod, in Cape Cod Bay, and north to the vicinity of Cape Ann and Ipswich Bay. It is limited in all directions by deep water, although to the south and north there are narrow strips of water of the preferred depth. Production from this stock has been comparatively stable. It rose to a moderate peak in 1944 of about 3⅓ million pounds, declined to about 1½ million pounds in 1948, and rose again to about 2¾ million pounds in 1949. In this area, the yellowtail is a species of minor importance sought only at certain seasons by vessels out of New Bedford, Plymouth, Boston, Provincetown, and Gloucester, Mass. It is heavily fished when available, but changes in catch may be related to changes in effort because other species are sought at times in preference to it.

4. *Northern Gulf of Maine Stock.*—This stock contributes the very few yellowtail that are taken on the scattered shoal areas of the northern gulf along the coast of Maine. This extremely small catch is taken by otter trawlers and line trawlers incidentally to other species. No significance can be attached to the small fluctuations in catch, which may be caused by changes in fishing as well as by changes in the stock.

5. *Nova Scotian Stock.*—It is completely distinct from the New England stocks. Moreover, it is of slight importance to New England fishermen. United States vessels have rarely gone to the Nova Scotian Banks especially to catch yellowtail, and therefore the catch is related to the fishing for other species. The great increase in the take of yellowtail from a low of 40,000 pounds in 1942 to a high of 4,700,000 pounds in 1945 appears to have been caused by the removal of wartime restrictions. The subsequent reduction in yellowtail catches coincided with the declining market for cod in the later years, because the large catches of yellowtail were produced by vessels fishing primarily for cod.

The United States landings from these five stocks are shown in table 6.

THE SOUTHERN NEW ENGLAND STOCK

LANDINGS

The total landings from the southern New England stock are readily computed from table 3 by combining the landings from the statistical areas designated as Nantucket Shoals and Lightship Grounds, off No Mans Land, southern Massachusetts, Rhode Island shore, and Long Island. These have been combined in table 7 to show the landings, by month and quarter, for the years 1942 to 1949. The annual totals for 1940 and 1941 are also included.

TABLE 7.—*Landings of yellowtail from southern New England stock, by month and quarter, 1940–49*

[In thousands of pounds]

Month and quarter	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	Average 1942–49
January			4,881	4,905	3,701	1,323	2,123	2,641	2,009	1,162	2,843
February			3,719	3,855	3,730	1,573	1,144	737	1,260	1,402	2,178
March			6,756	4,929	3,516	3,401	3,299	2,037	1,704	884	3,316
1st quarter			15,356	13,689	10,947	6,297	6,566	5,415	4,973	3,448	8,336
April			5,610	2,993	2,518	652	583	1,401	1,274	406	1,930
May			2,847	1,629	1,142	454	511	1,058	1,026	216	1,110
June			4,598	2,232	977	381	1,538	1,706	1,749	424	1,701
2d quarter			13,055	6,854	4,637	1,487	2,632	4,165	4,049	1,046	4,741
July			5,982	3,538	2,641	1,827	2,162	2,903	3,262	477	2,849
August			7,403	5,770	2,914	2,386	1,509	1,750	1,258	527	2,940
September			5,389	4,979	151	2,560	1,696	2,662	1,677	956	2,509
3d quarter			18,774	14,287	5,706	6,773	5,367	7,315	6,197	1,960	8,297
October			7,886	2,166	647	3,221	3,286	3,961	1,808	519	2,937
November			4,308	1,920	829	4,073	2,765	2,645	3,025	1,325	2,611
December			3,418	861	640	1,010	3,251	3,205	1,820	2,007	2,026
4th quarter			15,612	4,947	2,116	8,304	9,302	9,811	6,653	3,851	7,574
Grand total[1]	36,924	47,933	62,797	39,777	23,406	22,861	23,867	26,706	21,872	10,305	28,949

[1] Slight discrepancies occur due to rounding off of the figures.

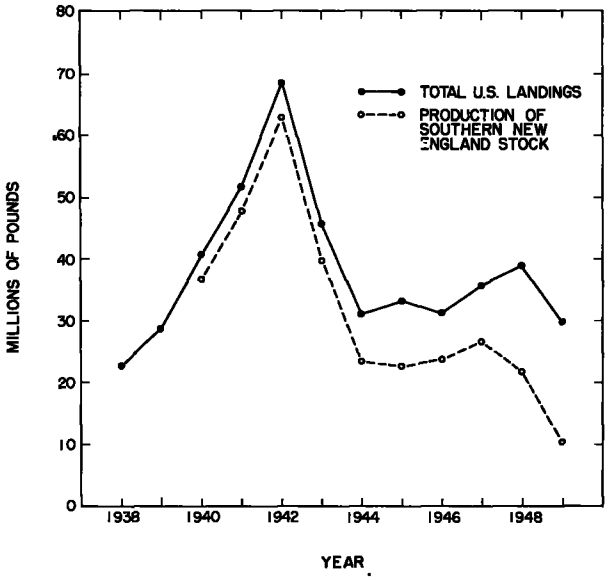

FIGURE 6.—Production of yellowtail, 1938 through 1949.

Four distinct periods in the southern New England fishery may be recognized from these data (fig. 6). First there was the increasing production to a peak of 63 million pounds in 1942, then an abrupt decline to 23 million pounds in 1944, fairly steady production from 1944 to 1947, and another abrupt decline from 27 million pounds in 1947 to 10 million pounds in 1949.[2] Since this stock has contributed the bulk of the United States yellowtail production for many years, fluctuation in its numbers is the principal cause for concern for the species.

A seasonal trend is apparent in the average catch per month (table 7). There were distinctly lower catches from April through June which, as will be shown later, are the months of the spawning season. The small variations in the average catch during the other months probably have no biological significance, being due to the seasonal weather pattern or to shifts of the fishermen to other species.

Turning from the average catch to the catches of the individual years, it is apparent that the seasonal changes in the landings have been variable. During the peak years of 1942 and 1943, there were large summer and winter fisheries with lower catches made in May and December. In 1944, the summer fishery lasted only a short time and the fall fishery was practically a failure. In 1946 and 1947, the summer landings were lower than those of the period October to December. Finally, in 1949 when a new low in the catch was reached, the landings were extremely small during all the summer months.

[2] This decline continued to 7.2 million pounds in 1950 then leveled off at 4.0 in 1951, 4.8 in 1952, and about 4.5 million pounds in 1953. Total landings in United States ports declined to 23.5 million pounds in 1950, 18.4 in 1951, 16.3 in 1952, and about 13.5 in 1953.

LENGTH COMPOSITION OF THE CATCH

Data on lengths of yellowtail in the landings were collected routinely at New Bedford from October 1942 through 1947. In addition to these routine measurements, a few were obtained irregularly at other ports. Also, some measurements were made occasionally during 1941 and the first 9 months of 1942. The total number of measurements available are listed in table 8, and detailed length frequencies are given in appendix tables C–14 and C–15, pages 244 and 245.

TABLE 8.—*Numbers of yellowtail measured from southern New England stock, by statistical area, 1941–47*

[See fig. 1 for chart of statistical areas]

Year and quarter	Statistical area—				Total
	New England Banks			Southwestern Long Island	
	O	Q-R	S		
Year 1941:					
1st quarter					
2d quarter		77			77
3d quarter					
4th quarter		317			317
Year 1942:					
1st quarter			504	240	744
2d quarter		161	684		845
3d quarter					
4th quarter	455	805			1,260
Year 1943:					
1st quarter	1,221	959			2,180
2d quarter		1,449	137		1,586
3d quarter	1,024	1,751			2,775
4th quarter		609			609
Year 1944:					
1st quarter	172	1,354	459		1,985
2d quarter		454			454
3d quarter	207	413			620
4th quarter	513	403	100	228	1,244
Year 1945:					
1st quarter	1,481	2,098	201		3,780
2d quarter			402		402
3d quarter	701	2,223			2,924
4th quarter	1,417	1,280	202		2,899
Year 1946:					
1st quarter	1,202	1,351			2,553
2d quarter		100			100
3d quarter	1,304	805			2,109
4th quarter	2,873	1,404			4,277
Year 1947:					
1st quarter		1,005	187		1,192
2d quarter		803	803	100	1,706
3d quarter	1,402	367	202		1,971
4th quarter	301	1,008	400		1,709
Total	14,273	21,196	4,281	568	40,318

The routine measurements were obtained with the primary objective of having them representative of the landings. To ensure that the area of

origin was known, only the catches from vessels that fished a single area were sampled. A sample of about 100 fish was selected for measuring in as nearly random a manner as working conditions would permit. The standard practice at the port of New Bedford was to pack the fish in 125-pound boxes as they were being unloaded. The boxes were accessible to the measurers before being iced and closed, and it was convenient to measure 20 or 25 fish from each box. A sample of 100 fish was obtained from 4 or 5 boxes taken one at a time from the unloading line as needed. Usually from 1,000 to 2,000 pounds of fish were unloaded between the boxes sampled. The fish were taken from one end of each box from the top to the bottom, with a special effort to avoid any selection. In view of the difficulties of obtaining an accurately representative sample (Hayne 1951), a slight bias may have favored the large fish; but the same technique was followed throughout the investigations, and the bias, if any, should not affect the interpretation of trends in fish lengths.

Measurements were of the total length of the fish—from the tip of the lower jaw (with the mouth closed) to the end of the caudal fin. Almost all measurements were recorded on a measuring board slotted to receive an aluminum strip. The measurement was taken by pricking a hole in the strip, which was marked off in two parts to keep separate the records of the lengths of males and females. This method of measuring is very satisfactory, provides a rapid field method suitable for use when fingers are too wet or too cold to write, and is free of "digit bias," which has troubled other investigators who have measured large numbers of fish (Sette 1941). Later in the laboratory, the lengths were tallied to the half centimeter by superimposing a graduated celluloid strip over the marked aluminum strip.

It became apparent quite early in the study that the sexes differed in size composition, and commencing in October 1942 most measurements were kept separate by sex although the total sample was obtained in as random a manner as possible so that the number of each sex measured would be representative of its numbers in the landings. After opening a few fish to determine the condition of the sex organs, it was discovered that the yellowtail could be sexed easily and accurately by holding the white side to the light and looking through the fish. In this way, the outline of the ovary extending posteriorly from the mass of viscera can readily be seen even in immature females.

The program of sampling was planned to obtain a sample from nearly every vessel landing that had fished but a single area. It was expected that this would supply representative samples of the entire landings, but pressure of other duties and changes in field personnel made it impossible to maintain the program at the same level at all times. Some gaps also occurred because of the fishermen's habit of working in two or more areas when fish are scarce. This was particularly true in the yellowtail fishery, and many months when the landings from an area were low it was not possible to obtain a sample because the few landings made were always mixtures of fish from several areas. This tendency led to some undersampling of areas poorly represented in the landings at New Bedford. Furthermore, the catches from the Block Island and Long Island areas, which are fished mostly by Rhode Island and New York fishermen, were landed to a large extent in ports not covered by our sampling.

To obtain the best representation of the length composition of the yellowtail for the period October 1942 through December 1947, it would be best to weight the length frequencies by the quantities landed. This would be difficult, however, because of lack of data in numerous quarters and from some statistical areas (table 8). Therefore, we have tested the representativeness of our unweighted data in two ways: First, by comparing the distribution of measurements with the distribution of catch according to area and time, and second, by computing the effect of the maldistribution of the catch on the average length.

A comparison of the distribution of measurements with the distribution of catch shows that the discrepancies were not serious. When considered according to area, it is apparent that the areas off No Mans Land and Nantucket Shoals, which provided the bulk of the catch, were somewhat oversampled and the areas off Block Island and Long Island were somewhat undersampled (table 9). The distribution according to years showed similar discrepancies, with 1943, 1944, and 1947 being undersampled and 1945 and 1946 being oversampled. However, the distribution accord-

ing to the calendar quarter shows excellent agreement, with the maximum discrepancy between measurements and landings being only 2.3 percent. The effect of these maldistributions on the average is very slight. The average size of the yellowtail measured from 1943 through 1947 was 35.87 cm. If the average lengths by area are computed separately and weighted according to the quantity landed from each area, the overall average is decreased only 0.18 cm. Similarly, if we separate the measurements according to the year and weight them according to quantities landed, the overall average is increased by only 0.14 cm. Finally, computations according to quarter show even less change, 0.03 cm. Because of these very small differences, we present the average length compositions in the ensuing pages on the basis of the actual number measured, and we consider them representative.

TABLE 9.—*Quantities of yellowtail landed and numbers measured, by area, quarter, and year, 1943–47*

	Fish landed		Fish measured	
	Thousand of pounds [1]	Percent	Number	Percent
Area:				
Subarea O	39,672	29.0	13,818	37.3
Subareas Q–R	63,011	46.1	19,836	53.5
Subarea S	24,110	17.6	3,093	8.3
XXIII	9,825	7.2	328	.9
Total [1]	136,618	99.9	37,075	100.0
Quarter:				
1st	42,914	28.2	11,690	30.5
2d	19,775	13.0	4,248	11.1
3d	39,448	25.9	10,399	27.1
4th [2]	50,092	32.9	11,998	31.3
Total [1]	152,229	100.0	38,335	100.0
Year:				
1943	39,777	29.1	7,150	19.3
1944	23,406	17.1	4,303	11.6
1945	22,861	16.7	10,005	27.0
1946	23,867	17.5	9,039	24.4
1947	26,706	19.5	6,578	17.7
Total	136,617	99.9	37,075	100.0

[1] Slight discrepancies occur because of rounding off of the figures.
[2] Includes data from 4th quarter in 1942.

The samples obtained during 1941 and 1942 were less representative than later samples; they were taken as opportunity afforded and sex data are lacking. No attempt was made to sample more heavily during the seasons with heavy landings, and the third quarter of 1942, with the heaviest landings in the history of the yellowtail fishery, was not sampled at all. Thus, these length compositions are not fully representative and reservations will be made in using them.

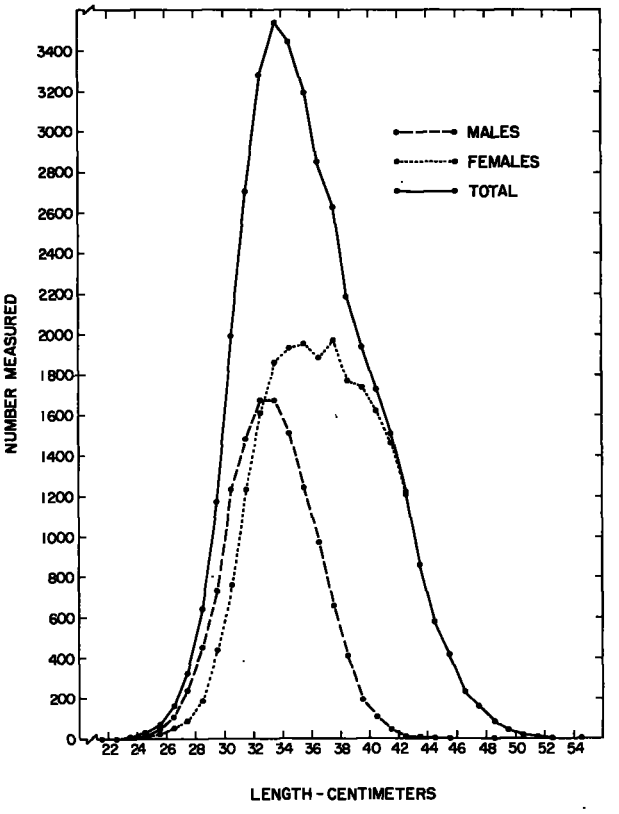

FIGURE 7.—Length composition, by sex, of the yellowtail from the southern New England stock, 1943 through 1947.

The predominance of the females in the landings from 1943 through 1947 with respect to both numbers and length is shown in table 10 and figure 7. The females accounted for 65.33 percent of the total number in the samples. The grand average length of the sexes combined was 35.87 cm.; the females averaged 37.21 cm., whereas the males averaged only 33.34 cm. It will be shown that this difference in size is caused by a difference between the sexes in rate of growth, which apparently also results in the preponderance in numbers of females in the catch. In table 10 it may be seen that above 33 cm. the females were more numerous in the landings; under 33 cm. the males were more numerous. It may be judged also from the curves in figure 7 that the fishery is fully utilizing only male yellowtail more than 33 cm. or females more than about 40 cm. in length, if we assume that this species decreases normally in numbers as it increases in size. However, if the total curve is considered, it may be judged that both sexes are fully available when more than

33 cm. long. Since the fishery did catch more males in the smaller sizes and was obviously not catching them with full effectiveness, we see no reason to suspect that the sex ratio of the unfished population is other than equal. The unequal representation in the catch may be due entirely to gear selectivity and the unequal rate of growth of the sexes.

TABLE 10.—*Length composition of yellowtail landed from the southern New England stock, by sex, 1943–47*

Total length	Number measured		
	Male	Female	Total
21.5 cm	1		1
22.5 cm	2	1	3
23.5 cm	5	5	10
24.5 cm	17	10	27
25.5 cm	44	21	65
26.5 cm	116	49	165
27.5 cm	237	84	321
28.5 cm	460	193	653
29.5 cm	729	440	1,169
30.5 cm	1,227	762	1,989
31.5 cm	1,478	1,232	2,710
32.5 cm	1,673	1,610	3,283
33.5 cm	1,674	1,865	3,539
34.5 cm	1,517	1,935	3,452
35.5 cm	1,246	1,951	3,197
36.5 cm	972	1,886	2,858
37.5 cm	660	1,973	2,633
38.5 cm	413	1,774	2,187
39.5 cm	195	1,740	1,935
40.5 cm	111	1,622	1,733
41.5 cm	44	1,466	1,510
42.5 cm	16	1,209	1,225
43.5 cm	14	861	875
44.5 cm	2	579	581
45.5 cm	1	415	416
46.5 cm		228	228
47.5 cm		163	163
48.5 cm	1	79	80
49.5 cm		40	40
50.5 cm		16	16
51.5 cm		8	8
52.5 cm		2	2
54.5 cm		1	1
Total	12,855	24,220	37,075
Mean length (cm.)	33.34	37.21	35.87

The average size composition during each quarter of the year (table 11, fig. 8) showed a definite seasonal change, which is in accord with the changes expected in most species of fish. The average length was greatest in the first quarter, January to March (37.40 cm.), least in the third quarter, July to September (34.37 cm.), and intermediate in the second and fourth quarters. The curves, when plotted on a percentage basis to facilitate comparison, show little change in shape. The changes appear to arise from the entrance into the fishery of young fish during the spring and summer and their subsequent growth and mortality during the winter. There is also a possibility that some of the differences arose from heterogeneity of the population, since tagging experiments indicated some segregation of

TABLE 11.—*Percent length composition, by quarter, of yellowtail landed from the southern New England stock, fourth quarter, 1942 through 1947*

Total length	1st quarter	2d quarter	3d quarter	4th quarter
21.5 cm	0.01			0.02
22.5 cm		0.02	0.01	.12
23.5 cm	.02	.02	.03	.21
24.5 cm	.07	.12	.02	.45
25.5 cm	.31	.28	.07	.51
26.5 cm	.68	.99	.30	.38
27.5 cm	.75	1.58	1.32	.44
28.5 cm	.97	2.19	3.53	.90
29.5 cm	1.10	3.22	6.14	2.62
30.5 cm	2.30	5.37	8.64	5.63
31.5 cm	4.32	8.05	9.64	7.94
32.5 cm	5.94	10.66	10.37	9.78
33.5 cm	7.82	11.91	10.11	9.68
34.5 cm	8.39	9.86	9.46	9.68
35.5 cm	8.54	8.94	8.74	8.35
36.5 cm	8.23	7.27	7.27	7.68
37.5 cm	7.98	5.70	6.65	7.09
38.5 cm	7.42	4.38	4.89	5.72
39.5 cm	6.06	4.33	4.30	5.37
40.5 cm	6.07	4.07	3.20	4.62
41.5 cm	5.24	3.70	2.36	4.38
42.5 cm	5.18	2.99	1.52	3.05
43.5 cm	4.13	1.88	.81	2.01
44.5 cm	2.88	1.11	.35	1.44
45.5 cm	2.29	.73	.17	.87
46.5 cm	1.34	.31	.06	.48
47.5 cm	1.04	.14	.03	.28
48.5 cm	.50	.07	.02	.15
49.5 cm	.21	.02		.12
50.5 cm	.10	.05		.02
51.5 cm	.06	.02		
52.5 cm	.02			
54.5 cm				.01
Total	99.97	99.98	100.01	100.00
Mean length (cm.)	37.40	35.17	34.37	35.70

the southern New England stock during the winter (p. 180). However, there is no way to distinguish the two sources of variation with these data.

Segregating the length data according to statistical area for 1943 through 1947 (table 12, fig. 9) reveals a small geographical gradient in length, with the largest yellowtail coming from the more easterly area. The yellowtail from the Nantucket Shoals area averaged 36.35 cm., from off No Mans Land 35.66 cm., from off Block Island 35.23 cm., and from off Long Island 34.27 cm. These figures show statistically what is common knowledge among the fishermen, but since the figures are associated with the seasons there is no certainty that the differences are due entirely to geography. Table 3, which shows the catch by statistical subarea, indicates that the landings from the Nantucket Shoals area (O) were usually the heaviest when those from off No Mans Land (Q) were light, and vice versa. The landings from the westward, off Rhode Island (S) and Long Island (XXIII) run smaller regardless of season, but there was no clear-cut seasonal pattern in the size changes. It should be noted that in areas from Block Island to Nan-

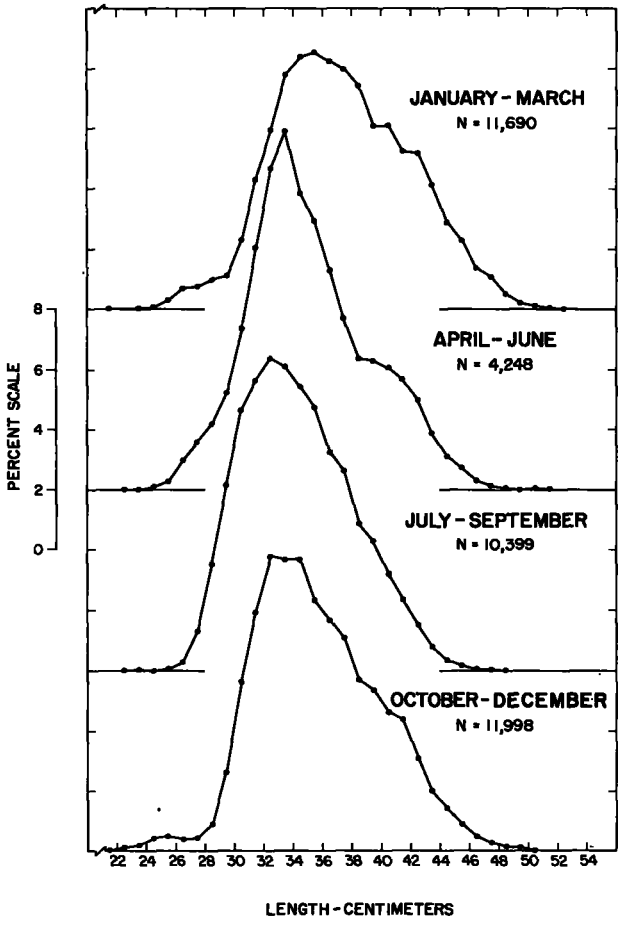

FIGURE 8.—Percent length composition, by quarter, of yellowtail from the southern New England stock, fourth quarter 1942 through 1947. (N=number of fish.)

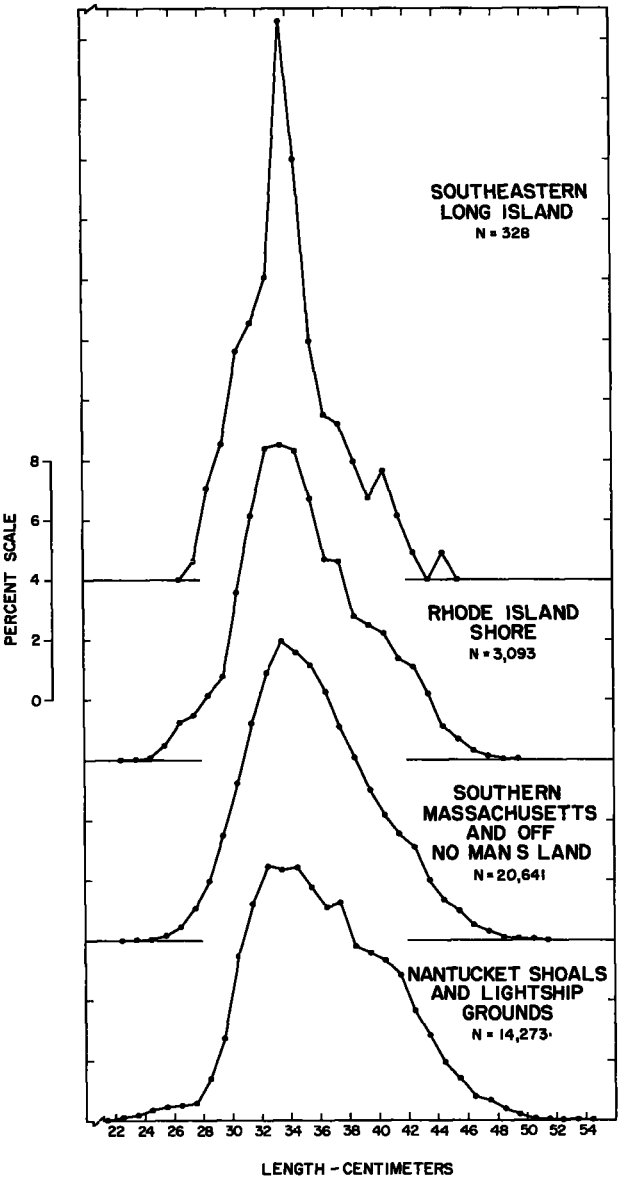

FIGURE 9.—Percent length composition, by statistical area, of yellowtail from the southern New England stock, 1943 through 1947. (N=number of fish.)

tucket Shoals for which we have adequate samples, the difference in average size (1.12 cm. maximum) was markedly less than the difference among seasons (3.02 cm. maximum).

The length compositions from 1941 to 1947 are particularly interesting (table 13; fig. 10) because they cover a period that includes the peak catch of 63 million pounds in 1942 and much of the subsequent decline. Only slight changes in the average length occurred during the period 1941–47, and there was no trend toward smaller fish in the catches, as might be expected.[3]

The yellowtail were smallest in 1942 (34.22 cm.) and largest in 1945 (36.37 cm.). Even this small difference (2.22 cm.) probably was largely the result of a change in the habits of the fishermen. The length-composition curve for 1942 (and to a lesser degree for 1941) differs appreciably from the curves for later years by including a mode of smaller fish. Very probably this mode occurred because of failure of the fishermen to cull their catches at sea. At this time the filleting industry in New Bedford was just becoming established and there were no general agreements regarding the size of fish acceptable to the trade. The fish-

[3] Such a trend apparently did develop according to reports, after 1951, when the very small annual catches were largely comprised of "peewee" yellowtail.

TABLE 12.—*Percent length composition, by statistical area, of yellowtail landed from the southern New England stock, 1943–47*

[See fig. 1 for chart of statistical areas]

Total length	Subarea O	Subareas Q-R	Subarea S	Area XXIII
21.5 cm	0.01			
22.5 cm	.01	0.01	0.03	
23.5 cm	.03	.03		
24.5 cm	.09	.06	.10	
25.5 cm	.10	.18	.48	
26.5 cm	.26	.46	1.23	
27.5 cm	.45	1.06	1.52	0.61
28.5 cm	1.28	2.01	2.17	3.05
29.5 cm	2.69	3.51	2.78	4.57
30.5 cm	5.61	5.12	5.59	7.62
31.5 cm	7.30	7.16	8.15	8.54
32.5 cm	8.58	8.79	10.38	10.06
33.5 cm	8.49	9.98	10.54	18.60
34.5 cm	8.55	9.60	10.35	14.03
35.5 cm	7.86	9.15	8.73	7.93
36.5 cm	7.20	8.25	6.69	5.49
37.5 cm	7.32	7.06	6.60	5.18
38.5 cm	5.86	6.13	4.78	3.96
39.5 cm	5.70	5.04	4.49	2.74
40.5 cm	5.43	4.23	4.24	3.66
41.5 cm	4.94	3.60	3.39	2.13
42.5 cm	3.69	3.11	3.10	.91
43.5 cm	2.94	2.02	2.20	
44.5 cm	1.99	1.35	1.13	.91
45.5 cm	1.43	.99	.71	
46.5 cm	.80	.54	.32	
47.5 cm	.68	.32	.16	
48.5 cm	.40	.12	.06	
49.5 cm	.18	.07	.06	
50.5 cm	.06	.04		
51.5 cm	.04	.02		
52.5 cm	.01			
54.5 cm	.01			
Total	99.99	100.01	99.98	99.99
Mean length (cm.)	36.35	35.66	35.23	34.27

TABLE 13.—*Percent length composition, by years, of yellowtail from the southern New England stock, 1941–47*

Length	1941	1942	1943	1944	1945	1946	1947
20.5 cm		0.04					
21.5 cm		.08				0.01	
22.5 cm		.65			0.01	.01	0.02
23.5 cm		.98	0.01	0.07	.04	.02	
24.5 cm	0.25	2.08	.04	.21	.10	.03	.03
25.5 cm		2.20	.12	.28	.19	.14	.18
26.5 cm	.25	1.80	.49	.37	.54	.29	.52
27.5 cm	1.52	1.96	.91	.86	.88	.67	1.06
28.5 cm	1.27	2.29	1.58	1.35	1.74	1.78	2.23
29.5 cm	.76	3.23	2.48	2.49	3.24	3.35	3.92
30.5 cm	7.87	5.84	4.01	5.18	4.60	6.53	6.52
31.5 cm	6.85	7.90	6.35	8.55	6.42	7.56	8.56
32.5 cm	6.34	10.25	8.78	9.32	7.28	9.38	10.31
33.5 cm	7.11	9.07	9.50	10.83	8.08	9.82	10.61
34.5 cm	8.63	9.48	8.88	9.83	8.36	9.87	10.11
35.5 cm	11.17	9.27	9.31	8.92	8.44	7.79	9.11
36.5 cm	10.66	7.56	8.24	7.64	8.02	7.30	7.25
37.5 cm	9.64	6.17	7.51	7.23	7.87	6.97	5.59
38.5 cm	5.58	4.90	6.76	5.30	6.61	5.72	4.53
39.5 cm	5.84	4.21	6.10	5.18	5.52	5.16	3.92
40.5 cm	5.84	3.47	4.91	3.72	5.21	4.82	4.03
41.5 cm	3.55	2.45	4.52	3.12	4.17	4.38	3.63
42.5 cm	3.55	1.84	3.10	3.21	3.83	3.08	3.10
43.5 cm	1.52	.98	2.60	1.88	2.91	2.08	1.96
44.5 cm	.51	.65	1.40	1.84	2.03	1.35	1.17
45.5 cm	.51	.23	1.02	1.14	1.69	.78	.82
46.5 cm	.76	.37	.54	.63	1.07	.40	.29
47.5 cm			.43	.44	.64	.34	.27
48.5 cm		.04	.17	.21	.36	.16	.12
49.5 cm			.14	.14	.08	.13	.06
50.5 cm			.04	.03	.07	.03	.03
51.5 cm			.03		.03	.01	.03
52.5 cm			.01			.01	
54.5 cm				.02			
Total	99.98	99.99	99.98	99.98	100.03	99.97	99.98
Mean length (cm.)	35.86	34.15	36.12	35.69	36.37	35.67	35.22

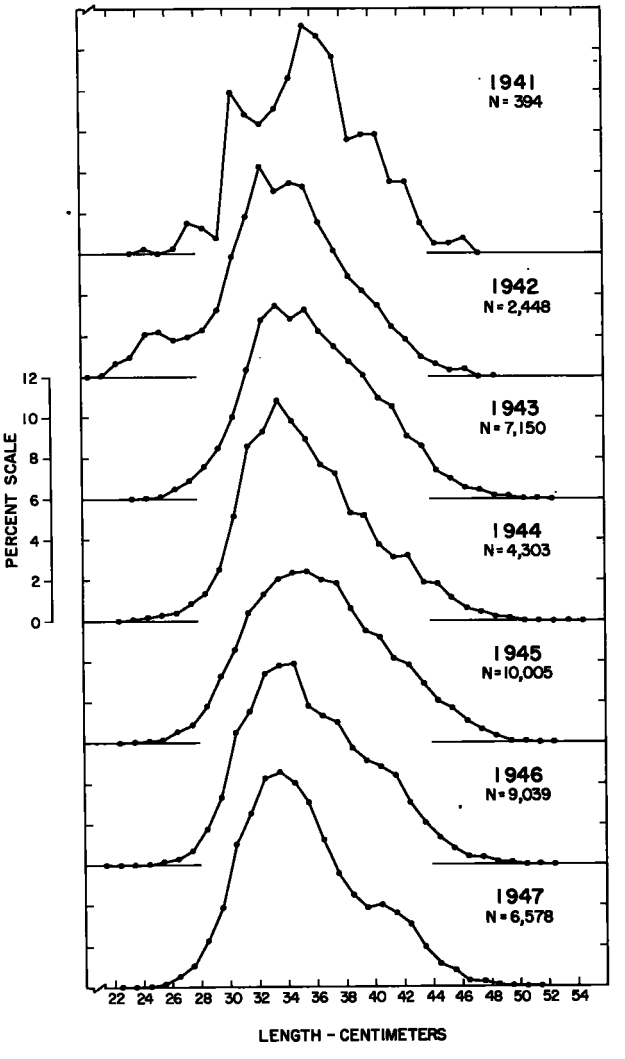

FIGURE 10.—Percent length composition, by year, of yellowtail from the southern New England stock, 1941–47. (N=number of fish.)

ermen were catching yellowtail in great quantities accompanied by few other fish, and in such situations there is an understandable tendency to ice down the entire catch and neglect the few fish that might otherwise be culled. Furthermore, these small fish were mostly from the 1941 year class, which we later found was the largest year class to occur during the period included in our study.

Another explanation of the smaller average size in 1942 might be less-representative sampling. We have previously pointed out that routine sampling began in October 1942 and, of course, a preponderance of measurements were obtained during the fall season; however, the size composition by quarters indicates that the size during the fourth

quarter of the year is almost exactly the same as the average for the year. Therefore, if 1942 were an average year, insofar as the size of the yellowtail is concerned, we would expect our average (mostly during the fourth quarter) to be fairly representative of the entire year.

This lack of a decrease in the average size during a period of heavy fishing is particularly significant because it is not in agreement with theory or with actual events in closely comparable fisheries. The theory of the effect of fishing developed by Baranoff (1918) and expounded by Thompson (1937) indicates that a marked decrease in the proportion of older and larger fish is to be expected when fishing mortality increases. The development of Baranoff's theory was stimulated by observations on the plaice, which was being heavily fished in the North Sea. Russell (1942, p. 77) reported that in 1907 the relatively unfished plaice population in the Barents Sea was almost entirely mature and averaged about 48 cm. in length. At the same time in the North Sea the marketable plaice population was more than one-half immature and averaged less than 40 cm. in length even though their size at maturity was about the same as that of the Barents Sea plaice (39–40 cm.).

The European plaice and the yellowtail which it closely resembles belong to the same family, the Pleuronectidae. The plaice attains almost the same maximum size as the yellowtail, although it grows a little more slowly. The plaice appears in maximum numbers in the catch at age 4 and individuals as old as ages 10 and 11 are fairly common, whereas the yellowtail is taken in maximum numbers at age 3 (p. 209), and few individuals older than age 7 are found. Both species are subject to otter-trawl fisheries, though the North Sea plaice has been subject to a heavy fishery for 70 years or more, whereas the American yellowtail has been especially sought only since about 1938.

Despite the difference in the length of time the plaice and the yellowtail fisheries have been in operation, a nearly parallel situation is to be found in a comparison of the peak and decline of the yellowtail fishery with the peak and decline of the plaice fishery immediately after World War I. That war caused almost a complete cessation of fishing in the North Sea for about 4 years and permitted the stocks of fish to accumulate far above their prewar levels. Thursby-Pelham (1939, p. 53) has shown that the proportion of large plaice in the landings began to decline about 2 years after fishing was resumed, and reached a minimum in about 7 years.

That reduction in size of the fish did not occur in the yellowtail fishery as a result of fishing is shown in figure 11, where part of Thursby-Pelham's figure 6 has been reproduced for comparison of plaice length data with similar data from the yellowtail. We have arbitrarily established a large yellowtail category as including fish of more than 40 cm. total length and a small, as including fish of less than 30 cm. These categories differ somewhat from the large and small market categories of Thursby-Pelham, but each category forms a significant fraction of the landings. There obviously was no trend toward a decreasing proportion of large fish in the yellowtail fishery during the period of observation, 1941–49.

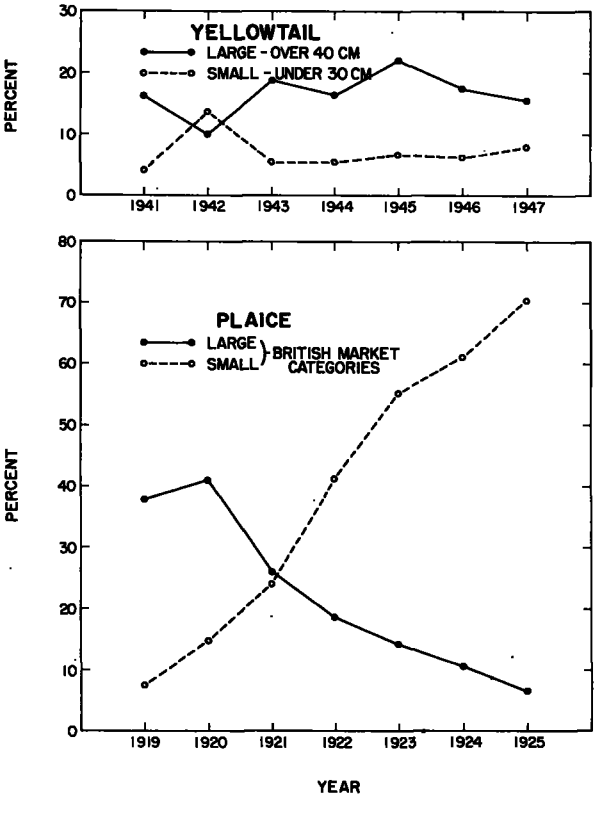

FIGURE 11.—Comparison of the trends in proportions of large and small yellowtail from the southern New England stock and of European plaice of the North Sea stock. The medium-size category has been omitted from both graphs.

This matter will be discussed further after data on abundance, age, and rate of growth have been presented.

LENGTH-WEIGHT RELATION

The regression of weight on length of the yellowtail flounder was determined (1) to provide data to convert the landings from pounds to numbers of fish, and (2) to provide data on fatness of the yellowtail which may furnish clues to changing ecological conditions. Information obtained during each quarter of 1943 provided a good basis for estimating weight from length during the several years of our study, assuming that the relation did not change from year to year. In addition, it provided a critical comparison of the differences in the length-weight relation between the sexes and among the seasons. The reduced statistical data are presented to permit further comparison with data which may be collected later.

Samples were obtained near the middle of each calendar quarter of 1943 (table 14). The fish to be weighed and measured were taken at random from the landings in the same manner as those measured for length (p. 186). Usually a sample of 50 fish was weighed and measured from a vessel that had fished in a single statistical subarea. No attempt was made to equalize the numbers of each sex.

TABLE 14.—*Numbers of yellowtail from the southern New England stock, by subarea and by sex, weighed and measured during 1943*

Date	Statistical subarea			Sex		Total
	O	Q	S	Male	Female	
Feb. 5		151		153	223	376
Feb. 6	75	50				
Feb. 19	50					
Feb. 27	50					
May 25		100		54	204	258
May 31			50			
June 2		58				
June 3	50					
Aug. 4		50		21	255	276
Aug. 9		98				
Aug. 11		43				
Aug. 12		47				
Aug. 16		38				
Nov. 8		49		62	141	203
Nov. 12		50				
Nov. 22		54				
Nov. 24		50				
Total	225	838	50	290	823	1,113

The lengths were obtained on a measuring board and the weights on balances provided with special scales graduated in 2-place logarithms to simplify the computation. The balances were of the spring type, one with a capacity of 5 pounds, the other of 1 pound. Since the weighing was done in the field it was necessary to set up the balances for each sample. Check weights were used prior to, midway through, and at the end of the weighing of a sample. The scales were adjusted at the beginning of the weighing and subsequent checks revealed no error of more than 1 percent in the weighing.

The regression of weight on length was computed with the assumption that the relation is of the form

$$W = aL^b.$$

Changing this to logarithms, of course, reduces it to

$$\text{Log } W = \text{Log } a + b \text{ Log } L,$$

which is a straight-line relation easy and convenient to compute by the standard method of minimizing the squared deviations. (The reduced logarithmic data from the observations are presented in table 15.) Plots of all the data in logarithms were made to test the assumption of linearity and as a final check on the computations. These plots showed no deviation from linearity, but they did identify two aberrant observations, which were located away from the regression line by several times the standard error of estimate. These two observations—one male and one female from the sample of August 9, 1943—were omitted from the analysis.

The several regression formulas (table 16) have been computed to permit estimating the weight from the length of the yellowtail for each sex in each quarter and for combinations of the sexes and quarters. When these formulas are used to estimate the weight of each sex at the mean length of 35.869 cm. (table 17), the females are consistently heavier than the males. The difference varies from 0.041 pound in the first quarter to 0.119 pound in the second quarter—amounts which are 4.5 percent and 14.4 percent of the average weight of the males. The greater difference (in the second quarter) reflects the greater weight of the females laden with ova. However, the samples were taken slightly after the middle of the spawning season when 67 percent of the mature females in the samples were spent (see Spawning Season, p. 216). Therefore, the differ-

TABLE 15.—*Reduced length-weight data for yellowtail from the southern New England stock, by quarters, 1943*

[n=number of specimens; Σ=summation; x=logarithm of length in decimeters; y=logarithm of weight in tenths of pounds]

Factors	1st quarter		2d quarter		3d quarter		4th quarter	
	Male	Female	Male	Female	Male	Female	Male	Female
n	153	223	54	204	21	255	62	141
Σx	82.78	103.63	27.90	110.15	10.66	137.53	32.50	81.31
$\Sigma(x-\bar{x})^2$	44.9604	77.0631	14.4832	59.7513	5.4468	74.7535	17.1322	47.1623
Σy	140.44	241.93	44.03	188.90	16.69	228.21	53.35	148.04
$\Sigma(y-\bar{y})^2$	130.9540	269.0343	36.4677	179.7234	13.5071	209.5729	46.7119	158.5402
$\Sigma(x-\bar{x})(y-\bar{y})$	76.5292	143.5529	22.9311	103.2014	8.5628	124.7938	28.2332	86.2542

TABLE 16.—*Length-weight regression formulas for yellowtail from the southern New England stock, by quarter and sex, 1943*

Quarter and sex	Number of specimens	Formula [1]
1st quarter:		
Male	153	$y=3.1558x-0.7895$
Female	223	$y=3.3838x-.8972$
Both sexes	376	$y=3.4102x-.9187$
2d quarter:		
Male	54	$y=2.6730x-.5057$
Female	204	$y=3.0348x-.7078$
Both sexes	258	$y=3.0567x-.7239$
3d quarter:		
Male	21	$y=2.5448x-.4971$
Female	255	$y=2.9577x-.7002$
Both sexes	276	$y=2.9469x-.6917$
4th quarter:		
Male	62	$y=2.7894x-.6017$
Female	141	$y=3.2340x-.8150$
Both sexes	203	$y=3.2377x-.8229$
All quarters:		
Male	290	$y=3.0092x-.7188$
Female	823	$y=3.2353x-.8249$
Both sexes	1,113	$y=3.2310x-.8259$

[1] x=logarithm of length in decimeters; y=estimated logarithm of weight in tenths of pounds.

TABLE 17.—*Comparison of the weight of male and female yellowtail, by quarter, at the mean length of 35.869 cm.*

[In pounds]

Quarter	Male	Female	Difference	Ratio of difference to weight of males
				Percent
1st	0.914	0.955	0.041	4.5
2d	.826	.945	.119	14.4
3d	.822	.872	.050	6.1
4th	.882	.953	.071	8.0
Average	.892	.933	.041	4.6

ence between the sexes at the onset of spawning in early April is probably even greater.

The differences in the length-weight relation among quarters also are considerable. Yellowtails of the average length of both sexes are heaviest in the first quarter and lightest in the third. This is a little surprising since one would expect the females, at least, to be heaviest during the spawning season. However, as was previously mentioned, 67 percent of the females in the samples were spent, and even in this condition the average weight was only slightly less (0.010 pound) than that of the first quarter. Probably the females are their heaviest at the onset of spawning in early April.

Most of these differences are statistically significant. Covariance analysis (table 18), according to the method used by Kendall (1952, p. 239) indicates that the differences between the sexes are highly significant in each quarter except the third, which immediately follows the spawning season. It is not certain whether this lack of a significant difference is due to the small number of males (21) or to the fact that the females are recovering from spawning and have ovaries of minimal size. The differences among quarters for each sex also are highly significant.

Further consideration of the covariance analysis indicates that the slopes of the regression lines of the males, which are consistently lower than those of the females, are significantly so during the third and fourth quarters. Thus it appears that the males, in addition to being surpassed in numbers and dominated in length by the females (p. 188), become more slender compared with the females as they grow older.

These differences between the sexes and among the seasons indicate the necessity of classifying the data by sex and time of capture, if critical comparisons of condition are to be made and if the data are to be used for transforming the weight of yellowtail to numbers of fish. For the latter purpose we have segregated our data by quarters, but

TABLE 18.—*Summary of covariance analysis of length-weight data on yellowtail*

I. COMPARISON OF SEXES BY QUARTER

Source of variation	1st quarter			2d quarter			3d quarter			4th quarter		
	Degrees of freedom	Mean square	F	Degrees of freedom	Mean square	F	Degrees of freedom	Mean square	F	Degrees of freedom	Mean square	F
Deviations from individual sample regression	372	0.00184		254	0.00212		272	0.00105		199	0.00154	
Difference between regression coefficients	1	.0069	3.75	1	.0079	3.73	1	.0058	[1] 5.52	1	.0141	[2] 9.16
Difference between adjusted means	1	.0245	[2] 13.17	1	.0867	[2] 40.51	1	.0004	.38	1	.0225	[2] 13.98
Difference between samples	2	.0157	[2] 8.53	2	.0473	[2] 22.31	2	.0031	2.95	2	.0183	[2] 11.88

II. COMPARISON OF QUARTERS BY SEX

Source of variation	Male			Female		
	Degrees of freedom	Mean square	F	Degrees of freedom	Mean square	F
Deviations from individual sample regression	282	0.00168		815	0.00165	
Difference between regression coefficients	3	.0068	[1] 4.05	3	.0202	[2] 12.24
Difference between adjusted means	3	.0140	[2] 8.04	3	.0855	[2] 50.00
Difference between samples	6	.0104	[2] 6.19	6	.0528	[2] 32.00

[1] Expected less than once in 20 times by chance.
[2] Expected less than once in 100 times by chance.

since the length-weight data were from samples taken at random and include representative numbers of males and females we regard the total values for each quarter as representative and have not segregated the data by sex.[4]

The estimated weight at each length occurring in the landings has been obtained from the combined data for males and females in the preparation of table 19. This will be used in the next section to determine the number of fish landed. Figure 12 indicates the average length-weight relation. Meanwhile, it is interesting to note the range in weight of the yellowtail in the landings. When the central 98 percent was selected from the data on average length composition (table 10) to avoid the few very small or very large specimens, the "lower limit" of size was 27.3 cm. (0.38 lb.) and the "upper limit" was 46.7 cm. (2.17 lb.). The average length was 35.87 cm. (0.93 lb.). The smaller value reflects selection by the fishermen as influenced by buyers interested in filleting the fish. The buyers estimate that an average of 40 percent of the weight is recoverable as fillets. If

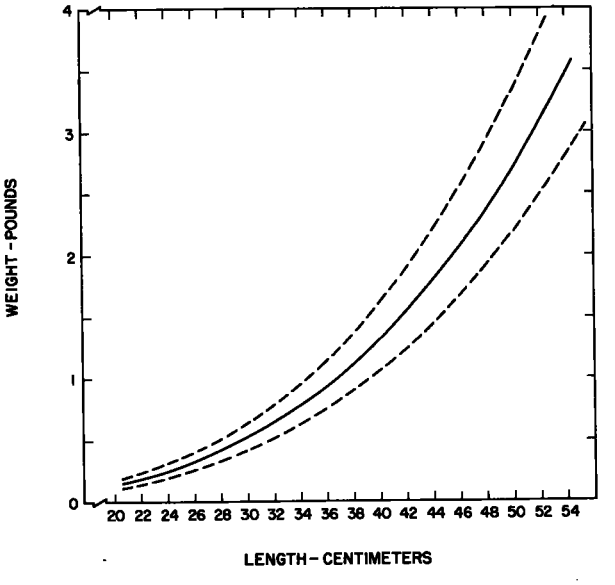

FIGURE 12.—Average length-weight relation of yellowtail landed from the southern New England stock during 1943. The dotted lines are plus and minus twice the standard error of estimate and enclose about 95 percent of the observations.

this was true of the small fish,[5] the lower limit of desirable fillet weight would be about 0.076 pound, or just over 1 ounce. The average-size fillet weighed 0.186 pound, or about 3 ounces, and the maximum 0.434 pound, or about 7 ounces.

[4] We have estimated the discrepancy arising from varying proportions of the sexes by calculating the average weight of the yellowtail in the second quarter (when the greatest difference between the sexes occurs) for each sex by using the aggregate formula, and we found that the maximum difference between the sexes in average weight was 3.7 percent. Because of the small difference and the poor representation of males in the length-weight data for the second and third quarters, it appears unnecessary to compute the averages separately by sex.

[5] Small fish were disliked by the filleters because of higher cost and lower yield, but data on fillet recovery were not obtained.

TABLE 19.—*Estimated weight, by quarters, of yellowtail of each length group in the landings from the southern New England stock, during 1943*

[In pounds]

Length	1st quarter	2d quarter	3d quarter	4th quarter	Year
20.5 cm	0.14			0.15	0.15
21.5 cm	.16			.18	.18
22.5 cm	.19	0.22	0.22	.21	.20
23.5 cm	.22	.25	.25	.24	.24
24.5 cm	.26	.29	.28	.27	.27
25.5 cm	.29	.33	.32	.31	.31
26.5 cm	.33	.37	.36	.35	.35
27.5 cm	.38	.41	.40	.40	.39
28.5 cm	.43	.46	.44	.45	.44
29.5 cm	.48	.51	.49	.50	.49
30.5 cm	.54	.56	.54	.56	.55
31.5 cm	.60	.62	.59	.62	.61
32.5 cm	.67	.68	.65	.68	.67
33.5 cm	.74	.75	.71	.75	.74
34.5 cm	.82	.82	.78	.83	.82
35.5 cm	.91	.90	.84	.91	.89
36.5 cm	1.00	.98	.92	.99	.98
37.5 cm	1.09	1.06	.99	1.08	1.07
38.5 cm	1.20	1.15	1.07	1.18	1.16
39.5 cm	1.30	1.24	1.16	1.28	1.26
40.5 cm	1.42	1.34	1.24	1.39	1.37
41.5 cm	1.54	1.44	1.34	1.51	1.48
42.5 cm	1.68	1.56	1.43	1.63	1.60
43.5 cm	1.81	1.68	1.54	1.76	1.73
44.5 cm	1.96	1.79	1.64	1.89	1.86
45.5 cm	2.11	1.92	1.75	2.03	2.00
46.5 cm	2.28	2.05	1.87	2.18	2.14
47.5 cm	2.45	2.19	1.99	2.33	2.29
48.5 cm	2.63	2.33	2.11	2.50	2.45
49.5 cm	2.82	2.48	2.24	2.67	2.62
50.5 cm	3.02	2.64		2.84	2.80
51.5 cm	3.23	2.80		3.03	2.98
52.5 cm	3.44	2.97		3.23	3.17
53.5 cm	3.68			3.43	3.37
54.5 cm				3.64	3.58

CALCULATING NUMBERS OF FISH LANDED

In many of the later computations, it will be desirable to deal in numbers rather than pounds of fish to avoid a constant accounting for change due to growth.

The landings, given by quarters in thousands of pounds in table 7, may be converted to numbers of fish if we know the average weight of the fish. The average weight, W (table 20), is estimated by summing the weights of the fish measured for length as follows:

$$W=\frac{\Sigma N_L W_L}{N_T}$$

N_L=number in each length group (appendix tables C–14 and C–15, pp. 244–5), W_L=average weight of yellowtail of the corresponding length in that quarter (table 19), N_T=total number measured during the quarter. After determining the average weight of the fish, the landings in thousands of pounds are converted to number of fish (table 21).

CATCH PER UNIT OF EFFORT

We determined the catch per unit-of-effort to obtain an estimate of the relative size of the population or the equivalent as defined by Marr (1951), the relative apparent abundance.[6]

TABLE 20.—*Average weight of yellowtail, by quarters, landed from the southern New England stock, 1942–47*

[In pounds]

Quarter	1942	1943	1944	1945	1946	1947
1st		1.17309	1.05247	1.26689	1.07662	1.05420
2d		.90554	.74412	.94403	.87770	.95305
3d		.86310	.80208	.76025	.78116	.75504
4th	0.83036	1.04952	.99991	1.00915	.98079	.95558

TABLE 21.—*Number of yellowtail, by quarters, landed from the southern New England stock, 1942–47*

[In thousands of fish]

Quarter	1942	1943	1944	1945	1946	1947
1st		11,669	10,401	4,970	6,099	5,136
2d		7,569	6,232	1,575	2,999	4,370
3d		16,553	7,114	8,909	6,866	9,688
4th	18,801	4,714	2,116	8,229	9,484	10,267
Total	18,801	40,505	25,863	23,683	25,448	29,461

In developing this measure of abundance, we sought one that would be stable, continuous, and representative of the fleet's activities. We desired a figure that would not vary with changes in the composition of the fleet, with seasonal changes in the weather, or with changes in the relative attractiveness to the fishermen of yellowtail and other species. Of course, this measure should be continuous and uninterrupted in order to provide data in all seasons of all the years under study. Finally, since vessels seeking yellowtail fish as a fleet and freely exchange information by radio and in port, they naturally concentrate where the fish are concentrated. Their fishing is far from randomly distributed. They avoid for months, or even years, areas where yellowtail are judged to be scattered and the risk of an unproductive trip is too great. There appears to be no possibility of obtaining a measure of abundance from this fishing activity that would be based on fishing effort distributed over the range of the stock. We, therefore, considered as an alternative obtaining a measure representative of the activities of the entire fleet.

[6] We shall use the terms in the sense defined by Marr as follows: Abundance, the absolute number of individuals in the population; availability, the degree or percentage to which a population is accessible to the fishery; apparent abundance, abundance as affected by availability; and catch per unit of effort, an index number related to the apparent abundance.

Meeting these three criteria was necessarily a compromise with the characteristics of the fishing fleet. Throughout the period of our study, yellowtail were taken entirely by otter trawlers ranging in size from about 10 to 75 gross tons. The majority of these vessels, and the most successful, were those of about 25 to 40 gross tons, which could carry a crew of 4 to 6 men and make fairly regular trips of 3 to 6 days' duration.

All of the vessels fishing for yellowtail used similar gear, but since every fisherman has his ideas of how an otter-trawl net should be rigged, probably no two were identical. Essentially, however, they used lightweight trawl nets of cotton or manila twine with head ropes ranging in length from 50 to 70 feet and with foot ropes of chain, perhaps protected by a wrapping of old rope but never with large rollers. Usually, the doors were attached on pennants from 1 to 3 fathoms from the net. Vignernon-Dahl gear was never used.

During the period of study, the yellowtail fishery was only one of the major fisheries in the area and a large proportion of the fleet turned from one fishery to another as the markets and the fish dictated. Early in the yellowtail fishery many of the fishermen who had formerly sought the winter flounder would regularly return to that fishery in the spring season from April to June. Other vessels occasionally interspersed their fishing for yellowtail with periods of fishing for whiting, scup, or other species. The larger vessels (of more than 50 gross tons) usually sought yellowtail only in the winter when the weather was too rough for them to go to Georges Bank for sea scallops or haddock, and the crews preferred to fish the nearby yellowtail grounds. Our study of yellowtail abundance was further complicated by the fact that other species of fish were sometimes abundant near the yellowtail grounds and vessels on the same trip would catch a mixture of several species.

After several attempts to select particular vessels from the fleet, which would provide a continuous record, we found that no sizeable part of the fleet had fished throughout the period studied. We therefore decided to select vessels of 26 to 50 gross tons. This range in weight included the majority of the vessels, but it eliminated the very small ones which were most affected by the seasonal weather changes and likewise the very large ones which usually entered the fishery only in periods of poor weather. Vessels in this group fished only part of the time for yellowtail flounders, and many times they landed a mixture of yellowtail and other species; consequently, we further restricted our data to landings comprised of more than 75 percent yellowtail.

Most of the vessels fished day and night while on the fishing grounds, although a few of the smaller ones fished only during daylight hours. It was decided to select as a unit of effort a day of 24 hours actual fishing on the grounds and to consider the small amount of entirely daylight fishing according to the actual time fished. Information on fishing effort was obtained almost entirely at the port of New Bedford, where the captain of each vessel landing was interviewed to determine where he had fished, what he had caught, and how long he had fished in each statistical subarea to the nearest tenth of a day.

The interviews were commenced in October 1942 and were obtained a few days each week until the early part of 1943 after which they were made daily (except for some interruptions caused by personnel changes). Prior to October 1942, a considerable number of cooperating captains had kept detailed logbook records, which made it possible for us to estimate the catch per unit of effort during the first 3 quarters of 1942.

Despite the restriction on size of the vessels, condition of the catch, and necessity of landing the catch at New Bedford, a considerable percentage of the total catch has been included in our data. The percentage of the landings included in the catch per unit-of-effort data was low (1.4) during the early months of 1942 when only logbook records were available, but rose to 16.7 percent during the last quarter of 1942 (table 22). Subsequently, it varied from 14.1 percent in 1944 to as much as 39.2 percent in 1948. In order to reduce the effect of sampling variation during the first 3 quarters of 1942 and during the second quarter of 1945, we have included the catch and adjusted days fished for trawlers of between 5 and 25 gross tons. The days fished were multiplied by 0.796, the ratio of the catch per day of the small trawlers to the catch per day of our selected group during the period 1943 to 1947. Considering the generally substantial proportion of the landings included and the fact that the New Bed-

ford fishing fleet usually fished the concentration of yellowtail flounder wherever it was found within the range of the southern New England stock, we believe that our calculation of the catch per unit of effort is representative of that experienced by the entire fleet.

TABLE 22.—*Percent of yellowtail landings from the southern New England stock included in catch per unit-of-effort data*

Period	Percent	Period	Percent
1942:		1945	25.1
Jan.–Sept.	1.4	1946	31.6
Oct.–Dec.	16.7	1947	32.7
1943	24.0	1948	39.2
1944	14.1	1949	38.0

The most obvious phenomenon in the resulting catch-per-day data is the pronounced seasonal fluctuation (table 23). In every year (1942–49) the catch per day during the third quarter was greater than in any other quarter. The remaining quarters were more variable with the first, second, and fourth leading in one or more of the years. The average landing per quarter for the 8 years, 1942 through 1949, was 5,808 pounds of yellowtail per day for the first quarter; 5,242 pounds for the second quarter, 9,480 pounds for the third quarter, and 6,400 pounds per day for the fourth quarter, with an unweighted average of 6,732 pounds for the year.

This seasonal fluctuation does not hide the general downward trend of the relative apparent abundance of the yellowtail from 1942 to 1949. The trend is similar in all quarters (fig. 13). The annual average catch per day differs somewhat from the trend in the total landings (fig. 14): the change in the relative apparent abundance is not so great as the change in quantities landed. This is to be expected from the fleet's habit of concentrating on a species when it is abundant and of changing to other fisheries when it becomes scarce. Also, a considerable increase in the relative apparent abundance occurred in 1945, which was associated with a decrease in fishing effort and therefore was not accompanied by an increase in the catch.

The catch per day has been computed also in terms of numbers of fish to provide data which will be used later in the estimation of mortalities. It is of interest to note that the catch per day in terms of numbers of fish landed greatly accentuates the seasonal fluctuation because of the tendency for yellowtail to run larger in the winter fishery and smaller in the summer.

TABLE 23.—*Catch per unit of effort of yellowtail from the southern New England stock, by year and quarter, 1942–49*

[Averages not weighted]

Year and quarter	Catch (thousands of pounds)[1]	Days fished[1]	Catch per day	
			Pounds	Number of fish[2]
Year 1942:				
1st quarter[3]	702.9	84.3	8,338	
2d quarter[3]	301.0	43.6	6,904	
3d quarter[3]	731.2	39.6	18,465	
4th quarter	4,487.6	435.4	10,307	12,413
Average[4]		602.9	11,004	
Year 1943:				
1st quarter	3,298.5	489.7	6,736	5,742
2d quarter	986.6	178.9	5,515	6,090
3d quarter	4,035.7	377.9	10,679	12,373
4th quarter	1,231.1	209.0	5,890	5,612
Total and average	9,551.9		7,205	
Year 1944:				
1st quarter	1,482.3	243.4	6,090	5,786
2d quarter	226.9	44.7	5,076	6,821
3d quarter	1,433.8	178.0	8,055	10,043
4th quarter	161.0	38.6	4,171	4,171
Total and average	3,304.0		5,848	
Year 1945:				
1st quarter	1,079.8	159.4	6,774	5,347
2d quarter[3]	50.6	8.8	5,750	6,091
3d quarter	1,736.5	181.1	9,589	12,613
4th quarter	2,863.6	310.7	9,217	9,133
Total and average	5,730.5		7,832	
Year 1946:				
1st quarter	1,218.4	188.4	6,467	6,007
2d quarter	370.3	52.3	7,080	8,066
3d quarter	2,134.4	263.5	8,100	10,369
4th quarter	3,829.1	543.2	7,049	7,187
Total and average	7,552.2		7,174	
Year 1947:				
1st quarter	1,482.6	259.7	5,709	5,415
2d quarter	736.6	142.8	5,158	5,412
3d quarter	2,468.5	265.1	9,311	12,332
4th quarter	4,047.2	749.6	5,399	5,650
Total and average	8,734.9		6,394	
Year 1948:				
1st quarter	1,895.8	540.1	3,510	
2d quarter	1,388.3	292.0	4,754	
3d quarter	2,289.1	412.6	5,548	
4th quarter	2,997.6	591.3	5,070	
Total and average	8,570.8		4,720	
Year 1949:				
1st quarter	1,692.0	594.9	2,844	
2d quarter	216.3	76.5	2,827	
3d quarter	449.5	73.8	6,091	
4th quarter	1,555.7	379.5	4,099	
Total and average	3,913.5		3,965	
Average, 1942–49:[4]				
1st quarter			5,808	
2d quarter			5,242	
3d quarter			9,480	
4th quarter			6,400	
Grand average			6,732	

[1] Catch (in thousands of pounds) and days fished from interviewed vessels of 26 to 50 gross tons landing more than 75 percent yellowtail on each trip.
[2] Estimates based on average weights from table 20, p. 195.
[3] Includes the catch and days fished times 0.796 of trawlers from 5 to 25 gross tons. (See text, p. 196.)
[4] Unweighted average.

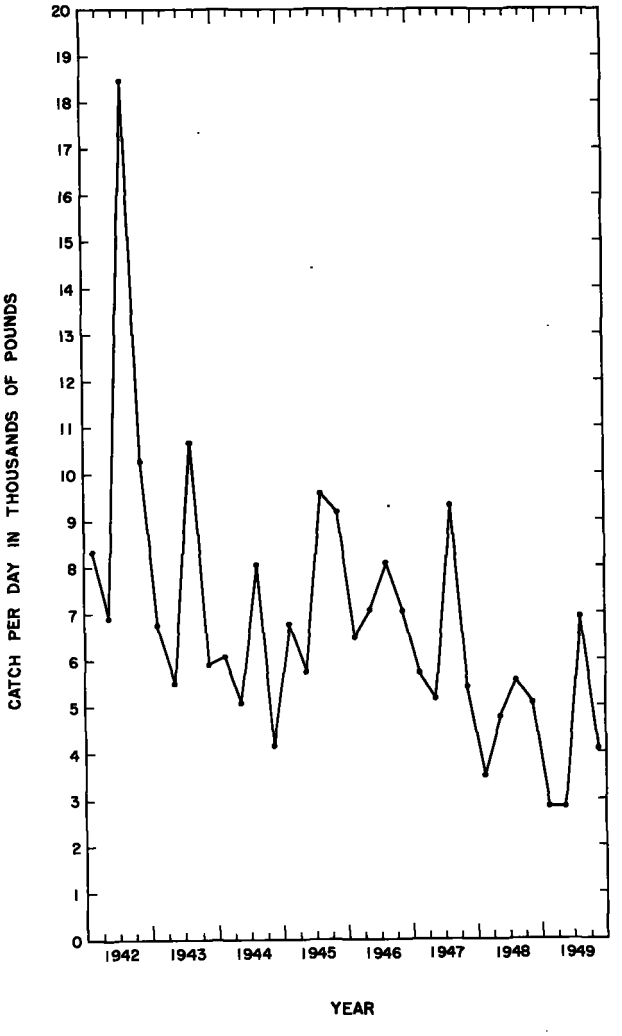

FIGURE 13.—Trend in relative apparent abundance, by quarters, of yellowtail from the southern New England stock, 1942 through 1949.

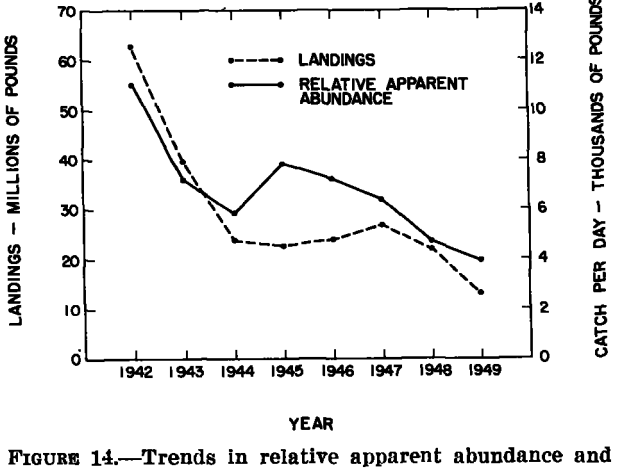

FIGURE 14.—Trends in relative apparent abundance and landings of yellowtail from the southern New England stock, 1942 through 1949.

Fishing Effort

The catch per unit of effort as computed for the selected trawlers leads naturally to an estimate of the amount of fishing for yellowtail in terms of the standard day, i. e., days fished by small otter trawlers of between 26 and 50 gross tons that landed more than 75-percent yellowtail in the catch. The data (table 24) have been computed from tables 7 and 23.

TABLE 24.—*Number of standard days fished for yellowtail on southern New England grounds, by quarters, 1942–49*

[Data computed from tables 7 and 23]

Quarter	1942	1943	1944	1945	1946	1947	1948	1949
1st	1,841	2,032	1,798	930	1,015	948	1,417	1,212
2d	1,891	1,243	914	322	372	807	852	370
3d	1,017	1,338	708	706	662	786	1,117	322
4th	1,515	840	507	901	1,320	1,817	1,312	939
Total	6,264	5,453	3,927	2,859	3,369	4,358	4,698	2,843

It is obvious immediately that the seasonal distribution of fishing effort did not parallel the seasonal distributions of catch and abundance. Usually there was more fishing for yellowtail in the first and fourth quarters of the year, less in the third quarter, and least in the second quarter. This is a reflection of a seasonal trend in the price received for yellowtail and the relative attractiveness of other fisheries. During the winter, yellowtail usually was higher in price and more easily caught than other species, but during the spring and summer the price declined as winter flounder, scup, whiting, and other species became available. The large decrease in the amount of fishing for yellowtail during the summer months between 1948 and 1949 is of interest. This occurred because of a diversion of the fleet to the newly developed "trash" fishery as described by Snow (1950).

AGE DETERMINATION

The ages of a large number of yellowtail flounder were determined for two purposes: (1) To estimate the age composition of the landings in each year and thereby obtain an estimate of the recruitment and mortality rates; and (2) to estimate the rate of growth.

Early in the investigation consideration was given to the best method of determining the age of the fish. The Petersen method of using modes in the length-frequency distribution showed little

promise in the first data examined. The study of scales and otoliths was then undertaken. Both show regular growth rings, and while the otoliths may be more easily read in the larger fish, we chose the scales.[7] These are readily readable for several growth rings, are much easier to obtain from the fish, and can be handled with much less trouble in the laboratory. The choice of scales also was influenced to some extent by the fish dealers, who were accustomed to boxing and shipping fresh fish to the market. Early in the investigation a substantial part of the catch went to the consumer as whole fish, and as it was desirable to have clean, good-looking fish, several dealers refused to permit the mutilation necessary to obtain the otoliths.

It was then necessary to determine which scales were the most satisfactory to use. Careful examination of 13 different areas on the yellowtail revealed that the largest[8] symmetrical scales are located near the anterior end of the caudal peduncle on the eyed side. Scales from this area show more distinct growth rings than do those from other areas; consequently, they were used throughout the investigation. The limits of the area are not critical: scales from near the lateral line on the posterior half of the eyed side are similar in size and in clarity of growth rings.

The scales were taken from the landings in the same manner as the length measurements (p. 186), and usually they were obtained at the same time: 25 fish were measured and scales obtained, and another 75 fish were measured. The fish were measured to the nearest half centimeter. They were taken only from catches of vessels fishing in a single statistical subarea in order to make certain of their origin.

After considerable experimentation with various methods of mounting the scales on slides, it was found that they could be handled speedily and entirely satisfactorily by obtaining an impression on small strips of cellulose acetate, using a rollertype press. The strips, 2½ inches long by ½ inch wide by 0.020 inch thick, were warmed on a metal box heated by a 60-watt bulb to a temperature a little hotter than the hand could stand. Four or five scales were placed on a strip with the rough sides in contact. The scales were selected without aid of a microscope because the regenerated scales are readily distinguished with the naked eye. The only criteria for the selection of scales to be mounted were that they be symmetrical and lack regeneration. Information concerning the date, locality, length, and sex of the fish was transferred to the strip with a special celluloid ink.

The growth rings vary in character according to their position on the scale (fig. 15). The first ring, near the center, is rather indistinct at the magnification generally used when examining scales. It consists of a group of closely spaced circuli and is terminated by the first complete circulus that can be traced around the anterior portion of the scale, followed by the widely spaced circuli. This first growth ring is so narrow that it might have been considered a "natal" ring; that is, one associated with the larval stage, had it not been for our finding yellowtail that possessed this recently completed ring in the spring just before the spawning season.

Each of the succeeding three growth rings consist of a zone of widely spaced circuli enclosed by a zone of closely spaced circuli. The outer circuli of the latter are usually incomplete. The outer edge of the growth zone is marked by a prominent, complete circulus, which is concentric with the margin. The second growth ring is always very prominent. It consists of a broad zone in which the circuli are widely spaced at first but gradually come closer together at the outer edge of the ring. The third growth ring is usually about one-half the width of the second, and it, too, consists of widely spaced circuli gradually coming closer together. The fourth ring is about one-third to one-half the width of the third, has very few widely spaced circuli, and in some cases the transition from wide spacing to narrow is abrupt. The fifth and succeeding growth rings are usually very narrow and can be most easily identified if one examines the sides of the scale and attempts to trace the rings around to the apex. These include few, if any, widely spaced circuli. The outer part of the ring usually is just an interruption of the closely spaced circuli.

[7] Scott (1954) used otoliths in his studies of the yellowtail from Cape Cod and the Nova Scotian Banks. He found otoliths about as difficult to read as scales from the Cape Cod area but much easier than scales from the Nova Scotian area.

[8] The size of the scale is an important criterion because the first growth ring appears in a tiny area near the center of the scale and is completely missing from smaller scales near the head and along the edges of the fins.

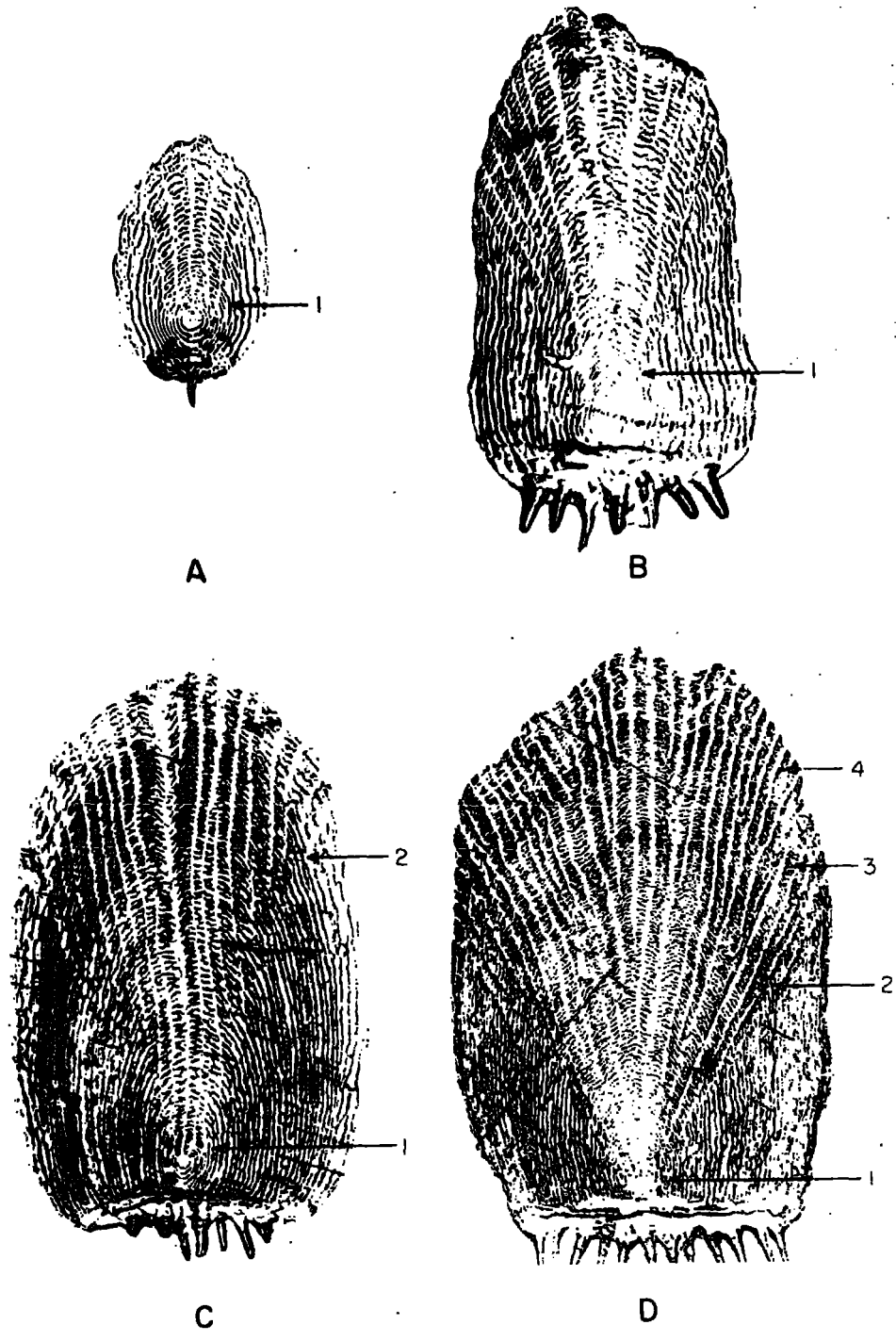

FIGURE 15.—Scales of yellowtail flounder: A, 8.2 cm. specimen, 1 annulus, April 1944; B, 16.6 cm. specimen, 1 annulus, September 1944; C, 27 cm. specimen, 2 annuli, May 1943; D, 36 cm. specimen, 4 annuli, June 1942.

In the third growth zone, frequently a very narrow ring of closely spaced circuli is visible in the midst of the widely spaced ones. This ring is less prominent than the rings of closely spaced circuli terminating the second and third growth zones. We have considered that this ring is associated with spawning and is not a true growth ring comparable to the others which we have counted. If it is a spawning mark, it would be expected to appear in subsequent growth zones, but it is not apparent because the widely spaced circuli are so few in growth zones after the third.

Examination of a series of scale samples taken throughout the year revealed that the new growth ring begins to form from January to March, and that it is apparent earliest in fish with two completed rings and later in the older fish. By the middle of March, almost all scales show the beginning of the new growth ring. Since the spawning season commences in late March, we have designated April 1 as beginning another year in the life of the fish, and in counting the growth rings, we have not included those rings completed during January, February, or March.

The consistent appearance of new growth at one season of the year is evidence that these growth rings are true annuli. Additional evidence appears from the facts (which will be developed later in this paper) that the growth rings are added systematically as growth proceeds, that a progression of modes in length-frequency data agrees closely with the length of the fish at corresponding ages estimated from the scales, and that there are consistencies in the data on age composition and in the changes in the average length of each age group which would be unlikely if the rings were not annuli. It will also be shown that there is good agreement between the mean lengths of yellowtail aged by scales during this study and those aged by otoliths by Scott (1954). Furthermore, the theoretical ultimate length computed from the lengths at each age is very close to the maximum length observed.

The age determinations used in this paper were made by Raymond J. Buller and Dexter S. Haven during a single period of a few months. The scale impressions were enlarged by a microprojector and read independently by each worker. After preliminary trials to establish a uniform technique, the two men were able to agree on the reading of more than 90 percent of the scales examined. Due to the scarcity of older scales and the difficulty of reading them, the scales aged 6 years and older were combined in one group in the first quarter and ages 7 and older in the other quarters.

Scales that were not read identically by the two readers were discarded. Since the scales become more difficult to read with increasing age of the fish, discarding them could change the proportions of older fish in the samples. Fortunately this did not happen, as indicated in figure 16 where the percentage length distributions of the yellowtail whose ages were determined from scales are compared with the percentage length distributions of the fish that were measured. Only very small differences in composition are evident, the greatest difference being a greater percentage of females in the 39- to 43-cm. group of aged fish which was compensated by a smaller percentage in the 35- to 38-cm. group. The proportion of males was almost identical—34.50 percent in the aged fish, 34.67 percent in the measured fish.

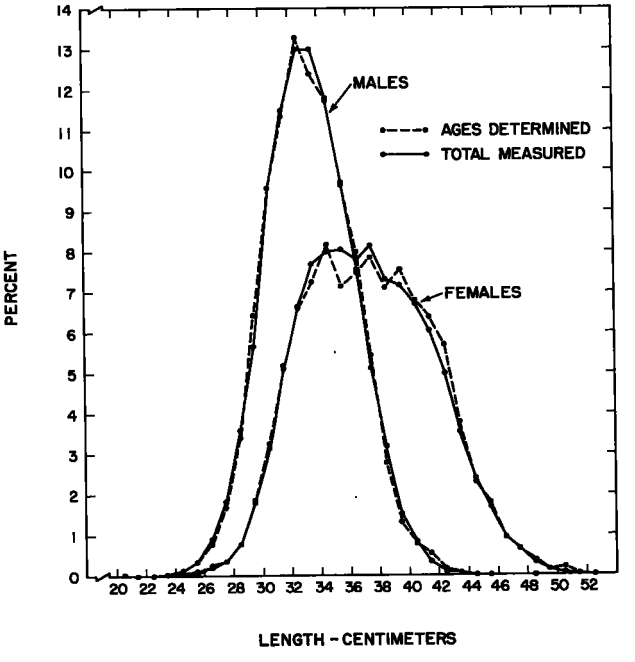

FIGURE 16.—Comparison of the percent length distributions of 7,924 yellowtail whose ages were determined from scales with 37,075 fish that were measured, 1943 through 1947.

Rate of Growth

Growth data have been developed from the attained length at time of capture of 9,204 yellowtail for which the ages were determined from scales. These fish were included in the samples collected from 1942 to 1947. The data are listed in detail in appendix D, p. 246, and summarized in table 25. The mean length of each age group in each calendar quarter during which 10 or more age determinations were obtained has been computed (table 26). It may be recalled that we have assumed that the annulus is complete on March 31, and therefore the yellowtail's year of life does not correspond to the calendar year. The first quarter in the fish's year is the second quarter in the calendar year. For example, the 2-annuli, male yellowtail that averaged 32 cm. in the fourth quarter of 1942 were actually in the third quarter of their third year of life.

The average attained length for each quarter of the yellowtail's life is plotted in figure 17. It is readily apparent from this chart that the females

TABLE 25.—*Number of age determinations of yellowtail, by sex and quarter, from the southern New England stock, 1942–47*

Year and quarter	Male	Female	Undetermined sex	Total
Year 1942:				
1st quarter	10	15		25
2d quarter			368	368
3d quarter			74	74
4th quarter	48	50	158	256
Year 1943:				
1st quarter	23	49	133	205
2d quarter	160	430	89	679
3d quarter	30	145		175
4th quarter	42	81	279	402
Year 1944:				
1st quarter	20	30	43	93
2d quarter	56	68		124
3d quarter	46	85	13	144
4th quarter	77	167		244
Year 1945:				
1st quarter	298	586		884
2d quarter	39	61		100
3d quarter	256	412		668
4th quarter	264	475		739
Year 1946:				
1st quarter	239	408		647
2d quarter	13	12		25
3d quarter	326	582		908
4th quarter	326	572		898
Year 1947:				
1st quarter	79	121		200
2d quarter	146	279		425
3d quarter	149	350		499
4th quarter	144	278		422
Total	2,791	5,256	1,157	9,204

TABLE 26.—*Mean lengths of yellowtail at time of capture, by sex and age, from southern New England stock, 1942–47*

[Computed from 10 or more age determinations]

Time of capture	Mean length (in centimeters) of—																		
	Males with—					Females with—							Undetermined sex with—						
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli
Year 1942:																			
2d quarter														29.4	33.4	34.5	35.9	37.3	39.8
3d quarter														29.6	34	37.1			
4th quarter		32	35.3				32.6	36.1						32.3	36.2	38.8	41.3		
Year 1943:																			
1st quarter		32						38.1	41.3		46.2		27.1	32.4	35.3	37.2	40.8		
2d quarter			32.8	35.5			29.6	34.2	38.2	40.6	42.1	44.9		28.7	32.7	37.4		42.7	
3d quarter		30.2	34.2				31.7	34.6	38.8										
4th quarter		32.5	34.2				33.3	36.9	39.3					33.9	36	39.4	42.8		
Year 1944:																			
1st quarter								37.9						31	35.6				
2d quarter			31.8					33.6											
3d quarter			31.9					33.8	38.2										
4th quarter		30.6	33.8	37.4			32.4	36.6	39.9	42.1	45								
Year 1945:																			
1st quarter	27.5	33	35.6	37.5	38.5		34.8	38.1	41.2	43	45.9								
2d quarter			32	33.6				33.7	37			43.4							
3d quarter		30.4	33.4	34.5			31.7	35.7	37.4	39.9	41.8								
4th quarter		32	34.2	35.7	38.2		33.6	36.4	38.5	41.3	43.2	46.4							
Year 1946:																			
1st quarter	28	33.5	35.8	38.2		28.1	34.8	37.6	41	43.2	46.1								
3d quarter		30.2	33.8	34.9			31.5	35.2	37.7	40.1	42.4								
4th quarter		31.8	34.5	35.9	37.3		33.3	36.7	39	40.7	42.8	46							
Year 1947:																			
1st quarter		33.8	37.2			29.9	35.2	38.2	41.8	42.4	45.9								
2d quarter		29.5	32.6	35.7	37.1		31.1	34.9	37.9	40.7	42.3	44.9							
3d quarter		30.5	32.8	35	37.5		32.1	34.9	37.7	40.3	42.8								
4th quarter		32	34.3	36			33.5	36.6	38.8	41.5	42.8								
Average, 1942–47:																			
1st quarter	27.9	33.3	35.8	37.7	39.4	28.8	34.8	38	41.1	43	46		27.1	32	35.4	37.5	40.2	43.5	
2d quarter		29.1	32.5	35.2	37.2		30.4	34.2	37.9	40.6	42.2	44.5		29	33.2	34.7	36.6	38.8	39.8
3d quarter		30.3	33.1	34.9	37.1		31.7	34.8	37.7	40.1	42.4	44.3		30.1	33.9	37			
4th quarter		31.9	34.4	35.9	37.6		33.3	36.7	39	41.1	43.2	46.4		33.6	36.4	39.5	42.6	44.9	

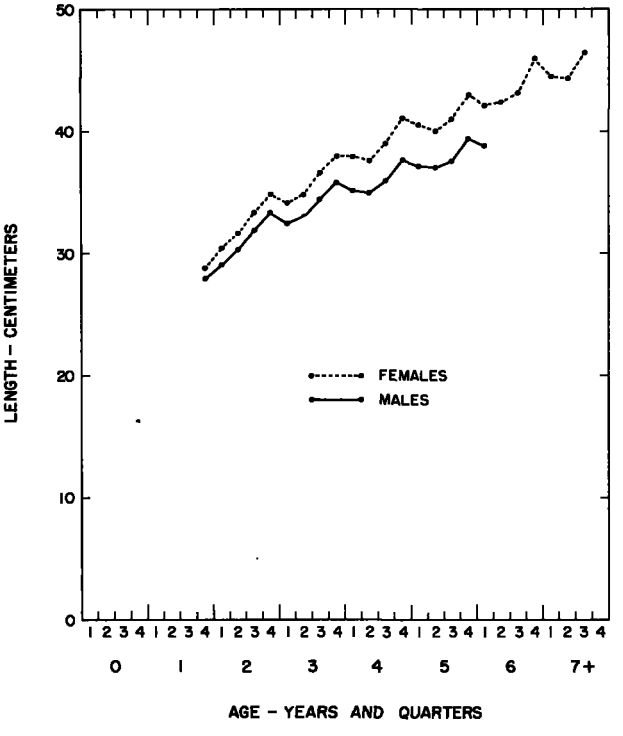

FIGURE 17.—Mean lengths of yellowtail, by ages and quarters, in the landings from the southern New England stock, fourth quarter 1942 through 1947.

grow faster than the males, as was to be expected from the observation that females attain a greater size. They were 4.5 percent longer than the males at age 2 and up to 9.1 percent longer at age 5. The lack of males prevents such comparison in the older age groups.

On the other hand, figure 17 indicates an unexpected constant seasonal cycle in the growth curve. The mean length during the fourth quarter of the fish's year of life (first calendar quarter) is usually slightly greater than during the succeeding first and second quarters, in both of which the fish are of about the same average size. One would expect slow growth in winter and rapid growth in summer, except perhaps during the spawning period from April through June. Although reduction of the mean length of an age group might occur among the younger groups because of seasonal changes in gear selectivity, it would not be expected consistently in all age groups.

The possibility of this seasonal change in average length being due to errors in reading the scales was not overlooked. If too few rings were counted in the fourth quarter of the fish's year of life and/or too many rings were counted in the succeeding first quarter, such a cycle might result. Error in reading the scales seems improbable, however, because any evidence of a new annulus forming at the edge of a scale during the fourth quarter was disregarded, and too few rings could have been read only by disregarding annuli which were counted in similar scales from second and third quarters. Most important is the similarity of the cycle in all age groups after the yearling. Since scales from the 2- and 3-year-old groups are so much easier to read than from the older age groups, we feel certain that any reading errors would have been much more common among the older fish; consequently, a change in the cycle would have occurred between the young and old groups. We, therefore, believe that reading errors are not responsible for the seasonal change in average length. Rather, the most probable explanation of this seasonal growth pattern is that different populations of flounders occurred in the landings in different quarters of the year and that these populations were growing at slightly different rates.

The differences in rate of growth of yellowtail among quarters are accentuated when the lengths are converted to weights (using the formulas from table 16), because when the fish were longer they were also correspondingly heavier. The weights (table 27) when plotted (fig. 18) show a markedly faster growth in the first quarter of the fish's year of life, intermediate and about equal growth during the second and fourth quarters, and slow growth during the third quarter. The differences, especially among females, are so great that they indicate population differences rather than seasonal differences. For example, females with three annuli were heavier in the first quarter than in the following second and third quarters, and in their next year of life were heavier in the first quarter than during the subsequent second, third, and fourth quarters. In addition, the heaviest fish were found during the coldest season when we would expect the rate of growth to be minimal.

These curves (fig. 18), which are nearly straight lines passing through the point of origin, indicate nearly equal weight increments during each year of life in the fishery. This results, in part,

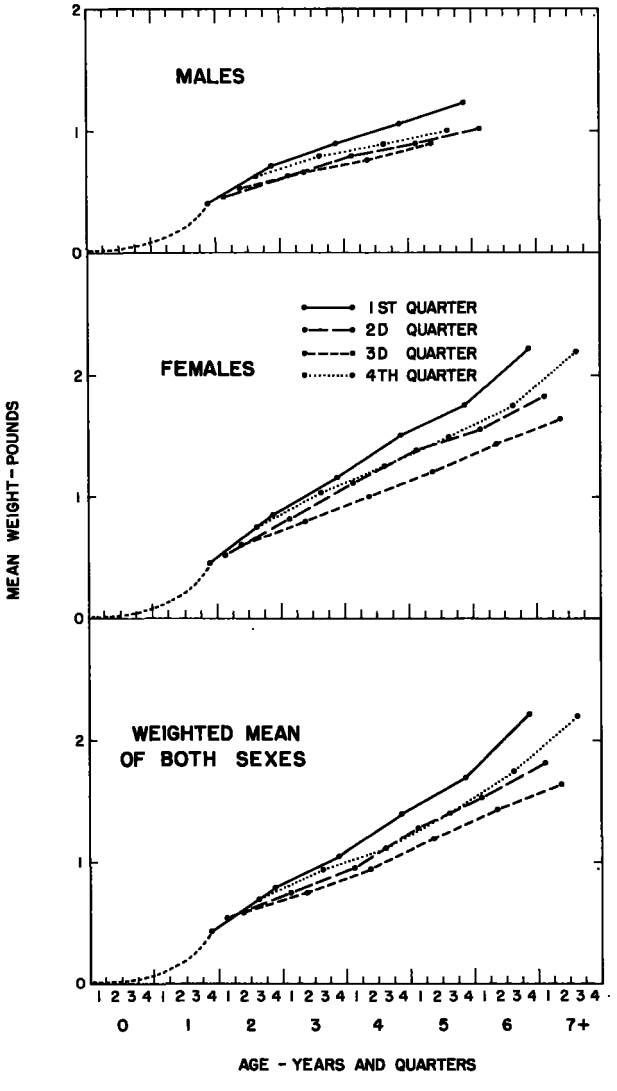

FIGURE 18.—Growth in weight of yellowtail from the southern New England stock caught during different calendar quarters. Dashed line indicates probable growth during early life.

from certain characteristics of the data. There is little doubt that the average weight of the yellowtail taken during the third year of life (2-annuli) is greater than the average weight of the fish remaining in the sea, because the fishery selects fish above a certain size. We shall note subsequently that growth during the first year of life is very small, as suggested by the dotted lines in figure 18. At the other end of the curve we have combined the 6-annuli and older fish in the first quarter and 7-annuli and older fish in other quarters. This combination of age groups is probably responsible for the greater growth among females in the first and fourth quarters.

TABLE 27.—*Mean weights and growth rates of yellowtail, by quarter, age, and sex, from the southern New England stock, 1942–47*

Number of annuli	Males		Females		Sexes combined, weighted mean	Instantaneous growth rate
	Mean weight	Number	Mean weight	Number		
1st quarter:	*Pounds*		*Pounds*		*Pounds*	
1 annulus	0.4137	51	0.4543	28	0.4281	
2 annuli	.7229	250	.8619	268	.7948	0.619
3 annuli	.9089	238	1.1607	295	1.0483	.277
4 annuli	1.0696	97	1.5129	285	1.4003	.290
5 annuli	1.2293	23	1.7634	172	1.7004	.194
6 annuli			2.2168	146	2.2168	.265
2d quarter:						
1 annulus						
2 annuli	.4724	55	.5724	95	.5357	
3 annuli	.6347	219	.8181	389	.7520	.340
4 annuli	.7854	104	1.1172	120	.9632	.248
5 annuli	.9104	33	1.3769	128	1.2813	.285
6 annuli	1.0191	3	1.5485	77	1.5286	.176
7 annuli			1.8200	41	1.8200	.174
3d quarter:						
1 annulus		3		3		
2 annuli	.5346	432	.6052	578	.5750	
3 annuli	.6694	210	.7974	366	.7507	.267
4 annuli	.7661	145	1.0010	334	.9299	.214
5 annuli	.8954	17	1.2124	216	1.1893	.246
6 annuli			1.4307	63	1.4307	.185
7 annuli			1.6280	14	1.6280	.129
4th quarter:						
1 annulus	.3792	5	.2890	5	.3341	
2 annuli	.6362	398	.7489	427	.6945	.732
3 annuli	.7854	226	1.0260	316	.9257	.287
4 annuli	.8845	166	1.2491	308	1.1214	.192
5 annuli	1.0055	52	1.4791	323	1.4134	.232
6 annuli		6	1.7386	141	1.7386	.207
7 annuli			2.1903	53	2.1903	.231
All quarters		2,733		5,191		

SUMMARY

Age groups:	*Mean instantaneous growth rate*
1–2 annuli	0.673
2–3 annuli	.291
3–4 annuli	.233
4–5 annuli	.238
5–6 annuli	.206
6–7 annuli	.173

The mean growth rate, computed from the data in table 27, will be of use to us later in population studies. Such a mean should be representative if we give proper consideration to differences between the sexes and among quarters, because we found no trends in the growth rate during the period of our study. The estimated weights for each sex in each quarter have been combined in quarterly averages through weighting the means of the sexes combined by the number of each sex in the scale samples at each age from 1943 through 1947. We then computed the instantaneous growth rate (k) for each age in the four quarters from the formula

$$e^k = 1 + b$$

in which b is the fractional increase in weight over that at the beginning of the year (after

Ricker 1945). The values for each quarter were then combined in a geometric mean for each age.

The resulting growth rates commence at 0.673 between ages 1 and 2, drop abruptly to 0.291 the next year, and then decrease to 0.173 between ages 6 and 7. The first of these growth rates is probably much too low—not only because of the gear selectivity mentioned earlier, but because the yearling group was represented only during the last half of its year of life (fourth and first calendar quarters) when the fish had already accomplished most of their season's growth. The growth rate from 2 to 3 years is probably somewhat low also because of gear selectivity.

The measurements of the fish for which we have scale readings provide valuable checks on the validity of the readings. First, the mean lengths are in close agreement, except in the older age groups, with those obtained by Scott (1954), who aged his fish by otoliths. In table 28 we have compared Scott's readings from otoliths collected during July 1946 in the New Bedford fishery with our determinations from scales collected during the entire third quarter of 1946. Agreement between scale and otolith readings is very good except among age-groups 5 to 7 where the mean lengths of the fish whose ages were determined by otoliths are somewhat less. This lack of agreement in the older groups might be attributed to the finding of a greater number of annuli on the otoliths because a slightly greater proportion of older fish were found; but we also notice that no fish of greater age were found in either sex by means of the otoliths. Moreover, the possibility remains that the scales and otoliths were obtained from somewhat different populations because of an abrupt change in the principal fishing grounds between July and August 1946 (table 3). Therefore we do not consider that these discrepancies indicate faults in the scale-reading technique.

TABLE 28.—*Mean lengths of yellowtail flounder, by age groups and sex, as determined from otoliths and from scales, third quarter 1946*

[In centimeters; number of specimens in parentheses]

Age group	Length of males determined from—		Length of females determined from—	
	Otoliths[1]	Scales	Otoliths[1]	Scales
1				17.5 (1)
2	29.1 (23)	30.2 (212)	30.2 (23)	31.5 (281)
3	34.0 (14)	33.8 (35)	35.0 (20)	35.2 (38)
4	34.4 (23)	34.9 (73)	37.3 (18)	37.7 (109)
5	35.3 (12)	36.8 (6)	38.8 (40)	40.1 (126)
6			38.7 (11)	42.4 (22)
7			42.0 (5)	43.7 (5)

[1] Collected in July (Scott 1954).

The differences among populations within the southern New England stock, as suggested by comparison of the otolith and scale samples and by the discrepancies in attained size in different quarters, are much smaller than those between the southern New England and Nova Scotian yellowtail. Scott (1954) found that the yellowtail on Middle Ground and Western Bank areas of the Nova Scotian Banks grew much more rapidly than the Cape Cod yellowtail, except during the second and third years of life. However, in the second year the growth of the southern New England yellowtail so far exceeded the growth of the Nova Scotian fish that the attained length of the southern New England fish was the greater until about the seventh year. At this age, when the southern New England yellowtail had nearly all died, the female Nova Scotian yellowtail were just maturing. They continued to grow until the modal ages in the catch were 9 and 10 years at lengths of 44 to 47 cm. Contrast this with maturity and a modal age of 3 years at about 34 cm. in the southern New England stock.

Additional evidence of the reliability of the scale readings is available in a comparison of the attained sizes (table 26) with modes in the length frequencies of the females. We have plotted the percentages at each length as deviations from the grand mean for the years 1942 to 1947 (fig. 19). Two modes, suggestive of dominant year classes, progress from year to year. An eye-fitted line faired through one series of modes commences at 25.5 cm. in 1942, is missing in 1943, but continues to 34.5, 37.5, 41.0, and 42.5 cm. in the succeeding years. This is in good agreement with the mean attained lengths of the 1941 year class from scale readings which averaged 33.8, 37.4, 40.1, and 42.8 cm. in the third quarter (the season of heaviest landings) of the corresponding years. The shorter series of modes commences at 28.5 cm. in 1945 and continues at about 31.5 and 34 cm. in the following years. This also is in good agreement with the mean attained length of the females from the 1944

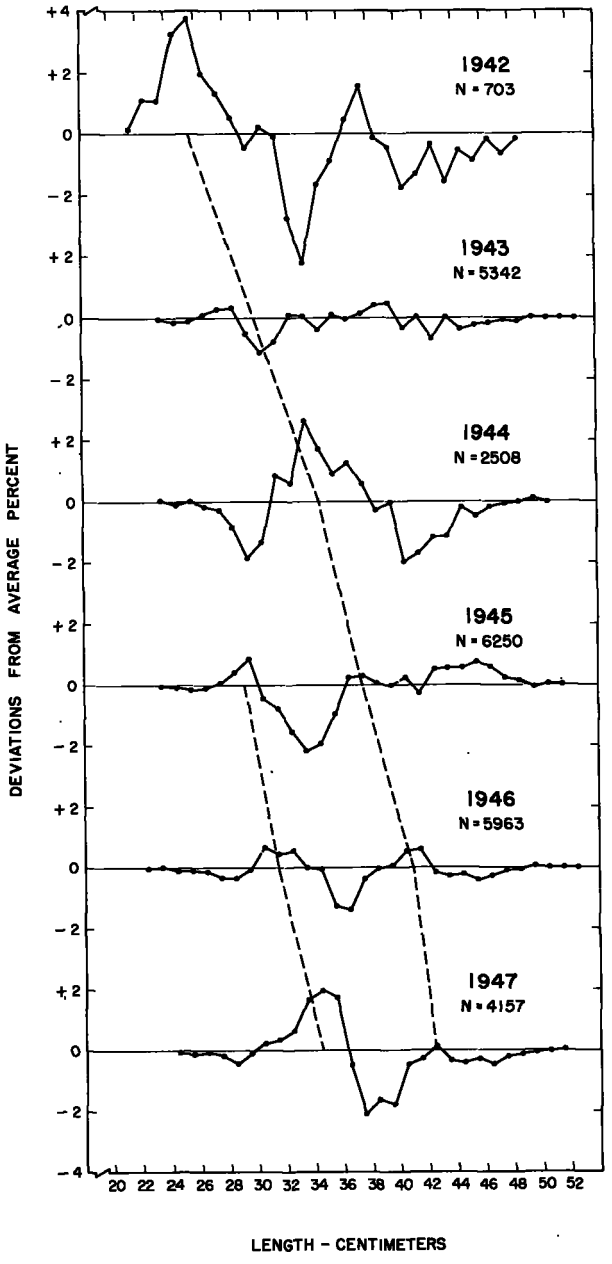

FIGURE 19.—Deviations from the mean percentage length distribution of female yellowtail from the southern New England stock, 1942–47. (N=number of fish.)

year class which were 31.5 and 34.9 cm. during the third quarters of 1946 and 1947.

It is highly significant that there was no trend in the mean length (and consequently in the growth rate) of each age group during the period of our study. The mean lengths of both males and females (table 26) for comparable quarters from 1942 to 1947 reveal no tendency toward an increasing or a decreasing growth rate among either older or younger fish. It is surprising that an increased growth rate has not occurred during this period of intense fishing in view of the both theoretical and empirical determination for many species that the growth rate increases as the stock decreases. Since we found no change in rate of growth, we conclude that the total environmental pressure remained essentially constant during the period of this study.

The rate of growth in the young yellowtail appears to be rather unusual. The proportions of the scale suggest that growth to the first annulus is only from 3 to 5 cm., whereas during the second year the fish attains a length of nearly 30 cm. Such a method of estimation is not precise, however, because some measurements of the scales from fish in the commercial catch showed that increase in size of the scales is not proportional to increase in size of the fish: the scale growth is heterogonic. For this reason and because we could not obtain appreciable numbers of juvenile yellowtail to determine the relation between scale size and fish size, we have not attempted to calculate fish lengths at early ages from scales.

Age Composition of the Landings

The proportion of each age in the landings is readily determined from the samples (appendix D, p. 246) because all of the yellowtail used in making the age determinations except those taken during the first three quarters of 1942 were taken at random from the landings (table 25). The samples not taken at random during the early part of the investigation may not be representative and must be considered with caution. These proportions, when plotted by quarters (fig. 20) offer rather striking evidence of an alternation of the populations between winter and summer from the winter of 1942–43 to the winter of 1944–45. The distribution of age groups was similar in the fourth quarter of 1942 and the first quarter of 1943. Then a marked change to a summer pattern existed in the second and third quarters of 1943. This pattern was followed by a winter pattern in the fourth quarter of 1943 and the first quarter of 1944, a summer pattern in the second and third quarters of 1944, and another winter pattern in the fourth quarter of 1944 and the first quarter of 1945.

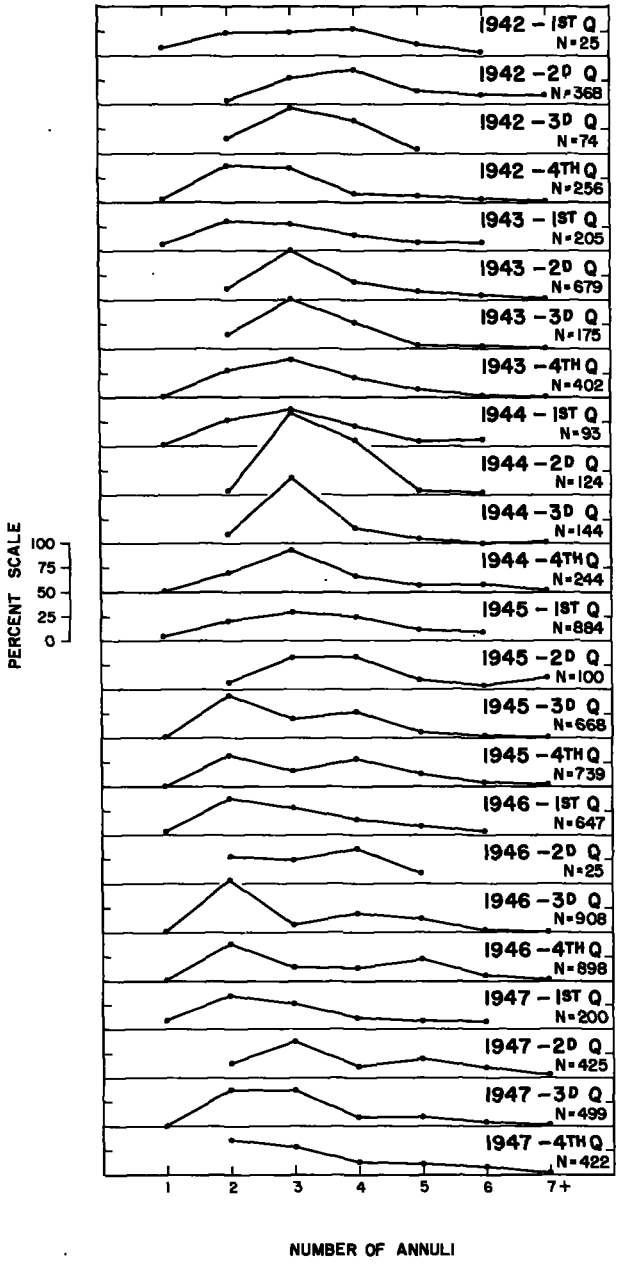

FIGURE 20.—Age composition of yellowtail from the southern New England stock during each quarter, 1942–47. (N=number of fish.)

An interruption in the sequence of summer and winter populations occurred in 1945. Here we find a close resemblance in the age distributions of the third and fourth quarters which persisted somewhat less clearly in the third and fourth quarters of 1946 and 1947. The change may be reflected also in the total landings, which were markedly greater in the fall months of 1945 through 1947 than in 1943 and 1944 (table 7). The first and second quarters in 1945, 1946, and 1947 have age distributions which appear to differ from those of the third and fourth quarters and also among themselves.

When we seek evidence of dominant year classes, these changes in age distributions within the southern New England stock emphasize the necessity of comparing each quarter only with the same period in other years and that with caution. When we do so for the first quarter (fig. 21) by plotting the deviations from the average age-frequency curve for the 6 years, 1942–47, we find one series of small modes as indicated by the dashed line. The series runs from the mode at the second annulus in 1943 to the mode at the fifth annulus in 1946. Recalling that the second annulus in the first quarter of 1943 was completed March 31, 1942, we identify this series of modes as representing a more abundant year class from the 1940 spawning. However, the age distribution during the first quarter was remarkably uniform, and this year class was only slightly more abundant than the others—its maximum deviation above the average being less than 9 percent.

Turning to the second quarter (fig. 21), we find little indication of a dominant year class passing through the fishery. Only two pairs of modes suggesting this appear—one from the 1941 year class in 1944 and 1945 and the other from the 1942 year class in 1946 and 1947. Since these modes are neither preceded nor followed by peaks, their interpretation as dominant year classes is dubious.

Much clearer is the succession of modes from the 1941 year class which appear as peaks from 1944 to 1947 in both the third and fourth quarters (fig. 21). Why both of these quarters in 1943 produced fewer fish from this year class, which was subsequently abundant, is of interest. Clearly the 1941 year class was not as available as other year classes at the 2-annuli stage during these quarters, nor was it more available during other quarters in 1943.

Other features of these curves are significant. The proportion of 2-annuli fish increased abruptly in 1945 in both the third and fourth quarters, and since no decrease occurred in the cull size (see length frequency data, p. 245) they must have become more available to the fishery. Significant, too, is the fact that they either did not remain

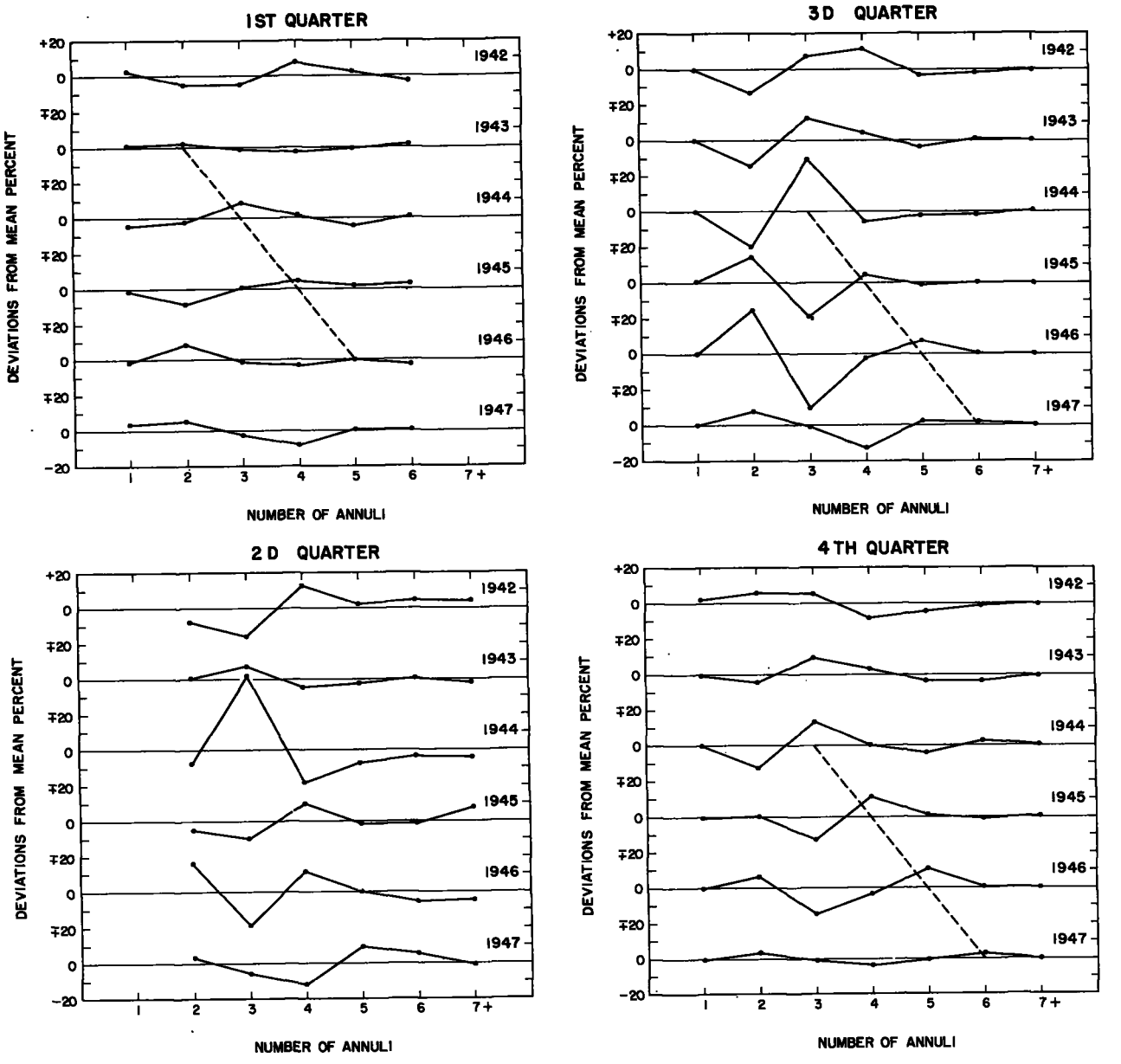

FIGURE 21.—Deviations from the mean percent age composition of yellowtail landed from the southern New England stock, 1942–47. Dashed lines indicate the series of small modes.

more available or else were mostly caught in 1945, since no similar increase in 3-annuli fish was noted in 1946 or 1947.

The data on age composition (table 29) are readily combined with the total landings in numbers of fish (table 21) to obtain an estimate of the landings of each age group in each quarter from the fourth quarter of 1942 through 1947 (table 30). These data will be used later in determining mortality. Meanwhile, we note that on the average, age-groups 2, 3, and 4 predominated, comprising 28.1, 35.5, and 19.3 percent of the catches. An exception to this might be taken for the average landings in the second quarter (the spawning season), when the 3-year-olds comprised more than half of the total; but this average is strongly influenced by the unusual sample from the second quarter of 1944, and probably is not representative. Also noteworthy is the fact that the average landings of young fish prior to age 2 years and 3 months were negligible. The youngest group strongly represented in the average catch was the group with 2 annuli in the third calendar quarter.

TABLE 29.—*Age composition, by quarters, of yellowtail landed from the southern New England stock, 1942–47*

Year and quarter	Number of fish	Percent of fish having—						
		1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli
Year 1942:								
1st quarter	25	8.00	24.00	24.00	28.00	12.00	4.00	------
2d quarter	368	------	4.08	27.17	36.68	13.86	9.78	8.42
3d quarter	74	------	16.22	45.94	33.78	4.05	------	------
4th quarter	256	3.12	38.67	35.55	9.38	7.42	4.30	1.56
Year 1943:								
1st quarter	205	6.34	31.22	27.80	17.56	8.78	8.29	------
2d quarter	679	------	12.52	50.37	19.59	9.28	6.04	2.21
3d quarter	175	------	15.43	50.86	26.86	3.43	2.86	.57
4th quarter	402	.25	28.11	39.30	20.90	8.46	1.99	1.00
Year 1944:								
1st quarter	93	1.08	26.88	37.63	21.50	5.38	7.53	------
2d quarter	124	------	4.03	84.68	5.64	4.03	1.61	------
3d quarter	144	------	9.72	68.06	16.67	4.86	------	.69
4th quarter	244	.82	20.08	43.03	17.62	7.79	8.20	2.46
Year 1945:								
1st quarter	884	3.85	20.25	29.64	24.77	11.65	9.84	------
2d quarter	100	------	7.00	33.00	34.00	10.00	4.00	12.00
3d quarter	668	.60	44.01	19.91	26.80	5.99	2.24	.45
4th quarter	739	.27	32.88	17.18	29.09	13.40	4.60	2.57
Year 1946:								
1st quarter	647	3.86	37.87	27.82	16.85	9.43	4.17	------
2d quarter	25	------	28.00	24.00	36.00	12.00	------	------
3d quarter	908	.11	54.30	8.04	20.04	14.54	2.42	.55
4th quarter	898	.56	38.86	15.26	14.36	22.72	6.12	2.11
Year 1947:								
1st quarter	200	9.00	34.50	26.50	12.00	10.50	7.50	------
2d quarter	425	------	15.29	37.41	12.24	20.70	11.06	3.29
3d quarter	499	.20	37.68	37.68	9.82	9.62	4.21	.80
4th quarter	422	------	36.26	28.67	13.74	10.90	8.53	1.90

TABLE 30.—*Estimated number of yellowtail of each age, landed from the southern New England stock, fourth quarter of 1942 through 1947*

[In thousands of fish. Based on tables 21 and 29]

Year and quarter	Number of fish having—							Total [1]
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli	
Year 1942: 4th quarter	587	7,270	6,684	1,764	1,395	808	293	18,801
Year 1943:								
1st quarter	740	3,643	3,244	2,049	1,025	967	------	11,669
2d quarter	------	948	3,812	1,483	702	457	167	7,569
3d quarter	------	2,554	8,419	4,446	568	473	94	16,553
4th quarter	12	1,325	1,853	985	399	94	47	4,714
Year 1944:								
1st quarter	112	2,796	3,914	2,236	560	783	------	10,401
2d quarter	------	251	5,277	351	251	100	------	6,232
3d quarter	------	691	4,842	1,186	346	------	49	7,114
4th quarter	17	425	910	373	165	174	52	2,116
Year 1945:								
1st quarter	191	1,006	1,473	1,231	579	489	------	4,970
2d quarter	------	110	520	536	158	63	189	1,575
3d quarter	53	3,921	1,774	2,388	534	199	40	8,909
4th quarter	22	2,706	1,414	2,394	1,103	378	211	8,229
Year 1946:								
1st quarter	235	2,310	1,697	1,028	575	254	------	6,099
2d quarter	------	840	720	1,080	360	------	------	2,999
3d quarter	8	3,728	552	1,376	998	166	38	6,866
4th quarter	53	3,685	1,447	1,362	2,155	580	200	9,484
Year 1947:								
1st quarter	462	1,772	1,361	616	539	385	------	5,136
2d quarter	------	668	1,635	535	905	483	144	4,370
3d quarter	19	3,650	3,650	951	932	408	78	9,688
4th quarter	------	3,723	2,944	1,411	1,119	876	195	10,267
Average, 1943–47:								
1st quarter	348	2,305	2,338	1,432	651	576	------	7,655
2d quarter	------	563	2,393	797	475	221	100	4,549
3d quarter	16	2,909	3,847	2,069	676	249	60	9,826
4th quarter	21	2,373	1,714	1,305	988	420	141	6,962
All years	385	8,150	10,292	5,603	2,790	1,466	301	28,992
Percent	1.3	28.1	35.5	19.3	9.6	5.1	1.0	------

[1] Slight discrepancies occur due to rounding off of the figures.

Good agreement appears between maximum lengths observed and Walford's (1946) ultimate length $l\infty$ for the yellowtail. This characteristic represents the length at which growth becomes zero and is computed from

$$l\infty = \frac{l_1}{1-k}$$

in which l_1 is the y intercept of a line fitting the points $(ln, ln + 1)$, ln is the length at age n years and k is the slope of the line. We have used the mean attained length by quarters from table 26, fitted lines by the least-squares method to determine l_1 and k, and estimated $l\infty$, for each quarter and sex. (We have omitted females age 7 years and older from the computation because this group contains older fish and probably has a higher average mean length than a group composed only of females age 7 would have.) The results (table 31) show reasonably good agreement with the maximum size observed in the length samples which comprised 38,335 fish from the fourth quarter of 1942 through 1947. If we assume that the samples from different quarters represent different populations and the estimates of $l\infty$ contain sampling variation, it is permissible to average them. Thus, we find that the mean estimate of $l\infty$ for males is 1.1 cm. lower and for females 2.0 cm. higher than the observed measurements. Moreover, the estimates of $l\infty$ from these data, particularly for males, are probably low because the fishery undoubtedly oversamples the larger fish in the younger age groups. This results in a high value for l_2, and perhaps for l_3, and correspondingly lower values for k and $l\infty$. Nevertheless, the close agreement gives us further confidence in our age readings and length samplings.

TABLE 31.—*Ultimate length* ($l\infty$) *and maximum length found in samples of the catch* (lm), *from the southern New England stock, by quarter and sex*

[In centimeters]

Quarter	Males		Females	
	lm [1]	$l\infty$	lm [1]	$l\infty$
1st	48.5	41.0	52.5	51.7
2d	45.5	44.2	51.5	49.4
3d	42.5	47.8	48.5	61.8
4th	43.5	42.7	54.5	52.2
Mean	45.0	43.9	51.8	53.8

[1] From appendix C, pp. 244–5, recorded in centimeter groups.

SURVIVAL, MORTALITY, AND AVAILABILITY

Three methods were used to estimate survival and mortality rates, no one of which is completely satisfactory but each of which contributes something to the sum of the information. These methods are as follows: (1) Immediate fishing mortality determined from the ratio of early returns of tagged fish to total number released; (2) total mortality determined from the ratios of the numbers of tag returns in successive years; and (3) total mortality determined from the ratios of the apparent abundance of certain age groups to comparable groups in successive years.

Immediate Fishing Mortality

The recaptures of tagged yellowtail during the first 10 days after release on the principal fishing areas usually show a high mortality rate (table 32). The recapture rate may be converted to the annual fishing rate, m,[9] if we assume that the 10-day mortality is equal to the instantaneous fishing mortality rate p, where $m=1-e^{-p}$.

The calculations (table 32) yield estimates of m ranging from 0.43 to 0.97 and averaging 0.86 from the sum of returns and releases. These values can be considered minimal estimates of the annual total mortality rate a of the group tagged because natural mortality is not included. They will, of course, have been reduced by deaths due to tagging during the 10-day period, but because only lively fish were released such deaths should not have been immediate.

TABLE 32.—*Early recaptures of tagged yellowtail released on the principal fishing grounds off Nantucket Shoals and No Mans Land*

Lot	Date released	Number released	Number recaptured in first 10 days	Annual rate of fishing (m)
No. 4	June 10, 1943	131	2	0.43
No. 5	Oct. 22–24, 1943	286	14	.83
No. 10	July 19, 1946	158	7	.80
No. 11	Aug. 21–23, 1946	228	21	.97
All lots		803	44	.86

Such a high rate of exploitation for a small group of fish is subject to criticism as not being representative of the rates experienced by the population, unless availability is not uniform among all parts of the population. However, rates calculated in this way are probably indicative of the mortalities experienced by groups of fish while completely available to the fishery. All of the lots except No. 10 were released from commercial fishing vessels, and in such an operation the tagged fish probably were released over a substantial part of the area that the fleet was fishing at the time. One characteristic of the yellowtail fishery has been the appearance of concentrations of yellowtail at various places with a subsequent shift of the fleet to those areas. We have actually observed a group of about 50 vessels fishing at one time in an area of not more than 300 square miles.

At the mean rate of fishing found from the tag returns, the "half life" (the period required to catch half of the fish exclusive of any natural mortality) would be 123 days.[10] At the maximum rate of fishing (lot No. 11), the half life would be only 72 days—a period similar to the length of time fishing was frequently pursued intensively in a small area.

Mortality from Tag Returns in Successive Years

Estimates of the rate of fishing, m, derived from the early recaptures are not greatly different from estimates of the total annual mortality rate, a, derived from the tag returns in successive years.[11] If we consider the same four experiments (lot Nos. 4, 5, 10, and 11) used to estimate immediate mortality, we note that 103 yellowtail were recaptured during the first year, 11 during the next year, and 1 in the third year (table 33). Ricker (1948) has pointed out that such a series of recaptures provides direct estimates of the survival rate, $s=1-a$, simply by taking $\frac{R_2}{R_1}$, $\frac{R_3}{R_2}$, et cetera. If we do this, we find $s=\frac{11}{103}=0.11$, $a=0.89$. Between the second and third years, $a=1-\frac{1}{11}=0.91$, but this estimate, of course, is much less reliable because of the small numbers. Similar computations for the total returns in successive years from all the lots released in the southern New England stock show $s=\frac{25}{212}$, $a=0.88$ between the first year and the second after tagging.

[9] This and other symbols for mortality rates are used as defined by Ricker (1948) and Widrig (1954).

[10] The half life was computed by substituting the observed recapture rate p and 0.5 for m in the "compound interest" formula $m=1-(1-"p")^n$ and solving for n. Then, n times the period in days gives the half life.

[11] These years start with each release date and are different for each lot released.

Between the second year and third after tagging $s=\frac{6}{25}$, $a=0.76$. The value of a calculated in this way indicates the total mortality—fishing mortality and natural mortality occurring simultaneously.

TABLE 33.—*Numbers of tagged yellowtail returned in successive years after release*

Stock and lot	Number released	Date released	Number returned in—					
			1st year	2d year	3d year	4th year	5th year	6th year
Southern New England:								
No. 1	227	Feb. 24, 1942	60	12	3	2	1	-----
No. 2	240	Mar. 2, 1942	47	2	2	-----	-----	-----
No. 4	131	June 10, 1943	9	2	-----	-----	-----	-----
No. 5	286	Oct. 22-24, 1943	19	2	-----	-----	-----	-----
No. 6	15	Feb. 28-29, 1944	2	-----	-----	-----	-----	-----
No. 10	158	July 19, 1946	27	2	1	-----	-----	-----
No. 11	228	Aug. 21-23, 1946	48	5	-----	-----	-----	-----
Sum	-----	-----	212	25	6	2	1	-----
Georges Bank:								
No. 7	189	Jan. 28-31, 1945	23	0	0	1	-----	-----
No. 8	100	Jan. 17-18, 1946	6	1	-----	-----	-----	-----
No. 14	51	Aug. 28-31, 1949	19	1	0	1	-----	-----
Sum	-----	-----	48	2	0	2	-----	-----
Cape Cod:								
No. 3	405	Mar. 18, 1942	24	-----	-----	-----	-----	-----
No. 9	138	June 14, 1946	22	8	4	0	1	1
No. 12	270	May 26-27, 1948	7	0	1	-----	-----	-----
No. 13	159	June 8, 1948	4	5	0	1	-----	-----
Sum	-----	-----	57	13	5	1	1	1

These estimates of mortality are subject to several tagging difficulties, as well as to changes in fishing pressure. First, as has been pointed out, we probably experienced some mortality among the tagged fish shortly after the fish were released. Whenever the tagged fish were exposed immediately to a heavy fishery, as was usually the case, undoubtedly some that would have died soon were caught, thus tending to give a larger number of returns in the first year than would be experienced in the second from the same rate of fishing. The result of this would be an estimate of the annual expectation of death greater than the actual value. Secondly, loss of tags through corrosion of the pins probably took place somewhat after the immediate tagging mortality; but we judge that our losses from this cause were small (see p. 180), although we cannot accurately evaluate them. Lastly, changes in fishing pressure influenced the number of returns. This cannot be accurately evaluated because we do not know the amount of fishing pressure on each population. The fishing pressure on the southern New England stock (table 24) declined from 6,264 days in 1942 to 2,859 in 1945, increased to 4,698 days in 1948 and dropped to 2,843 days in 1949. Except for 1949, it did not change more than 30 percent in any year. Since most of our sums of returns in successive years include experiments conducted during periods of both declining and increasing fishing effort, we have chosen not to adjust our return data by the amount of fishing.

The estimates of mortality in the southern New England stock are lower than similar estimates in the Georges Bank stock for which (table 33) almost all of the tags were returned during the first year. In the Georges Bank stock, the survival rate from the first year to the second was only $\frac{2}{48}$, or an annual expectation of death of 0.96. The proportion of returns in successive years was similar in all lots. Reference to table 4 indicates that in two of the releases off Georges Bank, lots No. 7 and No. 8, a great number of returns were experienced in the first week after tagging, but in lot No. 14 the returns were well scattered through the year after tagging, and yet no different proportion was obtained in successive years.

The mortality rate computed for the Cape Cod stock is lowest of all (table 33). Here we obtain the values for the annual expectation of death of 0.77 between the first year and the second after tagging and of 0.62 between the second year and the third after tagging. These values perhaps should be even lower than this because we have included lot No. 3, which was tagged under extremely difficult weather conditions and showed no returns after the first year. If we consider only lot Nos. 9 and 13, we find an annual expectation of death of 0.50 between the first year and the second after tagging.

When we associate these mortality rates with the trends in the yellowtail fishery we find a rather confusing relationship. As would be expected, the lowest mortality rate occurred in the Cape Cod stock where production was relatively stable, but the higher rates occurred, in one instance, when production was rapidly increasing and, in the other cases, when production was seriously declining. We have no explanation for this, but it is clear that a high mortality rate from such computations is not evidence per se of a dangerous fishing rate.

Mortality and Apparent Abundance of Age Groups

The basic data for our third method of estimating total mortality are to be found in tables 23 and 29, which show the percentage age composition and the catch per day in numbers of fish of the southern New England stock. These data, when combined in table 34, provide estimates of the catch per day in numbers of each age group in each quarter from the fourth quarter of 1942 through 1947. From these data we shall select the apparent abundance of homologous groups or age classes in successive years, and this may be done more easily if the data are reorganized to show the abundance of each year class in each year (table 35).

TABLE 34.—*Catch per day in numbers of yellowtail, of each age from the southern New England stock, 4th quarter of 1942 through 1947*

[Based on tables 23 and 29]

Year and quarter	Number of fish having—							All fish [1]
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli	
Year 1942:								
4th quarter	387	4,800	4,413	1,164	921	534	194	12,413
Year 1943:								
1st quarter	364	1,793	1,596	1,008	504	476	------	5,742
2d quarter	------	762	3,068	1,193	565	368	134	6,090
3d quarter	------	1,909	6,293	3,323	424	354	70	12,373
4th quarter	14	1,577	2,205	1,173	475	112	56	5,612
Year 1944:								
1st quarter	62	1,555	2,177	1,244	311	436	------	5,786
2d quarter	------	275	5,776	385	275	110	------	6,821
3d quarter	------	976	6,835	1,674	488	------	69	10,043
4th quarter	34	838	1,795	735	325	342	103	4,171
Year 1945:								
1st quarter	206	1,063	1,585	1,324	623	526	------	5,347
2d quarter	------	426	2,010	2,071	609	244	731	6,091
3d quarter	76	5,551	2,511	3,380	756	282	57	12,613
4th quarter	25	3,003	1,569	2,657	1,224	420	235	9,133
Year 1946:								
1st quarter	232	2,275	1,671	1,012	566	250	------	6,007
2d quarter	------	2,258	1,936	2,904	968	------	------	8,066
3d quarter	11	5,630	834	2,078	1,508	251	57	10,369
4th quarter	40	2,793	1,097	1,032	1,633	440	152	7,187
Year 1947:								
1st quarter	487	1,868	1,435	650	568	406	------	5,415
2d quarter	------	827	2,025	662	1,120	599	178	5,412
3d quarter	25	4,646	4,646	1,211	1,186	519	99	12,332
4th quarter	------	2,049	1,620	776	616	482	107	5,650

[1] Slight discrepancies occur due to rounding off of the figures.

We have computed the apparent survival, s,[12] between age groups as an average of the several years during which we observed the fishery by summing the catch per day for each year class that appears in each age group, and then determining the ratio between successive age groups (table 36). For example, in the first quarter we

[12] We computed the apparent survival to avoid difficulties with apparent minus mortalities resulting from changing availability.

TABLE 35.—*Catch per day in numbers of yellowtail, by year class and quarter, from the southern New England stock, 1937–44*

Quarter and year class	Number of fish caught having—						
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli
1st quarter:							
1937	------	------	------	------	504	436	------
1938	------	------	------	1,008	311	526	------
1939	------	------	1,596	1,244	623	250	------
1940	------	1,793	2,177	1,324	566	406	------
1941	364	1,555	1,585	1,012	568	------	------
1942	62	1,083	1,671	650	------	------	------
1943	206	2,275	1,435	------	------	------	------
1944	232	1,868	------	------	------	------	------
2d quarter:							
1937	------	------	------	------	------	------	------
1938	------	------	------	------	565	110	731
1939	------	------	------	1,193	275	244	------
1940	------	------	3,068	385	609	------	178
1941	------	762	5,776	2,071	968	599	------
1942	------	275	2,010	2,904	1,120	------	------
1943	------	426	1,936	662	------	------	------
1944	------	2,258	2,025	------	------	------	------
3d quarter:							
1938	------	------	------	------	424	------	57
1939	------	------	------	3,323	488	282	57
1940	------	------	6,293	1,674	756	251	91
1941	------	1,909	6,835	3,380	1,508	519	------
1942	------	976	2,511	2,078	1,186	------	------
1943	------	5,551	834	1,211	------	------	------
1944	------	5,630	4,646	------	------	------	------
4th quarter:							
1937	------	------	------	------	921	112	------
1938	------	------	------	1,164	475	342	235
1939	------	------	4,413	1,173	325	420	152
1940	------	4,800	2,205	735	1,224	440	107
1941	387	1,577	1,795	2,657	1,633	482	------
1942	14	838	1,569	1,032	616	------	------
1943	34	3,003	1,097	776	------	------	------
1944	25	2,793	1,620	------	------	------	------

have computed the ratio 1.024 between age groups 2 and 3 as follows:

$$s=\frac{\Sigma C3_{40}+\ldots C3_{43}}{\Sigma C2_{40}+\ldots C2_{43}}$$

in which $C3_{40}$ indicates the catch per day of 3-annuli fish of a 1940 year class, and so on. The data have been kept by quarters because of our previous observations that different populations tended to be available in different quarters.

TABLE 36.—*Mean apparent survival between age groups of yellowtail in the southern New England stock*

[Computed from abundance indexes for fourth quarter of 1942 through 1947]

Quarter	Ratio between age groups—				
	2 and 3	3 and 4	4 and 5	5 and 6	6 and 7+
1st	1.024	0.745	0.451	0.807	------
2d	3.157	.471	.454	.394	2.568
3d	1.054	.506	.376	.331	.385
4th	.637	.575	.632	.392	.376
Geometric mean	1.214	.565	.470	.451	.719
Mean instantaneous mortality rate, i	.194	.571	754	.796	.330

Several anomalies occur in the apparent survival data. The ratios greater than 1 between age-groups 2 and 3 are doubtless due to increasing

availability, because, as was presented in table 30, the 3-year-old yellowtail comprised the largest fraction of the landings. We suspect also that the mean apparent survival ratio of 0.565 between age-groups 3 and 4 may be a little high for the same reason. At any rate, the survival rate seems to level off at 0.470 between age-groups 4 and 5 and at 0.451 between age-groups 5 and 6. Beyond age-group 6, the apparent survival ratio jumps again to 0.719; but this is not a good estimate because too few age determinations were used and the age-groups 6 and older were combined in the first quarter and age-groups 7 and older in the other quarters.

The year-to-year survival rate has been obtained by comparing the catch per day for age-groups 3 and older with the same group a year later (table 37). For example, the comparison of 1943–44 in the first quarter was made from the following formula:

$$s=\frac{C4_{40}+C5_{39}+C6_{38}}{C3_{40}+C4_{39}+C5_{38}+C6_{37}}$$

$C3_{40}$ are the 3-annuli fish of the 1940 year class; $C6_{38}$ are the 6-annuli fish of the 1938 year class, et cetera. Here we find a low survival rate from 1943 to 1944, a high value for the next year, and a decline from 1945 to 1947. If we compare year-classes 1942 and 1943 for the fourth quarters only, we find the survival rate is even lower than from 1943 to 1944.

TABLE 37.—*Mean apparent survival between years of yellowtail in the southern New England stock*

[Computed from abundance indexes of age groups 3 and older]

Quarter	Ratio between—				
	1942 and 1943	1943 and 1944	1944 and 1945	1945 and 1946	1946 and 1947
1st	-------	0.556	0.593	0.450	0.464
2d	-------	.144	.558	.683	.441
3d	-------	.213	.494	.557	.638
4th	0.251	.374	1.375	.533	.455
Geometric mean	.251	.283	.668	.550	.494
Mean instantaneous mortality rate, i	1.382	1.262	.374	.596	.705

Survival rates computed from the abundance indexes average substantially higher than rates computed from the tagging returns in successive years. This discrepancy may result from several factors. The tagged yellowtail may have been caught from a group whose migratory habits made it more available to the fishery and thus actually suffered a higher mortality rate than the average for the stock. Other factors which we believe had only a small effect on the computing of survival rates were the immediate tagging mortality, the continuing loss of tags, and possibly the slightly higher, continuing death rate of tagged fish. The significance of the first factor will be more obvious after we examine the relation between fishing effort and total mortality.

We sought an estimate of natural mortality, q, by modifying the method proposed by Silliman (1943), who in effect considered the relation between the total instantaneous mortality rate, i, and fishing effort, f, and then extrapolated to zero fishing to find the natural mortality. We have estimated the total instantaneous mortality rate, i, for yellowtail 3 years and older (table 37), and related it to the appropriate amount of fishing, f, (table 24). For example, i computed for the fourth quarter of 1942 to the fourth quarter of 1943, was compared with the amount of fishing from the fourth quarter of 1942 through the fourth quarter of 1943. For the succeeding annual averages, the corresponding fishing effort was con-

TABLE 38.—*Relation of total mortality rate,* i, *to amount of fishing effort,* X

[The total mortality rate, i, has been computed from the relative apparent abundance of 3-year old and older fish in quarter N and the 4-year old and older fish in quarter $N+4$. The fishing effort X has been computed for various periods as follows: X_1=effort in quarter N, X_2 in quarters N and $N+1$, X_3 in quarters N, $N+1$, and $N+2$, X_4 in quarters N, $N+1$, $N+2$, and $N+3$]

Year and quarter	i	X_1	X_2	X_3	X_4
1942–43: 4th quarter	1.38	1,515	3,547	4,790	6,128
1943–44:					
1st quarter	.59	2,032	3,275	4,613	5,453
2d quarter	1.94	1,243	2,581	3,421	5,219
3d quarter	1.55	1,338	2,178	3,976	4,390
4th quarter	.98	840	2,638	3,552	4,260
1944–45:					
1st quarter	.52	1,798	2,712	3,420	3,927
2d quarter	.58	914	1,622	2,129	3,059
3d quarter	.71	708	1,215	2,145	2,467
4th quarter	−.32	507	1,437	1,759	2,465
1945–46:					
1st quarter	.80	930	1,252	1,958	2,859
2d quarter	.38	322	1,028	1,929	2,944
3d quarter	.58	706	1,607	2,622	2,994
4th quarter	.63	901	1,916	2,288	2,950
1946–47:					
1st quarter	.77	1,015	1,387	2,049	3,369
2d quarter	.82	372	1,034	2,354	3,302
3d quarter	.45	662	1,982	2,930	3,737
4th quarter	.79	1,320	2,268	3,075	3,861

CORRELATION COEFFICIENTS

	r
i X_1	0.37
i X_2	0.43
i X_3	0.55
i X_4	0.68

Regression:

$$i=-0.397+0.000312\ X_4$$

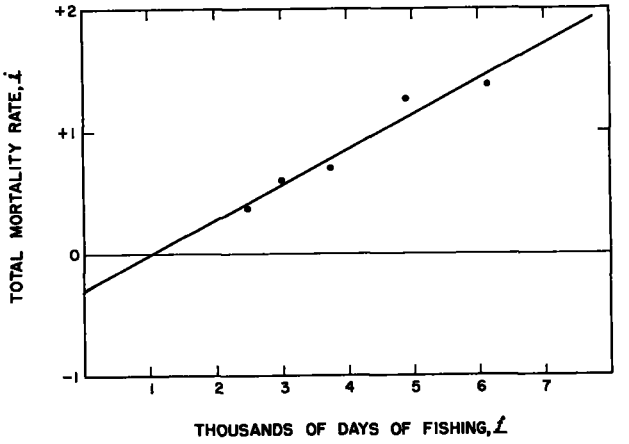

FIGURE 22.—Relation of total instantaneous mortality rate, i, and fishing effort, f, in the southern New England stock.

sidered to be from the third quarter of one year through the second quarter of the following year.[13]

When we assume a linear relation between fishing effort and mortality and compute the regression (fig. 22), we find

$$i = -0.302 + 0.288\,f$$

when f is the amount of fishing in thousands of days.

By definition $i=p+q$ and, of course, when $p=0$, $i=q$, but q must be positive. Therefore, an estimate of $i=-0.302$ with no fishing cannot be interpreted as $q=-0.302$. Since our estimate of i was based on abundance indexes computed from the fishing effort of the fleet, we immediately suspected that the availability of the fish was not constant. Not only was it not constant or even random, but there must have been an average annual increase in availability of $0.302 + q$, if we are to accept the relation of the apparent total mortality to the amount of fishing.

Some additional evidence of increasing availability may be found in the length composition curve (fig. 7). Ricker (1948) and others have considered that the ascending left limb and dome of age-frequency curves represent groups of fish not fully available to the fishery. This applies equally well to length-frequency curves when the rate of growth in length is uniform (as it very nearly is in yellowtail in the catch). If we accept this interpretation, then clearly the males less than 33 cm. long were not fully available nor were the females less than 39 cm., although this is less clear due to the spread-out curve. If we assume that changing availabilty is a function of length rather than age, we observe that among males most 2-year-olds, about half of the 3-year-olds, and some 4-year-olds, were below the 33-cm. point of inflection (age and length-frequency data in appendix table D–2, p. 254). Even older females were below the 39-cm. size, as well as most 2- and 3-year-olds, about half of the 4-year-olds, and some 5- and 6-year-olds. Such evidence suggests that there was increasing availability to a large extent among 2- to 4-year-olds, the most abundant age groups in the fishery, and to some extent among most of the other age groups.

Not only is there evidence of increasing availability with age, but also of erratic changes in availability due to other causes. Such is indicated by the increases in catch per day of certain year classes at advanced ages (table 35). The 1940 year class (age 5, fourth quarter) and the 1943 year class (age 4, third quarter) are examples. The great variability in the rate of decline of the year classes and the erratic changes in the seasonal catch (p. 197) suggest that changes in availability are common occurrences.

There is also evidence of increasing availability with time, because 2-year-old yellowtail apparently became more available to the fishery during the period of study. We have previously noted that the 1941 year class was probably an especially good one, and this is borne out by the data in table 35 which show that this year class usually was the most abundant among the fish with 3 or more annuli, from the second quarter through the fourth. We notice, however, that it was not especially available as 2-year-olds, for in none of the quarters did it make any particularly large contribution. On the other hand, the 1943 and 1944 year classes were especially abundant as 2-year-olds during the third and fourth quarters (table 35), but the 1943 year class was scarce among the older age classes in subsequent years.

[13] We also attempted to relate the annual mortality rate for each quarter to the fishing effort. The mortality, i, was computed from the relative apparent abundance of 3-year-old and older fish in quarter N and of the 4-year-old and older fish in quarter $N+4$. Various combinations of fishing effort (table 38) were tried to find the best correlation with mortality, and the most satisfactory combination was found to be quarters N through $N+4$ ($r=0.68$). The correlation between mortality and effort in quarter N was only 0.37, which is not statistically significant. The best regression was $i=-0.379+0.312f$, with f expressed in thousands of days.

The 1944 year class was abundant as 3-year-olds but probably not later, because the total yield of the fishery continued to decline.

With this problem of changing availability, we cannot fix the total annual mortality rate or even estimate the proportions due to fishing and natural causes. We can state that among fish on the grounds completely available to the fishery the total annual fishing rate is very high as indicated by the average m of 0.86, which was computed from early tag returns. Also it is certain that the total annual mortality rate of the whole stock was considerably less during the period of study as a result of not being fully available.

REPRODUCTION

Early in the yellowtail investigation we collected material from the commercial fishery at New Bedford, Mass., to provide information on the breeding habits of the yellowtail. Data were obtained on the age and length at maturity and on the spawning season of the yellowtail landed from the southern New England stock. Attempts to collect information on the juveniles were unsuccessful;[14] however, we are able to present data on yellowtail eggs and larvae which resulted from the extensive plankton work undertaken by O. E. Sette in his study of the eggs and larvae of the mackerel.

Age and Length at Maturity

At the peak of the spawning season in May 1943, 288 yellowtail were obtained at random from the commercial landings at New Bedford, measured, sex and condition of the gonads determined, and scale samples obtained. At this time it was simple to classify the individuals according to stage of maturity and, in mature females, whether ripe or spent (table 39).

Determination of the age of these fish revealed that most individuals of both sexes mature during their second and third years, although a larger percentage of the males mature at a younger age and smaller size. Of the females aged, 52 percent were mature at 2 years, 67 percent at 3 years, and 100 percent at 4 years and older. Of the males, 84 percent were mature at 2 years, 92 percent at 3 years, and 100 percent at 4 years and older.

If we extend the results of this sample to obtain an estimate of the proportion of immature individuals in the catch during the spawning seasons in the period during which we have studied this fishery, we must assume that the proportion of immature fish found in May 1943 is representative of that obtained in other years. This seems a likely assumption inasmuch as we have already pointed out that only very slight changes in growth rate and in length composition were noted during the period of study, 1942 to 1947. Therefore, if we apply our percentages of maturity to the summarized age composition for the second quarters of the years 1942 to 1947 (appendix table D–2, p. 254), we estimate that during the second quarters 94 percent of the males and 84 percent of the females in the landings would be mature. The same percentages would apply to the landings during the spawning season, since (as will be shown in the next section) almost all of the spawning occurs during the second quarter.

The same data provide us with an estimate of length of the yellowtail at maturity, but since the majority of the males mature before they appear in the commercial catch, it is not possible to relate maturity to length with any precision. For our purpose it is adequate to know that the males do mature before entering the commercial catch and mostly before they attain the length of 26 cm. Females, however, mature after reaching commerial size and our sample appears adequate for determining the size at which they mature. The most reliable estimates can be obtained by assuming that the data form a sigmoid curve and by transforming the data to the probability integral or "probit."[15]

A line fitted to the transformed data resulted in the formula $y=-0.2176+0.1631x$ in which y equals the estimated probit and x equals the length in centimeters. The estimated probit was then transformed back to a percentage to find the points for the sigmoid curve in figure 23, and to provide the estimates that 50 percent of the female yellowtail in the landings were mature at a length of 31.98 cm. and 90 percent were mature at 40.17 cm. We may further compute the variance of the

[14] Fifty-six tows with a 1½-inch mesh shrimp trawl, at times lined with ¾-inch mesh in the cod end, were made inside the 20-fathom contour between Nantucket and Long Island at various times from July to October in 1943, 1945, and 1946. No juvenile or larval yellowtail were taken. (Data on file at the Woods Hole laboratory of the U. S. Fish and Wildlife Service.)

[15] A discussion of the use of probits for this purpose will be found in appendix F, p. 266.

TABLE 39.—*Number of mature and immature yellowtail, by length, sex, and age, from the southern New England stock, May 1943*

[I = immature; M = mature]

Length of fish	Stage of maturity of females with—										Stage of maturity of males with—									
	1 annulus		2 annuli		3 annuli		4+ annuli		Total		1 annulus		2 annuli		3 annuli		4+ annuli		Total	
	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	M	I	M
26.5 cm			2						2					1						1
27.5 cm			2		1				3				1	1					1	1
28 cm			4						4					1						1
29 cm	1		2						3				1	2					1	2
30 cm			6	2					6	2				2		3				5
31 cm			2	3	1	1			3	4				4		6				10
32 cm			3	5	5	8			8	13			2	7		9			2	16
33 cm			3	9	4	7			7	16				1	1	4		2	1	7
34 cm			1	3	2	7			3	10				1	1	4		1	1	6
35 cm			1	2	5	4		1	6	7					2	7		3	2	10
36 cm				1	6	8		2	6	11						7		4		11
37 cm				2	1	5		2	1	9				1		2		2		5
38 cm				1	4	6		4	4	11								1		1
39 cm					1	6		5	1	11						1				1
40 cm						3		11		14										
41 cm						3		7		10										
42 cm						2		9		11										
43 cm								5		5						1		1		2
44 cm								2		2										
45 cm								4		4										
46 cm								2		2										
48 cm								1		1										
50 cm								1		1										
Total	1		26	28	30	60		56	57	144			4	21	4	44		14	8	79
Percent mature				52		67		100						84		92		100		

50-percent point as $s^2=0.946$. From this it follows that the standard error $s=0.973$ and the 95-percent fiducial limits are 30.03 and 33.93 cm.

Spawning Season

Only scattered information on the spawning season of yellowtail has been available. Bigelow and Welsh (1925: p. 499) observed that spawning commences near Gloucester, Mass., by the middle of March and seemingly lasts all summer. They also found young larvae off Sandy Hook, N. J., on August 1, 1913. Perlmutter (1939) found pelagic larvae off Long Island, N. Y., in the vicinity of Montauk Point, Jones Inlet, and Fire Island Inlet, between May 16 and June 17, 1938; and between June 8 and June 17 he found bottom-living postlarval stages near Moriches Inlet, Jones Inlet, and Fire Island Inlet. The larvae observed off New York and New Jersey belonged to the southern New England stock of yellowtail flounder, but they were considerably removed from the location of the fishery during the spawning season, which was centered off No Mans Land and Block Island during our study.

During the spring of 1943 the catch from these areas, which was being landed at New Bedford, was sampled periodically and the number of each sex and the stage of maturity of the females recorded (table 40). All females were dissected and the ovaries were easily classified into the three categories of immature, mature, and spent. The inside of the immature ovary appears reddish and somewhat gelatinous to the unassisted eye, whereas the developing ova cause the mature ovary to have a granular appearance several months before spawning. After the fish spawns, the ovarian contents are watery for several weeks, usually include some unspawned eggs, and often exhibit blood clots. Table 40 records the date on which the vessel landed; the fish were captured 1 to 4 days earlier. This lag could introduce error if the ripe fish have the spawn squeezed out of them by pressure in the fish hold and so be classified as spent. However observations indicated that pressure affected only a small proportion of the fish and no correction in the date was warranted.

Estimates of the peak and duration of the spawning period were obtained by transforming the data to probits (calculations are given in appendix F, p. 266), and by fitting a line as indicated in figure 24 which resulted in the formula $y=8.281+0.04348x$, in which y equals the estimated probit and x equals the day of the year less 100. From this formula the following points were

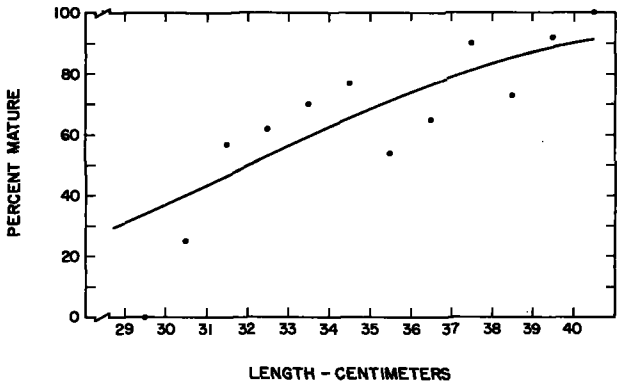

FIGURE 23.—Relation of length to percent mature of female yellowtail.

TABLE 40.—*Percentage of spent female yellowtail sampled from the southern New England stock during the 1943 spawning season*

Date vessel landed	Number of mature females examined	Spent		Date vessel landed	Number of mature females examined	Spent	
		Number	Percent			Number	Percent
Apr. 20	60	6	10.0	June 23	46	41	89.1
Apr. 20	62	3	4.8	June 28	50	49	98.0
Apr. 20	72	7	9.7	June 29	63	62	98.4
Apr. 20	50	9	18.0	July 4	50	50	100.0
Apr. 27	57	11	19.3	July 22	41	41	100.0
Apr. 27	66	14	21.2	July 23	25	25	100.0
May 4, 6 [1]	43	7	16.3	July 26	33	33	100.0
May 7	54	13	24.1	July 27	69	69	100.0
May 17	27	12	44.4	July 29	53	53	100.0
May 18	41	23	56.1	July 29	50	50	100.0
June 3, 7, 8 [1]	21	15	71.4	July 30	45	45	100.0
June 9	34	23	67.6				
June 16	45	41	91.1	Total	1,157	702	

[1] Included some unusually small samples.

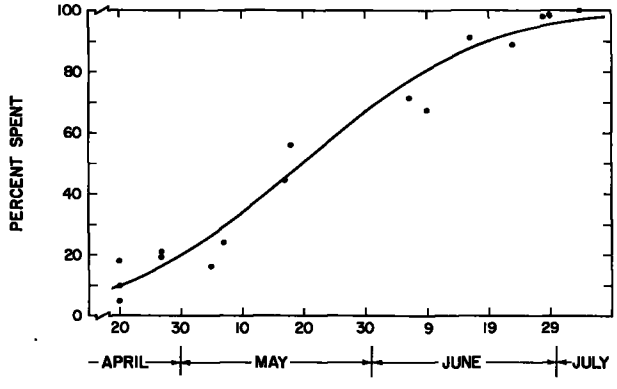

FIGURE 24.—Relation of date to percent spent in female yellowtail from the southern New England stock in 1943.

developed: (1) Ninety percent of the yellowtail spawned between April 12 and June 26; (2) the peak of spawning (the point of greater slope on a sigmoid curve) and the day on which half of the yellowtail spawned was May 20; (3) the period of heaviest spawning was from May 4 to June 4 during which 50 percent of the females became spent.

Distribution of Eggs and Larvae

Because the yellowtail shares with the mackerel the habit of spring spawning in the area between Cape Cod and Chesapeake Bay as well as the feature of pelagic eggs and larvae, we benefited from the mackerel investigations conducted by O. E. Sette (1943). The field work, from 1925 through 1932, included quantitative surveys of the distribution of mackerel eggs and larvae, and on these cruises large quantities of yellowtail eggs and larvae were taken in the plankton nets. Sette recalls that year after year the yellowtail seemed to be one of the most abundant spring spawners in the area. Quantitative data on yellowtail eggs and larvae from two cruises in April and May 1929 and on larvae only from a series of cruises in 1932 are available for analysis. In both years, a series of stations was established along section lines across the Continental Shelf. The lines were named after the nearest land feature and the stations were consecutively numbered seaward on each line from I (fig. 25).

Our task was eased by several reports that have appeared. The 1932 survey, the only one to cover adequately the range and spawning period of the mackerel (Sette 1943), included estimates of the mortality rates of the mackerel eggs and larvae and of the total number of eggs spawned. Other findings have been included in reports on the cycle of temperature by Bigelow (1933), the salinity by Bigelow and Sears (1935), and a volumetric study of the zooplankton by Bigelow and Sears (1939). A detailed account of methods used in the 1932 survey is given in Sette (1943) and the complete temperature and salinity observations for all years are reported by Bigelow (1933).

From our knowledge of the yellowtail spawning season, it appears that the period of the mackerel surveys, May 2 to July 24, 1932, covered the major part of the yellowtail spawning season (p. 217). Ninety percent of the yellowtail spawning off New Bedford in 1943 occurred between April 12 and June 26, but eggs have been taken from mid-March to September in various places (see p. 216). We would expect spawning to occur a little earlier in the warmer waters off New Jersey and a little later in the colder waters of the Gulf of Maine, north of Cape Cod.

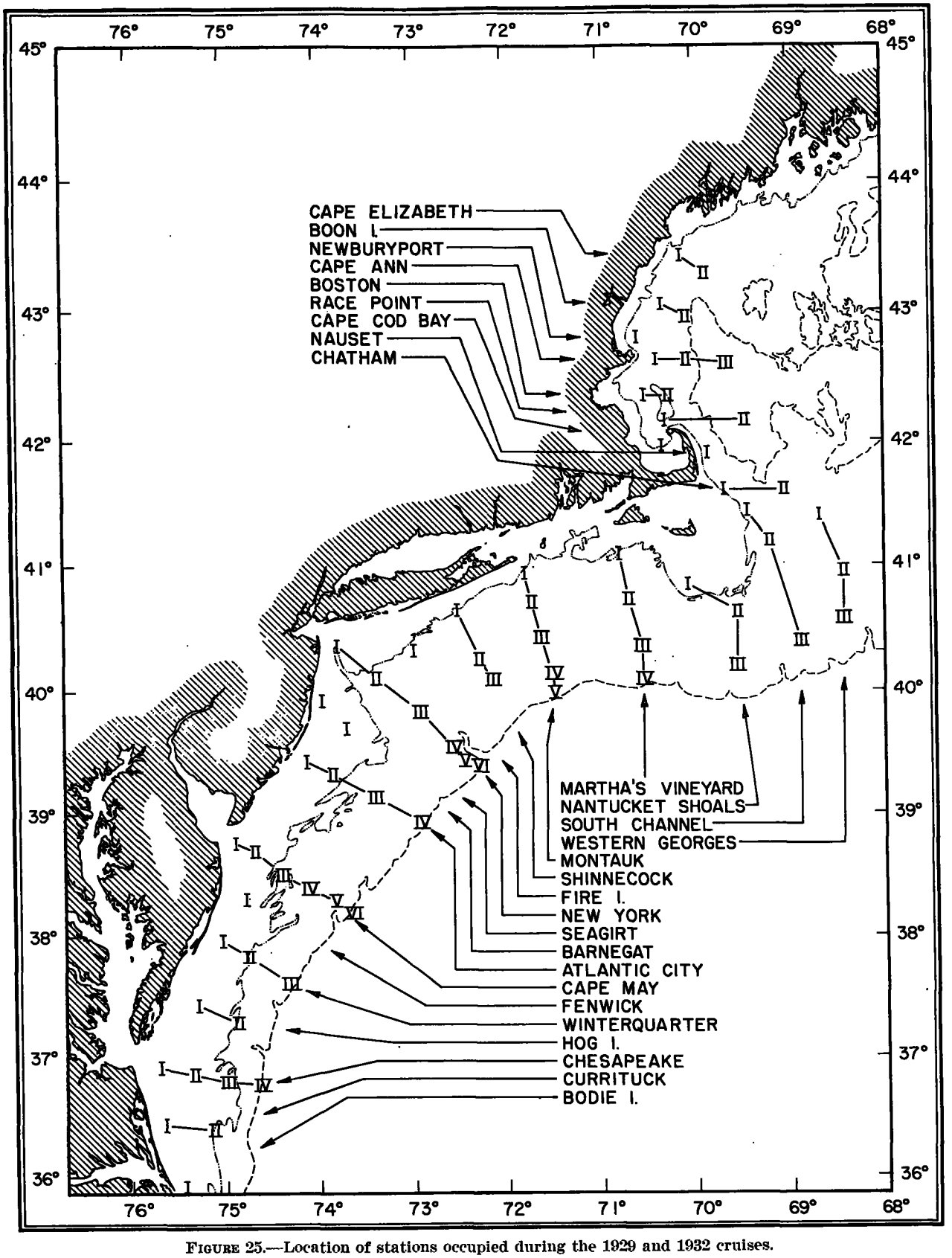

FIGURE 25.—Location of stations occupied during the 1929 and 1932 cruises.

Interpretation of the survey data would be easier if we had more information on the duration of the egg and larval stages. Bigelow and Welsh (1925) report that hatching takes place in 5 days at a temperature of 10° to 11° C. They judge further, from the stage of development, that the larvae descend to the ocean bottom when 14 mm. long, although Perlmutter (1939) reported that postlarvae caught in the bottom trawl ranged up to 12.6 mm. in length. This does not agree with Bigelow and Welsh's observation of 88 pelagic larvae 6.5 to 19 mm. long caught in a tow net off Sandy Hook on August 1, 1913. We conclude from these facts that the yellowtail may go to the bottom at lengths less than 12 mm., or even more than 19 mm., depending on conditions, but we remain ignorant of the duration of the larval period.

Horizontal distribution of eggs and larvae in 1929.—The plankton hauls during 1929 were made with nets, either 1 meter or ½ meter in diameter, towed horizontally at various levels at an average speed of 1.2 knots. The forepart of the nets had 29 to 38 meshes per linear inch, the rear part 48 to 54 meshes. For purposes of this paper, the hauls have been reduced to a standard basis of 20-minute tows with 1-meter nets.

During the April and May 1929 cruises, eggs and larvae of the yellowtail flounder were the dominant vertebrate form in the plankton (tables 41 and 42). The number of eggs taken ranged up to 37,000 at one station in April and to 79,000 in a tow in May. The eggs were taken on the April 12 to 24 cruise from the offing of Currituck, Va., to the northeasternmost stations off Block Island (fig. 26), but there was an impressive center of distribution off the coasts of northern New Jersey and Long Island. During the May 10 to 18 cruise, the southern limits of distribution of the eggs had moved about 150 miles to the northeast and a similar though less extensive movement was apparent in the principal center of the distribution, although a secondary center remained off Atlantic City. Distribution of the larvae corresponded closely to that of the eggs in both the April and May cruises though, of course, the numbers of larvae were markedly smaller.

The southern and offshore limits of the distribution of eggs in the April cruise agree well with the position of the 7°-C. isotherm at both surface

TABLE 41.—*Numbers of yellowtail eggs and larvae taken on the April 12–24 cruise in 1929*

[Weighted to basis of 20-minute tow with 1-meter net]

Locality and depth of tow	Station I		Station II		Station III		Station IV		Station V	
	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae
Montauk Point:										
Surface	2,880	1	490	0	0	0	10	0	0	0
Intermediate										0
Deep	2,900	3	100	0	0	3	0	0	0	0
Shinnecock:										
Surface	8,300	39	124	0						
Deep	1,800	18	3	0						
New York:										
Surface	10,200	440	31,500	11	180	0	0	0	1	0
Intermediate							0	0	0	0
Deep	5,000	170	5,400	210	34	0	0	0	0	0
Atlantic City:										
Surface	1,600	3	24,200	0	5,600	0	0	0		
Intermediate							0	0		
Deep	730	50	400	0	170	0	0	0		
Cape May:										
Surface	0	0	1,359	0	1,170	0	0	0		
Deep	0	0	70	3	30	0	0	0		
Fenwick:										
Surface		0								
Deep	3	0								
Winterquarter:										
Surface	16	0	173	0	0	0				
Deep	40	0	280	0	0	0				
Hog Island:										
Surface	7	1	400	0						
Deep	26	0	140	3						
Chesapeake:										
Surface	0	0	11	0	273	0	0	0		
Intermediate							0	0		
Deep	0	0	90	0	100	0	2	0		
Currituck:										
Surface	50	0	48	1						
Deep	0	0	21	0						
Bodie Island:										
Surface		0								
Deep		0								

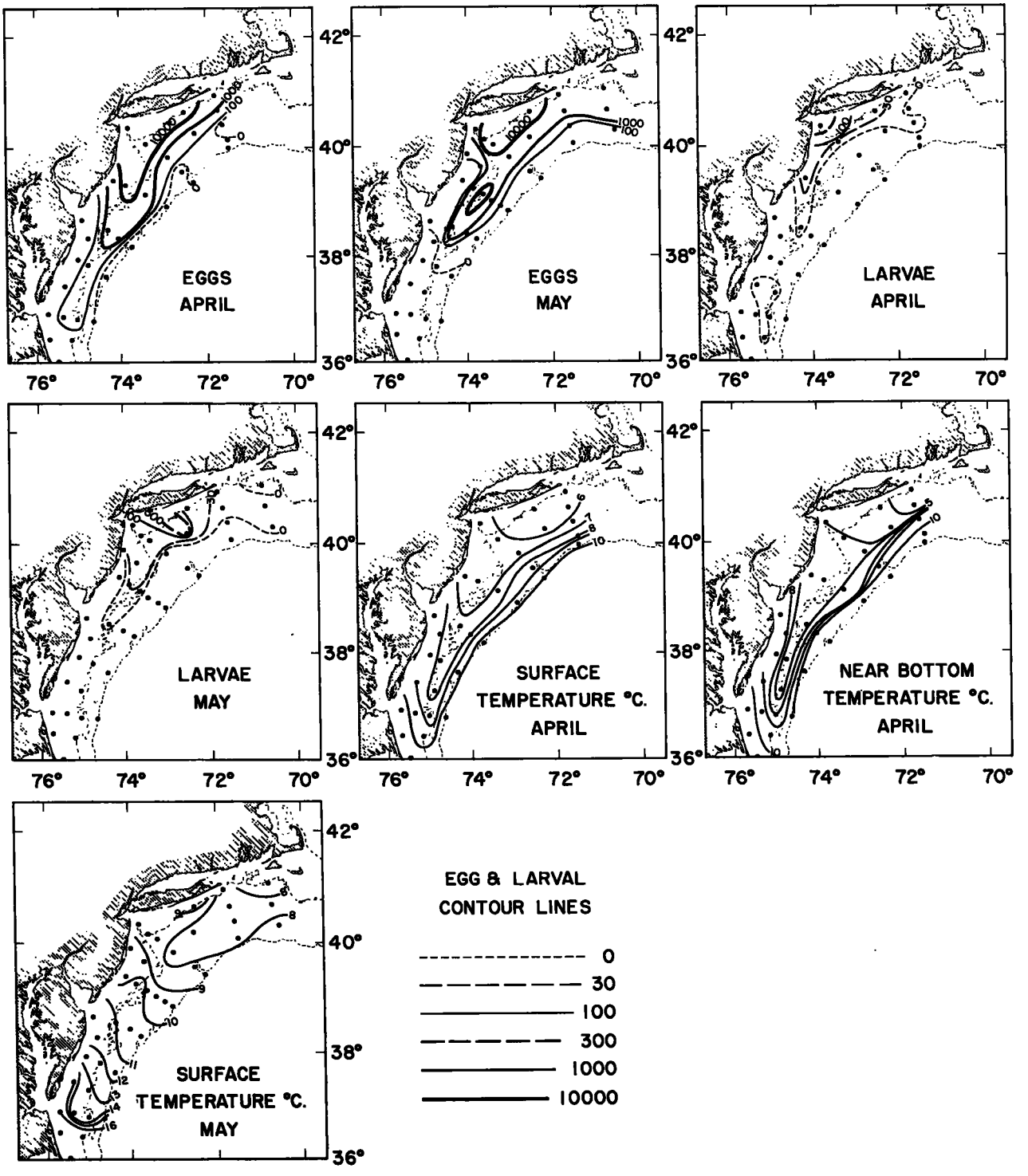

FIGURE 26.—Horizontal distribution of eggs and larvae, and surface and bottom temperatures during the 1929 cruises of April 12 to 24 and May 10 to 18. The egg and larval contour lines represent the numbers caught per standard tow of 20 minutes by a 1-meter net.

TABLE 42.—*Numbers of yellowtail eggs and larvae taken on the May 10–18 cruise in 1929*

[Weighted to basis of 20-minute tow with 1-meter net]

Locality and depth of tow	Station I		Station IA		Station II		Station IIA		Station III		Station IIIA		Station IV	
	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae
Martha's Vineyard:														
Surface	3,500	0			7,000	0			0	0				
Deep	1,600	0			900	2			1	1				
Montauk Point:														
Surface	4,000	0			1,000	0			9	0			0	0
Deep	2,400	15			20	2			1	0			16	0
Shinnecock:														
Surface	11,000	15			2,000	24								
Deep	3,000	65			350	25								
Fire Island:														
Surface			76,000	560										
Deep			2,800	48										
New York:														
Surface	2,000	1	24,000	2	32,000	7			157	0			2	0
Deep	2,400	95			2,700	35			20	0			0	0
Barnegat: Surface	300	1												
Seagirt: Surface	8	65												
Atlantic City:														
Surface	0	0			1,000	6	15,000	0	1,000	0	100	0	3	0
Deep	6	0			1,000	23			12	0			0	0
Cape May:														
Surface	8	0	8	1	2,400	0			7	0			11	0
Deep	0	0			210	0			3	0			3	0
Fenwick:														
Surface	0													
Deep	0													
Winterquarter:														
Surface	0		0		0				3					
Deep	0				4				0					

and bottom (fig. 26). (In these shoal waters at this time of year the upper 50 meters or so are nearly isothermal.) The lowest temperature recorded in any of the stations where eggs were taken was 4.8° C. at the bottom off Montauk Point. Evidently spawning had been proceeding prior to this April cruise when temperature conditions of 5° to 7° C. prevailed.

Recalling Bigelow's observation that hatching occurred in about 5 days at 10° C., we may deduce that hatching would require between 5 and 10 days at these lower temperatures of 5° to 7° C. Since larvae were found on April 18 that were several days old, it is apparent that spawning must have started in this area in early April at the latest. Size of the larvae during the April and May cruises (tables 43 and 44) provides a clue, however, that hatching had not long preceded the April cruise. During this cruise, the larvae ranged from 2 to 6 mm. in length, the bulk of them being about 3.5 mm. These larvae were smaller than those encountered during the May cruise, when the larvae ranged from 3 to 11 mm. in length, and were mostly 4 to 6 mm.

The close agreement in distribution of eggs and larvae suggests that hatching was completed and that the larvae had assumed their bottom-dwelling existence before much of the horizontal drift occurred. If this were not so we would expect a displacement in the centers and boundaries of the egg and larval distributions. Assuming that hatching was completed and the larvae had descended to the bottom, we may then note that the southernmost contingent of eggs and larvae off Virginia and Delaware disappeared from the surface waters by the time the temperature had risen above 11° C. Presumably, the eggs found in this area on April 17 to 19 had hatched and the larvae had descended to the bottom by May 14 to 16, when these southern stations were revisited.

At a station off Fire Island where yellowtail larvae were particularly abundant on May 17 and 18, 1929, a special series of tows was made to determine vertical distribution of the larvae (table 45). It may readily be seen that at all times the greatest number was located near the 10-meter level, but considerable numbers were taken during the night at the surface and at the 5-meter level. Relatively few were taken at any time at the 20- and 35-meter levels. This suggests some diurnal dispersion upward from the 10-meter level. Considerable differences are also apparent in the number of larvae taken during the night hauls—nearly twice as many larvae being obtained in the midnight series as were taken in the noon series, whereas morning and evening series were intermediate. Since there is no evidence that larvae retreated to levels below the net, it appears likely

TABLE 43.—*Yellowtail larvae taken April 12–24, 1929*

[Roman numerals indicate the localities (see fig. 25); numbers in parentheses indicate stations established during the mackerel studies, 1925–32 (see Sette 1943)]

Station and depth of tow	Number of larvae	Length (mm.)
Montauk Point:		
Station I (20456):		
Surface	1	3.5
Deep	1	5.0
Station III (20454): Deep	1	6.0
Shinnecock:		
Station I (20448):		
Surface	39	3.5
Deep	6	3.5
New York:		
Station I (20447):		
Surface	60	3.5
Deep	13	2.5–4.0
Station II (20446):		
Surface	11	4.0
Deep	19	3.5
Atlantic City:		
Station I (20439):		
Surface	3	3.0
Deep	14	2–3
Cape May: Station II (20438): Deep	1	4.0
Hog Island:		
Station I (20424): Surface	1	4.0
Station II (20432): Deep	1	4.0
Currituck: Station II (20428): Surface	1	4.0

TABLE 44.—*Yellowtail larvae taken May 10–18, 1929*

Roman numerals indicate the localities (see fig. 25); numbers in parentheses indicate stations established during the mackerel studies 1925–32 (see Sette 1943)]

Station and depth of tow	Number of larvae	Length (mm.)
No Mans Land:		
Station I (20457): Deep	1	6.0
Station II (20458): Deep	2	5 and 8
Station III (20459): Deep	1	6.0
Montauk Point:		
Station I (20463): Deep	16	4–6
Station II (20462): Deep	2	5 and 11
Shinnecock:		
Station I (20464):		
Surface	15	4–7, mostly 4.
Deep	71	4–6, mostly 5.
Station II (20465):		
Surface	4	3.5–5.5
Deep	8	3–4
Fire Island Station I (20498)		3–9
New York:		
Station I (20470):		
Surface	1	4.0
Deep	32	3–6
Station IA (20469): Surface	3	5.0
Station II (20468):		
Surface	9	4–8, mostly 6.
Deep	13	3–8, mostly 6.
Seagirt: Station I (20471): Surface	65	4–6, mostly 5.
Barnegat: Station I (20472): Surface	1	4.0
Atlantic City: Station II (20474):		
Surface	6	5–6
Deep	7	4–7
Cape May: Station IA (20482): Surface	1	8.0

that some of the larvae were escaping the net during the daylight hours. This is borne out in that the larvae averaged slightly larger (4.3 mm.) during the midnight tows than during the morning (3.6 mm.), noon (3.9), or evening (3.8) tows.

TABLE 45.—*Vertical distribution of yellowtail larvae (off Fire Island) at station A 20498, May 17–18, 1929*

Depth of tow	Estimated number of larvae taken in tows made—				Estimated total
	Morning	Noon	Evening	Midnight	
Surface	130	0	1	430	561
5 meters	58	0	98	521	677
10 meters	914	764	876	700	3,254
20 meters	81	34	4	34	153
35 meters	37			12	49
Total	1,220	798	979	1,697	4,694

Horizontal distribution of larvae in 1932.—Several factors prevented obtaining as complete information on the yellowtail during the cruises of the mackerel investigations in 1932 as in 1929. Between the 1929 and 1932 cruises, much was learned about the distribution of the mackerel eggs and larvae and better methods of quantitatively sampling them were developed. Some stations at the southern end of the series where mackerel eggs and larvae had not been taken in 1929 were dropped, and the 1932 cruises were delayed until May 1 so as to cover the mackerel spawning season more effectively. The method of towing was changed from horizontal to oblique, and the use of two nets, one at a lower level and the other at the upper level, was introduced. Compensation was made for variations in the amount of water strained by the addition of flowmeters to the nets which made it possible to convert the catch to the standard basis of numbers of larvae or eggs per 17.07 cubic meters of water strained per meter of depth fished. Finally, with the emphasis on mackerel, the large numbers of yellowtail eggs taken could not be counted; consequently, we have available counts only of the larvae taken on the 1932 cruises. These were divided into two sizes: large, those more than 5 mm. in length; and small, those from about 2.5 to 5 mm. Details of the methods of towing and counting may be found in Sette (1943). Complete counts of yellowtail larvae are given in appendix E, page 256.

The small larvae were found in considerable numbers on every cruise (fig. 27). On cruise 1 (May 2 to 6) the center of their distribution was from southern New Jersey to Virginia, but this changed abruptly during the following week, and on cruise 2 (May 9 to 16) two principal centers of distribution were found—off southern Massachusetts and off northern New Jersey. These centers

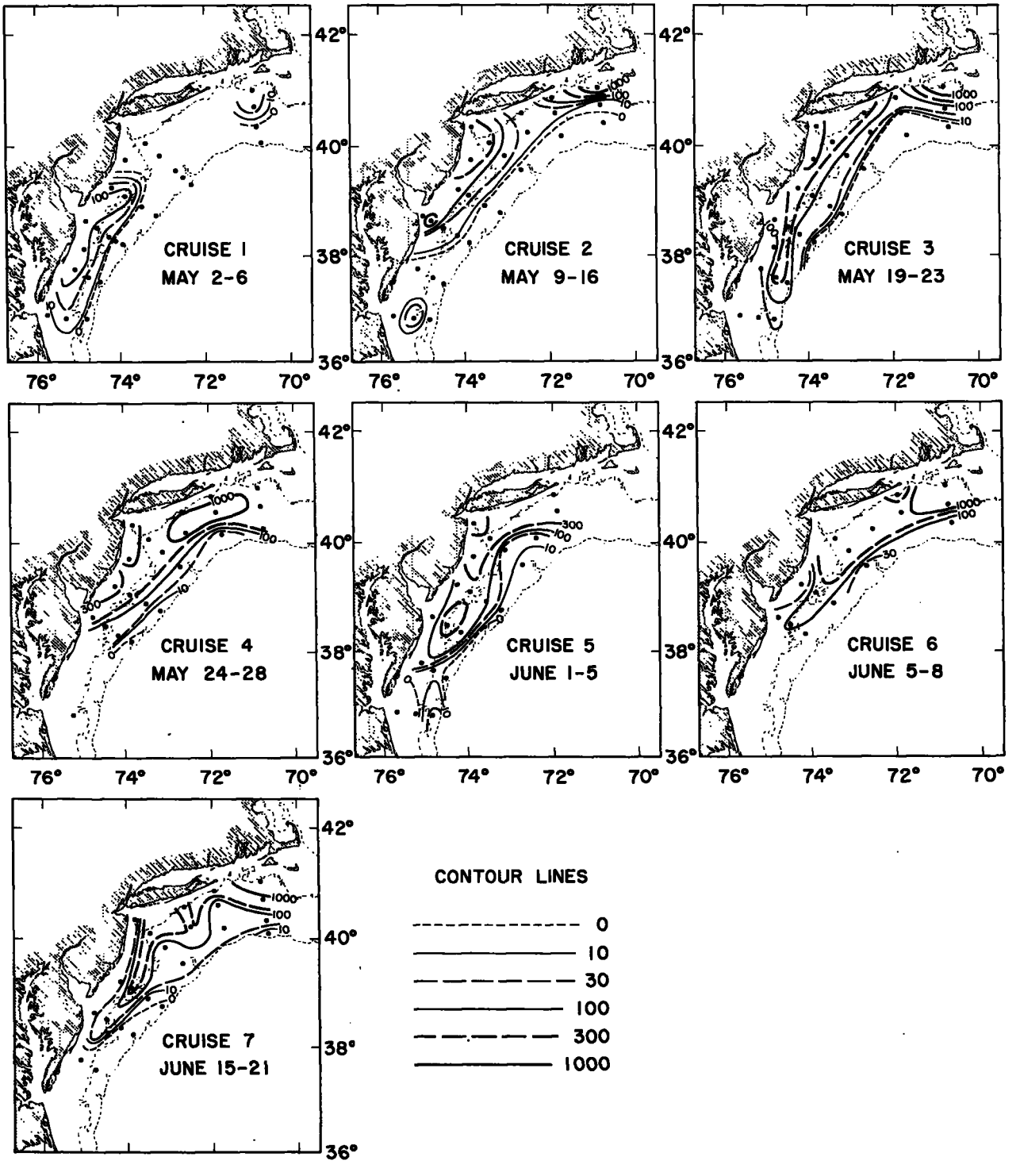

FIGURE 27.—Horizontal distribution of small yellowtail larvae during cruises in 1932. Contour lines represent the numbers taken in 17.07 cubic meters of water.

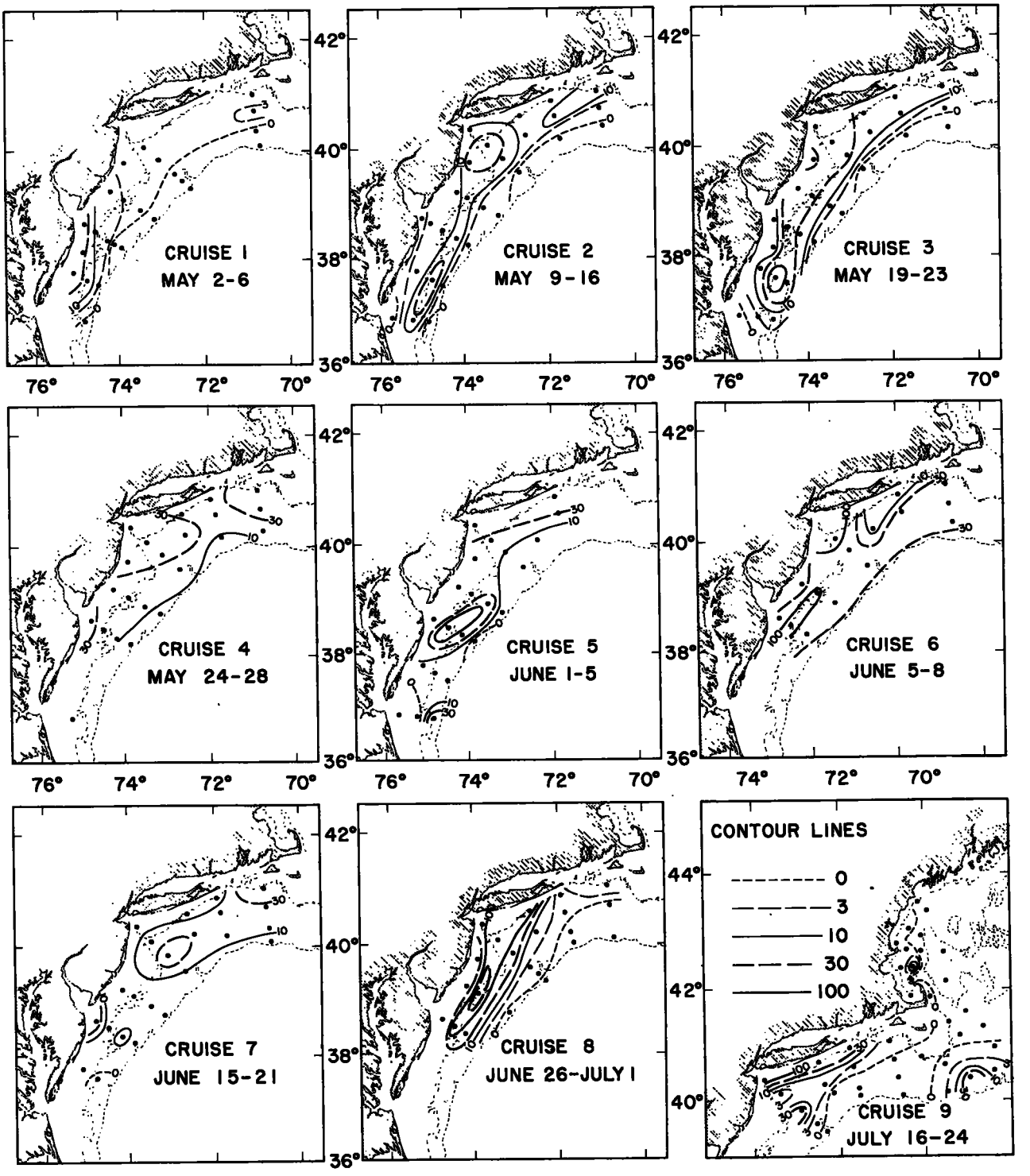

FIGURE 28.—Horizontal distribution of large yellowtail larvae during cruises in 1932. Contour lines represent the numbers taken in 17.07 cubic meters of water.

appear to have been augmented and spread out on cruise 3 (May 19 to 23), a pattern that continued to cruises 5 (June 1 to 5) and 6 (June 5 to 8). Beginning on cruise 6 and more noticeable on cruise 7 (June 15 to 19) is the reduction in the numbers of larvae found off New Jersey and Long Island as compared with those found off southern Massachusetts.

The distribution of the large larvae (fig. 28) was in most respects similar to that of the small, the principal differences being smaller numbers and the lesser variation in the catches of the large larvae. It is as though the peaks occurring in the distribution of the smaller larvae had had the opportunity to disperse somewhat.

The movement of one of the centers of distribution of the yellowtail is consistent with previous estimates of drift and, incidentally, provides an estimate of the duration of the small larval stage. In his study of the mackerel, Sette (1943) was able to identify and follow for a considerable period certain peaks in the frequency distributions of mackerel larvae, which he judged were produced by homologous groups that resulted from fluctuations in spawning. The movement during its passive phase of one of the most prominent of these groups, which he called the *S* group, was consistent with the wind movement. First found off Delaware Bay, this group moved about 60 miles south between cruises 1 and 2. The change in distribution of the small yellowtail larvae from that noted on cruise 1 and the northward movement of the southern center of large larvae observed on cruise 2 are in agreement with Sette's observations of the mackerel. This drift, coupled with the absence of small larvae at most of the stations where the southern center of large larvae was found on cruise 2, suggests further that the small yellowtail larvae progressed to the "large" stage in the 5 or 6 days intervening between the visits to the pertinent stations on cruises 1 and 2. If this were so, probably the groups of small larvae found on the later cruises had hatched from successive spawnings.

Further evidence of drift is suggested by the fact that the center of small larvae that persisted off Martha's Vineyard and/or Block Island from cruise 2 through cruise 7 was not followed by any special concentration of large larvae at these locations. We would expect a westerly or southwesterly drift to result from the prevailing coastal current—a conclusion strengthened also by Sette's discovery of a southwesterly drift of the northern center of larval mackerel off New Jersey during cruises 1 to 3. Since no special concentration of large larvae was found within a reasonable distance to the westward on cruise 3, these small larvae must have drifted north or east beyond the limits of the survey.

Further analysis of the drift of these groups of larvae appears fruitless because the yellowtail larvae were obviously more widely distributed than the mackerel which the cruises were designed to cover. In none of the cruises was the eastern limit of the yellowtail larvae included, and cruises 4, 6, and 9 (fig. 28) obviously did not cover the southwestern limits of their distribution. Furthermore, there was a considerable seaward spread of the large larvae, for on cruises 4 and 6 large larvae were found at every station that went to the edge of the Continental Shelf.

The depth distribution of yellowtail larvae found on the station off Fire Island in 1929 (table 45) was evidently not always typical of the distributions in 1932. No data from a similar special station are available for 1932, but at all of the deeper stations two levels were sampled by oblique tows. These were designed to sample the zone above the thermocline separately from the zone below. At this time the thermocline was usually about 20 meters down. On the average, more larvae were taken above the thermocline (appendix table E–3, p. 265), but at some stations all of the larvae were found below it (e. g., stations II and III off Atlantic City), and there were numerous instances of wide vertical distribution. No apparent relation existed between this distribution of the larvae and any factors of location, temperature, or time.

Temperature relationships found on these cruises (figs. 29 and 30) show the expected vernal warming with variations due to weather. The surface temperatures give evidence of a gradual seasonal increase interrupted by an invasion of cold water from the northeast at the time of cruise 2. This was compensated for by a spurt in the warming between cruises 4 and 5 followed by a gradual increase in water temperature through cruise 7. We note that the larvae were found in numbers when surface temperatures were as low as 8° C. on cruise 2 and as high as 20° C. on cruise 7.

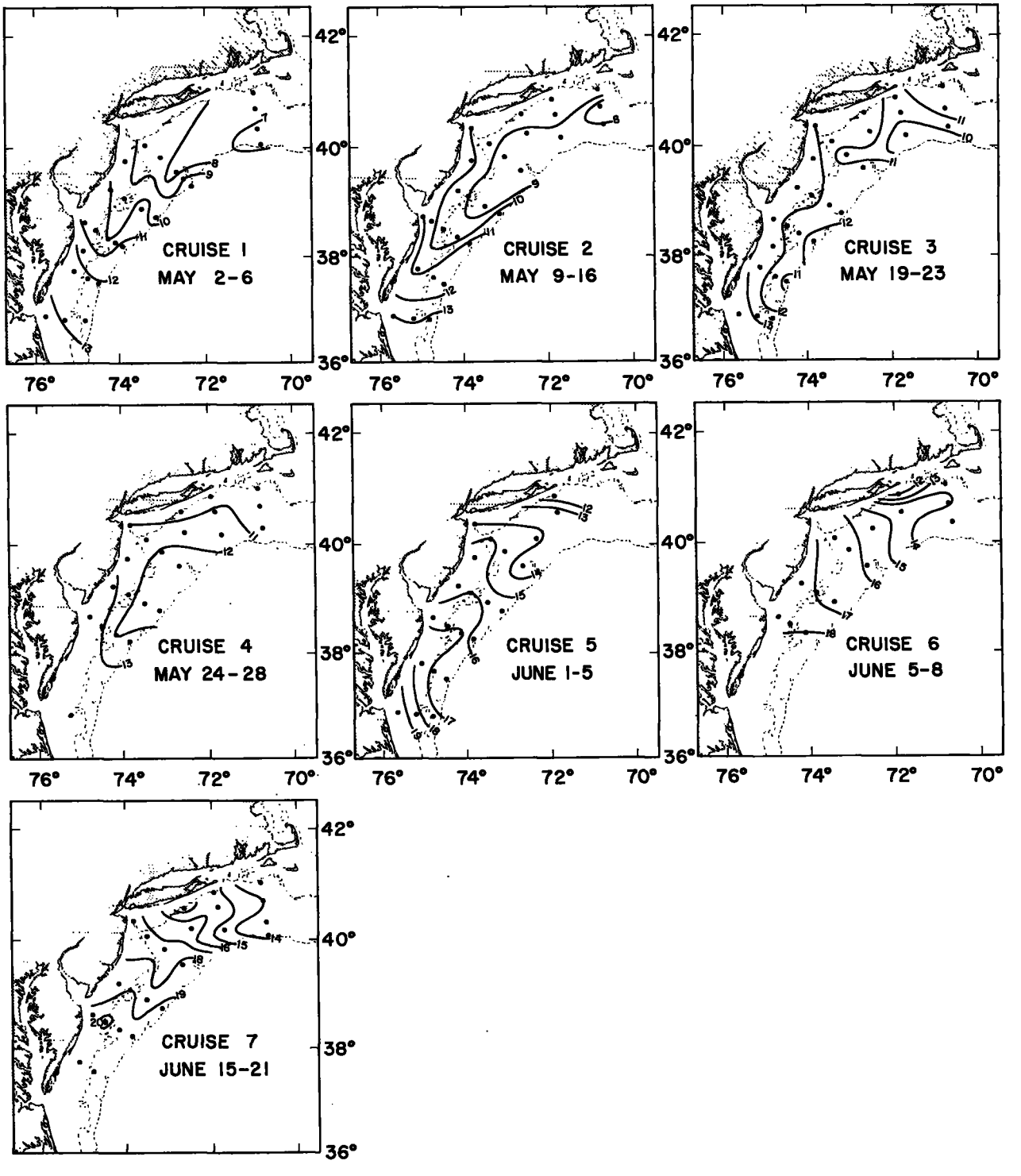

FIGURE 29.—Surface isotherms, 1932. (Temperature in degrees Centigrade.)

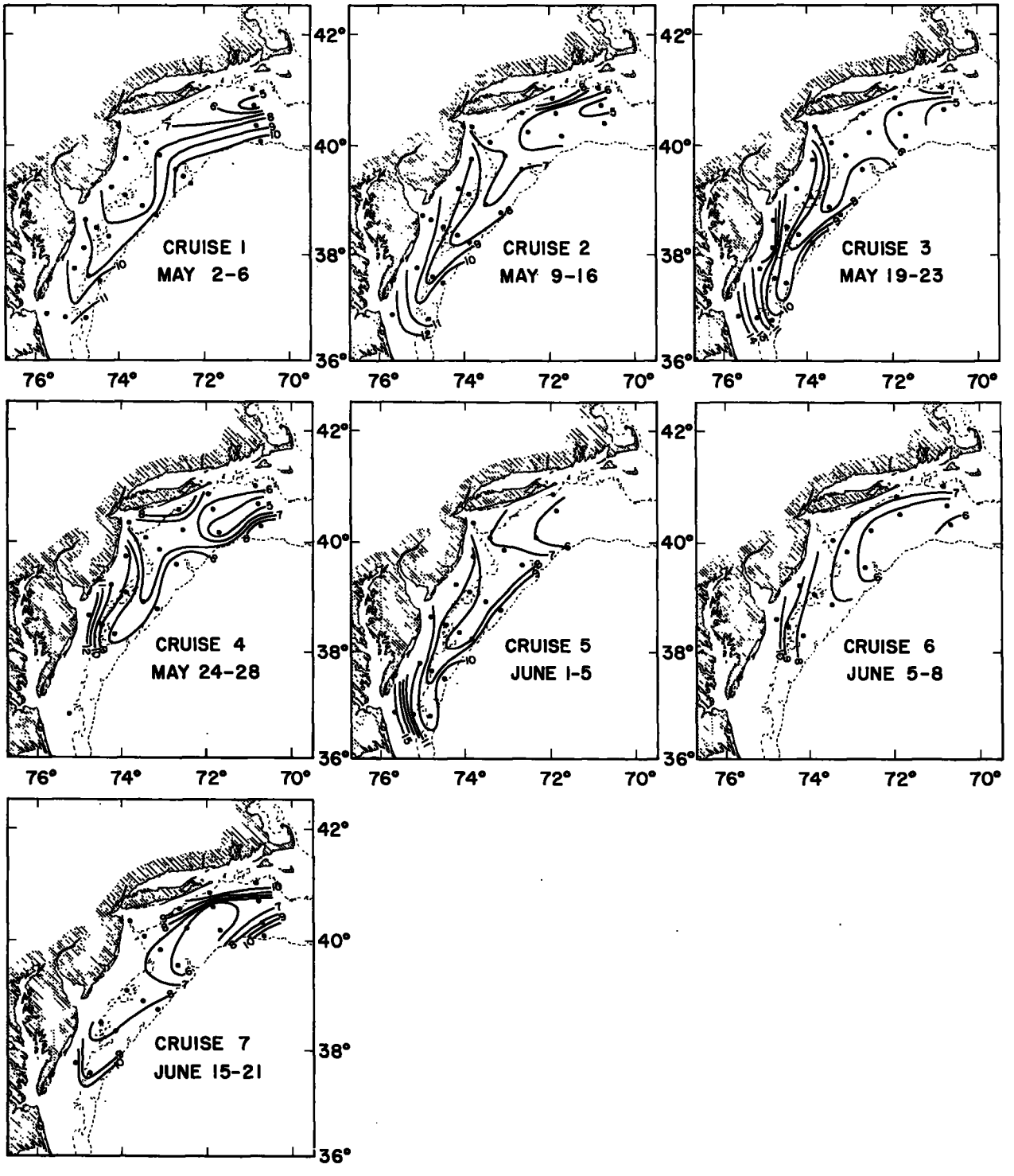

FIGURE 30.—Near-bottom isotherms, 1932. (Temperature in degrees Centigrade.)

The near-bottom temperatures, which may fairly well reflect the conditions actually pertaining during the spawning, were nearly all considerably lower than the surface temperatures. Near-bottom temperatures ranged from 4.9° C. off Martha's Vineyard on cruise 1 to about 12.3° C. on cruise 4 at the southern center of distribution of small larvae. Doubtless, spawning preceded these observations of temperature by some days, and therefore, at both ends of this range should perhaps be somewhat lower.

These temperatures give some evidence of considerable environmental changes. An invasion of warm water along the edge of the Continental Shelf south of Martha's Vineyard and Long Island occurred on cruise 1 and was strong enough to raise bottom temperatures to 10.9° C. at the edge of the shelf while the surface temperature was only 6.8°. The warming was immediately countered by cold water which persisted until after cruise 6 when at Martha's Vineyard station III the bottom temperature increased from 6.1° to 8° C. between cruises 6 and 7.

Such fluctuating temperature conditions probably occur most frequently along the edge of the Continental Shelf with the alternating invasion and retreat of the warm slope waters. The areas of gross temperature changes are not known to include the 15- to 35-fathom depth zone, which is probably inhabited by the spawning yellowtail, but Ketchum et al. (1951) found that the distribution of sea water diluted with river water in the New York bight varied greatly and could be altered suddenly by a storm. Such fluctuations in temperature must be a hazard to the larvae because of the accompanying movement of the water. The surveys show clearly that the larvae are distributed widely over the shelf and that when they descend to the bottom of the ocean they may encounter radically different bottom conditions and water temperatures. If yellowtail fry are as delicate as most fish fry, rather small differences in their environment may be fatal. Changes in temperature might even be catastrophic, as in the widespread destruction of the tilefish, which occurred along the edge of the Continental Shelf south of Block Island in March 1882 (Collins 1884). This occurrence is believed to have been caused by an invasion of cold water in an area normally warmed by the slope water during winter.

FAUNAL CHANGES ON THE YELLOWTAIL GROUNDS

In our studies of the fisheries in the New England area, we have found two examples of significant production of other species on yellowtail grounds. The first of these occurred when the landings of haddock from Nantucket Shoals rose to nearly 13 million pounds in 1928 and subsequently declined (table 46). These are the landings credited to the three principal ports in New England in the annual volumes of Fishery Industries in the United States, published by the Bureau of Fisheries and subsequently the Fish and Wildlife Service. Most of the haddock apparently came from almost exactly the depth range and location subsequently to become a major yellowtail producing area. Rounsefell (1948, fig. 6) plotted the areas fished by medium and large otter trawlers seeking haddock from 1928 to 1937. These plots show that the catches credited to the Nantucket Shoals area were centered at about latitude 40°40′ N., longitude 69°40′ W., in a depth of about 25 fathoms, although the spread of the fishing was from approximately 15 to 35 fathoms, with some tendency toward fishing shoaler waters from February through May. During most of our studies, the part of this area between 15 and 25 fathoms in depth was the second most important yellowtail producing ground (fig. 2), with production ranging from 22 million pounds in 1942 to a little over 5 million pounds in 1949.

TABLE 46.—*Landings of haddock and flounders at principal New England ports from the Nantucket Shoals, Lightship Grounds, and No Mans Land areas, 1925–49*

[In thousands of pounds]

Ports and year of landing [1]	Haddock	All flounders	Ports and year of landing [1]	Haddock	All flounders
Boston, Gloucester, and Portland:			1938	2,204	772
1925	6,488	No data.	1939	1,834	2,245
1926	9,987	Do.	1940	764	4,295
1927	6,246	Do.	1941	489	2,501
1928	12,808	2,060	1942	557	3,160
1929	4,083	1,000	Boston, Gloucester, Portland, and New Bedford:		
1930	4,890	495	1943	299	21,571
1931	2,969	609	1944	1,728	13,869
1932	1,650	203	1945	2,259	15,361
1933	360	114	1946	2,609	18,606
1934	151	21	1947	3,639	21,589
1935	116	19	1948	1,775	17,996
1936	171	225	1949	890	12,355
1937	900	1,090			

[1] For source see appendix A, p. 237.

We think that few flounders were landed from the Nantucket Shoals area in the late twenties because the fish were scarce and not just because it was the practice in the fleet to discard them. In the first place, large quantities of both haddock and yellowtail have never been caught on the same grounds at the same time in other parts of the New England Banks. Secondly, had the abundance of yellowtail in the twenties equalled that found on those grounds in 1942 when production by a small trawler reached nearly 20,000 pounds a day, it would have created so much work in sorting that fishermen not wanting the yellowtail would have moved to other areas. On the other hand, the subsequent failure of these grounds to produce haddock no doubt was due to a lack of haddock and not to a failure to fish for them. Haddock has been a much sought-after species on the New England Banks, and when vessels began to fish the grounds for yellowtail after 1940 it is certain that any significant haddock concentrations would have been discovered and fished, had they existed.

Coincident with the fishery for haddock on the grounds near Nantucket Shoals was the occurrence of yellowtail farther west off the coast of New Jersey. The presence of adults there during the spawning season is indicated by the capture of eggs and larvae in 1929 and 1932, as discussed in the preceding section. These eggs and larvae could not have been found consistently off the New Jersey coast if the spawners had been off southern Massachusetts, as they were after 1942. The residual drift of the waters on the shelf is slowly westward, but as Sette (1943) and Ketchum et al. (1951) have found, the surface water is drifted primarily by the wind. The wind direction is variable, but during May it is usually southwesterly (Sette 1943, p. 205), though it was northeast in 1932. Furthermore, the rate of drift was found by both investigators to be in the order of 10 miles a day or less. Since hatching occurs in 10 days or less and the "small" larval stage lasts only about 10 days, the spawning adults evidently were not far from the places where the eggs and larvae were found.

During the course of his mackerel investigations, 1925–32, Sette gained the impression that the yellowtail was consistently one of the principal spring spawners in the area. In 1932, the only year for which comparative data are available, the mackerel larvae were 1.97 times as numerous as yellowtail larvae in the tows of the first six cruises (Sette 1943, table 19; our appendix table E–1, p. 256). The yellowtail was the second most abundant species in the tows; consequently, the number of adults must have been large. The population of mackerel in 1932 was estimated at between 45,000,000 and 400,000,000 by Sette. We may surmise that yellowtail have similar fecundity, if we balance the slightly greater size of the egg of the mackerel against the slightly smaller size of the yellowtail. If so, the population of yellowtail was in the order of at least some tens of millions. Too, the limited migratory habits of the species indicate that it must have been a resident population, not a coastwise migrant like the mackerel.

Why such an abundant fish was not well known before 1935 is not clear, but we have mentioned that yellowtail were not marketed in those earlier years, they rarely occur within 10 miles of shore, and they are not easily caught by hooks; so it seems entirely possible that they were present but were not fished. On the other hand, any such concentration of yellowtail as was found after 1942 would have been fished, for enough small otter trawlers operated off the New Jersey coast to have found the fish if they had been there.

The second radical faunal change on the yellowtail grounds occurred after the decline in the southern New England stock. With yellowtail especially scarce in 1949 and with an expanding market for fish meal, the fishermen turned to "trash" fish, which they sold to the reduction plants. They saved everything they caught in their nets, but the principal species taken were red hake (*Urophycis chuss*), eelpout (*Zoarces anguillaris*), and several species of skates of the genus *Raja* (Sayles 1951). The principal fishing ground at the start of this fishery in 1949 was in from 10 to 20 fathoms of water south of the eastern end of Martha's Vineyard, and a secondary center was located about 15 miles southeast of this point. Both of these grounds had previously produced substantial quantities of yellowtail (fig. 2), and yet very few yellowtail were included in the catch of the trash fishery. After 1949, this fishery spread over more of the yellowtail grounds, fishermen reported.

476995 O—59——5

Such changes in the habitat of a few species of fish must be evidence of fundamental environmental changes. In seeking an explanation for the change in habitat, we note that the known geographical range of both the haddock and the yellowtail extends only a little south of the southern New England grounds, but much farther north. Bigelow and Schroeder (1953) report that haddock have been found from the deep water off Cape Hatteras north to the west coast of Greenland and the yellowtail from Chesapeake Bay to the Labrador side of the Straits of Belle Isle. We note, too, a retreat of the haddock from the grounds west of Nantucket Shoals northeasterly to Georges Bank in the early thirties, and a subsequent retreat of the yellowtail from off the New Jersey coast in the twenties to off southern New England in the early forties, and then to Georges Bank about 1949 (table 6). Perhaps these retreats have occurred because of the warming of the area (Conover 1951).

Some additional evidence from our study of the yellowtail flounder populations supports the concept of a retreat toward the northeast. We have already noted that the summer fishery weakened after 1944 and by 1949 was the smallest of all the fisheries, whereas it had been the largest in 1942 and 1943 (p. 172). Our tagging operations in 1942 and 1943 off Long Island showed that the summer fishery off No Mans Land included fish that moved west in winter and east in summer (p. 180). Perhaps it is significant that the fishery on this population was the first to fail. Perhaps, too, it is significant that old fish (5 years and older) were a smaller fraction of the landings (table 29) during the third quarter than during most other quarters even just after the peak years. Were these fish migrating from the west subject to greater environmental pressure than other groups?

We also ask why the southern New England yellowtail grew so much more slowly than Nova Scotian yellowtail (Scott 1954) except during their second and third years of life. Is this evidence of greater environmental pressure on the very young fish and those 4 years and older? Why was the life span of the southern New England yellowtail so much shorter than that of Nova Scotian fish, and why did they attain a smaller maximum size? Obviously, living conditions for the older fish from the southern New England stock must have been less favorable, but why? Perhaps the answers to these questions may be learned from a study of changing climatic conditions. Certainly here are problems deserving of more study.

EFFECTS OF THE FISHERY ON YELLOWTAIL STOCKS, 1942–49

How has the fishery affected the yellowtail flounder stocks? Although the exact effect is not known, as a result of our studies from 1942 to 1949 we can provide a working hypothesis.

Unquestionably, the fishery on the southern New England stock suffered a disastrous decline in landings and catch per unit of effort from 1942 to 1949. This decline was accompanied by the near disappearance of fishable schools of yellowtail from the usual fishing grounds on the Continental Shelf between New Jersey and Nantucket Shoals. Furthermore, extensive trawling to a depth of 200 fathoms by the *Albatross III* in 1949 revealed no concentrations of yellowtail outside the regular fishing grounds. These declining landings were accompanied by a high total mortality rate. On the other hand, there were none of the symptoms of heavy fishing, such as a declining average size, an increasing proportion of young fish in the catch, or an increasing growth rate due to the thinning of the stock.

This contradictory evidence cannot be fully explained with the limited data from so short a period of study. To it may be added the evidence of a heterogeneous stock composed of an unknown number of semi-independent populations; a mysterious absence of fish less than a year old and of yearlings from the fishing grounds; and an apparent northeasterly shift of the principal yellowtail population from off the New Jersey coast to off southern New England, where the big fishery occurred from 1941 to 1948, and then to Georges Bank.

The most striking finding from our study of the yellowtail fishery has been the changing availability, which appears, directly, in fluctuations in abundance of the fish during the year and in the abundance of year classes at different ages, and, indirectly, in the minus value of the average apparent natural mortality. It is evidence either that fishing pressure was not uniform on the south-

ern New England stock or that the populations of yellowtail were not uniformly distributed. That both conditions exist is indicated by the irregular tag returns from certain releases and by the differences in size, age, and sex composition at different times in different statistical subareas (figs. 9 and 20, and appendix C).[16] These phenomena prevent the conventional determination of the effect of fishing on the stock because we cannot satisfy the assumption that the fishing is uniform on all parts of the stock.

The changes in availability also prevent any clear determination of the recruitment resulting from spawning. The assumption that larger recruitment results from larger spawning stocks is being challenged for many species as data become available. Likewise, we doubt that large populations of spawning yellowtail produce more young, because we have evidence that only one slightly dominant year class (1941) was produced during the years of large spawning populations (1939 to 1942, and perhaps earlier). Probably, natural conditions greatly affect the survival of the young, because the collections of eggs and larvae indicate that the young drift widely in their pelagic stages at which time they must be vulnerable to changing weather conditions, especially winds that may blow them far from suitable bottom.

Obviously, a great population of yellowtail accumulated through unknown but favorable circumstances and was ready for the fishery, which sought it increasingly after 1938. The fish were centered on a rather restricted kind of coarse red-sand bottom and extended from there beyond the scope of the fishery. We postulate that as the fishery removed them from the favorite grounds scattered groups or individuals moved in to be caught and to make way for others. The new groups of yellowtail became available as others were caught at an estimated annual rate of 35 percent (the approximate annual equivalent of an instantaneous rate of +0.30) over and above any natural mortality. This process continued until 1949, when there were no other yellowtail to move in and parts of even their favorite grounds were used by other species. Why the stock, both on and beyond the fishing grounds, was not replenished by young as the adults were removed is unknown. It appears that the fishery used up the accumulated stock during years when few young survived. Further, the unchanging growth rate indicates that the removals by the fishery did not leave better living conditions for the remaining fish.

MANAGEMENT OF THE YELLOWTAIL FLOUNDER

We believe it is probable, although it cannot be proved, that the major changes in the yellowtail flounder fishery were not caused by overfishing although that may have hastened its decline. Many of the documented facts about the yellowtail populations are not in accord with theoretical changes caused by heavy fishing nor, with the limited data available, can we develop a theory that will, with a reasonable probability, associate fishing with the decline. Therefore, we have no answers to the fundamental questions of what sizes and numbers of fish can be expected from a given fishing effort or what measures would result in the greatest desired return from the fishery.

A negative approach to the question of protective measures is warranted because only a few practical measures have been devised to conserve an ocean fishery of this kind. These measures are all restrictive and should be adopted when they probably will increase the catch or, as Graham (1951) has suggested, fix the fishing level, methods, or seasons, and give the fishermen peace. Restriction for either of these reasons must be considered in conjunction with all of the fishing in the area, not merely for the yellowtail, which after 1945 amounted to less than half of the landings from the southern New England Banks. We have little knowledge of these other fisheries, but with what is available on them and the yellowtail we can eliminate most of the measures usually employed from further consideration.

A closed season on yellowtail appears to offer no help except that which might accrue from reduction of the total catch (to be discussed later). The period usually considered for closure is the spawning season and with the yellowtail this has

[16] Note especially in appendix C, p. 239, the usually, but not always, greater size in subarea O compared with Q and S, the great preponderance of 86 percent females (of small size) during the third quarter 1943 in subarea Q, and the reversal of the size of females in the large samples from subareas O and Q in the fourth quarter of 1945 and the first quarter of 1946. The females averaged 38.81 cm. in length in Q and 37.07 in O at first, and then 37.46 in Q and 38.83 in O.

been the season of poorest fishing. The fish have been consistently more available during the third quarter of the year, and while a closed season at that time would cause a greater reduction in the total catch it offers no obvious advantage in growth of the fish which might result in a greater catch after the period of restraint.

A minimum size limit may offer some small theoretical advantages, but we suspect that the practical difficulties in its application will overbalance any advantages. We cannot calculate the effect of a minimum size limit on yellowtail stocks because we do not know the natural mortality and therefore, cannot use the method developed by Ricker (1945). In principle, however, if natural mortality is low and growth rate high, it is desirable to save the fish to a larger size before capture because they will grow more than the group will lose through death. The reverse is also true: if natural mortality is high and growth rate low, the fish should be harvested as early as practicable. By the time the yellowtail enter the fishery, they have passed through the period of maximum growth in their second summer (1 annulus). When they are fully available at 3 years of age or older, the growth rate has slowed down markedly; therefore, we doubt whether even with a very moderate natural mortality, there would be a significant advantage from setting a size limit.

A second consideration that frequently enters into the establishment of a size limit is protection of the fish until they have had an opportunity to spawn. The southern New England yellowtail spawns at such an early age that during the period of our study only a negligible portion of the landings were immature; consequently, we could not advocate a size limit on this basis.

A serious limitation on the effectiveness of a size limit would ensue from the use of the otter trawl in the fishery combined with the certainty that virtually all small yellowtail, after being landed on deck and sorted in the usual manner, would die before or shortly after their return to the water. Consequently, an effective minimum size limit would have to be accompanied by a minimum mesh size, which would be most difficult to apply in a fishing fleet that seeks numerous other species of varying body shapes and minimal acceptable sizes along with the yellowtail.

There may, however, be a need to prohibit the landing of fish smaller than are acceptable for filleting. Such a need arises from the development of the trash fishery on and near the former yellowtail grounds and the possible inclusion of yellowtail among the fish destined to be reduced to fish meal. After commencement of the trash fishery, there were scattered reports of yellowtail being included in the catch, but evidently the proportion was small, for in the samples from trash-fish catches (Snow 1950) no significant quantities of yellowtail were included. If, however, an unusually successful spawning of yellowtail occurs, large quantities of young below filleting size may be attractive to the trash-fish boats. Such yellowtail would be in their most rapid period of growth and it might be more economical to allow them to remain in the sea to become available as food fish later. A prohibition against landing small fish should be effective, because the trawlers usually can avoid concentrations of such fish.

The closure of certain fishing areas has sometimes been recommended to protect spawning fish, young fish, or fish especially vulnerable to an efficient gear. Such a measure offers no solution in the yellowtail because only one kind of gear, the otter trawl, has ever caught significant quantities of them, the fish have been scarcer during their spawning season than at other times, and we have found no well-defined spawning or nursery area.

A restriction of the total catch might well have saved some of the fish and prolonged the fishery during and after the period of our study if our hypothesis of a large accumulated stock being gradually caught is correct. On the other hand, such a restriction might have meant a lowering of the total catch because the fish saved would have suffered some natural mortality that might or might not have been compensated by growth. Even a loss might have been desirable if it evened out the landings over a longer period. Advocacy of the measure for this reason requires studies beyond the scope of this report.

CONCLUSIONS

If, as appears probable, the abundance of the yellowtail is determined largely by natural causes beyond our control, no definite size or kind of catch can be expected from a given fishing effort. No action is necessary to prevent extinction of the

species; the high cost of fishing them will ease the pressure in time to save a spawning nucleus. The greatest catch from the yellowtail stocks may be obtained by fishing them when available without restriction other than the inevitable economic ones, which are necessarily greater in a highly fluctuating fishery.

Such erratic catches as characterize the yellowtail fishery cause serious economic consequences among short-range vessels of the kind prevalent in the southern New England fishery. If the fluctuations in yellowtail catch cannot be smoothed out, the earnings of the fishermen would be better maintained by turning to other species—some of which replaced the yellowtail when it declined. Finding uses and markets for these species should be helpful.

Not much is known about the yellowtail and the factors influencing the size of the stocks. One of the most troublesome features of our study has been the lack of knowledge of the yellowtail populations not being taken by the fishery. The study of these apparently numerous populations and subpopulations which do not fully intermingle can be accomplished only by thorough sampling of the commercial landings and of the fish in other areas of the sea by a research vessel. Such a study should also include proper consideration of the relation of the yellowtail to its environment and to other species in the area—vertebrate and invertebrate, competing and noncompeting, predator and prey. Other aspects of its life history need to be investigated. We know little of its food habits or fecundity, the requirements and habits of the larvae and juveniles, or of other factors which may limit the size of the stock.

Adequate answers to these questions will require considerable effort; however, a satisfactory guardianship of the stocks can probably be maintained with a limited study to determine trends in total catch, abundance, and size composition of the fishery, supplemented by a watchfulness for evidence of any significant waste of young fish either through discard at sea or reduction to fish meal. Such a study will not lead to a full understanding of the causes of fluctuations in the fishery, but it can be maintained at a cost commensurate with the value of the fishery and will provide invaluable data for any future, more elaborate investigation that may become desirable.

SUMMARY

An intensive study of the yellowtail flounder (*Limanda ferruginea*) was undertaken in 1942 and continued through 1947, with additional data on landings and catch per unit of effort collected through 1951.

Following the decline in the populations of the winter flounder—mainstay of the otter-trawler fleet in southern New England—in the mid-thirties, the abundant yellowtail proved a suitable substitute. The total United States landings of this flounder rose from 23 million pounds in 1938 to 70 million in 1942, then declined to about 30 million pounds annually from 1944 through 1949. Price changes were not the cause of the declining catch.

Between 1942 and 1949, a total of 2,597 yellowtail was tagged and released at 14 points along the New England coast, covering all the major United States fishing grounds. Through December 1952, a total of 377 tags, or 14.5 percent, had been recovered. The recoveries indicated that the yellowtail occur in relatively localized populations and that they make short, seasonal migrations. The majority of the recaptures were within 50 miles of the release points and the most distant recapture was only 170 miles from the release point. Almost all the fish were recaptured in depths between 15 and 35 fathoms.

The mingling of the tagged yellowtail and the fishing concentrations indicated the existence of five more or less distinct stocks:

1. A complex southern New England stock between Nantucket Shoals and Long Island, part of which may have begun to move to Georges Bank in the summer of 1947.

2. Georges Bank stock on the shoal parts of the Bank.

3. Cape Cod stock from east of Cape Cod north to the vicinity of Cape Ann.

4. A northern Gulf of Maine stock along the coast of Maine.

5. One or more Nova Scotian stocks which are fished incidentally by United States boats seeking other species.

The bulk of yellowtail production in the United States has come from the southern New England stock, hence any fluctuations in its numbers are a cause for concern. Because of the great importance of the southern New England stock to

United States fishermen, this study was largely limited to an investigation of that stock and following comments apply to it.

1. Landings from the southern New England stock declined from 63 million pounds in 1942 to 10 million pounds in 1949. During this same period, landings from Georges Bank stock increased from 2 million pounds to 16 million.

2. Between 1943 and 1947 a total of 37,075 fish were selected randomly from the landings and measured and their sex recorded. Females were twice as numerous in the catch as males. The mean length of both sexes was 35.69 cm., with males averaging 33.34 cm. and females 37.21 cm. There was no trend toward smaller fish in the landings between 1942 and 1947; however, later reports show that such a trend developed after 1951.

3. The length-weight relation, by sex and quarter, was determined for 1,113 yellowtail taken from the landings during 1943. Regression formulas were used to estimate the weight of each sex at the mean length of 35.869 cm., and the females were consistently the heavier—this difference between the sexes probably being even greater at onset of spawning in early April. Differences in the length-weight relation among the quarters also were considerable, and yellowtail of average length of both sexes were heaviest in the first quarter of 1943 and lightest in the third.

4. Data collected by quarters on the catch by area and time fished from about 30 percent of the landings revealed that the catch per day was greatest during the third quarter of the year. Despite this seasonal fluctuation, the change in apparent relative abundance as reflected in the catch per unit of effort approximately paralleled the downward trend in the catch during the years 1942 through 1949.

5. Growth data were developed from the attained length at time of capture of 9,204 yellowtail for which the ages were determined from scales. The females attained a greater length than the males of the same age, being 4.5 percent longer than the males at age 2 and up to 9.1 percent longer at age 5. The mean lengths of both sexes for comparable quarters revealed no upward or downward trend in length and only a slight change in growth rate from 1942 to 1947. Scale readings indicated an unusual rate of growth in the young yellowtail. The first year's growth appears to be only from 3 to 5 cm., whereas during the second year the juvenile attains a length of nearly 30 cm.

6. There was no trend toward a greater proportion of young fish in the catch between 1942 and 1947. The average age composition of yellowtail in the landings, in numbers of fish, was 1.3 percent 1-year-olds, 28.1 percent 2-year-olds, 35.5 percent 3-year-olds, 19.3 percent 4-year-olds, 9.6 percent 5-year-olds, 5.1 percent 6-year-olds, and 1.0 percent 7-year-olds and older.

7. The estimated total mortality rate among yellowtail completely available to the fishery was 86 percent a year.

8. Study of the age and length at maturity of 288 fish taken at random from the landings at the peak of the spawning season in May 1943 revealed that most yellowtail of both sexes mature during their second or third year of life. Of the females aged, 52 percent were mature at 2 years and 100 percent at 4 years or more; of the males, 84 percent were mature at 2 years and 100 percent at 4 years or older. Most males mature before entering the fishery and mostly before they attain 26 cm., while 50 percent of the females in the landings were mature at 31.98 cm. and 90 percent at 40.17 cm. The catch during the spawning season in 1943 included only 6 percent immature males and 16 percent immature females.

9. Examination of the ovaries of 1,157 females sampled periodically from the landings in the spring of 1943 revealed that 90 percent of the fish spawned between April 12 and June 26, and that the peak of spawning was May 20. The period of heaviest spawning was from May 4 to June 4 during which 50 percent of the females became spent.

10. We were unable to collect either eggs or larvae of the yellowtail during our investigations, but Sette (1943) recorded considerable data relative to these stages during his mackerel investigations in 1929 and 1932. During those earlier surveys, eggs and larvae of the southern New England yellowtail were found to be abundant over most of the Continental Shelf off New York, New Jersey, and Delaware—much farther southwest than the center of the fishery during the spawning seasons from 1942 to 1949.

11. Marked faunal changes have occurred on the yellowtail grounds. The area southeast of No Mans Land at one time produced large quantities of haddock, later yellowtail, and still later "trash" fish. These changes in fish populations may be associated with fundamental ecologic changes, possibly a warming of the climate.

12. The exact effect of the fishery on yellowtail stocks is not known, but our studies indicate that as the fishery removed the yellowtail from their favored bottom new populations moved in, becoming available to the fishery at an estimated 35 percent a year, in addition to any natural mortality. Unreplenished by young, the accumulated stocks were used up by the fishery until there were no other yellowtail to move in. There is evidence that no significantly greater recruitment was produced by larger spawning populations, as but one slightly dominant year class resulted during the years of large spawning populations from 1938 to 1942.

13. We do not believe that the great decline in the catch of the southern New England stock was caused by catching too many yellowtail, too small yellowtail, or spawning yellowtail. There was no evidence of a significant waste of small fish during the period of this study. Therefore, no restrictive legislation appears needed unless there is a radical change in the conduct of the fisheries.

LITERATURE CITED

BARANOFF, THEODOR I.
1918. On the question of the biological basis of fisheries. Nauchnyi issledovatelskii iktiologisheskii Institut, Izvestiia, vol. 1, No. 1, pp. 81–128. (Institute for Scientific Ichthyological Investigations, Proceed., vol. 1, No. 1, pp. 81–128. Reports from the Division of Fish Management and Scientific Study of the Fishing Industry.) Moscow. [Trans. from the Russian by William E. Ricker with the assistance of Natasha Artin.]

BIGELOW, HENRY B.
1933. Studies of the waters on the Continental Shelf, Cape Cod to Chesapeake Bay. I. The cycle of temperature. Papers in physical oceanography and meteorology, Massachusetts Inst. Technology and Woods Hole Oceanographic Inst., vol. 2, No. 4. 135 pp. Cambridge, Mass. [Contribution No. 34 Woods Hole Oceanographic Inst.]

BIGELOW, HENRY B., and WILLIAM C. SCHROEDER.
1953. Fishes of the Gulf of Maine. United States Fish and Wildlife Service, Fishery Bull. 74, vol. 53, pp. 1–577.

BIGELOW, HENRY B., and MARY SEARS.
1935. Studies of the waters on the continental shelf, Cape Cod to Chesapeake Bay. II. Salinity. Papers in physical oceanography and meteorology, Massachusetts Inst. Technology and Woods Hole Oceanographic Inst., vol. 4, No. 1. 94 pp. Cambridge, Mass. [Contribution No. 70 Woods Hole Oceanographic Inst.]
1939. Studies of the waters of the continental shelf, Cape Cod to Chesapeake Bay. III. A volumetric study of the zooplankton. Harvard College, Memoirs Museum Comparative Zoology, vol. 54, No. 4, pp. 183–378. Cambridge, Mass. [Contribution No. 194 Woods Hole Oceanographic Inst.]

BIGELOW, HENRY B., and WILLIAM W. WELSH.
1925. Fishes of the Gulf of Maine. Bulletin United States Bureau of Fisheries, vol. 40, Part 1, pp. 1–567.

CALHOUN, A. J., D. H. FRY, JR., and E. P. HUGHES.
1951. Plastic deterioration and metal corrosion in Petersen disk fish tags. California Fish and Game, vol. 37, No. 3, pp. 301–314. July.

COLLINS, J. W.
1884. History of the tilefish. United States Commission of Fish and Fisheries, Report of the Commissioner for 1882, Part X, pp. 237–292.

CONOVER, JOHN H.
1951. Are New England winters getting milder? Weatherwise, vol. 4, No. 1, pp. 5–9.

FINNEY, D. J.
1952. Statistical methods in biological assay. 2d edition. 661 pp. Chas. Griffin Co., London.

FISHER, RONALD A., and FRANK YATES.
1948. Statistical tables for biological, agricultural and medical research. 3d edition. 112 pp. Hafner Publishing Co., New York.

GRAHAM, MICHAEL.
1951. Overfishing. Proceedings United Nations Scientific Conference on the Conservation and Utilization of Resources. Vol. 7. Wildlife and fish resources, pp. 20–24.

HAYNE, DON W.
1951. A study of bias in the selection of a "representative" sample of small fish. Papers Michigan Acad. Sci., Arts and Letters. Part II, Zoology, vol. 37, pp. 133–141.

HILDEBRAND, SAMUEL F., and WILLIAM C. SCHROEDER.
1928. Fishes of Chesapeake Bay. Bulletin United States Bureau of Fisheries, vol. 43 (1927), Part 1, 366 pp.

KENDALL, MAURICE G.
1952. Advanced theory of statistics. 5th ed. vol. 1, 457 pp. Chas. Griffin Co., London.

KETCHUM, BOSTWICK H., ALFRED C. REDFIELD, and JOHN C. AYERS.
1951. The oceanography of the New York bight. Papers in physical oceanography and meteorology, Massachusetts Inst. Technology and Woods Hole Oceanographic Inst., vol. 12, No. 1, 46 pp. Cambridge and Woods Hole, Mass. [Contribution No. 549 Woods Hole Oceanographic Inst.]

MANZER, J. I.
1952. The effects of tagging upon a Pacific coast flounder, *Parophrys vetulus*. Jour. Fisheries Research Board of Canada, vol. 8, No. 7, pp. 479–485. May.

MARR, JOHN C.
1951. On the use of the terms *abundance, availability* and *apparent abundance* in fishery biology. Copeia 1951, No. 2, pp. 163–169. June 8.

PERLMUTTER, ALFRED.
1939. An ecological survey of young fish and eggs identified from tow-net collections. A biological survey of the salt waters of Long Island, 1938. Supplement to 28th Annual Report, State of New York Conservation Dept., Part 2, sec. 1, pp. 11–71.
1946. The distribution of the winter flounder (*Pseudopleuronectes americanus*) and its bearing on management possibilities. Trans. Eleventh North American Wildlife Conference, pp. 239–245. American Wildlife Institute, Washington, D. C.

RICKER, WILLIAM E.
1945. A method of estimating minimum size limits for obtaining maximum yield. Copeia 1945, No. 2, pp. 84–94. June 30.
1948. Methods of estimating vital statistics of fish populations. Indiana University Publications, Science Series, No. 15. 101 pp.

ROUNSEFELL, GEORGE A.
1948. Development of fishery statistics in the North Atlantic. United States Fish and Wildlife Service, Special Sci. Report No. 47. 18 pp. February.

RUSSELL, EDWARD S.
1942. The overfishing problem. 130 pp. Cambridge University Press, London.

SAYLES, RICHARD E.
1951. The trash fishery of southern New England in 1950. United States Fish and Wildlife Service, Commercial Fishery Review, vol. 13, No. 7, pp. 1–4. July.

SCHUCK, HOWARD A.
1951. Studies of Georges Bank haddock. Part I: Landings by pounds, numbers, and sizes of fish. United States Fish and Wildlife Service, Fish. Bull. 66, vol. 52, pp. 151–176.

SCOTT, D. M.
1954. A comparative study of the yellowtail flounder from three Atlantic fishing areas. Jour. Fisheries Research Board of Canada, vol. 11, No. 3, pp. 171–197. May.

SETTE, OSCAR E.
1941. Digit bias in measuring and a device to overcome it. Copeia 1941, No. 2, pp. 77–80. July 8.
1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I: Early life history, including growth, drift, and mortality of the egg and larval populations. United States Fish and Wildlife Service, Fishery Bull. 38, vol. 50, pp. 149–237.

SILLIMAN, RALPH P.
1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 5.—A method of computing mortalities and replacements. United States Fish and Wildlife Service, Special Sci. Report No. 24. 10 pp.

SNOW, GEORGE W.
1950. Development of trash fishery at New Bedford, Massachusetts. United States Fish and Wildlife Service, Commercial Fishery Review, vol. 12, No. 7, pp. 8–10. July.

STETSON, HENRY C.
1938. The sediments of the continental shelf off the eastern coast of the United States. Papers in physical oceanography and meteorology, Massachusetts Inst. Technology and Woods Hole Oceanographic Inst., vol. 5, No. 4, 48 pp. Cambridge and Woods Hole, Mass. [Contribution No. 178 Woods Hole Oceanographic Inst.]

THOMPSON, W. F.
1937. Theory of the effect of fishing on the stock of halibut. Report International Fisheries Commission No. 12. 22 pp. Seattle, Wash. October.

THURSBY-PELHAM, D. E.
1939. The effect of fishing on the stock of plaice in the North Sea. Rapports et Procès-Verbaux, Cons. Perm. Internat. Explor. Mer, vol. 110, pp. 39–63. Copenhagen.

WALFORD, LIONEL A.
1946. A new graphic method of describing the growth of animals. Biological Bull., vol. 90, No. 2, pp. 141–147. April.

WIDRIG, T. M.
1954. Definitions and derivations of various common measures of mortality rates relevant to population dynamics of fishes. Copeia 1954, No. 1, pp. 29–32. February 19.

APPENDIX

A. SOURCES OF DATA ON LANDINGS OF YELLOWTAIL, 1940–49

The following documents[1] supplied the information on the production of yellowtail flounder by ports.

All ports[2]

1938. Fishery Industries of the United States, 1939. Administrative Report No. 41: total production for the year, pp. 279-336; also from original records by ports and counties.

1939. Fishery Statistics of the United States, 1939. Statistical Digest No. 1: total production for the year, pp. 44-89; also from original records by ports and counties.

Portland, Maine, Boston and Gloucester, Mass.

1940–1945. Landings at Certain New England Ports, *in* Statistical Bulletin and Current Fishery Statistics series: all data by statistical subarea.

1946–1949. New England Landings, *in* Current Fishery Statistics series: all data by statistical subarea.

New Bedford, Mass.

1940. Monthly landings copied from dealers' records.

1941. Monthly landings compiled from daily reports telephoned to Boston Fishery Market News Service by the port agent of the Atlantic Fishermen's Union.

1942. Landings of Fishery Products at New Bedford, Mass., *in* Current Fishery Statistics No. 108: landings by months.

1943 (Jan.–June). Monthly landings by statistical subarea compiled from dealers' records and daily interviews.

1943 (July)–1945. Landings by Fishing Craft at New Bedford, Mass., *in* Current Fishery Statistics series: all data by month and statistical subarea.

1946–1949. New England Landings, *in* Current Fishery Statistics series: monthly landings by statistical subarea.

Provincetown, Mass.

1940–1943 (July). Monthly landings compiled from daily reports to Boston Fishery Market News Service.

Provincetown, Mass.—Continued

1943 (Aug.)–1949. Monthly landings from records of the Massachusetts Department of Conservation, Division of Marine Fisheries.

Woods Hole, Mass.

1940–1943 (July). Monthly landings compiled from daily reports to Boston Fishery Market News Service.

1943 (Aug.)–1949. Monthly landings copied from records of the Massachusetts Department of Conservation, Division of Marine Fisheries.

Chatham, Mass.

1943 (Aug.)–1949. Monthly landings copied from records of the Massachusetts Department of Conservation, Division of Marine Fisheries: landings before 1942 unavailable and yellowtail landings considered negligible.[3]

Plymouth, Mass.

1944 (Oct.)–1949. Monthly landings compiled from dealers' records: landings before this date considered negligible.[3]

Nantucket, Mass.

1944–1949. Monthly landings compiled from dealers' records: landings before 1944 considered negligible.[3]

Rhode Island.

1940. Fishery Statistics of the United States, 1941. Statistical Digest No. 7. Total production for the year.

1941. Monthly landings compiled from daily shipments into New York City as reported by the New York Fishery Market News Service.

1942. Current Fishery Statistics No. 164. Total production for the year. Proportion by month estimated from daily reports of New York Fishery Market News Service.

1943–1949. Monthly landings compiled from daily reports of the New York Fishery Market News Service. The total production reported for 1942 was 3.505 times the daily shipments to New York City. This factor was used to estimate the total landings for 1943 to 1949. Earlier years were not adjusted because processing facilities were not built until 1943.

[1] Unless otherwise specified, all publications are those of the United States Department of the Interior, Fish and Wildlife Service, Washington 25, D. C.

[2] Although certain data on the landings of yellowtail flounder are available for the years before 1940, they are compiled by the home port of the vessel instead of the port in which the trips were landed. Thus, the data are not comparable with those of the later years. Furthermore, before 1938 all species of flounders were consolidated in the statistics.

[3] Diversion of landings to smaller ports commenced after price controls were applied in 1943.

Connecticut.

1940–1941. Twenty-fourth Biennial Report of the Connecticut State Board of Fisheries and Game, State of Connecticut, Public Document No. 19. Landings by months.

1942. New England Fisheries, *in* Current Fishery Statistics No. 164. Total production for the year. Proportion by month estimated from daily shipments into New York City.

1943–1949. Monthly landings compiled from daily shipments into New York City as reported by the New York Fishery Market News Service. The total landings for 1942 were 1.9 times the daily shipments into New York City. This factor was used to estimate the total landings for 1943–49. Earlier years were not adjusted because processing facilities were not built until 1943.

New York City, N. Y.

1940–1944. Landings by Fishing Craft at New York City, *in* Current Fishery Statistics No. 193. Landings by months.

New York City, N. Y.—Continued

1945. Landings by Fishing Craft at New York City, *in* Current Fishery Statistics No. 269. Landings by months.

1946–1949. Landings compiled by months from fishing craft weighouts as reported by the New York Fishery Market News Service.

Long Island, N. Y.

1940–1949. Total monthly shipments into New York City, as reported by the New York Fishery Market News Service; assumed to represent the entire landings.

New Jersey.

1940–1949. Monthly landings compiled from daily shipments into New York City, as reported by the New York Fishery Market News Service; assumed to represent the entire landings.

B. METHODS OF ESTIMATING CATCH BY STATISTICAL SUBAREA

Portland, Maine, Gloucester and Boston, Mass., 1938 to 1949, and New Bedford, Mass., October 1942 to 1949.

Data were collected daily from representatives of almost all vessels by the U. S. Fish and Wildlife Service and mostly published in the Service's Current Fishery Statistics series. After October 1942, more than 60 percent of the total yellowtail landings were included in the statistics.

New Bedford, Mass., January–September 1942.

Landings were assigned to statistical subareas according to information compiled from log-book records that had been kept by several of the captains fishing out of the port.

Chatham, Mass.

The fishing fleet consisted of 30 or more line trawlers, 35 to 45 feet in length, which, as a rule, fished the same nearby grounds on 1-day trips throughout the year. According to interviews with fishermen in 1946, the area fished extended from No. 6 buoy to No. 10 buoy on the western side of South Channel, in depths ranging from 15 to 30 fathoms on hard, rocky bottoms shunned by otter trawlers. All species of fish landed at Chatham were assigned to subarea G.

Provincetown, Mass.

The fleet consisted of 35 to 40 small otter trawlers, which followed a regular seasonal pattern of fishing for yellowtail. During the winter months of November to March, the fleet fished Cape Cod Bay and Massachusetts Bay, statistical subarea E, and during the rest of the year they fished east of Cape Cod on the western side of South Channel in statistical subarea G. On the basis of this information, which was gathered through interviews with captains of vessels operating out of Provincetown, the landings of yellowtail flounder have been assigned to these two subareas for the months indicated.

Plymouth, Mass.

The fleet fishing out of Plymouth consisted of less than 20 small otter trawlers which regularly fished Cape Cod Bay and Massachusetts Bay, statistical subarea E, and all landings of yellowtail flounders have been assigned to this subarea.

Woods Hole, Mass.

The regular fleet consisted of 15 or more small otter trawlers and 2 medium-sized otter trawlers that fished the same grounds fished by the New Bedford fleet of small otter trawlers. Trips were also landed there occasionally by New Bedford vessels. The landings of yellowtail flounder at Woods Hole have been assigned to statistical subareas in proportion to the landings at New Bedford by small otter trawlers.

Nantucket, Mass.

Most of the vessels landing in this port were small and medium-sized draggers that commonly fished the same grounds fished by the New Bedford fleet, and they land there or at Woods Hole occasionally. The landings at Nantucket have been assigned to statistical subareas in proportion to the landings by all otter trawlers at New Bedford.

Rhode Island, Conn., and Long Island, N. Y.

Landings at ports in these places were variously assigned to statistical subareas according to information gathered from interviews with fishermen from these ports during October and November 1946. This varied slightly from port to port and season to season, but virtually all of the fishing was west of Nantucket Shoals.

New York City, N. Y.

Landings of yellowtail flounders at this port were assigned to the subareas in proportion to the landings by all vessels at New Bedford from Georges Bank and southern New England areas. This was based on the opinion of captains of both small and medium-sized draggers landing fish at New York City.

New Jersey.

The very small amount of landings were assumed to have come from the statistical area designated Southwestern Long Island.

C. LENGTH FREQUENCIES OF YELLOWTAIL BY STATISTICAL SUBAREA, QUARTER AND SEX, 1941–47

TABLE C–1.—*Length frequencies of yellowtail: By area, quarter, and sex, southern Nova Scotia (XXI–0) and eastern Massachusetts grounds (XXII–E)*

Length of fish	Southern Nova Scotia		Eastern Massachusetts grounds						
	1945 2d quarter		1942 4th quarter	1944 3d quarter		1946 2d quarter		1947 2d quarter	
	Male	Female	Both sexes	Male	Female	Male	Female	Male	Female
26.5 cm				2					
27.5 cm			10	3	1				
28.5 cm			11	5					
29.5 cm			17	2	1			1	
30.5 cm			22	2				3	1
31.5 cm			24	5	3			5	2
32.5 cm			11	10	1	1		4	3
33.5 cm			9	10	3	1		5	5
34.5 cm	1	1	4	10	5			3	6
35.5 cm				6	2	4		4	8
36.5 cm	1			1	2	1		5	2
37.5 cm	3	2	3	1	5	2	2	1	5
38.5 cm	2	3	2	6	3	3	1	2	4
39.5 cm				3	7	4	1	1	7
40.5 cm				1	1	10	5	1	6
41.5 cm	4	5				8	5	1	2
42.5 cm	2	8		1	1	7	1		3
43.5 cm	1	10				2	6		3
44.5 cm	3	12					5		1
45.5 cm		11				2	9		3
46.5 cm		7				1	5		4
47.5 cm		5				1	4		
48.5 cm		7					1		
49.5 cm		7					1		1
50.5 cm							1		
51.5 cm		2					1		
52.5 cm		3							
Total	17	83	113	68	35	47	48	36	66
Mean length (cm.)	40.50	45.20	31.00	33.53	36.10	40.41	44.19	34.44	38.50

TABLE C–2.—*Length frequencies of yellowtail: By area, quarter, and sex, western side of South Channel (XXII–G)*

Length of fish	1945 1st quarter		1946 2d quarter	
	Male	Female	Male	Female
18.5 cm			1	
19.5 cm				
20.5 cm			1	
21.5 cm			2	
22.5 cm			4	5
23.5 cm			5	4
24.5 cm			6	3
25.5 cm			4	6
26.5 cm	2		4	5
27.5 cm			1	1
28.5 cm	1	1		1
29.5 cm	3		1	
30.5 cm	6		2	2
31.5 cm	3	1	1	1
32.5 cm	4	1	3	
33.5 cm	8	2	3	2
34.5 cm	6	3	2	1
35.5 cm	3	2	1	
36.5 cm	4	2		4
37.5 cm	10	3	1	5
38.5 cm	12	5	3	3
39.5 cm	10	9	2	2
40.5 cm	8	12	5	
41.5 cm	4	10	4	3
42.5 cm	4	5	3	7
43.5 cm	1	7	1	6
44.5 cm		7		5
45.5 cm	1	10		7
46.5 cm		5		3
47.5 cm				
48.5 cm		3		
49.5 cm		3		
50.5 cm		4		
Total	90	95	59	76
Mean length (cm.)	36.51	41.90	31.11	35.62

TABLE C–3.—*Length frequencies of yellowtail: By area, quarter, and sex, eastern side of South Channel (XXII–H)*

Length of fish	1942 4th quarter	1944 1st quarter		1944 4th quarter		1945 1st quarter		1946 1st quarter	
	Both sexes	Male	Female	Male	Female	Male	Female	Male	Female
26.5 cm						1			
27.5 cm						1			
28.5 cm				1		1	2		
29.5 cm		2				1			1
30.5 cm	1	4				3	1	1	
31.5 cm	2	7	1	2		4		5	1
32.5 cm	1	17	2	2	1	14	3	4	
33.5 cm	6	16	9	6	1	19	6	9	4
34.5 cm	6	21	7	8	1	28	9	6	17
35.5 cm	13	25	15	14	1	45	17	11	19
36.5 cm	8	34	17	24	7	67	23	23	25
37.5 cm	18	21	22	22	19	50	48	25	17
38.5 cm	16	22	24	28	27	69	73	19	26
39.5 cm	13	21	31	24	45	68	90	15	20
40.5 cm	21	8	44	14	57	43	101	13	32
41.5 cm	11	5	33	9	57	29	144	14	45
42.5 cm	20	5	37	5	71	17	142	5	42
43.5 cm	23		33	3	55	8	139	1	54
44.5 cm	11	1	20	1	53	2	99		40
45.5 cm	11		19	1	39		86		40
46.5 cm	8		7		38		64	1	24
47.5 cm	7		13		36		32		16
48.5 cm	6		2		20		22		14
49.5 cm	4		3		9		11		6
50.5 cm	1		2	1	3		6		1
51.5 cm							2		1
Total	207	209	341	165	540	470	1,120	152	442
Mean length (cm.)	40.98	36.34	40.97	38.07	42.93	37.77	42.22	37.68	41.86

TABLE C–4.—*Length frequencies of yellowtail: By area, quarter, and sex, central and southeast Georges Bank (XXII–M)*

Length of fish	1942 4th quarter	1944 4th quarter		1945 3d quarter		1946 3d quarter	
	Both sexes	Male	Female	Male	Female	Male	Female
27.5 cm						1	
28.5 cm				1		2	
29.5 cm				1	1	8	1
30.5 cm	1			1		6	
31.5 cm				3		14	
32.5 cm	1			4	2	17	
33.5 cm	5	2		6	2	17	1
34.5 cm	5		2	6	4	18	3
35.5 cm	5	1	1	7	1	21	5
36.5 cm	10	1		16	4	17	9
37.5 cm	8	3	1	7	3	13	17
38.5 cm	8	5	5	9	9	10	21
39.5 cm	10	4	6	7	12	6	16
40.5 cm	6		4	2	9	3	13
41.5 cm	9	1	10	2	13	1	6
42.5 cm	8	1	14	2	11		15
43.5 cm	4	1	8		12	1	14
44.5 cm	7		13		12		6
45.5 cm	8		6		12		8
46.5 cm	5		4		9		3
47.5 cm			2		8		4
48.5 cm			2		1		1
49.5 cm			1				1
50.5 cm							1
51.5 cm		1	2				
52.5 cm					1		
Total	100	20	81	74	126	155	145
Mean length (cm.)	39.87	39.05	42.88	36.32	41.96	34.64	40.56

TABLE C–5.—*Length frequencies of yellowtail: By area, quarter, and sex, southwest Georges Bank (XXII–N)*

Length of fish	1942 1st quarter	1947 3d quarter		1947 4th quarter	
	Both sexes	Male	Female	Male	Female
20.5 cm	1				
21.5 cm					
22.5 cm	1				
23.5 cm	2				
24.5 cm	5				
25.5 cm	8				
26.5 cm	4				
27.5 cm	4		1		
28.5 cm	2	1			
29.5 cm	1	4			
30.5 cm		9	1	2	
31.5 cm	1	15	4	3	
32.5 cm	2	12	1	10	2
33.5 cm	1	12	9	2	1
34.5 cm	1	19	11	5	3
35.5 cm	5	14	17	3	3
36.5 cm	3	19	21	1	2
37.5 cm	1	15	26	2	5
38.5 cm	5	10	21	1	9
39.5 cm	5	3	24	2	10
40.5 cm	3	1	35		4
41.5 cm	7	1	30		8
42.5 cm	6		22		9
43.5 cm	9		19		5
44.5 cm	9		10		3
45.5 cm	4		9		
46.5 cm	3		3		2
47.5 cm	2		2		
48.5 cm			2		3
Total	95	135	268	31	69
Mean length (cm.)	36.56	34.66	39.58	34.05	40.24

TABLE C–6.—*Length frequencies of yellowtail: By area, quarter, and sex, Nantucket Shoals and Lightship grounds (XXII–0)*

Length of fish	1942 4th quarter		1943				1944					
			1st quarter		3d quarter		1st quarter		3d quarter		4th quarter	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
21.5 cm	1	1										
22.5 cm	4	8										
23.5 cm	14	8										
24.5 cm	17	23		1							4	
25.5 cm	23	28		1							2	
26.5 cm	18	16	1		1	2		2	1		3	
27.5 cm	9	10		1	2		3		3		2	
28.5 cm	11	10	2	2	2	4	1		3		3	
29.5 cm	17	4	2		7	4	3		2		13	1
30.5 cm	8	3	12	2	18	14	6	5	13	1	18	4
31.5 cm	15	5	17	10	21	13	9	5	16	5	22	12
32.5 cm	13	10	17	22	42	25	6	6	13	3	22	11
33.5 cm	15	4	29	25	34	28	6	3	7	26	25	13
34.5 cm	7	13	23	27	27	58	10	2	5	11	16	30
35.5 cm	7	12	41	50	33	77	6	4	3	11	17	30
36.5 cm	7	11	36	50	23	76	6	6		13	5	31
37.5 cm	3	19	37	64	14	82	4	2	1	13	17	34
38.5 cm	5	15	34	76	5	65	4	7		11	6	21
39.5 cm	1	12	17	83	6	85	1	6	1	11	2	40
40.5 cm		16	16	87		78	4	10		8	3	19
41.5 cm		11	4	104	1	72		7		10	1	23
42.5 cm		9	3	83		48	2	6		8		14
43.5 cm		4	1	78		32		6		2	1	15
44.5 cm		5		49		13		5		2		11
45.5 cm		1		44		8		5		2		11
46.5 cm		2		23		3		7				3
47.5 cm				23		1		3		2		3
48.5 cm				11			1	2				3
49.5 cm				8				1				1
50.5 cm				2								1
51.5 cm				2								
52.5 cm				1								
53.5 cm												
54.5 cm												1
Total	195	260	292	929	236	788	72	100	68	139	181	332
Mean length (cm.)	29.30	32.84	35.90	40.35	33.89	38.10	34.42	39.46	31.87	37.32	33.14	38.44

TABLE C–7.—*Length frequencies of yellowtail: By area, quarter, and sex, Nantucket Shoals and Lightship grounds (XXII–0)*

Length of fish	1945						1946						1947			
	1st quarter		3d quarter		4th quarter		1st quarter		3d quarter		4th quarter		3d quarter		4th quarter	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
21.5 cm							1									
22.5 cm			1													
23.5 cm			1	1	1		1									
24.5 cm	2			1		2						2				
25.5 cm	3		1	1			2	1	1			2				
26.5 cm	12			1	1	2	1	2	1	1	1		1	1	2	
27.5 cm	10		2		3	1	4	2	9	2	2	3	10	1	1	1
28.5 cm	10	1	14	1	10	1	9	6	45	10	9	12	25	4	2	1
29.5 cm	9	2	16	7	24	11	5	2	51	34	38	50	62	23	4	2
30.5 cm	13		50	12	59	18	9	2	104	78	89	123	73	42	10	1
31.5 cm	14	6	37	25	87	44	37	4	62	112	101	166	71	90	17	6
32.5 cm	30	17	45	35	75	61	49	26	45	116	100	215	62	111	19	13
33.5 cm	33	17	42	43	78	73	52	65	39	76	68	189	44	128	9	21
34.5 cm	51	31	30	43	81	65	52	80	39	37	76	200	41	122	6	19
35.5 cm	56	38	15	40	56	78	29	60	31	27	60	155	27	122	3	17
36.5 cm	44	46	8	47	34	92	32	62	33	41	62	125	11	82	8	22
37.5 cm	59	69	2	55	11	98	25	82	12	61	42	146	6	58	5	12
38.5 cm	47	72	3	34	6	82	22	59	6	57	12	125	3	35		18
39.5 cm	18	91	1	32	4	63	15	47	2	51	8	154	2	37	2	9
40.5 cm	20	126		19	3	54	9	54		40	1	154	1	31	1	14
41.5 cm	9	93		11		46	9	67		36	2	138		32		18
42.5 cm	3	109	1	12		22	2	54		25		88		17		13
43.5 cm	2	95		6		23	2	53		8		53		17		12
44.5 cm		77		4		17		41		7		42		5		2
45.5 cm		56		2		13		24		2		21		3		6
46.5 cm		32				8		14		2		15		1		3
47.5 cm		31				4		15				11				1
48.5 cm		18				6		6		1		5		1		1
49.5 cm		4						4				7				
50.5 cm		3						1				1				
51.5 cm		2						1								
52.5 cm								1								
Total	445	1,036	269	432	533	884	307	835	480	824	671	2,202	439	963	89	212
Mean length (cm.)	35.22	40.96	32.30	36.08	33.14	37.07	34.58	38.83	32.06	35.06	33.34	36.48	31.96	35.18	32.89	37.77

TABLE C–8.—*Length frequencies of yellowtail: By area, quarter, and sex, off No Mans Land and southern Massachusetts (XXII–Q, R)*

Length of fish	1941		1942			1943							
	2d quarter	4th quarter	2d quarter	4th quarter		1st quarter		2d quarter		3d quarter		4th quarter	
	Both sexes	Both sexes	Both sexes	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
22.5 cm				1									
23.5 cm													1
24.5 cm		1		1	1	1		1					
25.5 cm						1	1	3	1		2		
26.5 cm		1				4	2	7	6	1	11		
27.5 cm	5	1		2	3			7	11	9	30	2	
28.5 cm	4	1	2	5	2	5	2	10	18	14	50	3	
29.5 cm		3	1	19	10	14	5	22	23	19	70	9	1
30.5 cm		31	2	45	26	43	5	26	46	24	69	12	6
31.5 cm	1	26	5	39	34	51	32	54	71	29	117	21	9
32.5 cm	3	22	12	73	21	54	51	52	115	45	139	22	21
33.5 cm	7	21	20	51	24	53	49	44	144	36	163	38	21
34.5 cm	7	27	31	39	34	61	40	42	99	25	162	29	29
35.5 cm	10	34	24	35	39	62	39	41	78	21	150	23	37
36.5 cm	9	33	14	25	47	46	37	31	72	13	129	19	41
37.5 cm	6	32	11	14	49	19	46	17	73	3	125	7	43
38.5 cm	3	19	18	7	35	18	46	7	66	1	109	8	40
39.5 cm	9	14	9	2	34	10	27	3	51	1	105		43
40.5 cm	5	18	5	4	17	2	30	3	53	1	47	1	26
41.5 cm	3	11	4		21	2	30		48	1	22		36
42.5 cm	3	11	1		22		27		36		3		21
43.5 cm	1	5	1		9		21	2	27		3		21
44.5 cm		2	1		7		12		15		2		9
45.5 cm		2			4		5		11				5
46.5 cm	1	2			3		2		8				3
47.5 cm							4		2				1
48.5 cm					1				1				
49.5 cm									1				1
50.5 cm									1				
Total	77	317	161	362	443	446	513	372	1,077	243	1,508	194	415
Mean length (cm.)	36.11	35.80	35.76	33.21	36.52	33.88	37.01	33.17	35.85	32.52	34.64	33.73	38.03

TABLE C–9.—*Length frequencies of yellowtail: By area, quarter, and sex, off No Mans Land and southern Massachusetts (XXII–Q, R)*

Length of fish	1944								1945					
	1st quarter		2d quarter		3d quarter		4th quarter		1st quarter		3d quarter		4th quarter	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
23.5 cm		2		1							1			
24.5 cm	2		1				1	1	1	1				
25.5 cm	3	2	1				1	1	6		2			
26.5 cm	2		2				2		14	2	6	1		
27.5 cm	5	3	8		4		3		18	1	38	3	1	1
28.5 cm	8		7	2	10	1	6		16	4	89	20		
29.5 cm	18	1	19	1	13		2	2	18	3	154	61	10	1
30.5 cm	21	16	35	5	27	3	10	7	30	10	136	69	28	2
31.5 cm	51	20	40	29	26	24	17	10	48	26	128	96	58	12
32.5 cm	48	23	40	50	26	35	23	9	59	33	140	61	66	27
33.5 cm	66	36	21	59	24	40	26	11	90	34	135	68	73	41
34.5 cm	83	43	10	34	17	38	17	14	88	35	83	127	78	47
35.5 cm	68	76	7	18	8	26	21	23	97	52	42	183	64	43
36.5 cm	66	71	10	13	4	12	7	28	85	89	13	170	34	82
37.5 cm	42	76	2	9	6	23	10	20	53	96	3	153	34	74
38.5 cm	35	57	1	8	1	9	3	24	58	130		88	11	79
39.5 cm	15	79		8	1	11	1	24	16	141	2	49	8	93
40.5 cm	7	65		5		9		17	12	122		43	1	87
41.5 cm	4	47		3		7		16	4	124		30	1	74
42.5 cm	1	67		3		7		15		132		21		64
43.5 cm	3	35		1				9	1	113		7		26
44.5 cm		38		1		1		13		67		1		27
45.5 cm		28						1		72				18
46.5 cm		11						4		56				7
47.5 cm		8						2		21				7
48.5 cm		2								11				1
49.5 cm								2		4				
50.5 cm										4				
51.5 cm										1				
Total	548	806	204	250	167	246	150	253	714	1,384	972	1,251	467	813
Mean length (cm.)	34.52	38.62	31.79	34.27	31.58	35.23	33.28	38.05	34.34	40.16	31.51	35.36	34.04	38.81

TABLE C–10.—*Length frequencies of yellowtail: By area, quarter, and sex, off No Mans Land and southern Massachusetts (XXII–Q, R)*

Length of fish	1946								1947							
	1st quarter		2d quarter		3d quarter		4th quarter		1st quarter		2d quarter		3d quarter		4th quarter	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
22.5 cm								1								
23.5 cm							1									
24.5 cm					1											2
25.5 cm	4	3							1	1	1				2	
26.5 cm	7	6	3	1	3				5	2	3				1	
27.5 cm	12	4	3		14	3	3		13	1	3	2	2	1	3	2
28.5 cm	3	2	3	3	32	18	8	1	20	10	11	1	9	3	10	
29.5 cm	8	4	4	7	30	41	25	4	10	7	20	10	8	17	26	9
30.5 cm	21	2	4	3	28	50	63	14	19	10	28	15	16	40	47	25
31.5 cm	35	9	3		16	39	66	33	38	12	32	27	25	30	48	39
32.5 cm	75	29	2		27	27	88	49	42	17	42	29	19	32	68	58
33.5 cm	100	80	6	1	41	13	94	64	58	30	34	46	12	30	49	49
34.5 cm	92	93	6		47	15	88	67	43	43	32	41	7	32	45	52
35.5 cm	79	82	4	5	24	29	68	51	40	49	28	56	7	24	35	55
36.5 cm	71	71	2	5	17	34	60	45	44	44	38	33	5	16	20	61
37.5 cm	44	64		9	8	56	37	44	39	45	20	28		6	19	48
38.5 cm	25	52		4	2	67	19	67	26	47	14	24	2	7	10	51
39.5 cm	10	50		9		42	9	69	8	42	13	32		2	2	23
40.5 cm	6	46		2		44	4	76	7	51	1	32	1	7	1	30
41.5 cm		42		7		17		78	4	40	1	30		4		43
42.5 cm		49		3		10	3	44	1	49		26		3		31
43.5 cm		32		1		8		31	1	23		20				16
44.5 cm		18				1		13	1	23		12				14
45.5 cm		12				1		11		15		10				8
46.5 cm		2						3		6		3				2
47.5 cm		3						2		10		2				2
48.5 cm		2						1		4		1				
49.5 cm		1								2						2
50.5 cm		1								1		1				
51.5 cm										1		1				
Total	592	759	40	60	290	515	636	768	420	585	321	482	113	254	386	622
Mean length (cm.)	34.27	37.46	31.75	36.55	32.30	35.63	33.78	37.76	34.13	38.44	33.73	37.15	32.15	33.52	33.03	36.69

TABLE C–11.—*Length frequencies of yellowtail: By area, quarter, and sex, Rhode Island shore (XXII–S)*

Length of fish	1942		1943		1944				1945					
	1st quarter	2d quarter	2d quarter		1st quarter		4th quarter		1st quarter		2d quarter		4th quarter	
	Both sexes	Both sexes	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
20.5 cm	1													
21.5 cm														
22.5 cm	3													
23.5 cm	2													
24.5 cm	9										3			
25.5 cm	3				1	1			1	1	4			
26.5 cm	8	2			4				3	1	11			
27.5 cm	12	12	1	2	3	2					10			
28.5 cm	14	14		1	6		2	1	1		6		1	
29.5 cm	23	6		1	11	3	4	1			3		3	2
30.5 cm	38	23	2	8	23	9	1	1	5		9	2	14	3
31.5 cm	42	56		9	32	25	2	4	6	3	18	4	22	8
32.5 cm	58	76	7	16	34	20	2	3	11	10	20	12	13	13
33.5 cm	42	86	3	12	28	22	8	2	17	3	30	8	11	12
34.5 cm	34	105	2	11	31	20	7	4	12	6	27	14	8	11
35.5 cm	36	98	4	10	27	14	4	5	11	6	18	25	8	12
36.5 cm	37	58	6	10	14	16	5	9	5	11	7	30	2	4
37.5 cm	29	37		7	10	20		10	10	11	10	27	2	20
38.5 cm	33	25		8	8	19		5	5	14		25	3	4
39.5 cm	23	31		5	1	13	1	4	1	13		13		7
40.5 cm	28	20		7	2	7		1		13		15	1	5
41.5 cm	13	15		3		11		1		5		17		3
42.5 cm	4	10		1		8		4		4		14		1
43.5 cm	6	5		1		4		5	1	4		8		5
44.5 cm	2	2				3		3		2	1	6		1
45.5 cm	2	1				2				3	1	3		1
46.5 cm	2	2				2				1		1		2
47.5 cm						1				1				
48.5 cm						1								
49.5 cm						1		1						
Total	504	684	25	112	235	224	36	64	89	112	178	224	88	114
Mean length (cm.)	34.01	34.90	33.86	35.04	33.21	36.16	33.53	37.52	34.15	38.00	32.52	37.97	32.85	36.22

TABLE C–12.—*Length frequencies of yellowtail: By area, quarter, and sex, Rhode Island shore (XXII–S)*

Length of fish	1947							
	1st quarter		2d quarter		3d quarter		4th quarter	
	Male	Female	Male	Female	Male	Female	Male	Female
22.5 cm			1					
23.5 cm								
24.5 cm								
25.5 cm	1	2	2				1	1
26.5 cm	4	6	9					
27.5 cm	4	2	14	5	4			
28.5 cm	4	1	22	7	9	4	2	
29.5 cm	2	2	14	11	3	16	10	
30.5 cm	5	1	32	6	7	24	18	3
31.5 cm	10	5	38	8	6	15	26	11
32.5 cm	8	8	42	20	13	17	38	14
33.5 cm	4	14	37	43	8	14	31	19
34.5 cm	7	8	24	62	4	14	27	21
35.5 cm	6	7	24	52	4	5	11	17
36.5 cm	3	7	25	22	2	7	15	7
37.5 cm	5	11	17	18	1	4	7	14
38.5 cm	2	4	4	21		4	2	30
39.5 cm	2	3	6	39		6	5	20
40.5 cm		14	2	45		4	2	13
41.5 cm		7		46		3	1	8
42.5 cm		5		44		3		12
43.5 cm		8		20		1		11
44.5 cm		1		11				7
45.5 cm		2		6				4
46.5 cm		1		1				2
47.5 cm		1		2				
48.5 cm				1				
Total	67	120	313	490	61	141	196	204
Mean length (cm.)	32.59	36.52	32.64	37.60	31.78	33.52	33.41	37.53

TABLE C–13.—*Length frequencies of yellowtail: By area, quarter, and sex, off Southeastern Long Island (XXII–I)*

Length of fish	1942 1st quarter	1944 4th quarter		1947 2d quarter	
	Both sexes	Male	Female	Male	Female
24.5 cm	3				
25.5 cm					
26.5 cm	3				
27.5 cm	1	1		1	
28.5 cm	1	7	1	1	1
29.5 cm	4	13		1	1
30.5 cm	10	17	1	2	5
31.5 cm	18	19		2	7
32.5 cm	27	21	6	1	5
33.5 cm	40	28	15	3	15
34.5 cm	32	18	13		15
35.5 cm	31	9	7	4	6
36.5 cm	10	1	12		5
37.5 cm	17		12		5
38.5 cm	14		9		4
39.5 cm	14		4	1	4
40.5 cm	8		4		8
41.5 cm	7		5		2
42.5 cm	5		3		
43.5 cm	3				
44.5 cm	2		2		1
Total	240	134	94	16	84
Mean length (cm.)	35.03	32.28	36.51	32.75	35.24

TABLE C–14.—*Length frequencies of yellowtail: By area, quarter, and sex, from the southern New England stock*

Length of fish	1942 4th quarter		1943								1944							
			1st quarter		2d quarter		3d quarter		4th quarter		1st quarter		2d quarter		3d quarter		4th quarter	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
21.5 cm	1	1																
22.5 cm	5	8																
23.5 cm	14	8								1		2		1				
24.5 cm	18	24	1	1	1						2		1				5	1
25.5 cm	23	28	1	2	3	1		2			4	3	1				3	1
26.5 cm	18	16	5	2	7	6	2	13			6	2	2		1		5	
27.5 cm	11	13		1	8	13	11	30	2		11	5	8		7		6	
28.5 cm	16	12	7	4	10	19	16	54	3		15		7	2	13	1	18	2
29.5 cm	36	14	16	5	22	24	26	74	9	1	32	4	19	1	15		32	4
30.5 cm	53	29	55	7	28	54	42	83	12	6	50	30	35	5	40	4	46	13
31.5 cm	54	39	68	42	54	80	50	130	21	9	92	50	40	29	42	29	60	26
32.5 cm	86	31	71	73	59	131	87	164	22	21	88	49	40	50	39	38	68	29
33.5 cm	66	28	82	74	47	156	70	191	38	21	100	61	21	59	31	66	87	41
34.5 cm	46	47	84	67	44	110	52	220	29	29	124	65	10	34	22	49	58	61
35.5 cm	42	51	103	89	45	88	54	227	23	37	101	94	7	18	11	37	51	65
36.5 cm	32	58	82	87	37	82	36	205	19	41	86	93	10	13	4	25	18	80
37.5 cm	17	68	56	110	17	80	17	207	7	43	56	98	2	9	7	36	27	76
38.5 cm	12	50	52	122	7	74	6	174	8	40	47	83	1	8	1	20	9	59
39.5 cm	3	46	27	110	3	56	7	190		43	17	98		8	2	22	4	72
40.5 cm	4	33	18	117	3	60	1	125	1	26	13	82		5		17	2	41
41.5 cm		32	6	134		51	2	94		36	4	65		3		17	1	45
42.5 cm		31	3	110		37		51		21	3	81		3		15		36
43.5 cm		13	1	99	2	28		35		21	3	45		1		2	1	29
44.5 cm		12		61		15		15		9		46		1		3		29
45.5 cm		5		49		11		8		5		35				2		12
46.5 cm		5		25		8		3		3		20						7
47.5 cm				27		2		1		1		12				2		5
48.5 cm		1		11		1					1	5						3
49.5 cm				8		1				1		2						4
50.5 cm				2														1
51.5 cm				2														
52.5 cm				1														
53.5 cm																		
54.5 cm																		1
Total	557	703	738	1,442	397	1,189	479	2,296	194	415	855	1,130	204	250	235	385	501	743
Mean length (cm.)	31.84	35.16	34.68	39.16	33.22	35.77	33.20	35.83	33.73	38.03	34.15	38.21	31.79	34.27	32.16	35.98	32.98	37.98

476995 O—59——6

TABLE C-15.—*Length frequencies of yellowtail: By area, quarter, and sex, from the southern New England stock*

Length of fish	1945								1946								1947							
	1st quarter		2d quarter		3d quarter		4th quarter		1st quarter		2d quarter		3d quarter		4th quarter		1st quarter		2d quarter		3d quarter		4th quarter	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
21.5 cm									1															
22.5 cm					1										1				1					
23.5 cm					2	1	1		1						1									
24.5 cm	3	1	3			1		2					1		2									2
25.5 cm	10	1	4		3	1			6	4			1		2		2	3	3				3	1
26.5 cm	29	3	11		6	2	1	2	8	8	3	1	4	1	1		9	8	12		1	1	3	
27.5 cm	28	1	10		40	3	4	2	16	6	3		23	5	5	3	17	3	18	7	16	2	4	3
28.5 cm	27	5	6		103	21	11	1	12	8	3	3	77	28	17	13	24	11	34	9	43	11	14	1
29.5 cm	27	5	3		170	68	37	14	13	6	4	7	81	75	63	54	12	9	35	22	73	56	40	11
30.5 cm	48	10	9	2	186	81	101	23	30	4	4	3	132	128	152	137	24	11	62	26	96	106	75	29
31.5 cm	68	35	18	4	165	121	167	64	72	13	3		78	151	167	199	48	17	72	42	102	135	91	56
32.5 cm	100	60	20	12	185	96	154	101	124	55	2		72	143	188	264	50	25	85	54	94	160	125	85
33.5 cm	140	54	30	8	177	111	162	126	152	145	6	1	80	89	162	253	62	44	74	104	64	172	89	89
34.5 cm	151	72	27	14	113	170	167	123	144	173	6		86	52	164	267	50	51	56	118	52	168	78	92
35.5 cm	164	96	18	25	57	223	128	133	108	142	4	5	55	56	128	206	46	56	56	114	38	151	49	89
36.5 cm	134	146	7	30	21	217	70	178	103	133	2	5	50	75	122	170	47	51	63	60	18	105	43	90
37.5 cm	122	176	10	27	5	208	47	192	69	146		9	20	117	79	190	44	56	37	51	7	68	31	74
38.5 cm	110	216		25	3	122	20	165	47	111		4	8	124	31	192	28	51	18	49	5	46	12	89
39.5 cm	35	245		13	3	81	12	163	25	97		9	2	93	17	223	10	45	20	75	2	45	9	52
40.5 cm	32	261		15		62	5	146	15	100		2		84	5	230	7	65	3	85	2	42	4	57
41.5 cm	13	222		17		41	1	123	9	109		7		53	2	216	4	47	1	78		39	1	69
42.5 cm	3	245		14	1	33		87	2	103		3		35	3	132	1	54		70		23		56
43.5 cm	4	212		8		13		54	2	85		1		16		84	1	31		40		18		39
44.5 cm		146	1	6		5		45		59				8		55	1	24		24		5		23
45.5 cm		131	1	3		2		32		36				3		32		17		16		3		18
46.5 cm		89		1				17		16				2		18		7		4		1		7
47.5 cm		53						11		18						13		11		4				3
48.5 cm		29						7		8				1		6		4		2		1		1
49.5 cm		8								5						7		2						2
50.5 cm		7								2						1		1		1				
51.5 cm		3								1								1		1				
52.5 cm										1														
Total	1,248	2,532	178	224	1,241	1,683	1,088	1,811	959	1,594	40	60	770	1,339	1,307	2,970	487	705	650	1,056	613	1,358	671	1,038
Mean length (cm.)	34.64	40.39	32.52	37.97	31.68	35.55	33.50	37.80	34.39	38.18	31.75	36.55	32.15	35.28	33.56	36.81	33.92	38.11	33.18	37.20	31.97	34.70	33.12	37.07

D. LENGTH AND AGE FREQUENCIES OF YELLOWTAIL FROM THE SOUTHERN NEW ENGLAND STOCK, BY QUARTER AND SEX, 1942–47

TABLE D–1.—*Length and age frequencies of yellowtail: Southern New England stock, by year, quarter, and sex*

[Age determinations during first quarters were not made for yellowtail with more than 6 annuli]

Length of fish	Male						Female							Sex undetermined						
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli
1942																				
First quarter:																				
25.5 cm	1																			
26.5 cm																				
27.5 cm																				
28.5 cm	1																			
29.5 cm																				
30.5 cm																				
31.5 cm																				
32.5 cm			1					3												
33.5 cm			1																	
34.5 cm		1		1				1												
35.5 cm		1																		
36.5 cm			1							1										
37.5 cm				1					2											
38.5 cm					1				1	2										
39.5 cm										2										
40.5 cm																				
41.5 cm																				
42.5 cm											2									
43.5 cm																				
44.5 cm																				
45.5 cm												1								
Total	2	2	3	2	1			4	3	5	2	1								
Mean length (cm.)	27.0	35.0	34.2	36.0	38.5			33.0	37.8	38.5	42.5	45.5								
Second quarter:																				
26.5 cm																	2			
27.5 cm															5	1	1			
28.5 cm															2	2	1			
29.5 cm															3	2				
30.5 cm															1	6	4			
31.5 cm															3	13	8	1		
32.5 cm																24	12	4		
33.5 cm															1	11	26	5	2	1
34.5 cm																20	32	8	5	1
35.5 cm																11	25	7	4	2
36.5 cm																3	8	12	7	3
37.5 cm																4	3	6	6	3
38.5 cm																2	7	3	2	4
39.5 cm																1	3	3	2	2
40.5 cm																	2	1	6	2
41.5 cm																		1	2	4
42.5 cm																				3
43.5 cm																				4
44.5 cm																				1
45.5 cm																				1
Total															15	100	135	51	36	31
Mean length (cm.)															29.4	33.4	34.5	35.9	37.3	39.8
Third quarter:																				
26.5 cm															1					
27.5 cm															3					
28.5 cm															1					
29.5 cm															2					
30.5 cm															1	1				
31.5 cm															3	3				
32.5 cm																5				
33.5 cm															1	8	3			
34.5 cm																9	1	1		
35.5 cm																5	3			
36.5 cm																1	3			
37.5 cm																	7			
38.5 cm																2	4	2		
39.5 cm																	3			
40.5 cm																	1			
Total															12	34	25	3		
Mean length (cm.)															29.6	34.0	37.1	37.2		

TABLE D-1.—*Length and age frequencies of yellowtail: Southern New England stock, by year, quarter, and sex*—Continued

Length of fish	Male						Female							Sex undetermined						
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6*K* annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7*K* annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7*K* annuli
1942—Con.																				
Fourth quarter:																				
21.5 cm														1						
22.5 cm							1								1					
23.5 cm																				
24.5 cm														1						
25.5 cm							1								1					
26.5 cm														2	1					
27.5 cm														1	1					
28.5 cm															3					
29.5 cm	1							1							4					
30.5 cm		9						3							6	1				
31.5 cm		3													10	1				
32.5 cm		4	2					2	2						9	2				
33.5 cm		5	4					2	2						11	4				
34.5 cm		1	4					2	3						12	7				
35.5 cm		1	2	1					1						1	7	1			
36.5 cm			6					1	3						2	10		1	1	
37.5 cm			2						6						3	9	3			
38.5 cm				1					2	1						5	3	1		
39.5 cm			1						1							2	4	1		
40.5 cm					1					2	3	1					2			
41.5 cm										4	2					1	1	5		
42.5 cm										1		1				1		3		
43.5 cm												1						1	3	
44.5 cm																		1	3	
45.5 cm												1								1
46.5 cm																				1
47.5 cm																				1
48.5 cm																				1
Total	1	23	21	2	1		2	11	20	8	5	4		5	65	50	14	13	7	4
Mean length (cm.)	29.5	32.0	35.3	37.0	40.5		24.0	32.6	36.1	41.0	40.9	43.0		25.3	32.3	36.2	38.8	41.3	42.9	47.0
1943																				
First quarter:																				
19.5 cm															1					
20.5 cm																				
21.5 cm																				
22.5 cm																				
23.5 cm														1						
24.5 cm																				
25.5 cm														3	1					
26.5 cm														2	1					
27.5 cm														2						
28.5 cm														1						
29.5 cm														3	3	1				
30.5 cm	1	5	1												6	1				
31.5 cm		1						2							9	2				
32.5 cm		1													5	2	2			
33.5 cm		2	1					2	1						6	5	2			
34.5 cm			1					1							6	8				
35.5 cm				1				1	1						3	5	3			
36.5 cm		1						2							3	7	2	1		
37.5 cm			2	3					2	1					1	7	1			
38.5 cm					1				3						1	3	3			
39.5 cm				1					1		1							3	1	
40.5 cm				1					1	4						1	4	2		
41.5 cm									1	4	3							1		
42.5 cm										2		2					1	1	3	
43.5 cm											1	1						1		
44.5 cm											1							1		
45.5 cm										1	1	2							1	
46.5 cm												3								
47.5 cm												1								
48.5 cm												1								
49.5 cm												2								
Total	1	10	5	6	1			8	10	12	7	12		12	46	42	18	10	5	
Mean length (cm.)	30.5	32.0	34.7	38.0	38.5			34.1	38.1	41.3	42.5	46.2		27.1	32.4	35.3	37.2	40.8	42.5	
Second quarter:																				
24.5 cm															1					
25.5 cm															1					
26.5 cm		1						5							1					
27.5 cm		2						6	1						3					
28.5 cm		2	1					10	1						5					
29.5 cm		1	4					10	4						3					
30.5 cm		2	11					12	6						2	7				
31.5 cm			20	1				8	16						3	5				
32.5 cm			22	6				6	34	1						13				
33.5 cm		1	14	2					49							5				
34.5 cm			7	9					26	2						3	1			
35.5 cm			7	11	1				31	4						2	2			
36.5 cm			6	10	3				22	18	1					2	1	1		
37.5 cm			1	6	2				12	9	7						2	2	1	
38.5 cm					1	1			7	14	5	2					3			

TABLE D–1.—*Length and age frequencies of yellowtail: Southern New England stock, by year, quarter, and sex*—Continued

Length of fish	Male						Female							Sex undetermined						
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli
1943—Con.																				
Second quarter—Con.																				
39.5 cm			1	2					2	15	2	4					2		1	
40.5 cm				1						4	11	4	1						3	
41.5 cm										3	10	2	1					2	1	
42.5 cm										4	5	4	3					1	1	
43.5 cm					1						3	6	1					2	2	
44.5 cm											3		1						2	
45.5 cm												3	3						1	
46.5 cm												1	2						1	
47.5 cm													1						1	
48.5 cm													1							
49.5 cm																				
50.5 cm													1							
Total		9	94	48	8	1		57	211	74	47	26	15		19	37	11	8	14	
Mean length (cm.)		29.2	32.8	35.5	37.8	38.5		29.6	34.2	38.2	40.6	42.1	44.9		38.7	32.7	37.4	40.5	42.7	
Third quarter:																				
27.5 cm		1						1												
28.5 cm		2						1												
29.5 cm		4						1												
30.5 cm		2						2	1											
31.5 cm		2	1					2	8											
32.5 cm		1	2					4	11											
33.5 cm		1	4						9											
34.5 cm			3		1			2	15											
35.5 cm			3					1	15	2										
36.5 cm				2					5	7										
37.5 cm									6	4										
38.5 cm			1						2	11	1									
39.5 cm									3	13	1									
40.5 cm										2		1								
41.5 cm										5	1									
42.5 cm										1		2								
43.5 cm											1	1								
44.5 cm											1									
45.5 cm																				
46.5 cm												1								
47.5 cm													1							
Total		13	14	2	1			14	75	45	5	5	1							
Mean length (cm.)		30.2	34.2	36.5	34.5			31.7	34.6	38.8	41.5	43.1	47.5							
Fourth quarter:																				
23.5 cm							1													
24.5 cm																				
25.5 cm																				
26.5 cm																				
27.5 cm																				
28.5 cm		1													1					
29.5 cm		1													3					
30.5 cm		3	1					2							2	1				
31.5 cm		2	1					4							13	1				
32.5 cm		3	2					1		1					7	10				
33.5 cm		2	5					2	2						18	6				
34.5 cm		1	4					3							13	12	2			
35.5 cm		1	4	2				2	5						11	23	3	1		
36.5 cm		2	3	2					10	1					7	14	3			
37.5 cm				2					8	2					3	21	5			
38.5 cm								1	4	5					4	10	13			
39.5 cm									3	4						7	6	1		
40.5 cm										7							9	4		
41.5 cm										2	1					1	9	4		
42.5 cm										1	1						2	4		
43.5 cm											2		1				1	3	1	
44.5 cm											2	2					1	5	1	
45.5 cm											1						1	4		
46.5 cm																		1	3	1
47.5 cm																				
48.5 cm																			1	1
49.5 cm																				1
Total		16	20	6			1	15	32	23	7	2	1		82	106	55	27	6	3
Mean length (cm.)		32.5	34.2	36.5			23.5	33.3	36.9	39.3	43.6	44.5	43.5		33.9	36.0	39.4	42.8	46.0	48.2
1944																				
First quarter:																				
24.5 cm															2					
25.5 cm																				
26.5 cm																				
27.5 cm	1														1					
28.5 cm															1					
29.5 cm															1					
30.5 cm															1					
31.5 cm		1													4					
32.5 cm		1													4	2				

TABLE D–1.—*Length and age frequencies of yellowtail: Southern New England stock, by year, quarter, and sex*—Continued

Length of fish	Male						Female							Sex undetermined						
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli
1944—Con.																				
First quarter—Con.																				
33.5 cm		1	1												2	1				
34.5 cm		1	2												1	1	1			
35.5 cm			3					1	5						1	3	1	1		
36.5 cm		1		2				1								3	1			
37.5 cm			3	1					1											
38.5 cm				1					2							1	2			
39.5 cm									4	2						1	1	2		
40.5 cm				1					2	2										
41.5 cm											1						1			
42.5 cm										2		1					1			
43.5 cm												1							1	
44.5 cm										1	1									
45.5 cm												2								
46.5 cm												1								
47.5 cm																				
48.5 cm																			1	
Total	1	5	9	5				2	14	7	2	5			18	12	8	3	2	
Mean length (cm.)	27.5	33.7	35.7	37.9				36.0	37.9	41.4	43.0	44.7			31.0	35.6	38.4	38.2	46.0	
Second quarter:																				
28.5 cm		1																		
29.5 cm		1	4																	
30.5 cm		2	12						2											
31.5 cm			11					1	5											
32.5 cm			12						13											
33.5 cm			3						16											
34.5 cm			4						14											
35.5 cm				2					5		1									
36.5 cm			1	2					3											
37.5 cm										2										
38.5 cm					1					1										
39.5 cm											2									
40.5 cm												1								
41.5 cm											1									
42.5 cm												1								
43.5 cm																				
Total		4	47	4	1			1	58	3	4	2								
Mean length (cm.)		29.8	31.8	36.0	38.5			31.5	33.6	37.8	39.2	42.0								
Third quarter:																				
28.5 cm		1							1						2					
29.5 cm		1	3																	
30.5 cm		2	7					1	3						1					
31.5 cm			9					1	7						1	1				
32.5 cm		1	9					1	9							1				
33.5 cm			4						13						1	1				
34.5 cm			4	1					11						1	2	1			
35.5 cm									7	2										
36.5 cm				1					2	2										
37.5 cm				2					2	3										
38.5 cm										7							1			
39.5 cm				1					1	1	4									
40.5 cm											2									
41.5 cm										1	1									
42.5 cm									1	1										
43.5 cm																				
44.5 cm																				
45.5 cm																				
46.5 cm																				
47.5 cm													1							
Total		5	36	5				3	57	17	7		1		6	5	2			
Mean length (cm.)		30.3	31.9	37.1				31.5	33.8	38.2	40.1		47.5		31.2	33.3	36.5			
Fourth quarter:																				
20.5 cm	1																			
21.5 cm																				
22.5 cm																				
23.5 cm																				
24.5 cm																				
25.5 cm																				
26.5 cm																				
27.5 cm	1	1																		
28.5 cm		5																		
29.5 cm		6						3												
30.5 cm		5						3												
31.5 cm		3	3					4	1											
32.5 cm		3	8					4	1											
33.5 cm		1	11	1				3	1											
34.5 cm		1	7	1				4	12											
35.5 cm		1	7	1				2	12	1										
36.5 cm			2	1					12	1										
37.5 cm				2					9	1										
38.5 cm				2					10	4										

TABLE D–1.—*Length and age frequencies of yellowtail: Southern New England stock, by year, quarter, and sex*—Continued

Length of fish	Male						Female							Sex undetermined						
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli
1944—Con.																				
Fourth quarter—Cont.																				
39.5 cm					1				7	13										
40.5 cm				1					2	6	2									
41.5 cm				1						3	7									
42.5 cm										3	6	1								
43.5 cm											2	2								
44.5 cm										1	1	8	2							
45.5 cm												5								
46.5 cm												2	1							
47.5 cm												2								
48.5 cm																				
49.5 cm													1							
50.5 cm													1							
51.5 cm													1							
Total	2	26	38	10	1			23	67	33	18	20	6							
Mean length (cm.)	24.0	30.6	33.8	37.4	39.5			32.4	36.6	39.9	42.1	45.0	47.8							
1945																				
First quarter:																				
24.5 cm	1																			
25.5 cm	3						1													
26.5 cm	7	1					1	1												
27.5 cm	7						1													
28.5 cm	7	2					1													
29.5 cm	3	7					1													
30.5 cm		5						2												
31.5 cm	1	15	2					3												
32.5 cm		17	6	1				18	2											
33.5 cm		10	15	1				11	2											
34.5 cm		12	13	4	1			19	4											
35.5 cm		15	29	6				8	12	1										
36.5 cm		3	22	14				12	31	3										
37.5 cm		3	12	9	3			5	26	8	1									
38.5 cm			6	13	3			4	19	9										
39.5 cm			3	7				2	32	22	1									
40.5 cm				2	2			4	14	27	6									
41.5 cm				3	1				8	26	10	1								
42.5 cm				1					2	39	30	2								
43.5 cm									1	16	26	9								
44.5 cm									1	3	10	8								
45.5 cm										3	5	28								
46.5 cm										1	2	19								
47.5 cm											2	13								
48.5 cm												3								
49.5 cm																				
50.5 cm												4								
Total	29	90	108	61	10		5	89	154	158	93	87								
Mean length (cm.)	27.5	33.0	35.6	37.5	38.5		27.5	34.8	38.1	41.2	43.0	45.9								
Second quarter:																				
25.5 cm		1																		
26.5 cm		2																		
27.5 cm		2																		
28.5 cm		1																		
29.5 cm		1	1																	
30.5 cm			3						2						2					
31.5 cm			2	2					3											
32.5 cm			6	1					5											
33.5 cm			1	9					2											
34.5 cm				4					1	2										
35.5 cm			1	1					1	4										
36.5 cm					1				2	2										
37.5 cm									3	4	1									
38.5 cm										3										
39.5 cm										2	1	1	1							
40.5 cm											1	1	1							
41.5 cm											4	1								
42.5 cm											2	1	3							
43.5 cm													2							
44.5 cm													2							
45.5 cm													2							
46.5 cm													1							
Total		7	14	17	1				19	17	9	4	12							
Mean length (cm.)		27.4	32.0	33.6	36.5				33.7	37.0	40.9	41.0	43.4							
Third quarter:																				
23.5 cm	1																			
24.5 cm							1													
25.5 cm	1																			
26.5 cm		1					1													
27.5 cm		8																		
28.5 cm		13						4												
29.5 cm		36						20												
30.5 cm		38	1					29												

TABLE D–1.—*Length and age frequencies of yellowtail: Southern New England stock, by year, quarter, and sex*—Continued

Length of fish	Male						Female							Sex undetermined						
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli
1945—Con.																				
Third quarter—Cont.																				
31.5 cm		28	4	2				36												
32.5 cm		15	18	8				29	1											
33.5 cm		5	24	9				17	6	1										
34.5 cm			12	11				11	17	8										
35.5 cm		1	4	8				23	20	16										
36.5 cm			1	2					12	26	1									
37.5 cm				3					7	43	8									
38.5 cm				1					4	21	4									
39.5 cm				1					2	14	7	1								
40.5 cm										3	8	4								
41.5 cm											8	4	1							
42.5 cm										2	2	3	2							
43.5 cm											1	2								
44.5 cm												1								
45.5 cm											1									
Total	2	145	64	45			2	149	69	134	40	15	3							
Mean length (cm.)	24.5	30.4	33.4	34.5			25.5	31.7	35.7	37.4	39.9	41.8	42.2							
Fourth quarter:																				
26.5 cm	1																			
27.5 cm		1																		
28.5 cm			1																	
29.5 cm		8						2												
30.5 cm	1	19						6												
31.5 cm		29	4					16												
32.5 cm		24	8	1				27	2											
33.5 cm		17	18	10				29	3											
34.5 cm		6	16	19	1			31	6											
35.5 cm		3	7	20				11	10	1										
36.5 cm			9	9	2			12	21	17	1									
37.5 cm			1	10	3			2	11	35	1	1								
38.5 cm			1	5	1				6	34	1									
39.5 cm				2	4				1	34	11	1								
40.5 cm				1		1			2	10	22	1								
41.5 cm					1					5	24	2								
42.5 cm										2	17	8	1							
43.5 cm											6	12	1							
44.5 cm											3	3	2							
45.5 cm											1	4	4							
46.5 cm												1	3							
47.5 cm													3							
48.5 cm													5							
Total	2	107	65	77	12	1		136	62	138	87	33	19							
Mean length (cm.)	28.5	32.0	34.2	35.7	38.2	40.5		33.6	36.4	38.5	41.3	43.2	46.4							
1946																				
First quarter:																				
23.5 cm	1																			
24.5 cm																				
25.5 cm	2																			
26.5 cm	2						3													
27.5 cm	2	1					2	1												
28.5 cm	2						4													
29.5 cm	3						1													
30.5 cm		2	1					1												
31.5 cm	1	14	1				1	1												
32.5 cm	1	26	3					7	1											
33.5 cm		27	10					28	6											
34.5 cm		23	14					39	2											
35.5 cm		10	18					27	9											
36.5 cm		7	17	5				19	15											
37.5 cm			13	6				9	20	4										
38.5 cm			8	3				3	21	7	1									
39.5 cm			2	1	1				9	9	1									
40.5 cm				3	2				4	26	1									
41.5 cm				1	4				3	19	9									
42.5 cm					2				3	15	9									
43.5 cm										9	16	4								
44.5 cm										1	10	4								
45.5 cm											2	8								
46.5 cm											2	2								
47.5 cm												5								
48.5 cm												1								
49.5 cm											1	1								
50.5 cm												2								
Total	14	110	87	19	9		11	135	93	90	52	27								
Mean length (cm.)	28.0	33.5	35.8	38.2	41.3		28.1	34.8	37.6	41.0	43.2	46.1								

TABLE D-1.—*Length and age frequencies of yellowtail: Southern New England stock, by year, quarter, and sex*—Continued

Length of fish	Male						Female							Sex undetermined						
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli
1946—Con.																				
Second quarter:																				
26.5 cm		1																		
27.5 cm		1																		
28.5 cm		1						3												
29.5 cm		1																		
30.5 cm																				
31.5 cm																				
32.5 cm			1																	
33.5 cm			4																	
34.5 cm				2																
35.5 cm				2						2										
36.5 cm										2										
37.5 cm									1	1										
38.5 cm																				
39.5 cm											1									
40.5 cm											1									
41.5 cm											1									
Total		4	5	4				3	1	5	3									
Mean length (cm.)		28.0	33.3	35.0				28.5	37.5	36.3	40.5									
Third quarter:																				
17.5 cm							1													
18.5 cm																				
19.5 cm																				
20.5 cm																				
21.5 cm																				
22.5 cm																				
23.5 cm																				
24.5 cm																				
25.5 cm								1												
26.5 cm		4						1												
27.5 cm		9						3												
28.5 cm		33						11												
29.5 cm		50						29												
30.5 cm		63						60												
31.5 cm		28	2	2				71												
32.5 cm		14	8	12				57	3											
33.5 cm		9	9	8				30	6	2										
34.5 cm			11	14	1			12	10	2										
35.5 cm		2	4	16	1			4	10	8	1									
36.5 cm			1	12	1			1	4	19	1									
37.5 cm				8	1			1		33	7									
38.5 cm				1	2				4	28	20									
39.5 cm										12	35	1								
40.5 cm									1	3	26	3								
41.5 cm											24	5								
42.5 cm										1	10	5	2							
43.5 cm										1	1	4	1							
44.5 cm												4	1							
45.5 cm													1							
46.5 cm											1									
Total		212	35	73	6		1	281	38	109	126	22	5							
Mean length (cm.)		30.2	33.8	34.9	36.8		17.5	31.5	35.2	37.7	40.1	42.4	43.7							
Fourth quarter:																				
23.5 cm	1																			
24.5 cm							3													
25.5 cm		1																		
26.5 cm																				
27.5 cm		1																		
28.5 cm		3					1	1												
29.5 cm		14																		
30.5 cm		36	1					10												
31.5 cm		47	2					24												
32.5 cm		39	7		1			33	2											
33.5 cm		21	13	5				46	2											
34.5 cm		13	10	14	1	1		39	10											
35.5 cm		1	10	9	5			11	19											
36.5 cm		3	10	17	5			4	15	5	1									
37.5 cm			2	8	11			2	17	16	7									
38.5 cm				4	5	1			8	16	11	2								
39.5 cm						1			5	16	29	3								
40.5 cm					1				2	12	51	1								
41.5 cm					1				1	4	44	9								
42.5 cm					1					2	21	11	1							
43.5 cm										1	7	15	3							
44.5 cm									1		2	6	4							
45.5 cm												4	4							
46.5 cm												1								
47.5 cm													1							
48.5 cm													4							
49.5 cm													1							
50.5 cm													1							
Total	1	179	55	57	31	3	4	170	82	72	173	52	19							
Mean length (cm.)	23.5	31.8	34.5	35.9	37.3	37.5	25.5	33.3	36.7	39.0	40.7	42.8	46.0							

TABLE D–1.—*Length and age frequencies of yellowtail: Southern New England stock, by year, quarter, and sex*—Continued

Length of fish	Male						Female							Sex undetermined						
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli
1947																				
First quarter:																				
26.5 cm							1													
27.5 cm							1													
28.5 cm	3																			
29.5 cm	1	1					5													
30.5 cm	1						3													
31.5 cm	1	4																		
32.5 cm		5					1	1												
33.5 cm		6			1		1	8												
34.5 cm		14	1					7												
35.5 cm		3	8					9	1											
36.5 cm		2	5	4				4	4	1										
37.5 cm			6	1	1			4	7											
38.5 cm			6						5	1	1									
39.5 cm									4	1	1	1								
40.5 cm			3					1	2	5	3									
41.5 cm					1				1	3	1									
42.5 cm				1						1	6									
43.5 cm										1	2	4								
44.5 cm										3	3	1								
45.5 cm										1		1								
46.5 cm										1		3								
47.5 cm											1	1								
48.5 cm												2								
49.5 cm																				
50.5 cm												2								
Total	6	35	29	6	3		12	34	24	18	18	15								
Mean length (cm.)	29.5	33.8	37.2	37.7	37.5		29.9	35.2	38.2	41.8	42.4	45.9								
Second quarter:																				
26.5 cm		1																		
27.5 cm		7						3												
28.5 cm		6																		
29.5 cm		6	1					7												
30.5 cm		4	13					5												
31.5 cm		3	6					7	4											
32.5 cm		3	16					7	7											
33.5 cm		1	13	2				3	18											
34.5 cm			7	9	2			2	29											
35.5 cm				7	5				17	2										
36.5 cm			3	8	4				17	1										
37.5 cm				4	5				6	8	1									
38.5 cm					3	1				6	7									
39.5 cm				1	4	1				4	8	3								
40.5 cm									1		26	5								
41.5 cm									1		13	11								
42.5 cm											7	12	3							
43.5 cm											2	7	1							
44.5 cm												6	4							
45.5 cm												1	4							
46.5 cm													1							
47.5 cm											1									
48.5 cm																				
49.5 cm																				
50.5 cm																				
51.5 cm													1							
Total		31	59	31	23	2		34	100	21	65	45	14							
Mean length (cm.)		29.5	32.6	35.7	37.1	39.0		31.1	34.9	37.9	40.7	42.3	44.9							
Third quarter:																				
27.5 cm		1																		
28.5 cm		8						1												
29.5 cm	1	12						12												
30.5 cm		16	6					19												
31.5 cm		12	10					35												
32.5 cm		7	18	1				26	8											
33.5 cm		1	15	4				17	19											
34.5 cm			11	6	1			17	39											
35.5 cm			1	4	1			3	38											
36.5 cm				4	2				20	5										
37.5 cm					2			1	2	16										
38.5 cm				1	2				1	6	6									
39.5 cm					1					1	9									
40.5 cm					1					1	9	2								
41.5 cm											13	4								
42.5 cm											1	6								
43.5 cm												5	2							
44.5 cm												2	1							
45.5 cm												2								
46.5 cm																				
47.5 cm																				
48.5 cm													1							
Total	1	57	61	20	10			131	127	29	38	21	4							
Mean length (cm.)	29.5	30.5	32.8	35.0	37.5			32.1	34.9	37.7	40.3	42.8	45.0							

TABLE D–1.—*Length and age frequencies of yellowtail: Southern New England stock, by year, quarter, and sex*—Continued

Length of fish	Male						Female							Sex undetermined						
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli
1947—Con.																				
Fourth quarter:																				
28.5 cm								1												
29.5 cm		6						3												
30.5 cm		6						3												
31.5 cm		26	2					6												
32.5 cm		17	11	1				20	1											
33.5 cm		10	8	1	1			19	2											
34.5 cm		3	13	1				18	10											
35.5 cm		2	7	5	2			5	14	2										
36.5 cm			4	4		1		4	16	3										
37.5 cm			2	3	4			1	14	5										
38.5 cm			1					2	11	12										
39.5 cm				1				1	3	14	3									
40.5 cm					1				2	3	8	3								
41.5 cm						1				2	19	4								
42.5 cm										1	5	12								
43.5 cm											1	10								
44.5 cm											2	5	1							
45.5 cm													3							
46.5 cm													1							
47.5 cm																				
48.5 cm													1							
49.5 cm													2							
Total		70	48	16	8	2		83	73	42	38	34	8							
Mean length (cm.)		32.0	34.3	36.0	36.9	39.0		33.5	36.6	38.8	41.5	42.8	46.9							

TABLE D–2.—*Length and age frequencies of yellowtail: Summary, by quarter and sex, 1942–47*

Length of fish	Male						Female							Sex undetermined						
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli
First quarter: [1]																				
19.5 cm															1					
20.5 cm																				
21.5 cm																				
22.5 cm																				
23.5 cm	1													1						
24.5 cm	1														2					
25.5 cm	6						1							3	1					
26.5 cm	9	1					5	1						2	1					
27.5 cm	10	1					4	1						2	1					
28.5 cm	13	2					5							1	1					
29.5 cm	7	8					7							3	4	1				
30.5 cm	2	12	2				3	3							7	1				
31.5 cm	3	35	3				1	6							13	2				
32.5 cm	1	50	10	1			1	29	3						9	4	2			
33.6 cm		46	28	1	1		1	49	9						8	6	2			
34.5 cm		51	31	5	1			67	6						7	9	1			
35.5 cm		29	58	7				46	28	1					4	8	4	1		
36.5 cm		14	45	25				38	50	5					3	10	3	1		
37.5 cm		3	36	21	4			18	58	13	1				1	7	1			
38.5 cm			20	17	5			7	51	19	2				1	4	5			
39.5 cm			5	9	1			2	50	36	4					1	1	5	1	
40.5 cm			3	7	4			5	23	64	10					1	4	2		
41.5 cm				4	6				13	52	24	1					1	1		
42.5 cm				2	2				5	59	47	5					2	1	3	
43.5 cm									1	26	45	19						1	1	
44.5 cm									1	8	25	13						1		
45.5 cm										5	8	42							1	
46.5 cm										2	4	28								
47.5 cm											3	21								
48.5 cm												7							1	
49.5 cm											1	3								
50.5 cm												8								
Total	53	252	241	99	24		28	272	298	290	174	147		12	64	54	26	13	7	
Mean length (cm.)	27.9	33.3	35.8	37.7	39.4		28.8	34.8	38.0	41.1	43.0	46.0		27.1	32.0	35.4	37.5	40.2	43.5	
Second quarter:																				
24.5 cm															1					
25.5 cm		1													1					
26.5 cm		5						5							1		2			
27.5 cm		12						9	1						8	1	1			
28.5 cm		11	1					13	1						7	2	1			
29.5 cm		10	10					17	4						6	2				
30.5 cm		8	39					17	10						3	13	4			
31.5 cm		3	39	3				16	28						6	18	8	1		
32.5 cm		3	57	7				13	59	1						37	12	4		
33.5 cm		2	35	13				3	85						1	16	26	5	2	1

[1] Age determinations during first quarter were not made for yellowtail with more than 6 annuli.

TABLE D–2.—*Length and age frequencies of yellowtail: Summary, by quarter and sex, 1942–47*—Continued

Length of fish	Male						Female							Sex undetermined						
	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli	1 annulus	2 annuli	3 annuli	4 annuli	5 annuli	6 annuli	7+ annuli
Second quarter—Con.																				
34.5 cm			18	24	2			2	70	4						23	33	8	5	1
35.5 cm			8	23	6				54	12	1					13	27	7	4	2
36.5 cm			10	20	8				44	23	1					5	9	13	7	3
37.5 cm			1	10	7				22	24	9					4	5	8	7	3
38.5 cm					4	2			7	24	12	2				2	10	3	2	4
39.5 cm			1	3	4	1			2	21	14	8	1			1	5	3	3	2
40.5 cm				1					1	4	39	11	2				2	1	9	2
41.5 cm									1	3	28	14	1					3	3	4
42.5 cm										4	15	17	9					1	1	3
43.5 cm					1						5	14	4					2	2	4
44.5 cm											3	6	7				1		2	1
45.5 cm												4	9						1	1
46.5 cm												1	4						1	
47.5 cm											1		1						1	
48.5 cm													1							
49.5 cm																				
50.5 cm													1							
51.5 cm													1							
Total		55	219	104	32	3		95	389	120	128	77	41		34	137	146	59	50	31
Mean length (cm.)		29.1	32.5	35.2	37.2	38.8		30.4	34.2	37.9	40.6	42.2	44.5		29.0	33.2	34.7	36.6	38.8	39.8
Third quarter:																				
23.5 cm	1																			
24.5 cm							1													
25.5 cm	1							1												
26.5 cm		5					1	1							1					
27.5 cm		19						4							3					
28.5 cm		57						17	1						3					
29.5 cm	1	103	3					62							2					
30.5 cm		121	14					111	4						2	1				
31.5 cm		70	26	4				145	15						4	4				
32.5 cm		38	55	21				117	32							6				
33.5 cm		16	56	21				64	53	3					2	9	3			
34.5 cm			41	32	3			42	92	10					1	11	2	1		
35.5 cm		3	12	28	2			11	90	28	1					5	3			
36.5 cm			2	21	3			1	43	59	2					1	3			
37.5 cm				13	3			2	17	99	15						7			
38.5 cm			1	3	4				11	73	31					2	5	2		
39.5 cm				2	1				6	41	56	2					3			
40.5 cm					1				1	9	45	10					1			
41.5 cm										6	47	13	1							
42.5 cm									1	5	13	16	4							
43.5 cm										1	3	12	3							
44.5 cm											1	7	2							
45.5 cm											1	2	1							
46.5 cm											1	1								
47.5 cm													2							
48.5 cm													1							
Total:	3	432	210	145	17		2	578	366	334	216	63	14		18	39	27	3		
Mean length (cm.)	26.2	30.3	33.1	34.9	37.1		25.5	31.7	34.8	37.7	40.1	42.4	44.3		30.1	33.9	37.0	37.2		
Fourth quarter:																				
20.5 cm	1																			
21.5 cm														1						
22.5 cm							1													
23.5 cm	1						1								1					
24.5 cm							3							1						
25.5 cm		1					1													
26.5 cm	1													2	1					
27.5 cm	1	3												1	1					
28.5 cm		9	1				1	2							2					
29.5 cm		35						8							6					
30.5 cm	2	69	2					25							6	1				
31.5 cm		116	12					57	1						19	2				
32.5 cm		89	36	2	1			85	6	1					17	11				
33.5 cm		55	57	17	1			101	12						27	8				
34.5 cm		29	54	35	2	1		97	40						24	16	2			
35.5 cm		9	39	37	7			33	63	4					23	30	3	1		
36.5 cm		6	30	34	7	1		20	75	27	2				8	21	4			
37.5 cm			11	25	18			6	62	59	8	1			5	31	5	1	1	
38.5 cm			4	11	6	1		3	45	71	12	2			7	19	16			
39.5 cm				4	5	1		1	21	82	43	4				12	9	2		
40.5 cm			1	2	2	1			9	38	83	5				2	13	5		
41.5 cm				1	3	1			1	18	98	16				1	11	4		
42.5 cm					1					13	52	32	2			1	3	9		
43.5 cm										2	18	40	5			1	1	6	1	
44.5 cm									1	1	10	25	8				1	6	4	
45.5 cm											2	13	8				1	5	3	2
46.5 cm												5	4					1	3	1
47.5 cm												2	4							2
48.5 cm													9						1	2
49.5 cm													2							
50.5 cm													2							
51.5 cm													1							
Total	6	421	247	168	53	6	7	438	336	316	328	145	45	5	147	156	69	40	13	7
Mean length (cm.)	26.5	31.9	34.4	35.9	37.6	38.5	24.8	33.3	36.7	39.0	41.1	43.2	46.4	25.3	33.6	36.4	39.5	42.6	44.9	47.1

E. YELLOWTAIL LARVAE TAKEN IN 1932

TABLE E–1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*

[Numbers in parentheses indicate stations for which complete data are available in Sette 1943, pp. 216–219; fractions indicate part of haul sorted for small and large larvae; adjusted totals represent number of larvae per 17.07 square meters of sea surface; see Sette (1943, pp. 211–215) for method of computing]

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 1				
Martha's Vineyard:				
Station I (21327), May 2:				
Upper haul:				
112/1500	4		54	
1388/1500		2		2
Adjusted total			38	1
Station II (21328), May 2:				
Upper haul:				
112/1500	6		80	
1388/1500		7		8
Lower haul:				
112/1500	3		40	
1388/1500		1		1
Adjusted total			76	7
Station III (21329), May 3:				
Upper haul:				
112/1500	0		0	
1388/1500		0		0
Lower haul:				
56/1500	0		0	
1444/1500		0		0
Adjusted total			0	0
Station IV (21330), May 3:				
Upper haul:				
112/1500	0		0	
1388/1500		0		0
Lower haul:				
56/1000	0		0	
1444/1500		0		0
Adjusted total			0	0
New York:				
Station II (21335), May 4:				
Upper haul:				
40/1600	0		0	
Remainder		1		1
Lower haul:				
60/2400	0		0	
Remainder		0		0
Adjusted total			0	1
Station III (21334), May 3:				
Upper haul:				
100/2000	0		0	
Remainder		0		0
Lower haul:				
80/1600	0		0	
Remainder		1		1
Adjusted total			0	1
Station IV (21333), May 3:				
Upper haul:				
160/1600	0		0	
Remainder		0		0
Lower haul:				
240/1200	0		0	
Remainder		0		0
Adjusted total			0	0
Station V (21332), May 3:				
Upper haul:				
200/2000	0		0	
Remainder		0		0
Adjusted total			0	0
Station VI (21331), May 3:				
Upper haul:				
112/1000	0		0	
880/1000		0		0
Lower haul:				
112/1500	0		0	
1388/1500		0		0
Adjusted total			0	0

TABLE E–1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 1—Continued				
Barnegat:				
Station I (21336) May 4:				
Upper haul:				
240/2400	0		0	
Remainder		0		0
Adjusted total			0	0
Atlantic City:				
Station I (21337), May 4:				
Upper haul:				
120/1200	13		130	
Remainder		7		7
Adjusted total			91	5
Station II (21338), May 4:				
Upper haul:				
60/1000	12		200	
Remainder		2		2
Lower haul:				
80/1600	11		220	
Remainder		3		3
Adjusted total			260	3
Station III (21339), May 4:				
Upper haul:				
200/4000	0		0	
Remainder		2		2
Lower haul:				
80/1600	0		0	
Remainder		0		0
Adjusted total			0	1
Station IV (21340), May 4:				
Upper haul:				
80/1600	0		0	
Remainder		0		0
Lower haul:				
80/1600	0		0	
Remainder		0		0
Adjusted total			0	0
Cape May:				
Station II (21345), May 5:				
Upper haul:				
100/2000	34		680	
Remainder		104		104
Adjusted total			476	73
Station III (21344), May 5:				
Upper haul:				
160/1500	1		9	
Remainder		0		0
Lower haul:				
200/2000	9		90	
Remainder		16		16
Adjusted total			62	10
Station IV (21343), May 5:				
Upper haul:				
100/1000	2		20	
Remainder		4		4
Lower haul:				
160/1500	2		19	
Remainder		2		2
Adjusted total			24	4
Station V (21342), May 5:				
Upper haul:				
80/1600	0		0	
Remainder		0		0
Lower haul:				
100/2000	0		0	
Remainder		0		0
Adjusted total			0	0
Station VI (21341), May 5:				
Upper haul:				
100/2000	0		0	
Remainder		0		0
Lower haul: All		0		0
Adjusted total			0	0

TABLE E–1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 1—Continued				
Fenwick:				
Station I (21346), May 5:				
Upper haul:				
180/1800	24		240	
Remainder		46		46
Adjusted total			168	32
Winterquarter:				
Station I (21347), May 5:				
Upper haul:				
80/1500	19		356	
Remainder		78		78
Adjusted total			249	55
Station II (21348), May 5:				
Upper haul:				
260/3000	0		0	
Remainder		17		17
Lower haul:				
200/1500	6		45	
Remainder		26		26
Adjusted total			28	26
Station III (21349), May 5:				
Upper haul:				
160/3000	0		0	
Remainder		2		2
Lower haul:				
260/2000	0		0	
Remainder		2		2
Adjusted total			0	2
Chesapeake Bay:				
Station I (21352), May 6:				
Upper haul:				
300/1000	3		10	
Remainder				
Adjusted total			7	
Station II (21351), May 6:				
Upper haul:				
1000/3000	13		39	
Remainder				
Adjusted total			27	
Station III (21350), May 6:				
Upper haul:				
500/2000	0		0	
Remainder				
Lower haul:				
1/10	0		0	
All		0		0
Adjusted total			0	0
CRUISE 2				
Martha's Vineyard:				
Station I (21381), May 16:				
Upper haul:				
56/1500	59		1,580	
1444/1500		14		15
Lower haul:				
56/1250	33		737	
1194/1250		11		12
Adjusted total			1,426	16
Station II (21380), May 16:				
Upper haul:				
56/1500	0		0	
1444/1500		1		1
Lower haul:				
56/1000	2		4	
944/1000		0		0
Adjusted total			3	1
Station III (21379), May 16:				
Upper haul:				
56/2000	0		0	
1944/2000		0		0
Lower haul:				
56/1500	0		0	
1444/1500		0		0
Adjusted total			0	0

TABLE E–1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 2—Continued				
Montauk Point:				
Station I (21375), May 15:				
Upper haul:				
56/1000	9		161	
944/1000		7		7
Adjusted total			113	5
Station II (21376), May 15:				
Upper haul:				
56/1000	1		18	
944/1000		16		19
Lower haul:				
56/1000	0		0	
944/1000		2		2
Adjusted total			11	12
Station III (21377), May 15:				
Upper haul:				
56/1500	0		0	
1444/1500		0		0
Lower haul:				
56/1500	0		0	
1444/1500		0		0
Adjusted total			0	0
Shinnecock:				
Station I (21374), May 15:				
Upper haul:				
112/1000	1		9	
888/1000		1		1
Lower haul:				
56/1000	0		0	
944/1000		5		5
Adjusted total			5	4
Station II (21373), May 15:				
Upper haul:				
56/1000	0		0	
944/1000		0		0
Lower haul:				
56/1000	2		36	
944/1000		2		2
Adjusted total			23	2
New York:				
Station I (21369), May 14:				
Upper haul:				
56/1000	33		590	
944/1000		15		16
Adjusted total			413	11
Station II (21370), May 14:				
Upper haul:				
56/2250	16		643	
2194/2250		75		77
Lower haul:				
56/1250	33		736	
1194/1250		38		40
Adjusted total			854	72
Station III (21371), May 14:				
Upper haul:				
56/1000	3		54	
944/1000		29		31
Lower haul:				
56/1000	4		71	
944/1000		9		10
Adjusted total			78	25
Station IV (21372), May 15:				
Upper haul:				
112/2000	0		0	
1888/2000		0		0
Lower haul:				
112/1500	0		0	
1388/1500		0		0
Adjusted total			0	0
Barnegat:				
Station I (21368), May 14:				
Upper haul:				
28/1000	33		1,180	
972/1000		48		49
Adjusted total			826	34

TABLE E–1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 2—Continued				
Atlantic City:				
Station I (21367), May 14:				
Upper haul:				
56/1500	9		241	
1444/1500		11		11
Adjusted total			169	8
Station II (21366), May 14:				
Upper haul:				
56/1000	3		54	
944/1000		18		19
Adjusted total			39	13
Station III (21365), May 14:				
Upper haul:				
56/1500	0		0	
1444/1500		1		1
Lower haul:				
56/1500	0		0	
1444/1500		1		1
Adjusted total			0	2
Station IV (21364), May 14:				
Upper haul:				
56/1500	0		0	
1444/1500		1		1
Lower haul:				
56/1500	0		0	
1444/1500		1		1
Adjusted total			0	2
Cape May:				
Station I (21359), May 13:				
Upper haul:				
56/1000	2		36	
944/1000		3		3
Adjusted total			25	2
Station II (21360), May 13:				
Upper haul:				
56/1000	40		714	
944/1000		11		12
Adjusted total			500	8
Station III (21361), May 13:				
Upper haul:[1]				
56/1000	2		36	
944/1000		7		7
Adjusted total			25	5
Station IV (21362), May 13:				
Upper haul:				
56/1000	0		0	
944/1000		0		0
Lower haul:				
56/1000	1		18	
944/1000		24		25
Adjusted total			11	16
Station V (21365), May 13:				
Upper haul:				
112/2000	0		0	
1888/2000		0		0
Lower haul:				
112/2000	0		0	
1888/2000		1		1
Adjusted total			0	1
Winterquarter:				
Station I (21358), May 10:				
Upper haul:				
56/1500	0		0	
1444/1500		7		7
Adjusted total			0	5
Station II (21357), May 10:				
Upper haul:				
56/1500	0		0	
1444/1500		0		0
Lower haul:				
56/1500	0		0	
1444/1500		61		63
Adjusted total			0	40

[1] Part of this haul may have been lost.

TABLE E–1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 2—Continued				
Winterquarter—Continued				
Station III (21356), May 10:				
Upper haul:				
56/1000	0		0	
944/100		1		1
Lower haul:				
56/1000	0		0	
944/1000		3		3
Adjusted total			0	3
Chesapeake Bay:				
Station I (21353), May 9:				
Upper haul:				
56/1000	0		0	
944/1000		0		0
Adjusted total			0	0
Station II (21354), May 9:				
Upper haul:				
56/1500	4		107	
1444/1500		37		38
Adjusted total			75	27
Station III (21355), May 9:				
Upper haul:				
56/1500	0		0	
1444/1500		0		0
Lower haul:				
56/1500	0		0	
1444/1500		0		0
Adjusted total			0	0
CRUISE 3				
Martha's Vineyard:				
Station I (21382), May 19:				
Upper haul:				
56/1000	76		1,357	
944/1000		14		15
Lower haul:				
56/1000	19		339	
944/1000		28		30
Adjusted total			1,131	28
Station II (21383), May 19:				
Upper haul:				
56/1000	2		36	
944/1000		0		0
Lower haul:				
56/1000	2		36	
944/1000		3		3
Adjusted total			45	2
Station III (21384), May 19:				
Upper haul:				
56/1500	0		0	
1444/1500		0		0
Lower haul:				
56/1250	0		0	
1194/1250		0		0
Adjusted total			0	0
Montauk Point:				
Station I (21387), May 20:				
Upper haul:				
56/1500	0		0	
1444/1500		0		0
Lower haul:				
56/1500	5		134	
1444/1500		30		31
Adjusted total			84	20
Station II (21386), May 20:				
Upper haul:				
56/1000	0		0	
944/1000		13		14
Lower haul:				
56/1250	0		0	
1194/1250		10		10
Adjusted total			0	15

TABLE E–1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 3—Continued				
Montauk Point—Continued				
Station III (21385), May 20:				
Upper haul:				
56/1000	0		0	
944/1000		0		0
Lower haul:				
56/1250	0		0	
1194/1250		0		0
Adjusted total			0	0
Shinnecock:				
Station I (21388), May 20:				
Upper haul:				
56/1250	32		714	
1194/1250		33		35
Adjusted total			500	24
Station II (21389), May 20:				
Upper haul:				
56/1000	0		0	
944/1000		8		9
Lower haul:				
56/1000	3		54	
944/1000		12		13
Adjusted total			34	14
New York:				
Station I (21393), May 21:				
Upper haul:				
56/1250	46		1,127	
1194/1250		66		69
Lower haul:				
56/1500	23		616	
1444/1500		86		89
Adjusted total			1,072	98
Station II (21392), May 21:				
Upper haul:				
56/1250	32		714	
1194/1250		45		47
Lower haul:				
56/1500	30		804	
1444/1500		93		97
Adjusted total			940	90
Station III (21391), May 21:				
Upper haul:				
56/1500	5		134	
1444/1500		73		76
Lower haul:				
56/1250	0		0	
1194/1250		15		19
Adjusted total			81	58
Station IV (21390), May 20:				
Upper haul:				
56/1500	0		0	
1444/1500		0		0
Lower haul:				
56/1000	0		0	
944/1000		0		0
Adjusted total			0	0
Barnegat:				
Station I (21394), May 21:				
Upper haul:				
56/2000	57		2,034	
1944/2000		36		37
Adjusted total			1,424	26
Atlantic City:				
Station I (21395), May 21:				
Upper haul:				
56/1250	21		469	
1194/1250		61		64
Adjusted total			328	45
Station II (21396), May 21:				
Upper haul:				
56/1500	6		161	
1444/1500		5		5
Lower haul:				
56/1250	3		67	
1194/1250		56		59
Adjusted total			140	41

TABLE E–1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 3—Continued				
Atlantic City—Continued				
Station III (21397), May 21:				
Upper haul:				
56/1500	2		54	
1444/1500		7		7
Lower haul:				
56/1250	1		22	
1194/1250		4		4
Adjusted total			47	7
Station IV (21398), May 22:				
Upper haul:				
168/2000	0		0	
1832/2000		2		2
Lower haul:				
56/1500	0		0	
1444/1500		0		0
Adjusted total			0	1
Cape May:				
Station II (21402), May 22:				
Upper haul:				
56/750	2		27	
694/750		10		11
Adjusted total			19	8
Station III (21401), May 22:				
Upper haul:				
56/1500	15		402	
1444/1500		76		79
Lower haul:				
56/1250	17		380	
1194/1250		29		30
Adjusted total			570	66
Station IV (21400), May 22:				
Upper haul:				
112/1500	0		0	
1388/1500		0		0
Lower haul:				
56/1500	3		80	
1444/1500		39		41
Adjusted total			50	26
Station V (21399), May 22:				
Upper haul:				
112/1500	0		0	
1388/1500		0		0
Lower haul:				
56/1500	0		0	
944/1500		1		1
Adjusted total			0	1
Fenwick:				
Station I (21403), May 22:				
Upper haul:				
56/1000	7		125	
944/1000		5		5
Adjusted total			87	4
Winterquarter:				
Station I (21404), May 22:				
Upper haul:				
180/1800	4		40	
Remainder		30		30
Adjusted total			28	21
Station II (21405), May 22:				
Upper haul:				
300/3000	74		740	
Remainder		255		255
Adjusted total			518	179
Station III (21406), May 22:				
Upper haul:				
160/1600	15		150	
Remainder		127		127
Lower haul:				
56/1250	6		134	
1194/1250		26		30
Adjusted total			176	96

TABLE E–1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 3—Continued				
Chesapeake Bay:				
Station I (21409), May 23:				
Upper haul:				
40/1600	0		0	
Remainder		0		0
Adjusted total			0	0
Station II (21408), May 23:				
Upper haul:				
300/3000	1		10	
Remainder		3		3
Adjusted total			7	2
Station III (21407), May 23:				
Upper haul:				
300/3000	0		0	
Remainder		1		1
Lower haul:				
56/1250	3		67	
1194/1250		9		9
Adjusted total			42	7
CRUISE 4				
Martha's Vineyard:				
Station I (21431), May 28:				
Upper haul:				
56/1500	50		1,340	
1444/1500		63		65
Lower haul:				
56/1750	3		94	
1694/1750		26		27
Adjusted total			873	57
Station II (21430), May 27:				
Upper haul:				
56/1500	25		669	
1444/1500		48		50
Lower haul:				
56/1000	30		536	
944/1000		7		7
Adjusted total			744	35
Station III (21429), May 27:				
Upper haul:				
84/1500	3		536	
1416/1500		32		34
Lower haul:				
56/1000	0		0	
944/1000		0		0
Adjusted total			325	21
Montauk Point:				
Station I (21426), May 27:				
Upper haul:				
56/1000	52		928	
944/1000		22		23
Adjusted total			650	16
Station II (21427), May 27:				
Upper haul:				
28/1250	78		3,481	
1222/1250		16		16
Lower haul:				
56/1250	11		245	
1194/1250		10		11
Adjusted total			2,269	17
Station III (21428), May 27:				
Upper haul:				
56/1000	1		18	
944/1000		0		0
Lower haul:				
56/1000	1		18	
944/1000		10		11
Adjusted total			22	7
Shinnecock:				
Station I (21425), May 27:				
Upper haul:				
28/1500	25		1,340	
1472/1500		36		37
Adjusted total			938	26

TABLE E–1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 4—Continued				
Shinnecock—Continued				
Station II (21424), May 27:				
Upper haul:				
28/1250	48		2,143	
1222/1250		72		74
Lower haul:				
56/1000	7		125	
944/1000		16		17
Adjusted total			1,381	56
New York:				
Station I (21420), May 26:				
Upper haul:				
56/1500	55		1,473	
1444/1500		82		85
Adjusted total			1,032	60
Station II (21421), May 26:				
Upper haul:				
28/1000	3		107	
972/1000		21		22
Lower haul:				
56/1500	45		1,205	
1444/1500		37		38
Adjusted total			761	37
Station III (21422), May 26:				
Upper haul:				
56/1300	9		241	
1444/1500		25		26
Lower haul:				
56/1250	20		446	
1194/1250		26		27
Adjusted total			478	32
Station IV (21423), May 26:				
Upper haul:				
56/1250	4		89	
1194/1250		33		35
Lower haul:				
56/1000	1		18	
944/1000		1		1
Adjusted total			65	21
Barnegat:				
Station I (21419), May 26:				
Upper haul:				
56/1300	73		1,955	
1444/1500		53		55
Adjusted total			1,369	49
Atlantic City:				
Station I (21418), May 26:				
Upper haul:				
56/1500	8		214	
1444/1500		17		18
Adjusted total			150	13
Station II (21417), May 26:				
Upper haul:				
56/1500	18		482	
1444/1500		13		14
Lower haul:				
56/1000	21		375	
944/1000		17		18
Adjusted total			530	120
Station III (21416), May 25:				
Upper haul:				
112/1500	5		67	
1388/1500		14		15
Lower haul:				
56/1000	0		0	
944/1000		3		3
Adjusted total			41	12
Station IV (21415), May 25:				
Upper haul:				
168/1500	1		9	
1332/1500		5		6
Lower haul:				
56/1250	0		0	
1194/1250		1		1
Adjusted total			6	4

TABLE E–1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 4—Continued				
Cape May:				
Station II (21411), May 25:				
Upper haul:				
56/1250	48		1,072	
1194/1250		42		44
Adjusted total			750	31
Station III (21412), May 25:				
Upper haul:				
56/750	3		40	
694/750		12		13
Lower haul:				
56/1000	2		36	
944/1000		14		15
Adjusted total			47	17
Station IV (21413), May 25:				
Upper haul:				
112/1250	0		0	
1138/1250		0		0
Lower haul:				
56/1500	2		54	
1444/1500		16		17
Adjusted total			34	11
Station V (21414), May 25:				
Upper haul:				
112/1000	0		0	
888/1000		0		0
Lower haul:				
56/1000	0		0	
944/1000		1		1
Adjusted total			0	1
Chesapeake Bay:				
Station II (21410), May 24:				
Upper haul:				
112/1250	0		0	
1138/1250		1		1
Lower haul:				
112/750	0		0	
638/750		1		1
Adjusted total			0	2
CRUISE 5				
Montauk Point:				
Station I (21432), June 1:				
Upper haul:				
56/1500	45		1,205	
1444/1500		18		19
Lower haul:				
280/2650	6		57	
2370/2650		62		69
Adjusted total			767	55
Station II (21433), June 1:				
Upper haul:				
56/2000	19		658	
1944/2000		39		40
Lower haul:				
112/1250	40		446	
1138/1250		8		9
Adjusted total			681	30
Shinnecock:				
Station III (21434), June 2:				
Upper haul:				
56/1250	1		22	
1194/1250		2		2
Lower haul:				
112/1250	0		0	
1138/1250		6		7
Adjusted total			13	5
New York:				
Station I (21438), June 2:				
Upper haul:				
56/1500	55		1,473	
1444/1500		62		64
Adjusted total			1,032	45

TABLE E–1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 5—Continued				
New York—Continued				
Station II (21437), June 2:				
Upper haul:				
56/1500	0		0	
1444/1500		0		0
Lower haul:				
56/1500	38		1,018	
1444/1500		43		45
Adjusted total			642	28
Station III (21436), June 2:				
Upper haul:				
84/1250	0		0	
1166/1250		1		1
Lower haul:				
112/1500	2		27	
1388/1500		14		15
Adjusted total			17	10
Station IV (21435), June 2:				
Upper haul:				
112/1000	1		9	
888/1000		1		1
Lower haul:				
112/1250	0		0	
1132/1250		1		1
Adjusted total			6	1
Barnegat:				
Station I (21439), June 3:				
Upper haul:				
112/1500	51		683	
1388/1500		36		39
Adjusted total			478	27
Atlantic City:				
Station I (21440), June 3:				
Upper haul:				
112/1250	14		156	
1138/1250		36		40
Adjusted total			109	28
Station II (21441), June 3:				
Upper haul:				
112/1000	0		0	
888/1000		0		0
Lower haul:				
112/1250	33		368	
1138/1250		34		37
Adjusted total			232	23
Station III (21442), June 3:				
Upper haul:				
112/1250	0		0	
1138/1250		2		2
Lower haul:				
112/2250	10		201	
2138/2250		111		117
Adjusted total			127	75
Station IV (21443), June 3:				
Upper haul:				
112/1500	0		0	
1388/1500		0		0
Lower haul:				
112/1500	1		13	
1388/1500		1		1
Adjusted total			8	1
Cape May:				
Station II (21447), June 4:				
Upper haul:				
112/1500	3		40	
1388/1500		39		42
Adjusted total			18	19
Station III (21446), June 4:				
Upper haul:				
112/1500	7		94	
1388/1500		22		24
Lower haul:				
56/1500	22		589	
1444/1500		440		457
Adjusted total			428	302

TABLE E-1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 5—Continued				
Cape May—Continued				
Station IV (21445), June 3:				
Upper haul:				
112/1500	19		254	
1388/1500		23		25
Lower haul:				
168/1750	12		125	
1582/1750		110		122
Adjusted total			233	92
Station V (21444), June 3:				
Upper haul:				
112/2750	0		0	
2638/2750		0		0
Lower haul:				
168/1500	0		0	
1332/1500		0		0
Adjusted total			0	0
Winterquarter:				
Station I (21448), June 4:				
Upper haul:				
28/1250	1		45	
1222/1250		6		6
Adjusted total			45	6
Station II (21449), June 4:				
Upper haul:				
112/1500	0		0	
1388/1500		0		0
Lower haul:				
112/1250	1		12	
1138/1250		2		2
Adjusted total			8	1
Station III (21450), June 4:				
Upper haul:				
112/1500	0		0	
1388/1500		0		0
Lower haul:				
336/3000	0		0	
2664/3000		3		3
Adjusted total			0	2
Chesapeake Bay:				
Station I (21453), June 5:				
Upper haul:				
56/1500	0		0	
1444/1500		0		0
Adjusted total			0	0
Station II (21452), June 5:				
Upper haul:				
112/2000	0		0	
1888/2000		0		0
Adjusted total			0	0
Station III (21451), June 4:				
Upper haul:				
112/1500	6		80	
1388/1500		44		48
Lower haul:				
112/1000	2		18	
888/1000		16		18
Adjusted total			60	41
CRUISE 6				
Martha's Vineyard:				
Station I (21468), June 8:				
Upper haul:				
28/1500	27		1,446	
1472/1500		8		8
Lower haul:				
56/1500	55		1,474	
1444/1500		43		45
Adjusted total			1,807	34
Station II (21467) June 8:				
Upper haul:				
28/1500	41		2,197	
1472/1500		90		92
Lower haul:				
56/1500	15		268	
1444/1500		42		44
Adjusted total			1,503	84

TABLE E-1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 6—Continued				
Martha's Vineyard—Continued				
Station III (21466), June 8:				
Upper haul:				
28/1250	2		89	
1222/1250		44		45
Lower haul:				
84/1250	0		0	
1166/1250		8		9
Adjusted total			54	33
Montauk Point:				
Station I (21464), June 7:				
Upper haul:				
56/1500	1		18	
1444/1500		1		1
Lower haul:				
84/1250	18		268	
1166/1250		3		3
Adjusted total			180	3
Station II (21465), June 7:				
Upper haul:				
28/1250	28		1,250	
1222/1250		29		30
Lower haul:				
112/1500	10		134	
1388/1500		25		27
Adjusted total			907	35
Shinnecock:				
Station II (21463), June 7:				
Upper haul:				
56/1000	32		571	
944/1000		6		6
Lower haul:				
112/1250	56		625	
1138/1250		7		8
Adjusted total			741	8
New York:				
Station II (21460), June 6:				
Upper haul:				
56/1250	24		536	
1194/1250		110		115
Lower haul:				
112/1250	26		290	
1138/1250		216		237
Adjusted total			508	219
Station III (21461), June 7:				
Upper haul:				
56/1500	21		562	
1444/1500		113		117
Lower haul:				
112/1500	27		362	
1388/1500		29		31
Adjusted total			569	91
Station IV (21462), June 7:				
Upper haul:				
112/1250	4		45	
1138/1250		27		30
Lower haul:				
112/2250	0		0	
2138/2250		51		54
Adjusted total			27	52
Atlantic City:				
Station I (21459), June 6:				
Upper haul:				
56/1000	2		36	
944/1000		38		40
Adjusted total			25	28
Station II (21458), June 6:				
Upper haul:				
112/1000	0		0	
888/1000		0		0
Lower haul:				
112/1500	24		321	
1388/1500		151		163
Adjusted total			202	103

TABLE E–1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 6—Continued				
Atlantic City—Continued				
Station III (21457), June 6:				
Upper haul:				
168/1500	0		0	
1332/1500		0		0
Lower haul:				
112/2000	8		143	
1888/2000		105		111
Adjusted total			91	70
Cape May:				
Station II (21454), June 5:				
Upper haul:				
56/1000	4		71	
944/1000		57		60
Adjusted total			50	42
Station III (21455), June 5:				
Upper haul:				
56/1000	9		161	
944/1000		153		162
Lower haul:				
56/2000	1		36	
1944/2000		17		73
Adjusted total			121	144
Station IV (21456), June 6:				
Upper haul:				
56/1000	1		18	
944/1000		45		48
Lower haul:				
56/1000	3		54	
944/1000		21		22
Adjusted total			45	43
Cape May: [1]				
Station II (21454), June 5:				
Upper haul: All		339		339
Station III (21455), June 5:				
Upper haul: 168/3500		160		3,332
Station IV (21456), June 6:				
Upper haul: 84/1000		55		655
CRUISE 7				
Martha's Vineyard:				
Station I (21490), June 19:				
Upper haul:				
28/1250	45		2,009	
1222/1250		91		93
Lower haul:				
56/1000	34		607	
944/1000		43		46
Adjusted total			1,596	85
Station II (21491), June 19:				
Upper haul:				
112/2000	31		552	
1888/2000		20		21
Lower haul:				
112/1500	68		910	
1388/1500		22		24
Adjusted total			908	28
Station III (21492), June 19:				
Upper haul:				
56/1500	0		0	
1444/1500		11		11
Lower haul:				
112/1500	4		54	
1388/1500		11		12
Adjusted total			34	14
Station IV (21493), June 20:				
Upper haul:				
112/1000	0		0	
888/1000		1		1
Lower haul:				
112/1250	1		11	
1138/1250		3		3
Adjusted total			7	3

[1] Oblique upper haul with 2-meter net.

TABLE E–1.—*Yellowtail larve caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Continued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
CRUISE 7—Continued				
Montauk Point:				
Station I (21489), June 19:				
Upper haul:				
20/1000	1		50	
980/1000		2		2
Lower haul:				
20/1200	11		660	
1180/1200		5		5
Adjusted total			446	4
Station II (21488), June 19:				
Upper haul:				
112/1250	0		0	
1138/1250		0		0
Lower haul:				
168/1500	6		54	
1332/1500		21		24
Adjusted total			34	15
Station III (21487), June 19:				
Upper haul:				
112/1500	4		54	
1388/1500		27		29
Lower haul:				
112/1500	1		13	
1388/1500		1		1
Adjusted total			41	18
Shinnecock:				
Station I (21485), June 18:				
Upper haul:				
40/1500	10		375	
1460/1500		10		10
Adjusted total			262	7
Station II (21486), June 18:				
Upper haul:				
112/1000	16		143	
888/1000		18		20
Lower haul:				
112/1500	25		335	
1388/1500		23		25
Adjusted total			298	28
New York:				
Station I (21484), June 18:				
Upper haul:				
56/1000	0		0	
944/1000		2		2
Adjusted total			0	1
Station II (21483), June 18:				
Upper haul:				
112/1000	13		116	
888/1000		11		12
Lower haul:				
112/1500	44		589	
1388/1500		27		29
Adjusted total			441	25
Station III (21482), June 17:				
Upper haul:				
250/1500	8		48	
1250/1500		70		84
Lower haul:				
250/1000	28		112	
750/1000		7		9
Adjusted total			56	57
Station IV (21481), June 17:				
Upper haul:				
300/1500	3		15	
1200/1500		8		10
Lower haul:				
100/2000	3		60	
1900/2000		14		15
Adjusted total			47	10

TABLE E–1.—*Yellowtail larvae caught during cruises 1 to 7 of the* Albatross II, *in 1932*—Contintinued

Station and haul	Count of larvae		Total larvae	
	Small	Large	Small	Large
Cruise 7—Continued				
Atlantic City:				
Station I (21469), June 15:				
Upper haul:				
100/1500	0		0	
1400/1500		4		4
Adjusted total			0	3
Station II (21477), June 17:				
Upper haul:				
168/1500	1		9	
1332/1500		1		1
Lower haul:				
250/1500	81		486	
1250/1500		11		13
Adjusted total			312	4
Station III (21478), June 17:				
Upper haul:				
120/1200	0		0	
1080/1200		0		0
Lower haul:				
400/2000	1		5	
1600/2000		1		1
Adjusted total			3	1
Station IV (21479), June 17:				
Upper haul:				
112/1000	0		0	
888/1000		1		1
Lower haul:				
250/1500	0		0	
1250/1500		0		0
Adjusted total			0	1
Cape May:				
Station II (21470):				
Upper haul:				
56/1500	1		27	
1444/1500		49		51
Adjusted total			19	36
Station III (21476), June 16:				
Upper haul:				
300/1500	0		0	
1200/1500		0		0
Lower haul:				
300/1500	17		85	
1200/1500		62		77
Adjusted total			54	4
Station IV (21475), June 16: [3]				
Upper haul:				
112/1500	0		0	
1388/1500		4		4
Lower haul:				
112/2000	0		0	
1888/2000		21		22
Adjusted total			0	16
Station V (21474), June 16: [4]				
Lower haul		1		1
Adjusted total				1
Winterquarter:				
Station I (21471), June 16:				
Upper haul:				
28/1500	0		0	
1472/1500		4		4
Adjusted total			0	3
Station II (21472), June 16:				
Upper haul:				
28/1250	0		0	
1222/1250		0		0
Lower haul:				
112/1250	0		0	
Remainder		0		0
Adjusted total			0	0

[3] An estimated three-quarters of the upper haul was lost, therefore the counts are multiplied by 4.
[4] No fish larvae in 15 liters of the upper haul; only one *L. ferruginea* larva in 8 liters of the lower haul.

TABLE E–2.—*Yellowtail larvae caught during cruises 8 and 9 of the* Atlantis, *in 1932*

[Numbers in parentheses indicate stations for which complete data are in Sette (1943, pp. 216–219); fractions indicate parts of haul sorted for small and large larvae]

Station and haul	Date	Count of larvae	Estimated total larvae	Adjusted total [1]
CRUISE 8				
Martha's Vineyard: [2]				
Station:				
I (1283): All	July 1	51	51	7
II (1282): All	do	3	3	0
IV (1280): All	do	0	0	[3] 0
Montauk Point:				
Station:				
I (1276): All	June 30	42	42	2
II (1277): All	do	16	16	[3] 2
III (1278): All	do	3	3	[3] 0
IV (1259): All	June 25	0	0	0
VI (1279): All	June 30	1	1	[3] 0
Shinnecock:				
Station:				
I (1275): 112/1000	June 29	106	946	133
II (1274): All	do	63	63	16
New York:				
Station:				
I (1270): All	June 28	521	521	71
II (1271): 196/2000	June 29	301	3071	270
III (1272): All	do	430	430	32
IV (1273): All	do	7	7	[3] 1
V (1260): All	June 26	12	12	1
VI (1261): All	do	0	0	0
Barnegat: Station I (1269): All	June 28	197	197	26
Atlantic City:				
Station:				
I (1262): All	June 26	195	195	26
II (1263): 168/1800	do	241	2581	661
IV (1265): All	June 27	1	1	0
Cape May:				
Station:				
II (1266): All	do	107	107	13
III (1267): 250/1250	do	130	650	127
IV (1268): 1/10	do	31	310	25
CRUISE 9				
Cape Elizabeth:				
Station I (1323): All	July 23	1	1	[4] 0
Boon Island:				
Station:				
I (1322): All	do	3	3	[4] 1
II (1325): All	July 24	0	0	[4] 0
Newburyport:				
Station I (1321): All	July 23	4	4	[4] 1
Cape Ann:				
Station:				
I (1320): All	July 23	6	6	[4] 1
II (1319): All	do	0	0	0
III (1326): All	July 24	0	0	[4] 0
Boston:				
Station:				
I (1317): All	July 22	12	12	[4] 2
II (1318): All	do	52	52	15
Cape Cod Bay:				
Station I (1316): All	do	9	9	1
Race Point:				
Station:				
I (1315): All	do	2	2	0
II (1327): All	July 24	0	0	[4] 0
Nauset: Station I (1314): All	July 22	4	4	[4] 1
Chatham: Station II (1328): All	July 24	1	1	0
South Channel:				
Station:				
I (1312): All	July 22	0	0	[4] 0
II (1311): All	July 21	0	0	[4] 0
IV (1307): All	do	110	110	75
Western Georges Bank:				
Station:				
I (1310): All	do	2	2	[4] 0
II (1309): All	do	0	0	[4] 1
III (1308): All	do	25	25	5
Nantucket Shoals:				
Station:				
I (1304): All	July 20	8	8	[4] 2
II (1305): All	do	11	11	[4] 2
III (1306): All	do	22	22	[4] 4

See footnotes at end of table.

TABLE E–2.—*Yellowtail larvae caught during cruises 8 and 9 of the* Atlantis, *in 1932*—Continued

Station and haul	Date	Count of larvae	Estimated total larvae	Adjusted total [1]
Martha's Vineyard:				
Station:				
I (1303): All	do	37	37	4
II (1302): All	do	4	4	1
III (1301): All	July 19	0	0	[4] 0
IV (1300): All	do	0	0	[4] 0
Montauk Point:				
Station:				
I (1288): 40/1000	July 16	25	625	63
II (1289): All	July 17	10	10	[4] 2
III (1290): All	do	2	2	0
IV (1291): All	do	0	0	[4] 0
Shinnecock:				
Station:				
I (1294): 60/1000	July 18	71	1183	59
II (1293): All	July 17	26	26	[4] 5
III (1292): All	do	2	2	[4] 0
New York:				
Station:				
I (1295): 100/1000	July 18	113	1130	[4] 229
II (1296): All	do	10	10	1
III (1297): 100/1000	do	16	160	[4] 32
IV (1298): All	do	3	3	[4] 1
V (1299): All	July 19	0	0	[4] 0

[1] Represents the number of larvae per 17.07 square meters of sea surface. See Sette (1943, pp. 211–215) for method of computing.
[2] Oblique hauls to surface with 2-meter net.
[3] Adjustment data are not available from Sette (1943) and these tows have been adjusted by the average of the other values, 0.136.
[4] Adjustment data are not available from Sette (1943) and these tows have been adjusted by the average of the other values, 0.203.

TABLE E–3.—*Summary of standard catches of small larvae in upper and lower hauls at certain stations on cruises 1 through 7 in 1932*

Station	Cruise 1		Cruise 2		Cruise 3		Cruise 4		Cruise 5		Cruise 6		Cruise 7	
	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower
Martha's Vineyard:														
Station:														
I			1,106	320	950	181	938	−65			1,013	794	1,406	190
II	56	20	0	3	25	20	468	276			1,538	−35	386	522
III	0	0	0	0	0	0	375	−50			62	−8	0	34
IV	0	0											0	7
Montauk Point:														
Station:														
I					0	84			843	−76	13	167	35	411
II			13	−2	0	0	2,437	168	461	220	875	32	0	34
III			0	0	0	0	13	9					38	3
Shinnecock:														
Station:														
I			6	−1										
II			0	23	0	34	1,501	−120			400	341	100	198
III									15	−2				
New York:														
Station:														
I					789	283								
II	0	0	450	404	500	440	75	686	0	642	375	133	81	360
III	0	0	38	40	94	−13	169	259	0	17	393	176	34	22
IV	0	0	0	0	0	0	62	3	6	0	31.5—	−4	10.5	37
V	0	0	0	0										
VI	0	0	0	0										
Atlantic City:														
Station:														
II	140	120	39		113	27	337.5+	192	0	232	0	202	6	306
III	0	0	0	0	38	9	47	−6	0	127	0	91	0	3
IV	0	0	0	0	0	0	6	0	0	8			0	0
Cape May:														
Station:														
III	6	56	25		381	189	28	19	66	362	113	8	0	54
IV	14	10	0	11	0	50	0	34	178	55	13	32	0	0
V	0	0	0	0	0	0	0	0	0	0				
VI	0	0												
Winterquarter:														
Station:														
II	0	28	0	0					0	8			0	0
III	0	0	0	0	105	71			0					
IV									0	0				
Chesapeake Bay:														
Station:														
II							0	0						
III	0	0	0	0	0	42			56	4				

F. PROBIT ANALYSIS

In the section on reproduction, we dealt with two lots of data which can be analyzed by probit transformation. These data consist of samples of yellowtail that are used to determine (1) length of the fish at maturity and (2) the date of spawning. Since the technique of probit analysis is not commonly employed in fishery research, yet it has been thoroughly tested, an explanation of its use in this study is in order.

Probit analysis has been used almost exclusively in analyzing the results of biological assay of chemicals tested on experimental animals, although psychophysicists have used closely related methods. It is the most thoroughly developed method known for the analysis of quantal (all or nothing) response data, such as occurs in tests of a chemical in which different concentrations cause varying proportions of the experimental animals to die. Developed largely from the studies of C. I. Bliss, probit analysis was brought to its most definitive form by Finney (1952), on whose work this discussion is based.

Our yellowtail data may be considered as analogous to such doseage-response data. In determining length of the fish at maturity, the state of maturity or immaturity is the quantal response to the stimulus of growth. For the description of the spawning season, the females are ripe or spent in varying proportions as they are stimulated by the vernal change in environment.

The probit of a proportion P is defined as the abscissa which corresponds to a probability P in a normal distribution with mean 5 and variance 1; in symbols the probit of P is Y where

$$P=\frac{1}{\sqrt{2\pi}}\int_{-\infty}^{Y-5} e^{-\frac{1}{2}u^2}du$$

The transformation from percentage to probit changes the usual sigmoid curve of percentage response against stimulus to a straight line of the type

$$Y=a+bX$$

in which Y is the probit and X is the stimulus.

In the analysis of bioassay results, the typical distribution curve of dosage X is decidely skewed with a long tail on the right caused by the high tolerance of a few animals (usually insects). Such a curve can usually be normalized by transformation to common logarithms, and this has become standard practice in bioassay. In our spawning data, however, we have no evidence that such a transformation is necessary. A satisfactory fit is obtained by using the measures of time and length directly.

Probit regression lines may be fitted by eye if there is little scatter of the points and an accurate measure of the precision of the estimates is not needed. Such a procedure is easy and rapid, but it requires familiarity with the data and expected results. The arithmetic method of fitting is, unfortunately, rather laborious, because a solution of maximum likelihood is required. This results from the increasing variance as the proportion P approaches 0 or 1. The values of the probit Y must be weighted according to the expected Y and also according to the number of observations used in obtaining the proportion P. The expected Y is obtained from the eye-fitted line and the weighting coefficients have been tabulated by Fisher and Yates (1948, table 11).

In our analysis of the spawning period, the computations for the regressions of percentage of spent fish against the date for the female yellowtail have been made as indicated in table F–1,

TABLE F–1.—*Probit analysis of the spawning period of yellowtail, in 1943*

Date	x [1]	n	Percent spent [2] P	Provisional probit Y	nw	Working probit y
Apr. 20	10	60	10.0	3.7	20.15	3.719
Apr. 20	10	62	4.8	3.7	20.82	3.415
Apr. 20	10	72	9.7	3.7	24.18	3.701
Apr. 20	10	50	18.0	3.7	16.79	4.186
Apr. 27	17	57	19.3	4.0	25.00	4.142
Apr. 27	17	66	21.2	4.0	28.95	4.220
May 4, 6	25	43	16.3	4.3	22.86	4.047
May 7	27	54	24.1	4.4	30.12	4.300
May 17	37	27	44.4	4.9	17.13	4.859
May 18	38	41	56.1	4.9	26.01	5.154
June 3, 7, 8	57	21	71.4	5.8	10.55	5.544
June 9	60	34	67.6	5.9	16.03	5.374
June 16	67	45	91.1	6.2	16.66	6.334
June 23	74	46	89.1	6.6	10.93	6.111
June 28	79	50	98.0	6.8	9.00	7.002
June 29	80	63	98.4	6.8	11.34	7.052
July 4	85	50	100.0	7.0	6.56	7.421

SUMMARY OF REGRESSION COMPUTATIONS

$\Sigma nw=$	313.08
$\Sigma nwx=$	10,407.47
$\bar{x}=$	33.242
$\Sigma nw(x-\bar{x})^2=$	177,838.04
$\Sigma nwy=$	1,479.3402
$\bar{y}=$	4.726
$\Sigma nw(y-\bar{y})^2=$	355.9088
$\Sigma nw(x-\bar{x})(y-\bar{y})=$	7,731.7693

[1] x=day of the year minus 100.
[2] From table 40, p. 217.

which follows Finney (1952, p. 52). These computations lead to

$$\hat{Y}=3.281+.04348X$$

in which $\hat{Y}$ is the estimated probit and X the day of the year minus 100.

The goodness of fit was estimated by χ^2 from

$$\chi^2=\Sigma nw(y-\bar{y})^2-\frac{[\Sigma nw(x-\bar{x})(y-\bar{y})]^2}{\Sigma nw(x-\bar{x})^2}$$

$$\chi^2=19.76$$

With 16 degrees of freedom this value for χ^2 will be exceeded by chance about once in five times. We judge, therefore, that our curve (fig. 24) is a satisfactory fit and our assumption that no transformation of X was needed is justified.

The variance of x about the 50-percent point was estimated from

$$V(m)=\frac{1}{b^2}\left[\frac{1}{\Sigma nw}+\frac{(m-\bar{x})^2}{\Sigma nw(x-\bar{x})^2}\right]$$

$$V(m)=1.808 \qquad \sqrt{V(m)}=1.345$$

in which m is the 50-percent point, $\bar{x}$ mean observed x, and b the slope of the regression line. The 95-percent fiducial limits are 50-percent point of

$$x\pm 1.96\sqrt{V(m)}$$

or

$$34.77\pm 2.64$$

If we consider that our day began at noon, then we may say that the peak of spawning (in the fish as landed) probably occurred on May 19 and the odds are 19 to 1 that it occurred between May 16 and 21.

Using similar computations (appendix table F–2) for the data on length at maturity of the female yellowtail, we find

$$\hat{Y}=-0.2176+0.1631x$$

in which $\hat{Y}$ is the estimated probit and x is the total length in centimeters.

$$\chi^2=13.15,\ df=10,\ P=0.2$$

again indicating satisfactory fit. The standard error of the 50-percent point,

$$\sqrt{V(m)}=0.9727$$

and 95-percent fiducial limits of the 50-percent point (31.98 cm.) are 30.07 and 33.89 cm.

TABLE F-2.—*Probit analysis of the length at maturity of female yellowtail, in 1943*

Length X	n	Percent mature[1] P	Provisional probit Y	nw	Working probit y
29.5 cm	3	0	4.28	1.58	3.51
30.5 cm	8	25	4.49	4.63	4.33
31.5 cm	7	57	4.70	4.31	5.19
32.5 cm	21	62	4.90	13.32	5.30
33.5 cm	23	70	5.11	14.57	5.51
34.5 cm	13	77	5.32	7.97	5.70
35.5 cm	13	54	5.53	7.46	5.06
36.5 cm	17	65	5.73	8.89	5.34
37.5 cm	10	90	5.94	4.58	6.23
38.5 cm	15	73	6.15	5.81	5.44
39.5 cm	12	92	6.36	3.79	6.40
40.5 cm	14	100	6.57	3.46	7.07

SUMMARY OF REGRESSION COMPUTATIONS

$\Sigma nw=$	80.37
$\Sigma nwx=$	2,794.267
$\bar{x}=$	34.77
$\Sigma (x-\bar{x})^2=$	610.9173
$\Sigma nwy=$	438.3684
$\bar{y}=$	5.454
$\Sigma nw(y-\bar{y})^2=$	29.407998
$\Sigma nw(x-\bar{x})(y-\bar{y})=$	99.6630

[1] From table 39, p. 216.

U. S. GOVERNMENT PRINTING OFFICE : 1959 O - 476995

Blank page retained for pagination

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

SOME USES OF STATISTICAL ANALYSIS IN CLASSIFYING RACES OF AMERICAN SHAD (*Alosa sapidissima*)

BY DONALD R. HILL

FISHERY BULLETIN 147

From Fishery Bulletin of the Fish and Wildlife Service

VOLUME 59

UNITED STATES GOVERNMENT PRINTING OFFICE • WASHINGTON : 1959

For sale by the Superintendent of Documents, U. S. Government Printing Office, Washington 25, D. C.
Price 20 cents

Library of Congress catalog card for this bulletin:

Hill, Donald R

Some uses of statistical analysis in classifying races of American shad (*Alosa sapidissima*) Washington, U. S. Govt. Print. Off., 1959.

iv, 269–286 p. tables. 26 cm. (U. S. Fish and Wildlife Service. Fishery bulletin 147)

"From Fishery bulletin of the Fish and Wildlife Service, volume 59."
Bibliography: p. 283.

1. Shad. I. Title: Statistical analysis in classifying races of American shad. (Series: U. S. Fish and Wildlife Service. Fishery bulletin, v. 59, no. 147)

[SH11.A25 no. 147] Int 59–7

U. S. Dept. of the Interior. Library
for Library of Congress

Library of Congress catalog card for the series, Fishery Bulletin of the Fish and Wildlife Service:

U. S. *Fish and Wildlife Service.*
Fishery bulletin. v. 1–
Washington, U. S. Govt. Print. Off., 1881–19

v. in illus., maps (part fold.) 23–28 cm.

Some vols. issued in the congressional series as Senate or House documents.
Bulletins composing v. 47– also numbered 1–
Title varies: v. 1–49, Bulletin.
Vols. 1–49 issued by Bureau of Fisheries (called Fish Commission, v. 1–23)

1. Fisheries—U. S. 2. Fish-culture—U. S. I. Title.

SH11.A25 639.206173 9–35239 rev. 2*

Library of Congress [r55e½]

CONTENTS

	Page
Statement of the problem	269
Source of meristic data	271
Representativeness of the samples	272
Statistical evidence for the existence of races	274
Discriminant function analysis	276
Discussion	281
Summary	282
Literature cited	283
Appendix	284

ABSTRACT

Each year pound nets fished in the ocean off the coasts of New York and New Jersey catch large quantities of shad. The majority of these fish are believed to be native to the Hudson and Connecticut Rivers and therefore, these catches should be considered in any management plan for the two rivers. To establish a management plan which would include the ocean fisheries, estimates of the racial composition of this catch must be made.

In this paper an analysis of some meristic counts for shad is presented to support the racial theory. Samples were examined and it was found that the meristic counts used could be considered representative of the populations. An analysis of variance of the characters gave evidence for the existence of races.

A discriminant function is presented whereby a mixed sample of Hudson and Connecticut River shad can be separated. Meristic data collected from Hudson River shad in 1939 and Connecticut River shad in 1945 are used to construct the discriminant function. The mean value of this function for the Hudson River, 1939, is 74.103 and for the Connecticut River, 1945, is 70.940.

The discriminant function obtained will correctly classify approximately 81 percent of a mixed sample of Hudson and Connecticut River shad. Meristic data collected from the Hudson River in 1940 were substituted into this discriminant function and out of 105 fish, 16 were incorrectly classified; this is in good agreement with the theoretical 19 percent misclassification. The number of misclassifications can be considerably reduced if the individuals falling close to the mid-point between the two populations are not classified. By refusing to classify about one-half of the sample, the number of wrong classifications is reduced to 3.7 percent. Several methods of estimating the population composition of a mixed sample of shad are presented.

SOME USES OF STATISTICAL ANALYSIS IN CLASSIFYING RACES OF AMERICAN SHAD (*Alosa sapidissima*)

By Donald R. Hill, Fishery Research Biologist, Bureau of Commercial Fisheries

The commercial catch of American shad (*Alosa sapidissima*) has declined since the beginning of the twentieth century. In 1950 a study of this species was undertaken by the Fish and Wildlife Service acting as the primary research agency of the Atlantic States Marine Fisheries Commission. The objectives of the investigation were to determine the causes for the decline in shad abundance, determine conditions favoring recovery, and provide basic information so that the fishery can be managed to obtain optimum yields.

Most American shad landed on the Atlantic coast are captured in rivers; however, pound nets fished off the coasts of New York and New Jersey take large numbers of them each spring. The racial origin of these fish must be known for the intelligent management of the species. In this study, use is made of meristic counts for shad to separate two races or populations.

Meristic data were collected under the supervision of Louella E. Cable of the U. S. Fish and Wildlife Service. Grateful acknowledgement is made to G. B. Talbot, Chief, Middle Atlantic Fishery Investigations, for supplying these data and reviewing the manuscript, to C. H. Walburg in preparing the manuscript for publication, to T. M. Widrig and D. D. Worlund for suggestions concerning the estimation of relative abundance; and to T. A. Bancroft of the Statistical Laboratory, and K. D. Carlander of the Zoology Department, Iowa State College, for numerous suggestions.

STATEMENT OF THE PROBLEM

Studies of the shad populations of the Hudson (Talbot 1954) and Connecticut (Fredin 1954) Rivers have shown the effect of fishing effort on catches made in subsequent years. As a result of analysis of catch-and-effort statistics and tagging experiments, the size of the runs in previous years was determined for each river. Table 1 shows the size of the catches for the two rivers for 1938–51 and the calculated fishing rates for each of these years. These catches include only the fish taken in the rivers and not fish caught in the ocean.

TABLE 1.—*Total shad catches and estimated fishing rates for the Hudson and Connecticut Rivers from 1938 to 1951*

Year	Hudson River		Connecticut River	
	Catch (1,000 pounds)	Fishing rate (percent)	Catch [1] (1,000 pounds)	Fishing rate (percent)
1938	2,417	74.3	376	46.1
1939	3,103	69.9	332	43.4
1940	3,036	67.2	278	33.5
1941	3,112	68.4	364	32.8
1942	3,164	68.3	344	34.2
1943	3,185	71.0	478	44.8
1944	4,175	76.3	636	56.1
1945	3,545	64.7	651	70.3
1946	3,274	78.6	899	81.9
1947	2,046	79.0	657	81.0
1948	2,461	76.3	532	73.5
1949	2,038	74.3	392	69.6
1950	992	70.9	231	58.8
1951	755	46.0	303	56.7

[1] Catch for Connecticut River estimated by a factor of 3 pounds per fish.

Through an analysis of data on scales of 6-year-old shad from the Connecticut River, Fredin (1954) found for shad an extraneous mortality of about 40 percent occurring outside the river fishery. This was nearly as great as the fishing mortality in the river. He suggested that the pound nets in the New York Bay area and along the New Jersey coast could be the cause of some of this mortality. The number of pound nets in operation increased from 144 in 1946 to 180 in 1950. For these same years, the estimated populations (estimated by a regression analysis of escapements in previous years) were higher than the populations calculated from the catch-and-effort data. Fredin stated that the increase in pound-net effort may account for these deviations.

NOTE.—Approved for publication December 4, 1957. Fishery Bulletin 147.

He made the following statement about these pound-net catches: (p. 258)

> The relation between pound-net catches and deviations from the expected populations in the Connecticut River cannot be fully evaluated at this time because the extent to which the Connecticut River shad contribute to these pound-net catches is not known. Additional tagging studies conducted in the areas where pound nets are fished would enable us to determine the effect of this fishing on the Connecticut River shad runs. The causes of the extraneous-mortality rate must be taken into consideration in a management program to restore the Connecticut River shad population to the level of abundance which it held in the early 1940's.

The extent of the shad fisheries in New York Bay and along the Long Island and New Jersey coasts can be seen from the 1945 catches of shad reported by the U. S. Fish and Wildlife Service (1949). Total catches in pounds, by county, are given south to north from southern New Jersey to Long Island.

Atlantic Co., N. J.	60, 700
Ocean Co., N. J.	690, 900
Monmouth Co., N. J.	1, 173, 600
Suffolk Co., L. I., N. Y.	217, 000

This total New Jersey coast, Long Island, and New York Bay catch is about two million pounds while the combined total catch for the Hudson and Connecticut Rivers is about 4.2 million pounds for the same year. Of course the composition of this New Jersey catch is the basic problem. If it is primarily shad from southern rivers, this catch can be disregarded in the management of the Hudson and Connecticut Rivers. Conversely, if this catch is predominantly Hudson and Connecticut River shad, it must be considered in any management program because it represents one-third of the total fishery.

The Fish and Wildlife Service has carried out some tagging experiments [1] in the areas under consideration. An examination of these tag returns can supply a partial solution to the composition of these three catches. In 1945, 125 shad were tagged at Seaside Park, N. J. The following areas and numbers of recaptures were reported:

Hudson River	20
Connecticut River	3
Delaware River	2
Chesapeake Bay	4
New York Ocean	2
New Jersey Coast	5
Maine Coast	1

[1] Unpublished data, U. S. Fishery Laboratory, Beaufort, N. C.

In the same year 97 shad were tagged off Fire Island Inlet, Long Island, N. Y., and were recovered in the following areas:

Hudson River	9
Connecticut River	24
Bay of Fundy	1

Shad have been tagged off Staten Island, New York Bay, in several different years, and the following table gives the recoveries from these experiments in which a total of 1,380 shad were tagged.

Hudson River	448
Connecticut River	24
Delaware River	5
Chesapeake Bay	1
Long Island	5
New Jersey Coast	13
Bay of Fundy	3

These tagging experiments furnish us with some information about the composition of the populations in these three areas. Most of the shad tagged on the New Jersey coast migrated into the Hudson River. Similarly, a major part of those tagged off Staten Island were recaptured in the Hudson River. On the coast of Long Island, most of the fish tagged were recaptured in the Connecticut River. Very few of the fish tagged in these areas were recaptured in other major shad rivers.

The tag returns could be used in conjunction with the catch statistics of the various areas to estimate the composition of the catches. They have been of considerable value in showing the general composition of the catches in the areas under question, and it is apparent that these catches should be included in any analysis of the catch and effort statistics for either river. Any increase or decrease in effort in these areas will be reflected in the number of shad entering the rivers.

Unfortunately, complete catch and effort statistics are not available for the New Jersey pound-net fishery, so it is impossible to compare directly past pound-net catches and mortality rates of Hudson or Connecticut River shad. However, a research project could be designed to show what effect pound-net catches have on these mortality rates. This could be done by dividing the pound-net fishing areas into a number of geographical strata. For each stratum the total catch and effort would be needed. It would also be necessary to estimate the composition of this catch (for

example, 70 percent Hudson shad, 30 percent Connecticut shad) for each stratum. From these quantities, the entire pound-net catch could be divided into two parts, Hudson River shad and Connecticut River shad.

Obtaining the total catch and effort statistics is rather straightforward and not expensive, but estimating the compositions of the catches is much more complex. At the present time, this would have to be done by tagging experiments. In each stratum, a number of shad would be tagged, preferably at various times throughout the season. If the fishermen are personally interviewed to obtain tag returns, the coverage on the two rivers should be equal. Even the fishing rates for the two rivers should be the same or some adjustment would be needed to place them on the same level. As a result, the problem of estimating the composition of a pound-net catch becomes complex and expensive when two river systems are canvassed for tag returns, and the tagging is done several hundred miles from the rivers.

This is one of many fishery problems where it would be advantageous to obtain a sample of fish and classify them according to the river system to which they belong. If this were done accurately, samples of fish from various strata could be obtained, and each fish could be assigned to the proper river. The composition of this sample would be used to estimate the composition of the stratum. The remainder of this paper will investigate the statistical techniques applicable to this problem.

SOURCE OF MERISTIC DATA

Races (populations) of fish can often be separated through the use of body measurements or meristic counts. If some of these counts or measurements are sufficiently different for two populations, it is possible to classify the individuals in a sample and estimate the relative abundance of each population in an area by the composition of the sample.

A large number of morphological data were collected on the American shad, both juvenile and adults, by the Fish and Wildlife Service between 1939 and 1945. Data on twenty-five different characters were collected from each fish. They were defined as follows:

MID-CAUDAL LENGTH.—Tip of snout to end of shortest rays between lobes of caudal fin.

TOTAL LENGTH.—Tip of snout to end of longest ray of caudal fin.

STANDARD LENGTH.—Tip of snout to branching of urostyle (modified vertebra).

DEPTH.—Longest measurement from dorsal to ventral profiles (in front of dorsal fin).

THICKNESS OF FISH.—Measurement from left to right through thickest part of fish.

CAUDAL PEDUNCLE.—Shortest dorsoventral measurement of tail anterior to caudal fin.

HEAD LENGTH.—Tip of snout to posterior margin of opercular bone.

SNOUT.—Tip of snout to anterior margin of eye socket.

EYE.—From anterior to posterior margin of eye socket.

INTERORBITAL.—Across top of head from dorsal margin of one eye socket to dorsal margin of the other eye socket above pupil of the eye.

MAXILLARY.—From posterior margin of maxillary to a vertical from tip of snout.

LENGTH OF DORSAL AND ANAL BASES.—From anterior margin of base of first ray to posterior margin of last ray.

LENGTH OF PECTORAL.—From articulation of first ray to tip of longest ray.

SNOUT TO DORSAL.—Tip of snout to articulation of first ray of dorsal fin.

SNOUT TO ANAL.—Tip of snout to articulation of first ray of anal fin.

PECTORAL TO VENTRAL.—From articulation of first ray of pectoral fin to articulation of first ray of ventral fin.

VENTRAL TO ANAL.—From articulation of first ray of ventral fin to articulation of first ray of anal fin.

ANTERIOR SCUTES.—All scutes having processes in front of ventral fins, including the scute between the fins which does not appear to have a process. It is beneath the process of the preceding scute.

POSTERIOR SCUTES.—All scutes posterior to ventral fins.

VERTEBRAE.—Urostyle included in count.

DORSAL RAYS.—Last undivided ray counted with divided rays, other undivided rays separate.

ANAL RAYS.—As for dorsal rays.

PECTORAL RAYS.—All rays on left and right sides of fish.

GILL RAKERS.—Only those on the lower limb of the first gill arch counted (at the bend of the arch, the bases of the rakers of the upper arm point in the opposite direction from those of the lower arm).

SCALES.—Oblique rows from the upper end of opercular slit to base of caudal fin. Horizontal rows from the median dorsal line to ventral scutes but not including either.

Since there were numerous rivers involved and samples were taken for several years from some rivers, analysis using all the data would become exceedingly complex. Table 2 gives the location, year, and number of adult specimens examined.

TABLE 2.—*Summary of areas from which meristic data were collected on adult American shad*

[The figures represent the number of shad in each sample. Data were not complete for all meristic characters in all samples]

Area	1938	1939	1940	1941	1942	1943	1944	1945
Connecticut River	------	------	------	------	------	------	------	101
Hudson River (N. Y.)	------	104	105	102	------	------	------	-----
Maurice River (N. J.)	------	------	------	------	------	------	------	100
Delaware River	------	------	------	------	------	------	68	-----
Chesapeake Bay	105	100	------	102	------	------	------	-----
Albemarle Sound (N. C.)	127	124	85	------	------	------	------	-----
Edisto River (S. C.)	50	99	------	99	96	------	------	-----
Ogeechee River (Ga.)	------	50	------	------	------	------	------	-----
St. Johns River (Fla.)	45	100	106	------	------	------	------	-----

This paper will not include a complete analysis of the data available. It is hoped that this preliminary analysis will show that a complete analysis would be warranted, and that further research along these lines would be fruitful. No analysis of the information on the juveniles has been attempted, hence there is still much to be learned by combining this with the data on the adults.

REPRESENTATIVENESS OF THE SAMPLES

The need for separation of races of fish is apparent. However, before races can be separated, it should be established that they are present. Tagging experiments have been offered as the best evidence supporting the theory of a separate race of shad in each Atlantic coast river. In numerous tagging programs carried out by the Fish and Wildlife Service, few tagged shad have been recaptured in rivers other than the one in which they were tagged. No shad tagged on the spawning ground of one river system has ever been recaptured on the spawning ground of another river system. The operation of the homing instinct may not be 100 percent for shad, but examination of tag returns indicates that the percentage is very high.

If there is a race of shad in each river, that is, a group of fish and their offspring which return to the same spawning area year after year, the fish within a river should be more like one another than to the shad from other rivers. This could be expected because of environmental differences or genetic isolation. Conversely, if the spawning ground of each fish is determined by a completely random process, a single homogeneous shad population would be expected. Therefore, if consistent differences between shad in the several rivers can be found for some measurable characters, this can be used as further evidence to support the race theory.

Before proceeding with an attempt to verify this theory, one assumption should be investigated. If the available data are to be used to establish differences between rivers, it is essential that the samples be representative of the various populations. It is impossible to assume that these are random samples, because the shad fishermen know that they can control the size of fish in their catches by changing the mesh size of their nets. They know that if they fish a 5¾-inch stretched-mesh gill net, they will catch large-roe shad, and if they use a 4¾- to 5-inch stretched-mesh net, they will catch proportionately more small shad of both sexes. This selectivity occurs with drift, anchor, and stake gill nets. Pound nets and haul seines may be much less selective, but if the gill nets are catching large fish and permitting smaller ones to escape, the population being sampled by the haul seines is not the total population of the river, but the total population minus the fish removed by gill nets. The result, of course, would be an excess of smaller fish in the haul seine samples.

Since it is known that some fishing gear tends to select fish by length (and all correlated measurements such as depth and thickness), it cannot be assumed that the samples are random. However, this selectivity may take place only in the size of the fish in the samples and not in some of the other characteristics. If the number of rays in the pectoral fin is being investigated, the samples may be representative of this character even if there is selectivity of size. This would be true of any character which is not correlated with length. Therefore, the characters were tested for a correlation with length and if none was found, the samples were considered representative.

In examining the catches of shad in the St. Johns River of Florida and the Connecticut River, it is apparent that the shad in the Connecticut are larger. Some of this can probably be explained by the difference in the age distributions of the two populations. Can these age distributions be used in separating races of shad? The author feels that they cannot be used, since they will fluctuate from year to year with changes in fishing effort and catches. Age and length are correlated, and this is another reason for excluding

length and all correlated characters from any racial investigation.

The choice of characters to be used in investigating races of shad was evident. To avoid the difficulties presented by selectivity of the fishing gear, those characters which are correlated with length were not considered. Thus, depth, thickness, weight and all of the other body measurements were eliminated, because they increase as the fish grows. Ratios of two such measurements will also be related to length, unless these two measurements increase at the same rate throughout the growth of the fish. These ratios have not been investigated because it is doubtful that this condition exists, particularly when both juveniles and adults are considered. Scattergrams of gill rakers and length exhibited a parabolic relation and were therefore eliminated. Scale counts have not been included because notations on the data sheets indicated that some of the scale counts were questionable. Of the 25 counts and measurements, all were eliminated for the above reasons except 6 meristic counts (anterior scutes, posterior scutes, dorsal rays, anal rays, pectoral rays, and vertebrae) and these were tested for correlations with length before they were used in any analysis.

Analysis of variance tables for the regression of these characters on length have been calculated for some of the samples. The assumptions necessary for this analysis are: (1) For each length, the character is normally distributed, (2) the variance of the character is homogeneous for each length, and (3) for each length interval, the samples are random. The values of F needed to test for a regression of the characters on length are given in the last column of table 3. F with 1 and 100 degrees of freedom is equal to 3.94 at the 5 percent level and 6.90 at the 1 percent level. There are three significant regressions in this table. Two of these regressions are for vertebrae in the Hudson River samples of 1939 and 1940. It is interesting to note that the F-value for vertebrae in the 1941 Hudson River sample is also high (3.11) but not significant. This significance does not occur in any of the other three samples which were tested for a regression of vertebrae on length. Of course, this is not enough evidence in itself to say that it is a racial difference between the populations, but it raises the question as to why this difference occurs for the Hudson River samples

TABLE 3.—*Regression analyses to test meristic characters for correlation with length*

Source of variation	df	Sum of squares	Mean square	F
ANTERIOR SCUTES				
HUDSON RIVER, 1940				
Regression	1	1.270	1.270	2.91
Deviation from regression	103	44.958	0.436	
Total	104	46.228		
ST. JOHNS RIVER, 1940				
Regression	1	1.241	1.241	2.33
Deviation from regression	104	55.297	0.532	
Total	105	56.538		
CONNECTICUT RIVER, 1945				
Regression	1	0.180	0.180	0.45
Deviation from regression	99	39.820	0.402	
Total	100	40.000		
POSTERIOR SCUTES				
HUDSON RIVER, 1940				
Regression	1	0.236	0.236	0.46
Deviation from regression	103	52.310	0.508	
Total	104	52.546		
ST. JOHNS RIVER, 1940				
Regression	1	0.024	0.024	0.44
Deviation from regression	104	57.176	0.550	
Total	105	57.200		
CONNECTICUT RIVER, 1945				
Regression	1	2.390	2.390	3.71
Deviation from regression	99	63.800	0.644	
Total	100	66.190		
ANAL RAYS				
HUDSON RIVER, 1940				
Regression	1	0.151	0.151	0.15
Deviation from regression	103	102.382	0.994	
Total	104	102.533		
ST. JOHNS RIVER, 1940				
Regression	1	0.002	0.002	0.002
Deviation from regression	104	106.762	1.027	
Total	105	106.764		
PECTORAL RAYS				
HUDSON RIVER, 1940				
Regression	1	0.644	0.644	1.64
Deviation from regression	103	40.346	0.392	
Total	104	40.990		
ST. JOHNS RIVER, 1940				
Regression	1	0.002	0.002	0.005
Deviation from regression	104	43.847	0.422	
Total	105	43.849		
CONNECTICUT RIVER, 1945				
Regression	1	1.425	1.425	2.15
Deviation from regression	98	65.075	0.664	
Total	99	66.500		
VERTEBRAE				
HUDSON RIVER, 1939				
Regression	1	2.606	2.606	*3.97
Deviation from regression	102	66.945	0.656	
Total	103	69.551		
HUDSON RIVER, 1940				
Regression	1	3.431	3.431	*4.41
Deviation from regression	103	80.089	0.778	
Total	104	83.520		
HUDSON RIVER, 1941				
Regression	1	2.386	2.386	3.11
Deviation from regression	96	73.746	0.768	
Total	97	76.132		

Footnote at end of table.

TABLE 3.—*Regression analyses to test meristic characters for correlation with length*—Continued

Source of variation	df	Sum of squares	Mean square	F
VERTEBRAE—Continued				
ST. JOHNS RIVER, 1938				
Regression	1	0.002	0.002	0.002
Deviation from regression	41	39.440	0.962	
Total	42	39.442		
ST. JOHNS RIVER, 1940				
Regression	1	0.115	0.115	0.17
Deviation from regression	104	69.942	0.672	
Total	105	70.057		
CONNECTICUT RIVER, 1945				
Regression	1	0.684	0.684	0.50
Deviation from regression	99	134.316	1.357	
Total	100	135.000		
DORSAL RAYS				
HUDSON RIVER, 1940				
Regression	1	0.001	0.001	0.002
Deviation from regression	103	58.532	0.568	
Total	104	58.533		
ST. JOHNS RIVER, 1940				
Regression	1	3.650	3.650	**6.71
Deviation from regression	104	56.580	0.544	
Total	105	60.230		

NOTE.—Asterisks denote significant.

and not for the St. Johns and Connecticut River samples. The other significant F is for the regression of dorsal rays in the St. Johns River sample of 1940.

This regression analysis of samples from the Connecticut River, Hudson River, and St. Johns River shows that none of the six characters has a consistent correlation with length. It is difficult to explain the regression of vertebrae on length for the Hudson River sample. This is also true for dorsal rays in the St. Johns River sample; however, with 19 regressions tested, three significant values is a small proportion. Since none of the characters is consistently correlated with length, the available samples were considered representative even though they are not random.

STATISTICAL EVIDENCE FOR THE EXISTENCE OF RACES

It has been shown that none of the six characters: anterior scutes, posterior scutes, dorsal rays, anal rays, pectoral rays and vertebrae, exhibits a consistent correlation with length; therefore, we can place a certain degree of confidence in treating the samples as representative. In the previous section it was pointed out that consistent differences between rivers for some measurable characters would support the racial theory. This can be studied by setting up the following mathematical model:

$$Y_{ijk}=\mu+\alpha_i+\beta_j+(\alpha\beta)_{ij}+\epsilon_{ijk}$$

where Y_{ijk} is the character under study, μ is the general mean, α_i represents the contribution of the ith river, β_j is the contribution of the jth year (year caught), and $(\alpha\beta)_{ij}$ is an interaction of years and rivers. The ϵ_{ijk} is an error term. The α_i, β_j, $(\alpha\beta)_{ij}$, and ϵ_{ijk} are all assumed to be normally and independently distributed with means zero and variance σ^2_R, σ^2_Y, σ^2_{RY} and σ^2, respectively.

This model could be changed so that the jth classification stood for year class, but this necessitates knowing the ages of all the fish in the samples. A model of the latter type may have an advantage, since differences between year classes would not be averaged as they are with the above model. Unfortunately, the present data do not include ages, hence the model indicated will be used. This will in no way invalidate the conclusions, but grouping by year class might be a refinement that would prove valuable.

The racial theory can now be investigated more fully. Using the above model and suitable data, several hypotheses can be tested which may give added support to this theory. First of all, an interaction of years with rivers ($H_0:\sigma^2_{RY}=0$) can be tested, next a test of differences between years ($H_1:\sigma^2_Y=0$), and third, a test for differences between rivers ($H_2:\sigma^2_R=0$). If H_0 and H_1 can be accepted while H_2 is rejected, the conditions necessary to support the race theory are present.

These hypotheses and their relations to the present problem will be explained in some detail. The first one, ($H_0:\sigma^2_{RY}=0$), is a test for an interaction between rivers and years. This interaction could best be described by assuming that temperature is a factor in determining the number of vertebrae of young shad. If there were a warm spring on a northern river and a cold spring on a southern river in 1953, and just the opposite in 1954, there might be produced the following average number of vertebrae for shad from the two rivers:

Year	Northern river	Southern river
1953	55.7	56.3
1954	56.2	55.8

In this situation, one would conclude that vertebrae offer no evidence for the presence of races, and most of the variation is in the form of an interaction between rivers and years.

The second hypothesis to be tested, ($H_1:\sigma^2_Y=0$), concerns a difference between years. If the average number of vertebrae for two rivers and two different years were of the following magnitude, they would offer no proof for the presence of races.

Year	River A	River B
1953	56.5	57.0
1954	57.0	57.5

In this case, the difference from year to year is as large as the difference between rivers.

The third hypothesis, ($H_2:\sigma^2_R=0$), to be tested is the one for a difference between rivers. If the difference between rivers is not significant, there would be no evidence for the presence of races. Thus if H_0 and H_1 can be accepted and H_2 rejected, the conditions necessary for the presence of races would be satisfied.

Analysis of variance tables with years and rivers as the two classifications were computed for five of the six characters mentioned above. Dorsal rays had to be omitted because the data were incomplete. Table 2 shows that there are data for 1938 and 1939 in four locations: the St. Johns River in Florida, the Edisto River in South Carolina, Albemarle Sound, N. C., and Chesapeake Bay. Since the samples from Chesapeake Bay came from several different rivers, those data were not included in the analysis. The remaining three areas were used as one classification, and the years 1938 and 1939 were used as the other. A table of the same size could have been constructed using Hudson River, Albemarle Sound, and St. Johns data for the years 1939 and 1940.

The various samples are of unequal size ranging from 45 to 127 for the 2×3 table. Exact methods are available for the analysis of a 2×3 table with unequal subclass numbers but they require considerable computing time. Several approximations are available (Anderson and Bancroft, 1952) utilizing the complete data. In this study random samples of 40 fish each were drawn from the various samples, avoiding the difficulties of the unequal subclass numbers (table 10, appendix). With samples of size 40, this method should be a good approximation to the more exact methods.

TABLE 4.—*Analyses of variance for the meristic characters to test for differences between years, differences between rivers, and interaction between years and rivers*

Source of variation	df	Sum of squares	Mean square	F
ANTERIOR SCUTES				
Between years	1	1.837	1.837	3.72
Between rivers	2	7.599	3.799	**7.69
Y×*R*	2	0.101	0.051	0.10
Error	234	115.125	0.494	
Total	239	124.662		
POSTERIOR SCUTES				
Between years	1	2.204	2.204	3.49
Between rivers	2	19.733	9.867	**15.64
Y×*R*	2	2.234	1.117	1.77
Error	234	147.125	0.629	
Total	239	171.296		
ANAL RAYS				
Between years	1	0.067	0.067	0.07
Between rivers	2	4.059	2.029	2.17
Y×*R*	2	1.408	0.704	0.76
Error	234	218.200	0.932	
Total	239	223.734		
PECTORAL RAYS				
Between years	1	0.416	0.416	1.20
Between rivers	2	11.808	5.904	**17.01
Y×*R*	2	1.859	0.929	2.68
Error	234	81.100	0.347	
Total	239	95.183		
VERTEBRAE				
Between years	1	0.066	0.066	0.09
Between rivers	2	19.200	9.600	**12.87
Y×*R*	3	1.634	0.817	1.10
Error	234	174.500	0.745	
Total	239	195.400		

NOTE.—Asterisks denote significant.

Analysis of variance tables for these five characters are shown in table 4. The *F* values for testing the hypothesis of no interaction are the lower numbers in column five of this table. These range in value from 0.10 for anterior scutes to 2.68 for pectoral rays. None of these is significant ($F_{2,200}=3.04$ at the 5-percent level), so the hypothesis of no interaction of years and rivers is accepted.

The F values for testing differences between years range in value from 0.07 to 3.72. Again, these are not significant ($F_{1,200}=3.89$ at the 5-percent level), so the hypothesis of no differences between years can be accepted.

The F values for testing differences between rivers range in value from 2.17 to 17.01. The value for anal rays, 2.17, is not significant at the 5-percent level ($F_{2,200}=3.04$ at the 5-percent level, $F_{2,200}=4.71$ at the 1-percent level); however, the other four are all significant at the 1-percent level.

While the differences between rivers are not significant for anal rays, they are for the other four characters, so it can be safely concluded that there are differences from river to river for four characters.

The F values for differences between years are rather large for anterior scutes and posterior scutes, and both are significant at the 10-percent level ($F_{1,120}=2.75$). At the present time, it is impossible to say definitely whether there are differences from year to year for these two characters. It is apparent that this is one phase of the problem that should be studied in more detail.

The fact that there may be differences from year to year for some characters does not disprove the racial theory. The magnitude of the differences between years relative to the differences between rivers is the essential quantity to be considered in this problem. If the differences between years are small in comparison to the differences between rivers, races can still be distinguished. In terms of the model presented on page 274, the river-effects (α_i) should be considerably larger than the year-effects (β_j). An estimate of the relative magnitude of these two effects can be obtained from the analysis of variance tables. Since none of the interactions was significant, the interaction mean square has been pooled with the error mean square to obtain an estimate of the error (σ^2). It has been assumed that both the years and the rivers are a sample from a large number of years and rivers. Therefore, the α_i and β_j obtained from the data are samples from some larger population of α_i and β_j which have variance σ_R^2 and σ_Y^2. From the mean squares in the fourth column of table 5, estimates of σ_R^2 and σ_Y^2 can be obtained. For anterior scutes: $\hat{\sigma}^2=0.488$, $\hat{\sigma}_Y^2=0.0112$, and $\hat{\sigma}_R^2=0.0414$; for posterior scutes: $\hat{\sigma}^2=0.633$, $\hat{\sigma}_Y^2=0.0131$, and $\hat{\sigma}_R^2=0.1154$. Thus, the variation between years for anterior scutes is about one-fourth as large as the variation between rivers. Similarly, for posterior scutes, the variation between years is about one-ninth the variation between rivers.

These analyses present evidence that there are no differences between years for anal rays, pectoral rays, and vertebrae. There may be differences between years for anterior and posterior scutes, but if they do exist, they are small compared to the variation between rivers. These analyses of variance have approached the racial problem in a more direct manner than in previous studies and have given further support to the racial theory.

TABLE 5.—*Analysis of variance with interaction term pooled with error term*

Source of variation	df	Sum of squares	Mean square	Expected mean square
ANTERIOR SCUTES				
Between years	1	1.837	1.837	$\sigma^2+120\sigma_Y^2$
Between rivers	2	7.599	3.799	$\sigma^2+80\sigma_R^2$
Error	236	115.226	0.488	σ^2
Total	239	124.662		
POSTERIOR SCUTES				
Between years	1	2.204	2.204	$\sigma^2+120\sigma_Y^2$
Between rivers	2	19.733	9.867	$\sigma^2+80\sigma_R^2$
Error	236	149.359	0.633	σ^2
Total	239	171.296		

DISCRIMINANT FUNCTION ANALYSIS

There are numerous ways of using the data from meristic counts to construct discriminant functions. Raney and de Sylva (1953) constructed such a function by adding the number of dorsal, anal, and pectoral rays for each fish. They called this a "character index," but actually it is a simple form of a discriminant function. By plotting a frequency histogram of this character index for several areas and a series of years, they were able to differentiate to some extent between striped bass from the Hudson River and from Chesapeake Bay. There was considerable overlap in these distributions, and if one were presented with a fish of unknown origin, it would be difficult to assign it to a particular population with any certainty.

For illustration purposes, a discriminant function of this type has been constructed using data on shad from the Connecticut River and the Hudson River. It is unfortunate that the data for the Hudson River were collected in 1939 and 1940 (tables 11 and 12, appendix) while the Connecticut data were collected in 1945 (table 13, appendix), but since it has been shown that the characters are consistent from year to year, the data can be used for discrimination. The discriminant function,

$$Z=X_1+X_2+X_3+X_4+X_5+X_6$$

where X_1 is the number of anterior scutes, X_2 the number of posterior scutes, X_3 the number of dorsal rays, X_4 the number of anal rays, X_5 the number of pectoral rays, and X_6 is the number of

TABLE 6.—*Frequency distributions of the discriminant function*

$$Z=X_1+X_2+X_3+X_4+X_5+X_6$$

Z	Connecticut River 1945	Hudson River 1939	Hudson River 1940
139	1		
140			
141	1	1	
142	3		
143	4	1	
144	14		1
145	10	2	2
146	18	3	6
147	10	6	3
148	10	11	8
149	9	18	18
150	6	18	15
151	4	18	23
152	1	12	9
153		8	12
154		5	3
155			2
156		1	
157			2
158			1

vertebrae, has been tabulated for the Hudson River samples of 1939–40 and the Connecticut River sample of 1945 in table 6. It is interesting to note that the means of these distributions are: Hudson River (1939), 149.962 (n=104), Hudson River (1940), 150.362 (n=105), and the Connecticut River (1945), 146.363 (n=91); the variances are 5.816, 6.465, and 6.400, respectively. The pooled average for the Hudson River is 150.163. (A t-test shows that there is a highly significant difference between the two rivers.) If one were to use such a function for discrimination, he would classify everything above 148.2 as coming from the Hudson River and everything below as coming from the Connecticut River. However, since the counts are discrete, it would be necessary to use either 148 or 149 as the dividing line. Table 7 gives the percentage of wrong classifications for these two values. This simple function of the type $Z=\Sigma X_i$ provides a method of classifying about 78 percent of the individuals correctly. Without the use of this function, it would appear impossible to distinguish Connecticut River shad from Hudson River shad.

If such good results were obtained by totaling the number of scutes, vertebrae and rays for each specimen, perhaps some other combination might be more efficient. Considering only linear forms of the type $Y=\Sigma a_i X_i$, that function which is best for discriminating between the two populations can be determined. It can be shown (Rao 1952) that the best linear discriminant function for two multivariate normal populations is:

$$D=l_1X_1+l_2X_2+l_3X_3+l_4X_4+l_5X_5+l_6X_6$$

where the l_i's are obtained by solving the following set of equations:

$$\begin{aligned} l_1w_{11}+l_2w_{12}+l_3w_{13}+l_4w_{14}+l_5w_{15}+l_6w_{16}&=d_1\\ l_1w_{21}+l_2w_{22}\quad\ldots\quad&=d_2\\ \vdots\qquad\qquad\qquad\qquad&\ \vdots\\ l_1w_{61}+l_2w_{62}\quad\ldots\quad l_6w_{66}&=d_6. \end{aligned}$$

w_{ij} is an estimate of the covariance (assumed to be equal in the two populations) between the ith and jth characters and d_i is the estimated difference in mean values of the ith character in the two populations. The w_{ij} are estimated from the following equations:

$$(N_1+N_2-2)w_{ij}=\sum_{k=1}^{N_1}(X_{i1k}-\overline{X}_{i1})(X_{j1k}-\overline{X}_{j1})+\sum_{k=1}^{N_2}(X_{i2k}-\overline{X}_{i2})\ (X_{j2k}-\overline{X}_{j2}).$$

N_1 and N_2 are the number of specimens in the first and second sample, respectively, and X_{i1k} is the count on the ith character for the kth fish from population 1. $\overline{X}_{i1}$ is the mean value of the ith character for population 1.

Using data from the Hudson River sample of 1939 and the Connecticut River sample of 1945,[2] the following set of equations is obtained:

$$\begin{aligned} &0.38197l_1+0.03742l_2+0.06242l_3-0.01515l_4+\\ &\qquad 0.02467l_5+0.15184l_6=0.41484\\ &0.03742l_1+0.71332l_2-0.02032l_3-0.01196l_4+\\ &\qquad 0.02301l_5+0.18071l_6=0.46016\\ &0.06242l_1-0.02032l_2+0.65354l_3+0.21084l_4+\\ &\qquad 0.03309l_5+0.09918l_6=0.71291\\ &-0.01515l_1-0.01196l_2+0.21084l_3+0.88481l_4+\\ &\qquad 0.00717l_5+0.13073l_6=0.38462\\ &0.02467l_1+0.02301l_2+0.03309l_3+0.00717l_4+\\ &\qquad 0.58499l_5-0.01020l_6=1.07555\\ &0.15184l_1+0.18071l_2+0.09918l_3+0.13073l_4-\\ &\qquad 0.01020l_5+1.05154l_6=0.55082 \end{aligned}$$

TABLE 7.—*Percentage of wrong classifications using the function*

$$Z=X_1+X_2+X_3+X_4+X_5+X_6$$

River	Year	147–148	148–149
		Percent	*Percent*
Connecticut	1945	33	22
Hudson	1939	12	22
Hudson	1940	11	19

[2] Only fish with complete meristic data were used; first 91 fish in table 13 (appendix).

TABLE 8.—*Coefficients of the discriminant function* $D_i=\Sigma l_i X_i$ *and successive values of* D_i^2

1	2	3	4	5	6	D_i^2	$D_i/2$	P($D_i/2$)
1.086	------	------	------	------	------	0.4505	0.34	63.3
1.028	0.591	------	------	------	------	0.6985	0.42	66.3
0.856	0.629	1.029	------	------	------	1.3782	0.59	72.2
0.878	0.630	0.952	0.231	------	------	1.4218	0.60	72.6
0.785	0.577	0.871	0.234	1.731	------	3.1632	0.89	81.3
0.694	0.518	0.850	0.200	1.743	0.246	3.2195	0.90	81.6

The solution of these six equations requires the inversion of a 6×6 matrix. Rao (1952) presents a method of solving these equations so that successive discriminant functions are obtained. At the first stage of solution, the discriminant function using anterior scutes only is computed while at the second stage the function using anterior scutes and posterior scutes is obtained. The discriminant function using all six characters is obtained at the sixth stage. The solution of these equations is given in table 8. Any particular discriminant function can be obtained by substituting the l_i from this table into the equation:

$$Y_i=\Sigma l_i X_i.$$

The variance of Y_i is D_i^2 and can be obtained at the same time as the coefficients l_i. It can be proved (Rao 1952) that $D_i/2$ is a normal deviate with mean zero and a standard deviation of one. The probability of obtaining a normal deviate equal to $D_i/2$ is identical to the probability of correctly classifying an individual from any one population. Values of D_i^2, $D_i/2$ and the probability of correct classification are also given in table 8. From this table it can be seen that the increase in D_i^2 with the addition of vertebrae is quite small; therefore, the number of vertebrae is not very useful for purposes of discrimination when used with the other five characters. From the estimates of w_{ij} it is apparent that the covariance between vertebrae and other characters is generally large. This correlation may reduce the usefulness of vertebrae for discrimination. Taking an extreme example where the correlation between two characters is one, it would be useless to include more than one of them in a discriminant function. Immediately the question arises as to how the correlation of the characters affects the relative efficiency of the function. This can be answered by a test of significance which tests the hypothesis of no added increase in D_i^2 in going from a discriminant function using the first p characters to one using p plus q. In this case p=5 and p plus q=6. Rao presents this test on page 253.

$$R=\frac{1+\dfrac{N_1N_2}{(N_1+N_2)(N_1+N_2-2)}D_1^2}{1+\dfrac{N_1N_2}{(N_1+N_2)(N_1+N_2-2)}D_s^2}$$

$$=\frac{1+\dfrac{(91)(104)}{(195)(193)}(3.22)}{1+\dfrac{(91)(104)}{(195)(193)}(3.16)}=1.0078$$

$$F=\frac{N_1+N_2-p-q-1}{q}(R-1)=1.46$$

This F [with q and $(N_1+N_2-p-q-1)$ d. f.] is not significant; therefore, the hypothesis of no added information being supplied by vertebral counts can be accepted. It must be remembered that this is true only when use is made of the data from the remaining five characters. Since vertebrae add nothing to the power of discrimination, they will be omitted from further calculations. The fact that vertebral counts can be eliminated from the discriminant function has considerable practical value, because these counts have to be made from x-rays or after careful dissection of the fish. This one count would probably be as costly in terms of time and money as the other five.

The next step is to find the means of the discriminant function for the two populations. This is done by substituting the mean values of the characters for each population into the discriminant function. The discriminant function as taken from table 8 (excluding vertebrae) is:

$$Y=0.785X_1+0.577X_2+$$
$$0.871X_3+0.234X_4+1.731X_5$$

The mean value of this function for the Hudson River, 1939, is 74.103 and for the Connecticut River, 1945, is 70.940. If this function were to be used to discriminate between the two populations, those fish with a value of Y less than 72.52 would be called Connecticut River fish and those above 72.52 would be classified as Hudson River fish. The error in this classification would be the proportion of Connecticut fish with a Y greater than 72.52 and the proportion of Hudson fish with a Y less than 72.52. The variance of Y is:

$$D^2=l_1d_1+l_2d_2+l_3d_3+l_4d_4+l_5d_5$$
$$D^2=3.163$$

The proportion of Connecticut River fish which lie in the area under the normal curve from $-\infty$ to 72.52 is equal to the probability of a normal deviate of

$$\frac{72.52-70.94}{\sqrt{3.16}}=\frac{1.58}{1.78}=0.89$$

The probability of this normal deviate is 0.81 (table 8); therefore, the error of misclassification for the Connecticut River population is 19 percent. This is also the error of misclassification for the Hudson River population. This function will correctly classify 81 percent or approximately 3 percent more than the simpler function first investigated.

Rao (1952) presents a test of significance to determine if the calculated discriminant function is better than some other assigned function. If the assigned function is:

$$Z=X_1+X_2+X_3+X_4+X_5+X_6$$

then $$D_Z^2=\frac{(\bar{Z}_1-\bar{Z}_2)^2}{V(Z)}$$

where

$$V(Z)=V(X_1)+V(X_2)+V(X_3)+V(X_4)+V(X_5)+V(X_6)+2\ \text{cov}\ (X_1X_2)+2\ \text{cov}\ (X_1X_3)+\ldots+2\ \text{cov}\ (X_5X_6).$$

Using values of w_{ij},

$$D_Z^2=\frac{12.9521}{6.0771}=2.131$$

To test if this function is as reliable as the one derived from the data, the following must be calculated:

$$U=\frac{1+N_1N_2D^2/(N_1+N_2)(N_1+N_2-2)}{1+N_1N_2D_Z^2/(N_1+N_2)(N_1+N_2-2)}-1$$

$$=\frac{1+\frac{(104)(91)}{(195)(193)}(3.22)}{1+\frac{(104)(91)}{(195)(193)}(2.13)}-1=0.169$$

$$F=\frac{U(N_1+N_2-1-p)}{p-1}=\frac{(0.169)(188)}{5}=6.35$$

F is a variance ratio with $(p-1)$ and (N_1+N_2-p-1) degrees of freedom. In the above instance, F has 5 and 188 degrees of freedom. This is a highly significant value indicating that the calculated function is significantly better than the simpler function.

Since the above discriminant function was based on the 1939 Hudson River sample and the 1945 Connecticut River sample, the 1940 Hudson River sample (table 12, appendix) can be used to demonstrate how the function works. Values for the Hudson River sample of 1940 were substituted in the formula:

$$Y=0.785X_1+0.577X_2+0.871X_3+0.234X_4+1.731X_5.$$

The resulting distribution of Y is tabulated in table 9. It can be seen that only 16 out of the 105 values are below 72.52, which is very close to the 19 percent expected. The mean Y for this sample is 74.25, which is in close agreement with the value of 74.10 obtained for 1939.

TABLE 9.—*Frequency distribution of the discriminant function* $Y=0.785X_1+0.577X_2+0.871X_3+0.234X_4+1.731X_5$ *for the 1940 Hudson River sample*

Y	Frequency	Y	Frequency
78.52–79.51	1	73.52–74.51	10
77.52–78.51	3	72.52–73.51	22
76.52–77.51	4	71.52–72.51	11
75.52–76.51	17	70.52–71.51	4
74.52–75.51	23	69.52–70.51	1

There are a number of assumptions upon which the preceding techniques are based. The two populations have to be multivariate normal populations with equal variances and covariances. It is assumed that the samples are large since sample values are substituted for population values when the discriminant function is calculated. There can be only two populations present, and any future individual that is to be assigned to one of these populations must belong to one of them. Of course if a third population is present with characters considerably different from the two original populations, it may be apparent that it represents a third group when the discriminant function is used.

The calculated discriminant function can be used for two different types of situations. In some studies one is interested in individuals (for example, to obtain scale samples) and would like to be certain that the fish chosen are from an assigned population. In other studies, the rela-

tive abundance or composition of a mixed population is desired. In this case there is little interest in the individuals.

If we are interested in classifying individuals, it is possible to adjust the classification region to reduce the chance of making errors. Those individuals that fall close to the division line (75.52) are the cause of the largest percentage of misclassifications. If some of these are not classified, the errors can be reduced. This amounts to dividing the sample into three groups: Hudson River shad, Connecticut River shad, and those that could be either with about equal probability. This third group consists of fish which remain unclassified because there is insufficient information upon which to make a positive identification. If only those fish with a Y less than 70.94 are called Connecticut shad and those with a Y greater than 74.10 are called Hudson River shad, the probability of misclassifying a Connecticut shad would be equal to the area under the normal curve from 74.10–70.94=3.16 to infinity. The corresponding normal deviate is 1.78 and the area above this value is 3.7 percent. Thus by not classifying approximately one-half of the sample, the number of wrong classifications is reduced to 3.7 percent.

The area of indecision could be extended even wider to further reduce the chance of error; however, if this procedure is carried too far, fish from other rivers might introduce a bias that would have to be considered. The assumption was made earlier that only fish from the Hudson and Connecticut Rivers were present in the sample; however, any fish that do not belong to one of these populations will be classified as though they did. Therefore, any appreciable number of fish from other rivers would cause additional errors. From the tagging experiments mentioned previously, it would appear that a very small percentage of shad present off the New Jersey coast do not belong to one of these two populations. If this is of the order of 5 percent, it might have little effect if all of the fish were classified. If a large portion of the sample remains unclassified, the errors introduced by these fish may be more harmful than those due to misclassifying fish from the two populations.

Estimates of the relative abundance of a mixed population can also be obtained. Three methods of accomplishing this will be presented. The most obvious is to use the discriminant function to classify each fish in the sample and then estimate the composition of the population from the composition of the sample. If there are only two populations present, this method may be quite satisfactory, but it does contain a bias. If a fishery is sampled which contains individuals from only one of these rivers, 19 percent of these fish would be classified as coming from the other race and the estimated composition would be 19 and 81 percent. Thus there would be a bias of 19 percent. If the region is modified so that the relative abundance is estimated from the individuals which are more likely to be classified correctly, then this bias will be reduced. By using the region Hudson>74.10>Unclassified>70.94>Connecticut the estimated composition of a sample which contains only Hudson River fish is

$$\frac{50}{50+3.7}=93.5 \text{ percent}$$

for a bias of 6.5 percent. If there are equal numbers of Hudson and Connecticut River fish present in a sample, then the errors of classification would cancel and the bias would be zero. The maximum bias would occur when a sample is composed of fish from only one river.

Another way of removing the bias is to assume that the error of classification in the sample is the same as the error in the discriminant function (i. e., 19 percent). Then the number of fish classified as Hudson River fish consists of 0.19 N_C and (1–0.19) N_H or $N_H=0.19N_C+(1-0.19)N_H$ where N_C and N_H are the numbers present in the population. Similarly for those classified as Connecticut River fish the following relation exists:

$$N_C=(1-0.19)N_C+0.19N_H$$

Substituting sample values (N_C and N_H), these two equations can be solved for N_C and N_H which can be used to determine the relative abundance.

A third estimate is obtained by using the following formula (Rao 1952, p. 300)

$$P=\frac{\overline{X}_H-\overline{X}_S}{\overline{X}_H-\overline{X}_C}$$

where $\overline{X}_H$, $\overline{X}_C$ and $\overline{X}_S$ are the averages of the discriminant function for the Hudson River, the Connecticut River and the sample of the mixed

population; P is an estimate of the proportion of the sample native to the Connecticut River.

It is not known which of these estimates would be best for the present problem. A few stray fish will have a greater effect on the first estimate than on the third, particularly if the strays are near one end of the distribution of the discriminant function. In the first type of estimate, they would be weighted more heavily because some of the individuals near the midpoints of the two populations would not be classified. In the third estimate, they would all receive the same weight. In any particular problem, perhaps all three of these estimates should be tried and the various estimates compared. If they are not in agreement, the factors causing the differences should be investigated. Plotting the distributions on probability paper may give some clue to the number of strays present in the samples.

DISCUSSION

The basic condition necessary for the demonstration of a distinct population of shad in each river is that the differences between rivers must be large compared to the differences between years. This condition has been met by the data examined in this study: however, some large differences between years have been reported and they are impossible to evaluate completely at this time. Warfel and Olsen (1947) reported average vertebral counts of 57.042 and 56.837 for 1945 and 1946 in the Connecticut River. This difference of 0.2 is significant. Raney and de Sylva (1953) also reported some differences between years for striped bass. They made the following statement about these differences: (p. 506)

> In any one river system such as the Hudson River there may be significant variations from year to year in any of the characters investigated. These fluctuations may be caused by differences in water temperature and perhaps other factors during larval life at the time when fin ray number is determined. The assumption is made that fin ray numbers are genetically fixed within narrow limits and the minor fluctuations which occur from year to year are due to different physical and perhaps chemical conditions at any one locality or differences in time of spawning, will tend to balance out when samples are taken over a period of several years.

From the statistical point of view, it does not matter what causes these differences when a mixed population is to be divided into its components. For example, the characters for the Hudson and Connecticut Rivers can change considerably from year to year, and the New Jersey catch can still be segregated providing samples are obtained from both rivers and a new discriminant function is calculated each year. Of course, it is essential that the populations be different.

From the biological point of view, the cause of these differences is important. If these differences are primarily genetic, the different populations should be considered taxonomically as races or even sub-species. Raney and de Sylva (1953) considered striped bass from the Hudson River and Chesapeake-Delaware area to be different taxonomic races and suggested calling them the Hudson race and Chesapeake-Delaware race. Similarly, future research may prove that there are actually taxonomic races (or sub-species) of shad.

From Rounsefell and Dahlgren's (1932) work on the herring, it appears that temperature may be one of the most important environmental variables to be studied. A rather simple experiment could be set up whereby it would be possible to hatch shad eggs in controlled water temperatures. This should produce a response curve between meristic counts and temperature, if such a relation exists. Such an experiment would be useful in evaluating the differences between years and rivers.

The human errors in making meristic counts should also be investigated. These certainly contribute to the total variation; therefore, the magnitude of such errors should be known. There are no doubt times when a certain amount of judgment must be used in deciding if a given ray actually should be included in a count. Similarly, gross errors of definition can be made in the counts. These various errors cannot be evaluated at this time, but any future work should certainly include a study of this part of the problem.

Future work with meristic counts will naturally require a great amount of statistical analysis. It is essential, therefore, that the surveys be planned in such a manner that a maximum amount of information can be obtained from them. Of the 1,800 fish collected from 1938 to 1945, only one-third of them could be utilized in a two-way analysis of variance. The surveys should include year classes, sampling dates within a year, different types of gear and different locations within

a river. It would also be worthwhile to study the relation between juveniles and the corresponding year class when it enters the fishery as adults. Probably many of the answers which can be obtained from meristic counts will lead to a better understanding of the biology of the various shad populations.

SUMMARY

It is a commonly accepted theory that shad from the different rivers on the Atlantic coast return to the same river to spawn when they reach sexual maturity. Tagging experiments have offered considerable evidence to support this theory. No shad tagged on the spawning ground of one river system has ever been recaptured on the spawning ground of another river system.

If a group of fish return to the same spawning ground year after year with little mixing from other populations, it would be expected that the fish within a river would be more like one another than like the fish from other rivers. Thus, if differences in some characteristics could be found between rivers, and, if these differences were large compared to the differences between years, the conditions necessary to support a "racial" theory would be present.

Because of the selectivity of the fishing gear used to obtain the samples of shad, it could not be assumed that the samples were random. This selectivity occurred in the size of the fish. The various characters under consideration in this paper were tested for a correlation with length; when no consistent correlations could be found, the samples were considered "representative," even though they were not random.

Analyses of variance of the various characters provided evidence that there were differences between fish from other rivers and, if differences were present between years, they were of a much smaller magnitude than the differences between fish from other rivers. This contributed additional evidence to support the theory of a separate population of shad in each major river.

A large commercial shad fishery exists along the coast of New Jersey, New York Bay, and Long Island. The fishermen in these three areas catch shad that are migrating to the Hudson or Connecticut Rivers. This ocean catch in some years is approximately one-third the size of the river catches and, therefore, should be included in any management plan for the two rivers. To establish a management plan which would include the ocean fisheries would require estimates of the composition of the catches made at these various locations. In the past, this would have had to be done by tagging experiments.

A discriminant function has been constructed in this study which will classify correctly about 81 percent of a mixed population of Hudson and Connecticut River shad. This function was constructed from data obtained from the Hudson River in 1939 and the Connecticut River in 1945. Data from a sample of Hudson River shad obtained in 1940 were substituted into this discriminant function. Out of the 105 fish, 16 were classified incorrectly; this is in good agreement with the theoretical 19 percent misclassifications.

Most of the individuals that are misclassified fall close to the midpoint between the two populations. It is possible to reduce the number of these mistakes by refusing to make a decision on the individuals that lie close to the dividing line between the two populations. This is equivalent to classifying the individuals into three parts: Hudson River, Connecticut River, and a third part for which no decision can be reached. Without using this procedure the chance of misclassifying an individual is 19 percent. By refusing to classify 50 percent of the sample, it is possible to reduce this error to 3.7 percent.

Several methods of estimating the relative abundance or composition of a mixed population are presented. These techniques could be used if one is interested in the population composition of a mixed sample rather than the identification of a particular individual.

LITERATURE CITED

ANDERSON, R. L., and T. A. BANCROFT.
1952. Statistical Theory in Research. McGraw-Hill Publishing Co., New York.

FREDIN, REYNOLD A.
1954. Causes of fluctuations in abundance of Connecticut River shad. U. S. Fish and Wildlife Service, Fish. Bull., vol. 54, pp. 247–259.

RAO, C. RADHAKRISHNA.
1952. Advanced Statistical Methods in Biometric Research. 390 pp. John Wiley and Sons, New York.

RANEY, EDWARD C., and DONALD P. DE SYLVA.
1953. Racial investigations of the striped bass *Roccus saxatilus* (Walbaum). Jour. of Wildlife Management, vol. 17, No. 4, pp. 495–509.

ROUNSEFELL, GEORGE A., and EDWIN H. DAHLGREN.
1932. Fluctuations in the supply of herring, *Clupea pallasii*, in Prince William Sound, Alaska. Bull. U. S. Bur. Fish., vol. 47, pp. 263–291.

TALBOT, G. B.
1954. Factors associated with fluctuations in abundance of Hudson River shad. U. S. Fish and Wildlife Service, Fish. Bull., vol. 56, pp. 373–413.

U. S. FISH and WILDLIFE SERVICE.
1949. Fishery Statistics of the United States, 1945. Statistical Digest 18. 298 pp.

WARFEL, HERBERT E., and YNGVE H. OLSEN.
1947. Vertebral counts and the problem of races in the Atlantic shad. Copeia, 1947, No. 3, pp. 177–183.

APPENDIX

TABLE 10.—*Frequency distribution of meristic counts used in the analysis of variance*

Location	Year	Number of anterior scutes							Number	Mean
		19	20	21	22	23	24	25		
Florida	1938	----	2	9	24	4	----	1	40	21.850
Do	1939	----	1	4	28	7	----	----	40	22.025
South Carolina	1938	----	1	22	12	5	----	----	40	21.525
Do	1939	1	----	14	22	3	----	----	40	21.650
North Carolina	1938	----	1	8	26	5	----	----	40	21.815
Do	1939	----	----	4	28	8	----	----	40	22.100
		Number of posterior scutes								
		12	13	14	15	16	17			
Florida	1938	----	2	12	24	2	----	----	40	14.650
Do	1939	----	1	11	18	10	----	----	40	14.925
South Carolina	1938	1	----	8	14	14	3	----	40	15.225
Do	1939	----	----	9	16	15	----	----	40	15.150
North Carolina	1938	----	1	3	20	15	1	----	40	15.300
Do	1939	----	----	2	12	23	3	----	40	15.675
		Number of anal rays								
		18	19	20	21	22	23			
Florida	1938	1	2	10	18	7	2	----	40	20.850
Do	1939	----	3	9	17	10	1	----	40	20.925
South Carolina	1938	----	4	12	13	9	2	----	40	20.825
Do	1939	----	1	12	18	8	1	----	40	20.900
North Carolina	1938	----	1	8	12	17	2	----	40	21.275
Do	1939	----	3	7	18	10	2	----	40	21.025
		Number of pectoral rays								
		14	15	16	17	18				
Florida	1938	----	2	25	15	----	----	----	40	16.325
Do	1939	----	2	34	4	----	----	----	40	16.005
South Carolina	1938	----	2	18	20	----	----	----	40	16.450
Do	1939	----	4	21	13	2	----	----	40	16.365
North Carolina	1938	----	13	23	4	----	----	----	40	15.775
Do	1939	1	5	30	4	----	----	----	40	15.925
		Number of vertebrae								
		53	54	55	56	57	58	59		
Florida	1938	----	1	2	11	19	7	----	40	56.725
Do	1939	----	----	2	16	19	3	----	40	56.575
South Carolina	1938	----	3	8	18	11	----	----	40	55.925
Do	1939	1	2	5	14	17	1	----	40	56.175
North Carolina	1938	----	----	1	16	19	4	----	40	56.650
Do	1939	----	----	6	6	25	2	1	40	56.650

TABLE 11.—*Meristic counts on samples of shad from the Hudson River, 1939*

Anterior scutes	Posterior scutes	Dorsal rays	Anal rays	Pectoral rays	Vertebrae
22	15	18	23	15	58
22	15	18	21	16	58
22	15	17	22	14	57
22	15	18	21	16	57
20	15	17	21	16	56
22	16	18	22	17	57
21	16	19	23	15	56
22	16	18	22	16	58
23	14	18	22	16	58
22	17	18	21	16	58
22	16	18	20	15	58
21	15	18	21	17	57
22	16	18	21	17	58
22	16	18	23	15	58
22	17	17	22	15	58
22	15	18	22	17	57
22	16	19	22	15	58
22	15	18	22	15	56
23	15	18	21	15	58
22	15	17	20	16	55
23	16	18	21	16	57
22	16	18	21	16	58
21	16	14	20	15	57
22	14	18	22	15	58
22	18	19	25	16	58
21	15	19	22	16	57
22	15	18	22	15	57
21	13	18	20	15	54
23	17	18	21	16	58
23	15	19	23	16	57
23	15	18	22	17	59
22	15	18	22	16	57
21	15	18	23	16	57
22	16	17	20	16	57
22	15	17	21	16	57
21	15	18	20	16	57
22	14	18	21	15	57
22	16	19	22	17	57
23	16	18	20	16	58
22	14	17	21	16	56
22	16	19	22	16	58
22	15	19	22	15	57
22	14	19	21	16	58
23	16	18	21	16	58
22	16	18	22	16	57
22	16	17	22	16	58
22	14	17	22	15	57
21	17	18	21	17	58
22	18	18	21	15	57
22	15	18	22	15	57
22	15	18	22	16	56
22	15	18	19	16	59
22	15	17	21	17	56
22	16	17	22	15	57
22	16	17	21	16	57
22	15	17	21	16	57
23	15	18	22	16	57
22	15	17	22	16	58
22	15	17	21	16	57
21	15	17	22	15	58
22	14	17	21	15	57
22	14	18	21	15	57
22	15	17	21	16	57
23	15	18	22	16	57
22	15	18	22	15	59
22	16	19	23	16	57

TABLE 11.—*Meristic counts on samples of shad from the Hudson River, 1939*—Continued

Anterior scutes	Posterior scutes	Dorsal rays	Anal rays	Pectoral rays	Vertebrae
22	16	18	22	17	57
22	14	18	20	16	57
22	15	18	21	16	58
22	15	19	23	15	57
22	15	17	21	16	57
23	15	19	22	16	57
23	16	18	22	17	58
22	15	17	23	15	58
22	16	18	22	16	57
21	16	17	21	15	57
22	17	19	22	16	58
22	16	19	20	15	57
22	15	18	22	17	56
21	14	19	22	16	56
22	15	19	22	16	57
23	14	19	21	16	57
22	15	20	23	16	58
23	15	18	22	16	56
22	16	18	22	15	59
22	16	18	22	16	57
21	16	18	22	16	57
21	15	18	23	15	57
22	14	19	23	15	57
22	15	18	22	15	57
22	15	18	21	16	57
22	15	18	22	15	57
23	15	18	23	17	58
21	16	18	22	14	58
22	15	17	21	17	58
22	16	18	22	16	57
22	16	17	21	16	57
23	15	18	20	16	57
23	15	18	21	16	58
23	16	18	22	16	57
23	14	18	22	15	58
23	16	17	23	16	58
22	15	18	23	16	59
22	16	19	22	16	58

TABLE 12.—*Meristic counts on samples of shad from the Hudson River, 1940*

Anterior scutes	Posterior scutes	Dorsal rays	Anal rays	Pectoral rays	Vertebrae
20	15	19	21	16	54
22	16	19	22	17	58
22	16	18	20	17	57
22	16	18	22	16	58
23	15	18	21	16	57
21	16	17	22	15	58
21	15	17	21	15	57
23	16	18	21	16	57
22	16	18	23	16	58
22	15	17	22	15	57
22	15	18	21	16	58
22	16	18	21	17	57
23	16	17	22	16	57
23	14	18	21	15	56
21	15	18	21	16	57
22	15	18	22	15	57
23	15	17	22	15	58
22	16	17	21	16	58
22	16	18	22	15	58
22	15	18	21	16	57
22	16	19	22	16	57
22	17	17	22	15	58
22	15	18	21	15	58
21	17	18	22	16	56
22	15	19	22	16	57
23	15	18	22	16	57
23	16	18	22	16	57

TABLE 12.—*Meristic counts on samples of shad from the Hudson River, 1940*—Continued

Anterior scutes	Posterior scutes	Dorsal rays	Anal rays	Pectoral rays	Vertebrae
22	15	19	23	16	58
20	15	17	22	15	55
22	16	18	21	15	57
22	16	18	22	15	58
23	16	20	24	16	59
22	17	19	20	17	58
22	15	19	24	15	59
22	16	18	22	16	56
21	16	17	21	15	57
22	16	18	21	16	58
22	15	18	21	16	57
22	16	17	21	15	57
21	15	17	20	16	56
22	17	18	22	15	57
23	16	19	22	16	58
22	15	17	22	16	57
22	16	18	23	15	58
23	15	17	19	16	57
22	15	19	21	15	57
22	17	19	21	16	58
22	16	19	21	17	57
22	16	18	21	16	58
22	16	18	22	16	58
23	14	19	22	16	55
22	16	18	21	16	58
22	17	18	21	16	57
22	16	17	20	16	57
22	17	17	20	15	58
23	16	18	22	15	58
21	15	17	22	16	58
23	16	20	23	17	58
22	16	18	21	16	57
23	15	18	21	15	57
22	16	19	21	16	57
22	14	16	20	16	58
22	16	17	21	16	58
22	16	18	22	16	56
21	16	18	21	15	58
24	16	17	20	15	59
23	16	18	22	16	58
23	15	17	21	16	58
24	16	18	21	16	58
22	16	18	22	15	57
23	16	18	22	16	57
22	15	19	23	16	58
22	15	17	20	15	57
22	16	17	23	17	58
22	15	17	23	16	58
22	16	19	21	16	59
21	15	17	23	16	56
22	16	18	20	15	57
21	15	18	22	16	56
23	15	18	20	16	58
22	16	17	22	15	59
22	16	18	22	16	57
23	15	18	21	15	58
22	15	18	22	16	57
22	16	17	22	17	57
23	15	17	20	15	56
22	16	19	20	16	58
22	17	19	22	15	58
22	15	18	22	14	57
22	15	17	20	16	56
23	15	18	22	16	57
22	15	17	23	15	57
22	16	18	21	15	57
22	14	19	22	16	57
23	16	19	23	16	58
21	15	18	23	16	57
22	16	18	22	17	58
22	16	18	22	15	59
22	16	19	24	16	60
22	17	18	22	15	57
22	15	18	21	15	55
22	17	18	22	16	60
22	17	18	20	16	58
22	17	18	22	16	58

TABLE 13.—*Meristic counts on samples of shad from the Connecticut River, 1945*

[The last 10 samples in table are incomplete and therefore were not used in the discriminant function analysis]

Anterior scutes	Posterior scutes	Dorsal rays	Anal rays	Pectoral rays	Vertebrae
21	15	18	21	14	57
22	14	16	20	15	55
21	14	17	21	13	57
22	15	17	21	15	57
22	15	17	20	14	56
21	14	16	22	14	57
22	14	16	21	13	57
21	14	16	20	13	55
22	14	17	21	16	55
22	13	18	23	14	56
22	16	18	21	15	59
22	14	18	22	15	57
22	15	17	20	15	56
20	14	18	22	15	55
22	14	18	23	15	58
21	14	17	22	15	57
22	15	16	21	15	57
21	14	16	20	15	57
21	16	18	19	14	58
23	17	17	21	13	60
22	15	18	20	14	55
23	14	17	22	14	57
21	15	17	22	16	55
21	15	18	22	14	57
22	15	18	21	15	58
23	15	16	19	16	57
21	14	18	21	14	58
23	15	18	21	15	59
22	14	18	22	15	55
21	14	16	22	15	57
22	15	17	21	16	58
21	16	18	21	14	59
21	14	17	21	14	56
23	15	17	21	15	57
21	14	18	22	14	55
22	16	18	20	15	57
21	15	19	21	15	55
22	14	19	21	14	58
20	16	17	21	16	54
21	15	17	21	16	55
22	16	18	20	14	57
22	14	18	21	14	59
22	15	18	22	16	56
22	15	17	20	14	57
21	15	16	21	15	57
21	14	18	21	14	56
21	16	17	22	15	57
21	16	17	22	16	59
22	15	18	21	15	58
21	15	17	21	14	56

TABLE 13.—*Meristic counts on samples of shad from the Connecticut River, 1945*—Continued

Anterior scutes	Posterior scutes	Dorsal rays	Anal rays	Pectoral rays	Vertebrae
22	15	17	21	14	55
22	15	18	21	16	58
22	15	16	22	15	57
21	15	17	22	15	58
22	14	19	22	16	57
21	13	17	21	15	55
21	15	17	21	15	57
22	16	17	21	14	55
21	14	17	20	16	56
22	14	17	20	14	57
22	16	17	21	13	57
21	16	17	23	14	56
22	14	18	21	16	57
21	14	18	23	16	59
22	16	17	23	14	57
22	15	17	22	16	58
21	15	16	20	15	55
22	15	17	22	15	58
21	13	17	23	15	59
21	15	17	21	15	55
22	16	18	23	15	56
22	14	18	21	15	56
22	16	17	20	14	57
21	15	17	21	15	56
23	16	18	21	14	57
22	15	15	19	14	56
22	14	17	20	15	56
22	15	15	20	15	57
22	16	18	23	14	56
22	16	17	23	13	56
22	16	17	21	15	56
21	14	16	23	14	57
22	14	19	21	13	57
21	16	17	21	15	58
22	14	18	21	15	56
21	16	16	21	15	57
21	15	16	22	14	57
22	14	17	22	15	57
21	16	17	21	15	57
21	15	17	22	16	55
22	16	18	22	16	58
22	15		21	15	57
21	15		20		57
21	15		19	14	56
22	15		21	14	57
21	16			13	56
22	15		23	15	57
22	15			14	56
20	16	18		15	57
22	15	17		15	55
22	15	17		14	55

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

SEXUAL MATURITY AND SPAWNING OF ALBACORE IN THE PACIFIC OCEAN

BY TAMIO OTSU AND RICHARD N. UCHIDA

FISHERY BULLETIN 148

From Fishery Bulletin of the Fish and Wildlife Service

VOLUME 59

UNITED STATES GOVERNMENT PRINTING OFFICE • WASHINGTON • 1959

For sale by the Superintendent of Documents, U. S. Government Printing Office
Washington 25, D. C. Price 20 cents.

Library of Congress catalog card for this bulletin:

Otsu, Tamio.

Sexual maturity and spawning of albacore in the Pacific Ocean, by Tamio Otsu and Richard N. Uchida. Washington, U. S. Govt. Print. Off., 1959.

iv, 287–305 p. illus., map, diagrs., tables. 26 cm. (U. S. Fish and Wildlife Service. Fishery bulletin 148)

"From Fishery bulletin of the Fish and Wildlife Service, volume 59."

Bibliography: p. 304–305.

1. Tuna fish. I. Uchida, Richard N., joint author. II. Title. (Series: U. S. Fish and Wildlife Service. Fishery bulletin, v. 59, no. 148)

[SH11.A25 vol. 59, no. 148] Int 59–11

U. S. Dept. of the Interior. Library
for Library of Congress

Library of Congress catalog card for the series, Fishery Bulletin of the Fish and Wildlife Service:

U. S. ***Fish and Wildlife Service.***
Fishery bulletin. v. 1–
Washington, U. S. Govt. Print. Off., 1881–19

v. in illus., maps (part fold.) 23–28 cm.

Some vols. issued in the congressional series as Senate or House documents.
Bulletins composing v. 47– also numbered 1–
Title varies: v. 1–49, Bulletin.
Vols. 1–49 issued by Bureau of Fisheries (called Fish Commission, v. 1–23)

1. Fisheries—U. S. 2. Fish-culture—U. S. I. Title.

SH11.A25 639.206173 9–35239 rev 2*

Library of Congress [r55e½]

CONTENTS

	Page
Source of materials	287
North Pacific	287
Hawaiian Islands	289
Central equatorial Pacific	289
Description of the gonads	289
Testes	289
Ovaries	289
Subsampling the ovary	290
Distribution of mature eggs within an ovary	290
Developmental stages of the egg	292
Early developing	292
Late developing	292
Advanced	292
Classification of ovaries	293
Results of gonad examination	293
North Pacific	294
Hawaiian Islands	294
Central equatorial Pacific	296
Evidence of spawning	299
Minimum size of spawning fish	300
Frequency of spawning	300
Fecundity	300
Ovary size as index of maturity	300
Discussion	302
Summary	303
Literature cited	304

ABSTRACT

This report presents the results of a study of gonadal development and spawning in the albacore, *Germo alalunga* (Bonnaterre). The study is based on examination of the reproductive organs, principally the ovaries from albacore collected in three general areas: the North Pacific, the Hawaiian Islands, and the central equatorial Pacific.

The ovaries were classified in three stages of relative maturity: early developing, late developing, and advanced, on the basis of the most advanced eggs present. According to this classification, the early developing category included the thin ribbonlike ovaries from sexually immature fish as well as ovaries from the larger, adult fish which showed no signs of egg development beyond this particular stage. The other two categories, on the other hand, included only ovaries from adult fish.

The North Pacific albacore were either juveniles or sexually dormant adults with early developing gonads. The Hawaiian albacore showed varying degrees of maturity from early developing to advanced, with the bulk of the ovaries in the late developing stage. The ovaries from central equatorial Pacific fish were in the early developing and late developing stages, with the early developing stage predominating.

Our data show that albacore taken north of Hawaii by research vessels of the Pacific Oceanic Fishery Investigations, as well as albacore taken by the Japanese in the spring live-bait and winter longline fisheries, and those in the American west coast summer fishery are nonspawning fish, either juveniles or adult fish whose gonads show no signs of incipient or past spawning. Albacore apparently do not spawn in the temperate waters of the North Pacific. On the other hand, it appears that the albacore in the region of the Hawaiian Islands and in the central equatorial Pacific represent a segment of the population which, after attaining a certain size in temperate waters of the North Pacific, moves south into tropical and subtropical waters to reproduce.

SEXUAL MATURITY AND SPAWNING OF ALBACORE IN THE PACIFIC OCEAN

By Tamio Otsu and Richard N. Uchida, *Fishery Research Biologists, Bureau of Commercial Fisheries*

The albacore, *Germo alalunga* (Bonnaterre), is a commercially important tuna, valued highly for its excellent canning qualities. In the Pacific the major fisheries for this species are conducted by the Japanese in an area extending from the coast of Japan to the vicinity of the International Date Line, and by the Americans along the west coast of the United States. Tag recoveries during recent years have shown that albacore undertake extensive migrations across the Pacific (Ganssle and Clemens 1953, Blunt 1954, Otsu and Uchida 1959), thus suggesting that these major fisheries may be dependent on a single population.

Albacore are also widely distributed throughout the tropical Pacific, but in this region they are generally taken incidental to the catch of other species of tuna. It is not known whether albacore of the tropics belong to the same population as those of temperate latitudes, or whether they form part of another population. According to present knowledge, albacore do not spawn in temperate waters. Information on the areas of spawning might provide a clue to the general distribution of the populations that support the American and Japanese albacore fisheries.

The research program of the Pacific Oceanic Fishery Investigations (POFI) of the Bureau of Commercial Fisheries has included a study of gonadal development and spawning in the albacore, which has been financed by the Saltonstall-Kennedy Act (Public Law 466, 83rd Congress). The present report on the albacore is based on examination of the reproductive organs, principally the ovaries, collected in three general areas: the North Pacific, the Hawaiian Islands, and the central equatorial Pacific. Important differences in gonad development were noted for fish from these three areas. The size at which albacore attain sexual maturity was determined, and what appears to be a major spawning locality can now be defined.

NOTE.—Approved for publication January 13, 1958. Fishery Bulletin 148.

We gratefully acknowledge the contributions of the following persons: R. S. Shomura and B. Wyatt who collected ovaries at the Honolulu auction markets; the managements of the United Fishing Agency, Ltd., and the Hawaii Fishing Co., Ltd., and the several fish dealers who permitted us to sample the albacore landings; Shoji Ueyanagi of the Nankai Regional Fisheries Research Laboratory in Kochi, Japan, who sent us samples of ovaries; and H. S. H. Yuen for valuable suggestions pertaining to sampling procedure.

SOURCE OF MATERIALS

NORTH PACIFIC

A total of 126 gonads from both sexes was collected between January 1955 and November 1956 in the North Pacific on POFI's exploratory fishing cruises (table 1 and fig. 1). Most of the sampled fish, ranging in length from 50 to 112 cm. (weight, 6 to 65 lbs.), were taken at the surface by gill nets or trolling; the few albacore larger than 87 cm. were taken exclusively on longline

TABLE 1.—*The number of albacore gonads obtained in the three areas [1] in various years*

Month	North Pacific				Hawaii		Central Equatorial Pacific			
	1955		1956							
	Male	Female	Male	Female	1955	1956	1952	1953	1956	1957
January	4	5	0	0	0	0	0	0	0	3
February	2	1	0	0	0	0	2	11	0	8
March	0	0	1	1	0	0	1	3	0	0
April	0	0	0	4	0	0	0	0	0	0
May	0	0	0	0	2	0	0	22	0	0
June	0	0	0	0	18	2	0	0	0	0
July	0	0	5	6	5	9	0	0	0	0
August	4	9	10	12	5	1	0	1	1	0
September	2	0	0	1	1	7	0	0	7	0
October	6	5	3	3	1	1	1	0	0	0
November	0	0	24	18	0	4	6	0	0	0
December	0	0	0	0	0	0	0	0	0	0
Total	18	20	43	45	32	24	10	37	8	11

[1] Fish of both sexes were sampled in the North Pacific but only females in the other two areas.

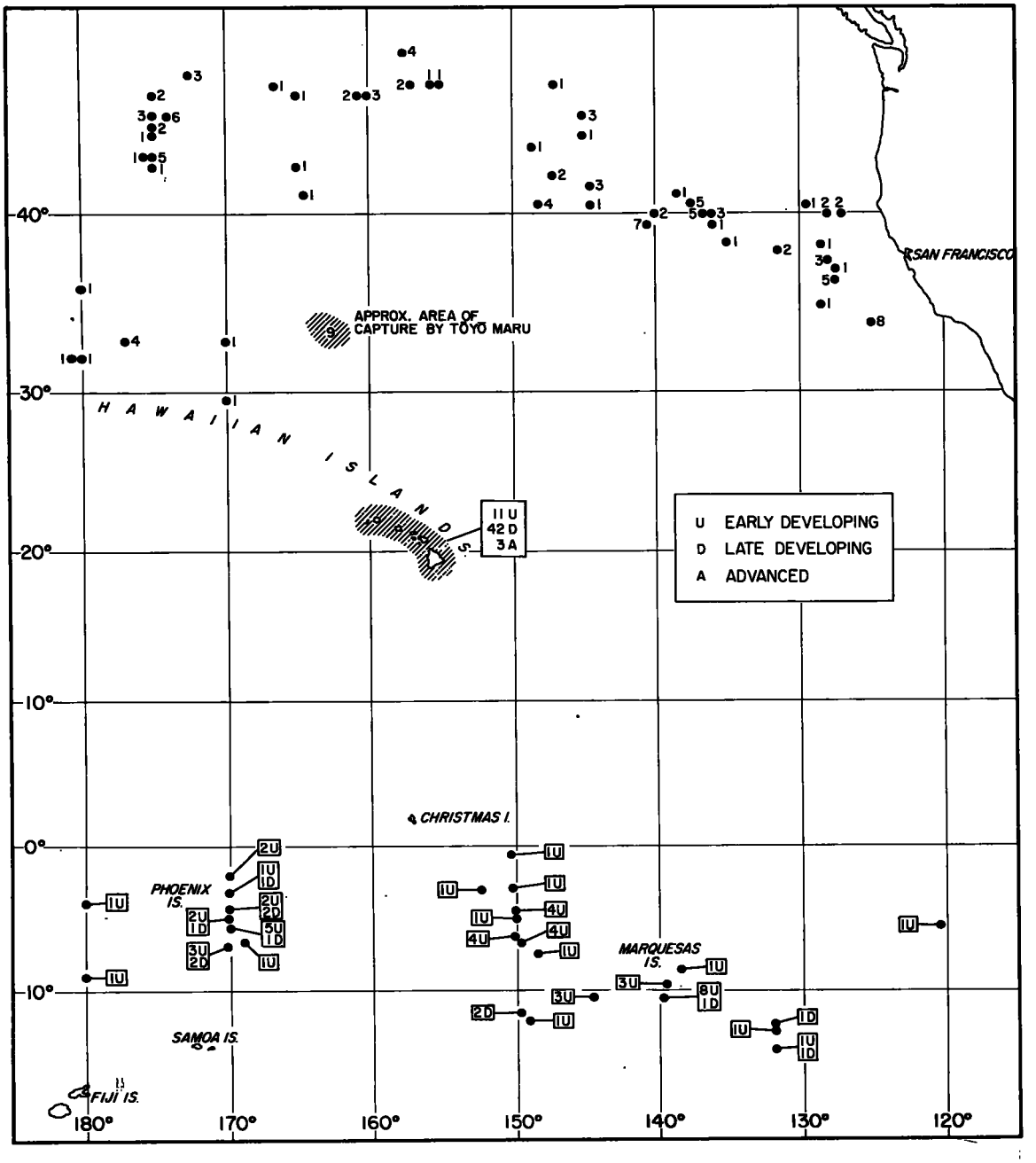

FIGURE 1.—Localities at which albacore gonads were collected. The Hawaiian and central equatorial Pacific samples consisted only of ovaries (stages of development shown); the North Pacific samples included testes and ovaries, all of which were in the early developing stage. (U=early developing, D=late developing, A=advanced stage).

(fig. 2). Immediately after the fish were landed the gonads were removed and preserved in 10-percent formalin. Data recorded were the date and locality of capture, fork length (weight was not always recorded), and the type of fishing gear.

In addition to the albacore taken on POFI vessels, we examined ovaries from a catch of albacore landed in Honolulu by a Japanese longline vessel, the *Tōyō Maru*, in January 1955. This vessel reportedly obtained her catch northwest of the

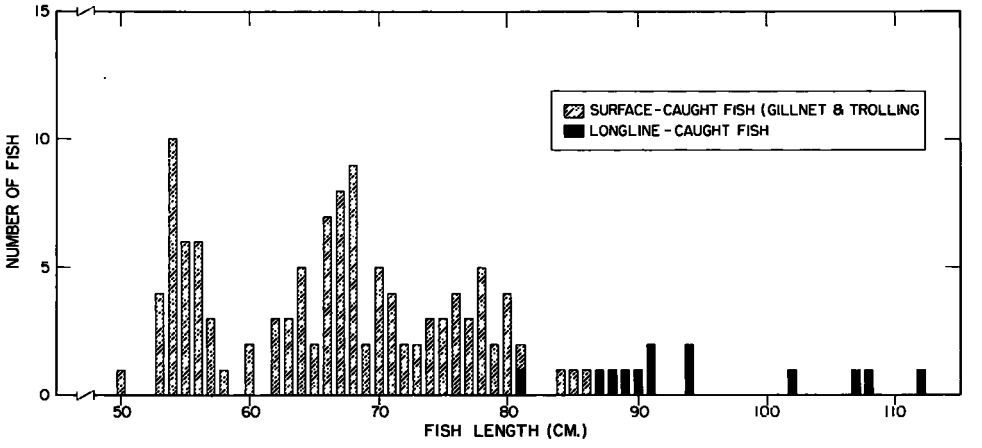

FIGURE 2.—Sizes of albacore sampled in the North Pacific.

Hawaiian Islands in the general area shown in figure 1.

HAWAIIAN ISLANDS

Ovaries from 56 fish ranging in length from 93.1 to 112.4 cm. (weight, 33 to 62 lbs.) were obtained in 1955 and 1956 from landings of the Hawaiian longline fishery (table 1, fig. 1). These fish were captured within 20 miles of the main Hawaiian Islands, mostly during the months of June to September. A detailed description of this fishery is given by June (1950) and Otsu (1954). These albacore and those taken by the *Tōyō Maru* were sampled at the auction markets of the United Fishing Agency, Ltd., and the Hawaii Fishing Co., Ltd., both in Honolulu. The ovaries were preserved in 10-percent formalin. Data obtained for each fish were the date of landing, locality of capture, fork length, and weight.

CENTRAL EQUATORIAL PACIFIC

The bulk of the samples from the central equatorial Pacific was obtained from three areas: (1) between the Equator and 7° S. latitude along 170° W. longitude; (2) between the Equator and 12° S. along 150° W. longitude; and (3) from the general region of the Marquesas Islands, 132° W. to 140° W. longitude (table 1, fig. 1). A total of 66 female albacore, all captured on longline on POFI cruises, was sampled between February 1952 and February 1957; these fish ranged in length from 84.6 to 104.8 cm. (weight, 29 to 54 lbs.). In general, sampling in this area was sporadic both in space and in time. The method of sampling the ovaries was similar to that described for the collection of gonads in the North Pacific.

DESCRIPTION OF THE GONADS

TESTES

The testes are paired, elongate organs suspended by the mesorchium in the body cavity. They are thin and ribbonlike in immature fish but with advance in maturity, they develop into somewhat flattened, whitish-yellow organs which are relatively solid. Their products are collected by a series of small ducts, vasa efferentia, leading posteriorly to a larger duct, the vas deferens, which opens to the exterior through the urogenital orifice.

June (1953) examined both the testes and ovaries in his study of the spawning of yellowfin tuna in Hawaiian waters but found that for this study "the testes were not suitable because no quantitative measure of their sexual products could be found that would provide reasonably accurate estimates of their relative stages of development." We found this to be true for the albacore also, and the testes were therefore merely designated in this report as immature or mature on the basis of their size and the presence or absence of milt.

OVARIES

The ovaries, like the testes, are paired, elongate organs suspended from the dorsal wall of the body cavity by the mesovarium. In immature fish, the ovaries are ribbonlike (fig. 3), may measure as little as 2 or 3 millimeters in diameter, and closely resemble the immature testes in appearance.

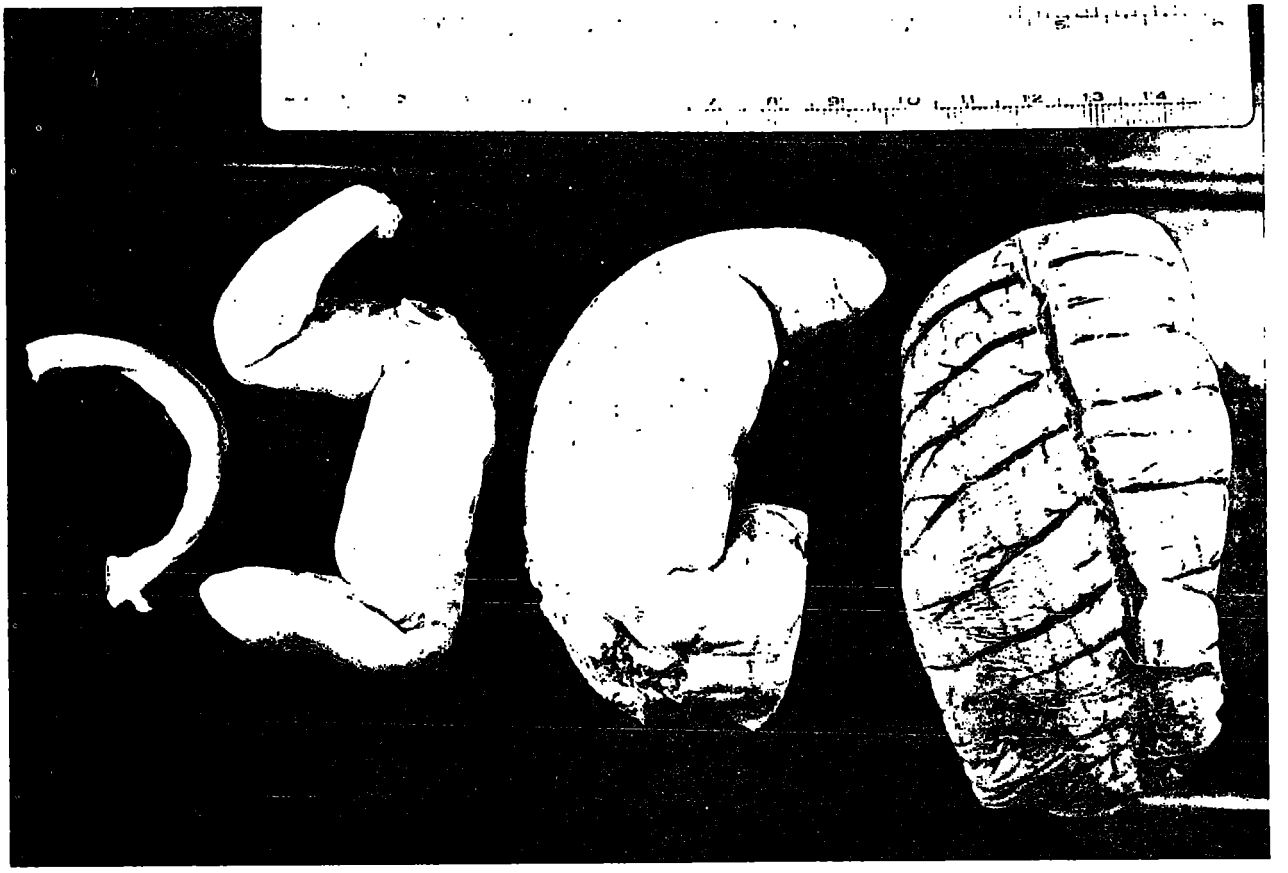

FIGURE 3.—Albacore ovaries in various developmental stages (only part of each ovary is shown). Left to right: a ribbon-like ovary taken from a sexually immature, 75.8-cm. fish (ovary weight 9 grams); an early developing ovary from a 99.2-cm. fish (ovary weight 74 gms.); a late developing ovary from a 98. 5-cm. fish (ovary weight 275 gms.); and an advanced ovary from a 107.6-cm. fish (ovary weight 916 gms.). Photograph by H. Yoshida.

They become progressively enlarged in length and girth as the fish attain sexual maturity, and with the final ripening of the eggs, they may attain a diameter of more than 40 mm. In the more advanced stages, the ovaries are nearly circular in cross section and the right ovary is usually slightly larger than the left. They have a ribbed internal cavity throughout their length and unite posteriorly with a thick-walled oviduct which opens exteriorly through the urogenital orifice.

SUBSAMPLING THE OVARY

An objective method for determining the degree of maturity of an ovary is to measure the diameters of the constituent eggs. In order to reduce the amount of work involved in measuring the tremendous number of eggs within an ovary, it was necessary in our study to resort to subsampling. To subsample an ovary with confidence, however, requires that the distribution of eggs of various sizes throughout an ovary as well as differences between the two ovaries of a pair be determined.

The procedure followed in this study was in general similar to that described by Yuen (1955) who investigated the maturity and fecundity of the bigeye tuna in the Pacific. Eggs from a sample were measured in a Sedgewick-Rafter counting chamber ruled with parallel guide lines. The parallel lines prevented duplicate measurements of the same egg. Measurements were made to the nearest micrometer unit (0.0167 mm.) using an ocular micrometer. Because the formalin-preserved eggs of the albacore are not perfectly spherical, we adopted the method of Clark (1934), June (1953), Yuen (1955), and others of measuring the random diameter parallel to the ruled lines in the counting chamber in whatever axis the egg lies.

DISTRIBUTION OF MATURE EGGS WITHIN AN OVARY

Several tests were conducted to evaluate sampling procedures. First, it was thought necessary to determine whether advanced eggs were evenly distributed within an ovary. For this test, thin cross sections were taken from the anterior, middle, and posterior parts of the right member of one of the most advanced ovaries in the collection (fig. 4a). The cross sections were

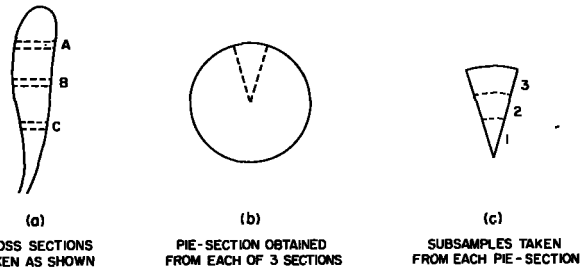

FIGURE 4.—Schematic representation of method used to obtain test samples for determining most efficient sampling procedure.

labeled A, B, and C, respectively. A triangular section was then obtained from each of the three cross sections (fig. 4b). Each triangular section was further subdivided into three subsamples representing, respectively, the center, mid-region, and periphery of the ovary (fig. 4c). Thus, for section A there were positions A_1, A_2, and A_3; for section B, positions B_1, B_2, and B_3; and for section C, positions C_1, C_2, and C_3. These samples were weighed to the nearest 0.001 gram. All of the eggs in the most mature group were then measured. The weights and measurements are given in table 2.

An analysis of variance (table 3) indicated a significant difference ($P<0.05$) between positions in the mean egg diameters but none between sections. The diameter means for sections A, B, and C were 0.842 mm., 0.848 mm., and 0.842 mm., respectively. The results showed that for sections A and B, the mean egg diameter was largest at the periphery of the ovary. The situation was reversed for section C where the mean diameter was least at the periphery and greatest near the central lumen (table 2). It has not been determined whether the differences between positions are real or an artifact of preservation.

The number of eggs in the most advanced group to be expected from 0.1 gram of each sample was

TABLE 2.—*Frequency distributions of diameters of the most advanced group of eggs from the various parts of an ovary (albacore No. 42—Hawaii)*

Diameter (in millimeters)	Sample No.								
	A_1	A_2	A_3	B_1	B_2	B_3	C_1	C_2	C_3
0.668	0	0	0	0	0	0	0	0	1
.685	0	1	0	1	0	0	0	1	1
.701	2	3	2	1	1	0	1	0	2
.718	1	4	4	1	0	1	2	1	2
.735	0	0	4	1	1	0	2	3	4
.752	1	7	3	1	1	1	2	8	9
.768	5	16	5	2	5	1	6	12	12
.785	11	13	10	5	2	1	7	13	10
.802	14	16	15	6	10	7	9	17	13
.818	14	16	15	9	9	4	12	11	14
.835	23	18	23	12	14	6	22	28	22
.852	13	22	13	15	14	7	23	14	19
.868	15	14	16	10	13	16	20	16	17
.885	10	18	9	12	7	5	13	10	12
.902	1	8	13	3	5	1	11	12	5
.918	2	11	8	1	6	3	6	6	6
.935	2	3	7	1	2	4	4	3	6
.952	1	3	5	2	2	2	3	4	0
.969	1	3	6	1	2	0	2	4	3
.985	0	2	1	0	0	1	1	1	3
1.000	0	1	2	0	0	0	1	0	2
Sum	116	179	161	84	94	60	147	164	163
Mean diameter (mm.)	0.833	0.838	0.850	0.842	0.848	0.858	0.850	0.838	0.837
Sample weight (gms.)	.053	.088	.080	.039	.047	.034	.088	.078	.070

then calculated from table 2 and tested by analysis of variance (table 4). The results showed that there was no significant difference ($P>0.05$) in the relative numbers per unit weight of ovary between sections A, B, and C.

A comparison was made of the egg-diameter frequencies of the right and left ovaries (albacore No. 74, Hawaii). A random sample was obtained from the central section of each ovary and all eggs larger than 10-micrometer units (0.167 mm.) were measured (table 5). The comparison resulted in a chi-square of 19.77 ($P=0.9$, 30 *d. f.*[1]) indicating a general similarity in the distributions between the two ovaries.

The results of the various tests suggested that representative samples of an ovary could be obtained anywhere along its length, provided a

TABLE 3.—*Analysis of variance of diameters of the most advanced eggs from different parts of the ovary (albacore No. 42, Hawaii)*

Source of variation	Degrees of freedom	Sum of squares	Mean square
Between sections	2	40.53	20.27
Positions within sections	6	165.85	*27.64
Individuals within positions	1,159	13,770.45	11.88
Total	1,167	13,976.83	

*Indicate significant ($p<0.05$) mean square value.

[1] The last four classes in the frequency distributions were combined because of the low numbers.

random subsample was obtained from the cross section. It was also shown that either of the two ovaries could be used. The procedure routinely used was to measure a random subsample from the mid-section of an ovary.

TABLE 4.—*Analysis of variance of numbers of most advanced eggs from different parts of the ovary (albacore No. 42, Hawaii)*

Source of variation	Degrees of freedom	Sum of squares	Mean square
Between sections	2	156.24	78.12
Positions within sections	6	3,152.96	525.49
Total	8	3,309.20	

TABLE 5.—*Egg diameter frequencies of right and left ovaries from the same fish (albacore No. 74, Hawaii)*

Diameter		Frequency	
Micrometer units [1]	Mm.	Right ovary	Left ovary
10	0.167	259	282
11	.184	137	147
12	.200	124	122
13	.217	117	101
14	.234	107	108
15	.250	115	93
16	.267	82	71
17	.284	72	64
18	.301	75	75
19	.317	69	64
20	.334	51	51
21	.351	48	44
22	.367	54	43
23	.384	56	55
24	.401	45	51
25	.418	59	46
26	.434	40	32
27	.451	39	30
28	.468	47	32
29	.484	29	32
30	.501	32	33
31	.518	16	19
32	.534	15	21
33	.551	26	32
34	.568	27	29
35	.584	27	28
36	.601	18	25
37	.618	20	19
38	.635	19	13
39	.651	10	8
40	.668	6	4
41	.685	2	1
42	.701	3	1
43	.718	1	0
Sum		1,847	1,776

[1] 1 micrometer unit = .0167 mm.

DEVELOPMENTAL STAGES OF THE EGG

Eggs were classified as early developing, late developing, and advanced. The descriptions are based on formalin-preserved material.

Early Developing

This category includes the primitive eggs found in all ovaries and eggs in the beginning stages of development. The primitive eggs vary from about 0.01 to 0.13 mm. in diameter, possess relatively large nuclei, and are transparent. In early development the eggs increase in size and become semi-opaque from deposition of yolk granules. The maximum diameter of eggs in the early developing stage is about 0.4 mm.

Late Developing

In this stage, the eggs are completely opaque from the heavy accumulation of yolk granules. They now range from 0.4 to about 0.8 mm. in diameter.

Advanced

Distinct changes occur in the eggs as they approach ripeness. They lose their opacity and become semitransparent; the nucleus cannot be detected at this stage, and a conspicuous golden-yellow oil globule appears. These advanced but not fully ripe eggs range from about 0.7 to 1.0 mm. in diameter in the most advanced sample available for study.

CLASSIFICATION OF OVARIES

The ovaries were classified into three categories of relative maturity, early developing, late developing, and advanced, according to the stages of development of the largest eggs. In this classification, the early developing category included the thin ribbonlike ovaries from sexually immature fish and ovaries from the larger adult fish which showed no signs of egg development beyond the early stage. The other two categories, on the other hand, included only ovaries from adult fish (fig. 3).

As an example of the classification, a frequency distribution of egg diameters from a fish classed as having late developing ovaries (fig. 5) is shown. In addition to the mode of largest eggs centering at 0.63 mm., other groups of eggs are evident. There are large numbers of early developing eggs less than 0.4 mm. in diameter, and there is evidence of a second group of late developing eggs, one with a mode at 0.43 mm. Both groups of late developing eggs were opaque, characteristic of this stage.

An advanced ovary (fig. 6) has a mode of semitransparent eggs centering at about 0.86 mm. In addition there is one or more groups of late developing eggs between 0.4 and 0.6 mm., possibly a less developed group at about 0.33 mm., as well as the usual large numbers of early developing eggs.

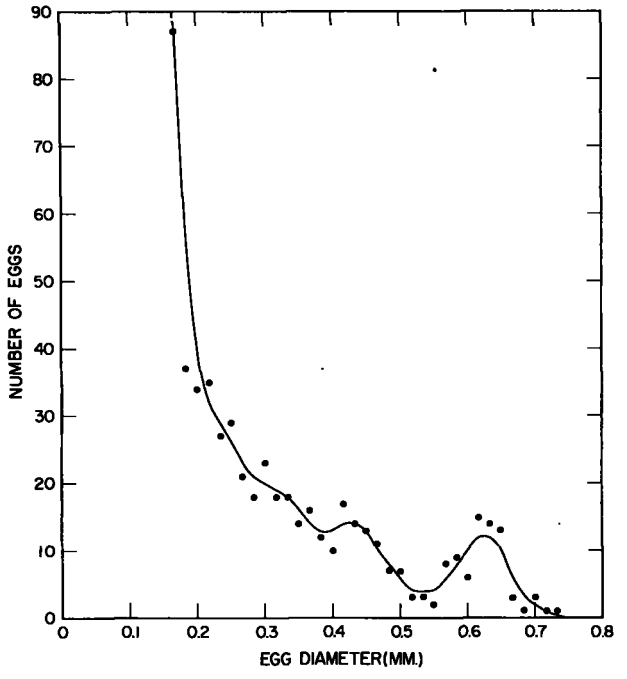

FIGURE 5.—Frequency curve of 550 egg diameters measured from a late developing ovary of a 55-pound albacore taken in Hawaiian waters on June 15, 1955. The curve was derived by smoothing the data twice by a moving average of three.

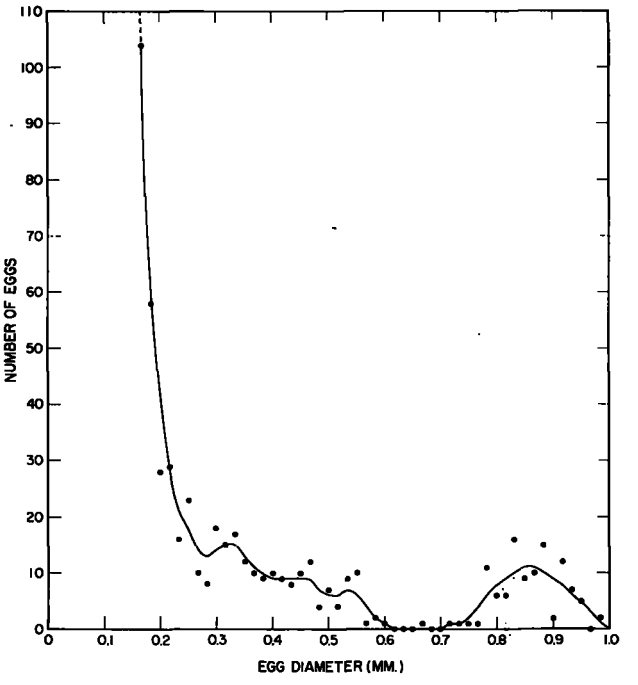

FIGURE 6.—Frequency curve of 550 egg diameters measured from an advanced ovary of a 47-pound albacore taken in Hawaiian waters on June 8, 1955. The curve was derived by smoothing the data twice by a moving average of three.

RESULTS OF GONAD EXAMINATION

NORTH PACIFIC

Since the gonads of albacore in the North Pacific are generally thin and ribbonlike (early developing), the sexes are often difficult to distinguish by gross examination in the field. For this reason, gonads of both sexes were collected and the sex was determined in the laboratory by microscopical examination. Of the gonads of 126 fish examined, 62 were ovaries and 64 were testes.

The ovaries, the bulk of which weighed less than 50 grams, contained only early developing eggs; the maximum egg diameter measured was 0.25 mm. The most enlarged pair of ovaries (131 grams) obtained from the largest female fish sampled (length 108.1 cm., weight 58 lbs.) contained eggs which measured less than 0.13 mm. in diameter. The testes were also immature.

Although large fish (longer than 90 cm.) were not well represented in the sample, field observations of the gonad condition of longline-caught fish gave supplementary evidence that North Pacific fish were either sexually immature juveniles, or adult fish with early developing gonads. Table 6 lists the observations, based strictly on gross inspection, recorded by various members of the POFI staff. Presumably, the gonads of these large fish were sufficiently enlarged so that sex could be determined with some assurance. While the observations recorded as "spent," "spawned-out," and "recovering" might be questioned, there is little doubt that the "immature" fish, corresponding to our early developing category, were correctly designated. The observation dated January 28, 1955 (table 6), for a male albacore of 93.3 cm., is not necessarily indicative of advanced maturity. Male albacore taken in tropical and subtropical waters almost invariably contain some milt in the testes regardless of the size of the gonads. Brock (1943) found that milt could be squeezed from the testes of albacore captured off the coast of Oregon, but the females from this region were judged to be immature.

Our observations indicate that albacore in the central and eastern North Pacific are either sexually immature fish, or are adults which do not show signs of near-spawning. Partlo (1955)

TABLE 6.—*Field observations on sex and maturity of large albacore (over 90 cm.) taken on longline during POFI cruises to the North Pacific* [1]

Date of capture	Position of capture		Fork length, cm.	Sex	Description of gonad condition
	Latitude	Longitude			
Jan. 22, 1954	26°28′ N.	159°39′ W.	107.5	M	Immature.
Jan. 27	33°58′ N.	159°44′ W.	118.3	M	Do.
Do	33°58′ N.	159°44′ W.	112.7	M	Do.
Do	33°58′ N.	159°44′ W.	111.6	M	Do.
Do	33°58′ N.	159°44′ W.	110.7	M	Do.
Do	33°58′ N.	159°44′ W.	109.7	M	Do.
Do	33°58′ N.	159°44′ W.	107.4	M	Do.
Do	33°58′ N.	159°44′ W.	107.4	M	Do.
Do	33°58′ N.	159°44′ W.	106.1	M	Recovering.
Do	33°58′ N.	159°44′ W.	106.1	M	Immature.
Do	33°58′ N.	159°44′ W.	105.7	F	Spawned-out.
Do	33°58′ N.	159°44′ W.	104.5	F	Spent.
Do	33°58′ N.	159°44′ W.	102.5	M	Immature.
Do	33°58′ N.	159°44′ W.	99.4	M	Do.
Jan. 28	35°27′ N.	156°38′ W.	109.1	M	Do.
Oct. 24	38°40′ N.	175°27′ W.	107.6	F	Spent.
Dec. 9	34°23′ N.	159°48′ W.	113.6	M	Immature.
Do	34°23′ N.	159°48′ W.	110.7	M	Do.
Dec. 12	36°14′ N.	159°55′ W.	115.9	M	Do.
Do	36°14′ N.	159°55′ W.	96.8	F	Do.
Dec. 14	35°35′ N.	158°21′ W.	116.1	M	Do.
Do	35°35′ N.	158°21′ W.	114.8	M	Do.
Do	35°35′ N.	158°21′ W.	110.4	M	Do.
Jan. 17, 1955	33°50′ N.	179°44′ W.	104.5	M	Do.
Jan. 18	35°48′ N.	179°49′ W.	116.8	M	Do.
Do	35°48′ N.	179°49′ W.	113.0	M	Do.
Jan. 20	31°25′ N.	178°08′ W.	110.0	M	Do.
Jan. 28	30°42′ N.	175°01′ W.	93.3	M	Some milt in testes.[2]
Do	30°42′ N.	175°01′ W.	90.6	M	No milt in testes.

[1] Includes only those observations in which both sex and gonad condition were recorded.

[2] The presence of milt in the testes does not necessarily indicate advanced maturity, as male albacore taken in tropical and subtropical waters almost invariably contain some milt in testes regardless of the degree of sexual maturity.

who examined histologically a series of male and female gonads, concluded that the British Columbia fishery is dependent on immature fish. Brock (1943) recorded a range in egg diameters of 0.01 to 0.1 mm. in Oregon albacore. He reported that "fish with ripening ova are not present in the Oregon fishery and have never been recorded from the California fishery." Kishinouye (1923) found no fish with maturing reproductive elements in Japanese waters. According to Suda (1954), albacore captured west of Midway Islands, north of the Subtropical Convergence, are all extremely immature, with gonad weights below 50 grams for both males and females. Thus, the albacore resource which furnishes the basis for the spring live-bait fishery in Japanese coastal waters and the Japanese winter longline fishery in midocean, as well as the American west coast fishery in the summer, is composed either of sexually immature fish, or of adult fish which show no signs of gonad development beyond the early developing stage. The implications are, therefore, that albacore do not spawn in the temperate waters of the North Pacific.

HAWAIIAN ISLANDS

Because of the great predominance of males in the landings of albacore in the Hawaiian Islands (fig. 7), coupled with the small numbers taken, we had hoped initially to utilize both male and female gonads in this study. We found, however, that the presence or absence of milt is not a

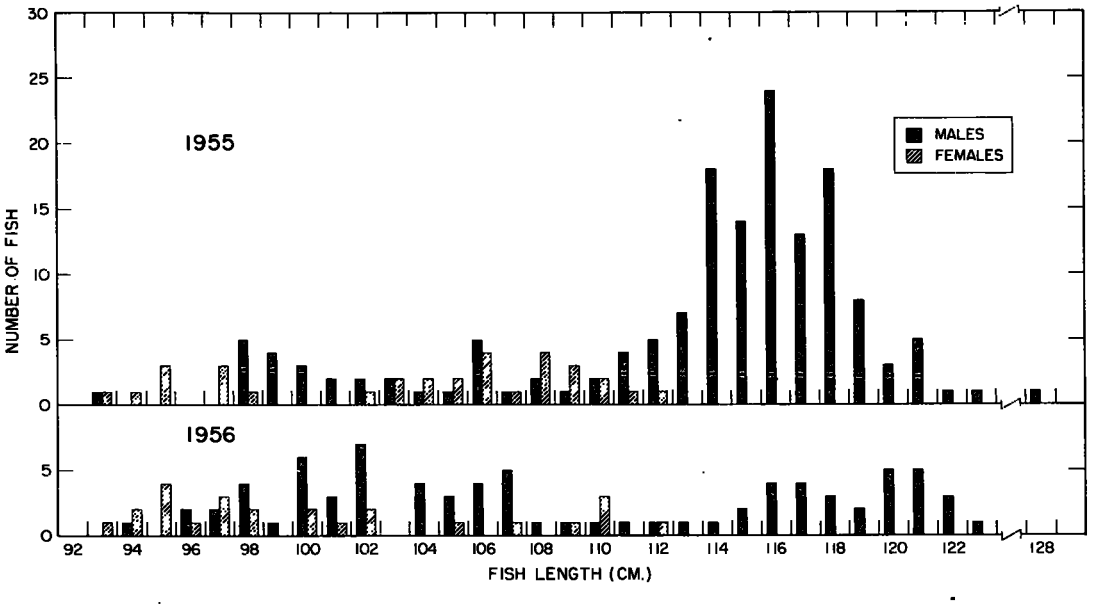

FIGURE 7.—Size and sex distribution of albacore sampled from landings in the Hawaiian Islands, (a) 1955 (b) 1956.

definitive measure of maturity, since regardless of their size, the testes of albacore in Hawaii invariably contain some milt. It was decided, therefore, that only the ovaries would be used for the study of sexual maturity of the Hawaiian and central equatorial Pacific albacore.

Examination of the ovaries from 56 fish revealed varying degrees of maturity from early developing to advanced. Eleven fish ranging in weight from 36 to 59 pounds possessed early developing ovaries; 42 fish, ranging from 33 to 62 pounds, had late developing ovaries; and 3 fish, of 41, 47, and 60 pounds, contained advanced ovaries. The frequency distributions of egg diameters for the 42 late developing and 3 advanced ovaries, and for 4 of the early developing ovaries are presented in table 7. No measurements were made on the remainder of the early developing ovaries with the exception of noting their maximum egg diameters; none exceeded 0.23 mm. The data (table 7) are arranged progressively from the early developing to the most advanced ovaries as determined by the position of the last mode. The modal diameters indicated here were selected by eye after the data had been smoothed twice by a moving average of three. Most of the ovaries showed a distinct second mode which is also indicated.

The modal diameters of the most advanced eggs in each of the 56 ovaries of Hawaiian fish are shown in figure 8 by date of landing. The modal diameters of the 11 early developing ovaries are plotted arbitrarily at 0.167 mm. (10 micrometer units) although the true mode was considerably below this value; only eggs larger than 10 micrometer units were measured.

Of the 36 ovaries sampled in May, June, and July, 3 were advanced and 33 were in the late developing stage; none was in the early developing stage. In August and September, however, of 14 examined, only 7 were in the late developing stage; the remainder were early developing. In October and November, of 6 examined, only 2 were in the late developing stage and 4 were early developing. The above may be an indication that some spawning took place during the summer months. Although the 3 advanced ovaries were not fully ripe, the appearance of the eggs suggested that spawning was not far distant. Clark (1929) examined 21 albacore from Hawaiian waters during the summer of 1929 and reported that all of these fish were "practically mature and ready to spawn." On the other hand, it is possible that albacore have a protracted spawning season, and that the apparent summer spawning season in Hawaii merely reflects seasonality in their occurrence in these waters (table 1).

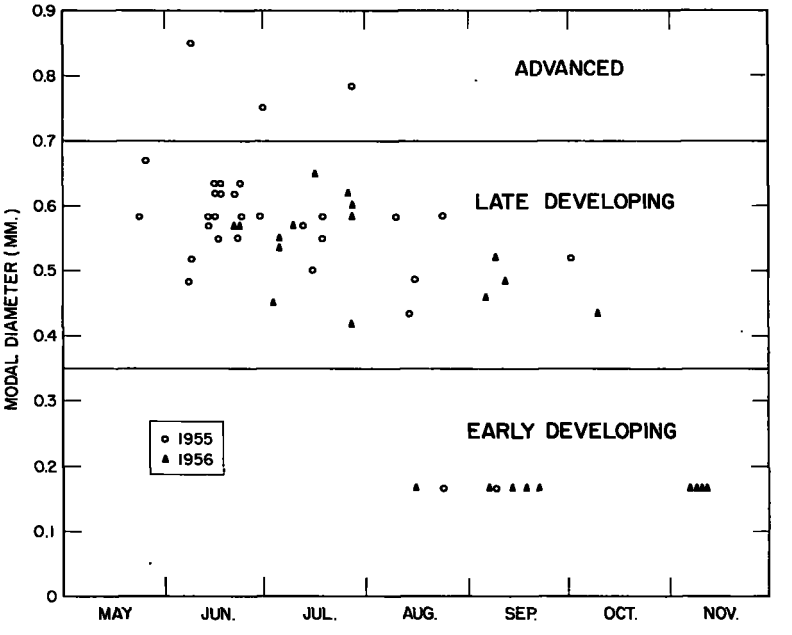

FIGURE 8.—Modal diameter of the most advanced group of eggs shown by date of landing for each of the 56 albacore from Hawaiian waters.

TABLE 7.—*Frequencies of egg diameters, in micrometer units (upper figure)*

[Asterisks mark modal diameters]

Ovary number	10 .167	11 .184	12 .200	13 .217	14 .234	15 .250	16 .267	17 .284	18 .301	19 .317	20 .334	21 .351	22 .367	23 .384	24 .401	25 .418	26 .434	27 .451	28 .468	29 .484	30 .501	31 .518	32 .534
200	175	119	119	65	38	23	5	4	2														
184	142	100	88	65	76	46	21	9	3														
318	57	37	26	27	14	15	8	7	8	1													
290	60	36	29	15	15	14	8	5	4	8	3	1	1	1									
276	125	79	65	52	52	35	24	16	10	10	12	2	2	9	12	*12	5	6	7	6	3	2	2
353	32	15	15	9	4	10	12	7	8	7	3	3	5	5	8	10	*16	11	9	3	4	4	
179	114	61	46	38	39	31	22	20	19	17	6	6	12	8	12	11	*12	16	10	8	6	5	5
264	105	66	38	39	40	39	24	24	18	29	12	10	13	13	6	8	10	*16	9	7	8	7	5
300	92	53	59	37	32	23	17	12	16	9	8	9	11	16	18	16	19	19	*24	19	18	13	4
32	64	31	25	35	25	30	18	21	16	14	12	11	5	19	11	15	16	21	21	*24	17	23	17
181	75	48	43	50	45	32	23	24	20	22	9	8	11	12	*22	18	14	7	13	*16	14	11	6
314	62	38	28	23	23	15	10	18	*22	14	12	13	12	25	14	16	15	23	34	*24	29	29	20
156	75	59	37	43	48	30	19	20	21	17	6	12	6	8	8	11	15	20	15	12	*24	12	15
41	58	36	31	22	12	14	24	*23	11	16	15	14	14	10	8	10	23	26	24	28	24	*36	29
305	85	48	37	33	33	22	11	13	18	12	8	20	*12	18	9	10	3	5	18	14	16	*24	22
209	43	24	18	15	15	11	19	19	8	12	14	15	9	8	6	17	18	30	31	30	34	*50	38
256	66	35	31	31	27	20	20	12	17	21	16	10	14	13	*13	20	9	13	15	14	16	30	*31
257	57	31	33	38	39	22	18	20	32	16	15	9	10	16	11	8	7	7	11	12	7	11	19
88	46	41	30	25	18	18	17	13	11	14	16	19	*13	24	10	17	11	9	12	9	7	12	30
116	74	59	42	36	28	38	17	15	16	13	15	10	4	15	13	11	10	4	8	9	6	16	19
159	71	45	35	30	31	36	11	25	22	24	18	13	17	20	11	10	5	8	14	7	9	9	18
251	72	42	27	28	27	24	19	18	23	23	14	13	13	*20	19	15	9	12	12	7	8	8	7
246	62	38	25	24	21	26	12	16	24	22	11	7	10	20	*23	20	10	13	16	11	8	11	11
259	62	30	26	21	12	20	19	19	30	17	10	11	14	14	14	*23	13	9	16	11	13	17	15
153	215	151	167	154	161	137	98	88	88	93	82	50	60	69	78	*87	56	67	38	41	25	34	54
74	259	137	124	117	107	115	82	72	75	60	51	48	54	*56	45	59	40	39	47	29	32	16	15
185	77	44	37	30	27	33	22	15	16	15	10	7	11	13	10	14	8	16	8	11	16	10	13
158	35	24	22	23	25	26	18	32	23	19	12	19	16	22	*17	24	9	11	6	4	14	11	15
275	87	43	39	30	36	29	14	17	16	15	13	9	13	12	*22	15	17	13	10	1	10	4	4
130	86	54	40	35	30	21	21	17	16	10	12	11	11	8	*13	14	8	10	7	8	7	5	10
79	76	55	42	36	36	29	22	12	17	21	12	9	9	14	*14	12	8	8	8	7	9	8	13
75	87	57	46	37	29	26	21	18	22	13	8	9	13	*14	9	11	9	8	7	5	2	8	10
80	105	51	34	38	39	40	27	29	27	17	13	13	15	14	*22	15	15	8	8	8	10	4	7
122	53	33	22	21	33	19	15	19	19	18	15	10	14	19	*21	22	11	16	10	7	7	4	9
174	61	37	23	26	22	40	20	17	19	33	17	13	19	9	15	*22	9	21	11	10	10	4	5
15	81	30	32	27	18	36	15	15	30	13	21	10	12	16	13	*22	13	9	17	6	6	1	8
277	102	54	40	40	34	29	15	17	15	15	12	13	6	12	10	*14	6	9	15	7	10	7	6
274	82	44	36	29	23	23	18	17	16	14	12	6	6	9	8	14	*7	8	13	8	9	7	6
110	61	30	36	18	27	40	14	23	13	17	21	16	14	11	15	*21	14	8	16	9	9	4	5
91	49	28	32	25	22	31	20	22	23	18	16	14	15	18	20	*15	6	17	14	13	15	5	10
82	87	37	34	35	27	29	21	18	23	18	18	14	16	12	10	*17	14	13	11	7	7	3	3
123	67	35	31	31	24	21	19	14	18	17	12	9	12	18	9	19	*13	14	22	7	3	1	3
84	72	40	33	25	22	24	17	15	25	13	12	9	13	17	20	*20	16	13	20	11	9	11	4
90	44	32	25	32	27	27	25	14	19	11	17	8	10	21	*16	21	8	16	19	12	12	4	4
269	32	22	24	25	11	17	21	21	12	11	16	7	12	19	15	*33	24	15	13	13	1	6	5
18	61	41	28	29	31	27	11	24	20	11	12	9	5	13	15	*16	12	16	13	4	10	0	1
145	189	94	83	85	74	93	52	61	66	46	44	36	38	47	40	49	42	*53	47	24	13	4	6
165	86	63	54	41	44	37	31	28	29	26	15	4	12	13	13	*15	10	12	12	8	6	6	3
42	104	58	28	29	16	23	10	8	18	15	17	12	10	9	10	9	8	10	12	4	7	4	*9

[1] No measurements were made on 7 of the 11 early developing ovaries with the exception of noting the maximum egg diameters; none exceeded 0.23 mm.

CENTRAL EQUATORIAL PACIFIC

While the vast region of the tropical Pacific is here treated as a single unit because of the small amount of data available, it is realized that a more detailed study of smaller units of area would be desirable.

The albacore caught in the equatorial Pacific (fig. 9) were intermediate in size between those from the North Pacific and those from Hawaii. If only the female fish are considered, however, their sizes were not much smaller than the female fish sampled from Hawaiian waters. One notable difference was in the sex ratio, which in this region was nearly 1:1, while in Hawaiian waters the males predominated (fig. 7).

Ovaries from 66 fish were examined. Of this total, 54 were in the early developing and 12 were in the late developing stage (table 8). In figure 10 the maximum egg diameter of each of the 66 ovaries is shown by date of capture of the fish. Maximum egg diameter was used, because no other measurements were made on most of the early developing ovaries. Most of the samples were collected during February and November 1952, in February and May 1953, September 1956, and January and February 1957. Some late developing ovaries were found during all of these periods with the exception of February 1952. The areas from which late developing ovaries were obtained are also indicated in figure 1. They appear to be randomly scattered. It is evident that no conclusions can be drawn from the amount of data available regarding the spawning time and locality.

and mm. (lower figure), for ovaries from the Hawaiian Islands [1]

[Asterisks mark modal diameters]

33 .551	34 .568	35 .584	36 .601	37 .618	38 .635	39 .651	40 .668	41 .685	42 .701	43 .718	44 .735	45 .752	46 .768	47 .785	48 .802	49 .818	50 .835	51 .852	52 .868	53 .885	54 .902	55 .918	56 .935	57 .952	58 .969	59 .985	Sum
																											550
																											550
																											200
																											200
0	2																										550
																											200
2	4	1																									531
3	1																										550
3	0	2	1																								550
18	8	13	7	8	2	1	0	2																			550
3	1	2	1																								550
16	8	5	2																								550
8	6	1	1	1																							550
22	6	5	4	3	2																						550
19	15	13	4	4	4	1																					550
27	12	12	9	4	1	1																					550
22	12	15	4	0	3																						550
*30	26	19	11	10	3	2																					550
*29	28	25	16	9	10	6	2	3																			550
*24	17	19	5	4	1	2																					550
*8	13	16	7	6	6	3	1	1																			550
18	*16	16	7	10	11	6	4	2																			550
25	*25	25	18	8	5	2	1																				550
27	*17	23	20	10	8	3	2	1	1	2																	550
74	*69	67	53	21	9	4	0	1																			2, 391
26	*27	27	18	20	19	10	6	2	3	1																	1, 847
13	*17	16	12	10	10	4	4	1																			550
28	*27	33	17	12	8	5	2	0	1																		550
10	9	*19	12	14	6	5	4	2																			550
10	13	*21	13	17	9	7	3	1	1	1																	550
12	10	*10	15	11	4	4	4	1	1	1																	550
14	15	*21	12	9	4	3	2	1																			550
9	15	*14	10	6	9	7	2	2	1																		634
14	20	*25	21	21	17	8	4	3																			550
8	13	*24	14	15	8	6	6	3																			550
16	13	*24	16	14	6	4	2	3	1																		550
6	3	10	*7	8	8	5	6	3	1	3	0	1	0	1													550
12	8	15	21	*25	21	13	8	6	4	2																	550
2	9	11	10	*25	7	11	11	7	7	6	0	2															550
12	9	9	8	*19	11	8	13	5	6	1	0	0	0	1													550
2	8	9	6	*15	14	13	3	1	3	1	1																550
6	10	15	17	17	*26	14	14	6	4	2																	550
5	2	1	9	7	*12	6	8	8	9	10	4	1	3	1	1	2											550
5	8	11	12	14	*22	9	21	11	7	3	1	1	0	1													550
6	10	10	20	16	27	*31	19	17	10	5	1	2	1														550
5	2	2	4	11	18	15	*21	15	11	15	7	10	0	3	1	1											550
2	4	7	3	11	11	13	15	11	16	23	24	*30	24	28	22	11	10	4	5	2	3	1	1	0	1		1, 568
3	2	0	1	0	1	1	1	2	6	5	5	5	7	*9	6	5	5	5	6	4	3	2	1	2			656
10	1	2	1	0	0	0	1	0	0	1	1	1	1	11	6	6	16	*9	10	15	2	12	7	5	0	2	550

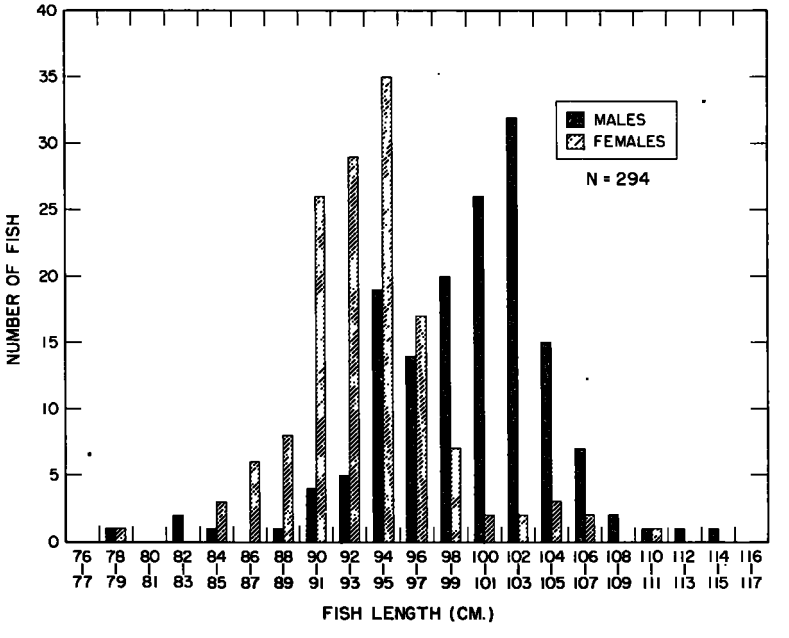

FIGURE 9.—Size distribution, by sex, of central equatorial Pacific albacore captured during the years 1952 to 1957, and for which sex and size data were recorded.

TABLE 8.—*Frequencies of egg diameters, in micrometer units (upper figure) and mm. (lower figure), for ovaries from the central equatorial Pacific Ocean* [1]

[Asterisks mark modal diameters]

Ovary number	10 .167	11 .184	12 .200	13 .217	14 .234	15 .250	16 .267	17 .284	18 .301	19 .317	20 .334	21 .351	22 .367	23 .384	24 .401	25 .418	26 .434	27 .451	28 .468	29 .484	30 .501	31 .518	32 .534	33 .551	34 .568	35 .584	36 .601	37 .618	38 .635	39 .651	40 .668	41 .685	42 .701	Sum
C-16	126	82	72	53	36	37	27	31	28	17	13	13	10	2	2	1																		550
C-49	39	23	16	20	18	7	18	13	5	5	*11	4	3	5	3	2	3	1	0	3	1													200
C-48	26	13	11	9	8	17	13	13	3	3	15	*10	10	7	8	8	10	4	5	4	3													200
C-3	57	42	35	22	28	33	30	14	18	16	14	18	19	20	22	*28	27	18	15	14	12	12	9	10	5	6	1	3	2					550
C-42	94	48	41	33	27	30	22	21	17	20	20	23	24	19	18	*24	27	12	15	5	4	3	0	0	2	0	1							550
C-20	67	39	38	22	23	19	16	*30	24	20	17	16	20	22	12	32	*21	27	27	10	18	14	7	6	2	1								550
C-31	126	77	57	31	19	20	13	8	10	3	6	12	9	12	12	13	20	*22	22	12	10	13	12	6	0	2	3							550
C-10	119	75	58	54	36	31	11	22	16	11	12	5	14	15	8	9	10	11	*16	7	2	3	2	2	1									550
C-61	61	35	30	39	32	30	25	23	24	15	22	20	19	19	13	18	23	22	*23	26	20	10	8	2	1									550
C-37	72	44	44	36	17	23	23	24	19	17	12	9	15	15	7	16	21	21	*20	20	16	8	9	9	12	8	3	3	3	3	0	0	1	550
C-1	58	28	25	19	15	14	14	15	14	20	20	16	16	17	22	15	20	22	16	18	26	*23	22	24	18	15	9	5	3	0	1			550
C-13	117	86	81	49	34	21	21	20	14	12	8	8	4	3	0	3	7	5	9	6	9	*13	3	4	5	5	1	1	1	0	0	0	1	550
C-2	96	56	36	25	23	20	11	20	12	10	15	11	10	11	9	12	17	16	19	11	16	*19	15	13	11	9	8	6	7	2	1	2	1	550

[1] Eggs from only one early developing ovary (albacore No. C-16) were measured.

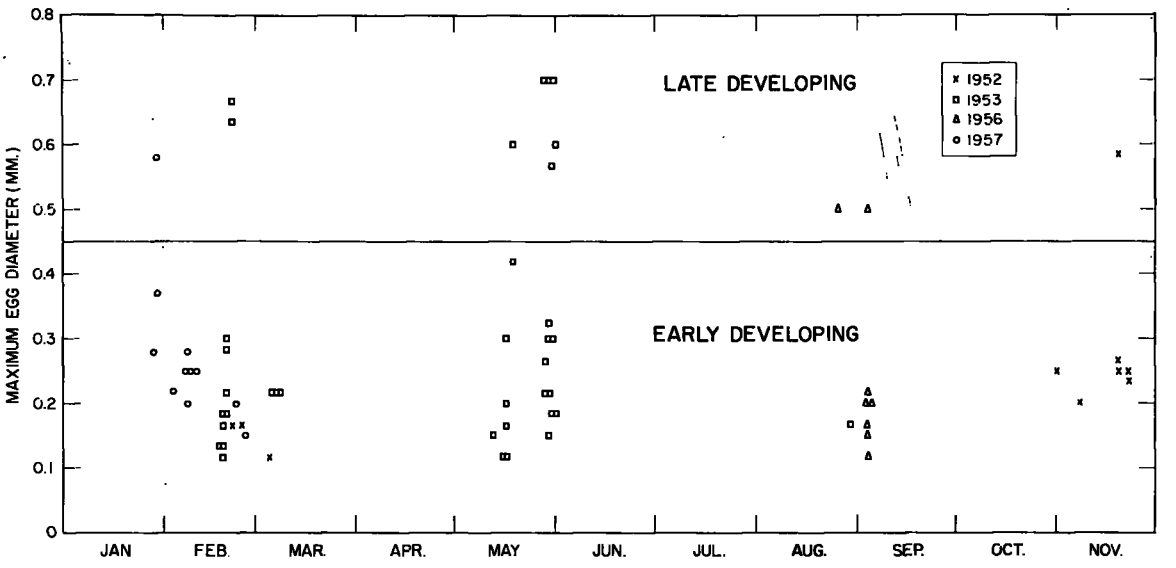

FIGURE 10.—Maximum egg diameter for each of the 66 central equatorial Pacific albacore by date of capture. (Since only the maximum egg diameter was recorded for most of the early developing ovaries, this measurement rather than the modal diameter is used.)

EVIDENCE OF SPAWNING

The spawned-out or spent stage is recognized by the presence of remnants of ripe eggs (residual eggs in the process of resorption) in the lumen of the ovary (Schaefer and Orange, 1956; Yuen and June, 1957). A fresh, unpreserved spent ovary is generally hollow and flaccid. In preserved specimens, however, it may resemble any of the other stages of maturity, even the early developing ovary, depending upon how recently spawning has occurred. Egg remnants were actually found in ovaries in all stages of maturity from early developing through advanced.

In this study we classified the ovaries into developmental stages without regard to the presence or absence of egg remnants. In figure 11 the maximum egg diameter for each of the Hawaiian and central equatorial Pacific albacore is shown by fish size, and the ovaries which contained egg remnants are indicated. No distinction was made of the quantity of remnants in the ovaries, nor of their stage of resorption. While the absence of egg remants may not be accepted as proof that the fish has never spawned, their presence constitutes good evidence that spawning has occurred (June 1953; Yuen 1955; Schaefer and Orange, 1956; Yuen and June, 1957). Of a total of 56 Hawaii samples, 47 contained egg remnants, indicating that these fish had spawned. Similarly of 66 central equatorial Pacific ovaries examined,

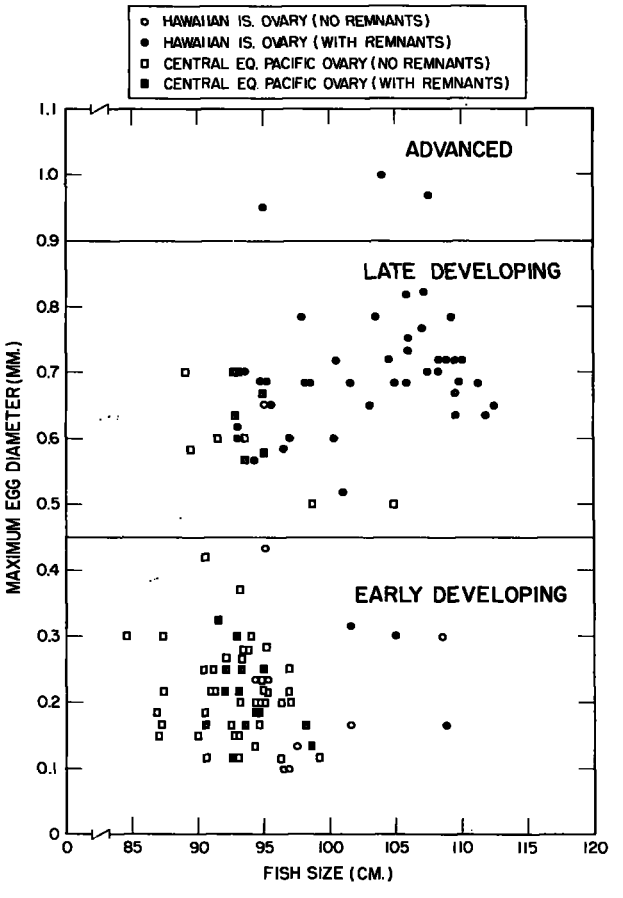

FIGURE 11.—Relation between fish size and maximum egg diameter. Ovaries with egg remnants are indicated.

20 contained egg remnants. None were found in the North Pacific ovaries, thus giving added weight to the conclusion that spawning does not occur in the North Pacific.

MINIMUM SIZE OF SPAWNING FISH

Ueyanagi (1955) has inferred from his studies that the albacore attains sexual maturity and may spawn at about 90 centimeters in length. Our observations are in agreement with this.

The 12 central equatorial Pacific ovaries in the late developing stage were obtained from fish ranging in length from 89.1 cm. to 104.8 cm. (weight, 33 to 54 lbs.); the 45 late developing and advanced ovaries from the Hawaiian area were taken from fish larger than 93.1 cm. (33 lbs.). Additional evidence regarding the minimum size at spawning can be found in figure 11. Although egg remnants were present in ovaries at all stages of maturity, none were found in fish less than 90 cm. in length. Therefore, our data suggest that the albacore attains sexual maturity at a size of about 90 cm. (33 lbs.), which coincides with Ueyanagi's findings.

FREQUENCY OF SPAWNING

The frequency distributions of egg diameters (figs. 5 and 6, tables 7 and 8) show clearly two or more modes which, depending on the growth rate of the egg, may represent eggs that will be spawned in a single season or in succeeding seasons. As the data do not permit determination of the growth rate of eggs, reference is again made to figure 11. The fact that the three advanced ovaries as well as most of the late developing ovaries contained egg remnants strongly indicates that the albacore undergoes multiple spawning. The lack of remnants in large, sexually inactive adults taken during late winter in the North Pacific suggests that remnants are not carried over from one year to the next, though in the absence of any knowledge regarding the rate of resorption of the unspawned eggs, no definite conclusions can be drawn. The presence of egg remnants together with a group of eggs approaching ripeness suggest, however, that albacore may spawn at least twice during a single spawning season.

FECUNDITY

Fecundity calculations were based on the assumption that all of the eggs comprising the most advanced group within an ovary were released in a single spawning. Eight Hawaiian fish of varying sizes were selected for this study. From each pair of ovaries, a random sample was obtained; this was weighed to the nearest 0.001 gram. All of the eggs comprising the most advanced group within the sample were then counted. The total number of such eggs in the pair of ovaries was estimated by multiplying the number in the sample by the ratio of ovary-weight to sample-weight. The results are shown in table 9. The data are arranged in the order of increasing fish size from 36 to 62 pounds. In addition, two calculations made by Ueyanagi (1955) are included.

TABLE 9.—*Estimations of the number of eggs in the most advanced group in the ovaries*

Albacore No.	Body wt. (lbs.)	Ovary wt. (gms.)	Sample wt. (gms.)	Number of mature eggs in sample	Estimated number of mature eggs in ovaries (millions)
158	36	183	0.1215	579	0.9
75	39	271	.1862	882	1.3
275	41	319	.1435	418	.9
42	47	538	.2367	482	1.1
74	54	513	.0560	513	1.6
84	57	552	.1983	582	1.6
145	60	916	.1197	238	1.8
153	62	194	.0811	411	1.0
A [1]	50	365	.2		2.1
B [1]	53	613	.2		1.8–1.9

[1] From Ueyanagi (1955).

There appears to be a slight tendency for larger fish to have more eggs per spawning but it is not as definite as that found for the yellowfin (June 1953) and bigeye tuna (Yuen 1955). The estimated total numbers of eggs in the most advanced group were remarkably uniform, ranging between 0.9 and 1.8 million eggs per individual female. Including Ueyanagi's estimates, the range is from 0.9 to 2.1 million eggs.

OVARY SIZE AS INDEX OF MATURITY

While the state of maturity of an ovary can be determined reliably by means of egg diameter measurements, a more simple and yet objective

method for making rapid field determinations is desirable. The size of the ovaries, if directly related to maturity, should provide a reasonable criterion. Our data show that all of the early developing ovaries from the central equatorial Pacific weighed less than 100 grams, and that late developing ovaries ranged from 104 to 363 grams. The early developing ovaries from the Hawaiian area, however, ranged in weight from 54 to 179 grams, the late developing ovaries from 123 to 805 grams, and the three advanced ovaries weighed 181, 538, and 916 grams, respectively. Thus, while the ovaries from the central equatorial Pacific fall conveniently into two stages of maturity according to their weights, there is considerable overlap in the Hawaiian samples. It appears, therefore, that ovary size is actually a poor criterion to follow in assessing the state of maturity of an ovary.

Recently, the relative ovary weight (ovary weight $\times$ 10^3/fish weight) has been found to be a fairly reliable measure of maturity for Hawaiian yellowfin (June 1953) and central Pacific bigeye tuna (Yuen 1955). This relation was therefore tested for the albacore ovaries. In figure 12 the relative ovary weight of each of the Hawaiian and central equatorial Pacific albacore is plotted against the maximum egg diameter. Here again, the data do not permit the use of modal diameters, for these were not determined for most of the early developing ovaries. The data presented in tables 7 and 8 indicate an acceptable correlation between modal and maximum diameters which justifies the use of the latter. The early developing ovaries, with only one exception, have relative ovary weights of less than 6, while all but three of the late developing ovaries have relative ovary weights greater than 6. Thus, with a reasonable amount of confidence, a relative ovary weight of 6 may be considered as the value which separates the early developing from late developing ovaries.

The late developing ovaries ranged in relative ovary weight from 6 to 30 with a general tendency for the ratio to increase with progressing maturity. The three advanced ovaries, however, failed to conform to any pattern and varied in relative ovary weights from 10 to 34. Despite the large variation exhibited by the three ovaries in the advanced stage, the data in general point to a definite relation between relative ovary weight and the state of gonad development.

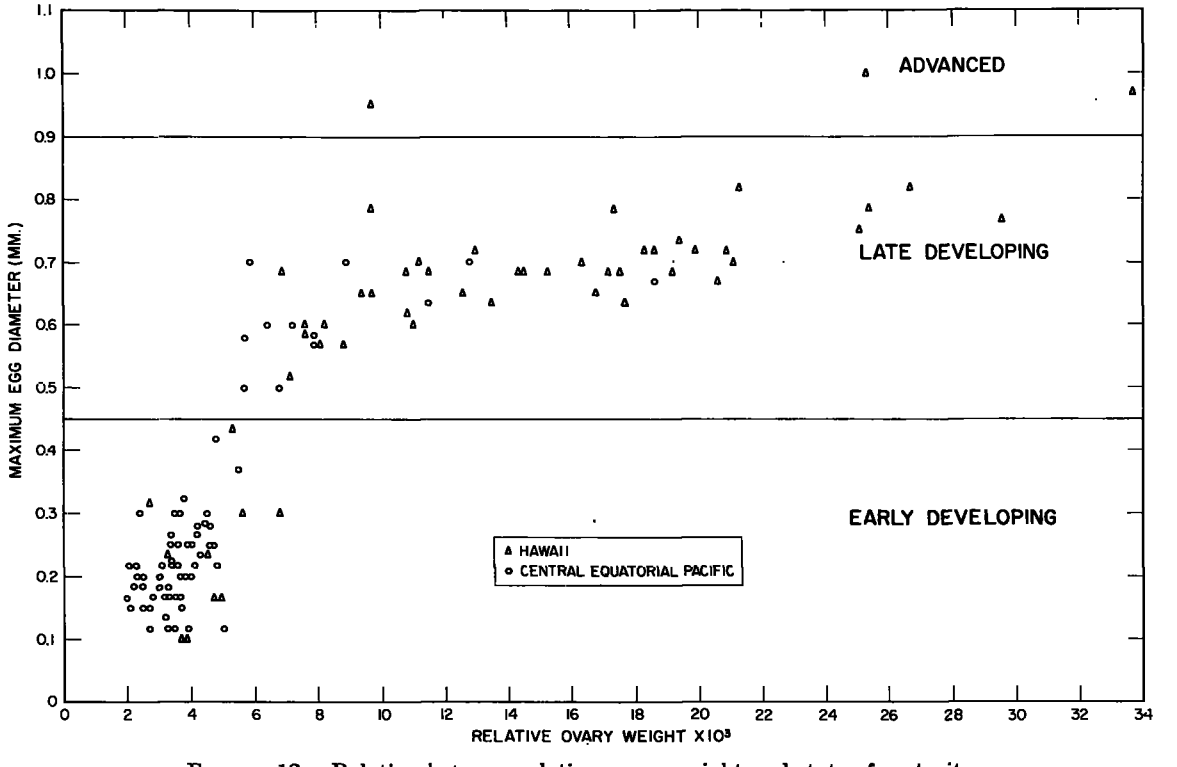

FIGURE 12.—Relation between relative ovary weight and state of maturity.

DISCUSSION

Our samples did not include any ovaries that were fully ripe. Three ovaries were classified as "advanced" on the basis of the appearance of the eggs. Although they were advanced in maturity, and presumably close to spawning, it has not been possible to determine the time required for these ovaries to attain a fully ripe stage. Because these advanced ovaries were collected during the summer months, and since a large percentage of ovaries collected in the fall were in the early developing stage (fig. 8), it was postulated that some spawning occurs during the summer in the vicinity of the Hawaiian Islands.

Fully ripe fish apparently are not available to the fishery. June (1953), working with Hawaiian yellowfin, concluded that this species spawns in Hawaiian waters. He found only one fully ripe ovary among his samples, however, and stated that "fish that are actually spawning either do not take the hook or migrate into deeper water outside the longlining grounds." Similarly, Schaefer and Orange (1956) stated that "apparently, when the yellowfin tuna imminently approach spawning, they become unavailable to the fishery." This behavior was noted earlier by Schaefer (1948) for yellowfin tuna and skipjack off Central America. Brock (1954) also found that fully ripe skipjack are not commonly available to the Hawaiian skipjack fishery. Thus, the possibility that fully ripe tunas are generally unavailable to the fishery may be one reason for the small number of advanced ovaries and the complete absence of ripe ovaries in our collections.

Most of the ovaries examined from the central equatorial Pacific were in the early developing stage, but a few late developing ovaries were present as well as those that contained relics of past spawning. Absence of advanced stages may mean that these fish do not spawn in this region. Unfortunately, not much is known of the maturity of the albacore taken in other regions of the tropical Pacific. Some field observations on the gonads of albacore landed by the Japanese tuna mothership expeditions between April and September of 1951 are available for the western equatorial Pacific between the Equator and 6° N. latitude and between 144° E. and 174° E. longitude (general vicinity of the Caroline and Marshall Islands). Descriptions of these expeditions are given by Shimada (1951), Ego and Otsu (1952), and Van Campen (1952). Of a total of 41 observations made by observers from POFI during this period, 33 were recorded as immature, 6 as spent, and only 2 as mature. Judging from these records, it may be assumed that the maturity of the western Pacific albacore during this period more nearly resembled that of the central equatorial Pacific albacore than that of the Hawaiian fish.

Ishii and Inoue (1956) postulated that the Coral Sea and adjacent New Caledonia area were spawning areas for the albacore. Their study was based on only two ovaries which, according to their descriptions, corresponded to our early developing and late developing stages. On the basis of these data, it is surmised that the maturity of the fish in this area is much like that found throughout the central and western equatorial Pacific. It is interesting to note that Ueyanagi (1955) reported on two well-advanced ovaries obtained in February 1953 from the southern waters of Sunda Islands (Indian Ocean); one of the ovaries he referred to as "ripe" and the other as "nearly ripe".[2] He has hypothesized that the albacore which occur in the Indian Ocean spawn in February, at least, in part. He believes that the area from south of the Sunda Chain to northwest of Australia may be the spawning grounds of the Indian Ocean albacore, since the fish taken there are generally large. Ueyanagi's size-frequency data of the Indian Ocean albacore (fig. 13)

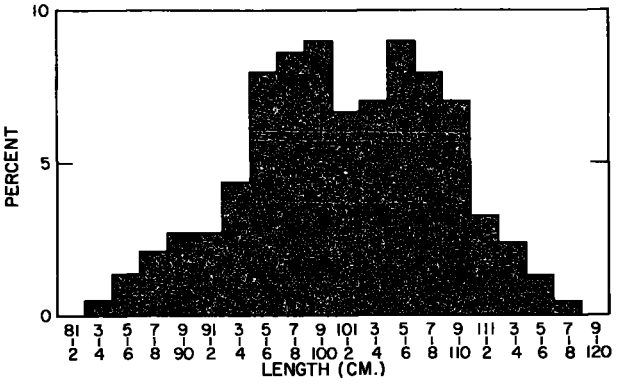

FIGURE 13.—Length composition of Indian Ocean albacore (reproduced from Ueyanagi 1955, fig. 2).

[2] Ueyanagi very kindly sent us samples taken from these two ovaries. The sample he referred to as "nearly ripe" corresponds in maturity to late developing ovaries, and the "ripe" to one of the advanced ovaries in the present study.

closely resemble that of the central equatorial Pacific albacore (fig. 9).

The best indications of albacore spawning are therefore available from two widely separated localities, the Hawaiian Islands in the central Pacific and Sunda Islands in the Indian Ocean, the former during the northern summer and the latter during the southern summer.

It is not known whether the albacore appearing in various parts of the Pacific Ocean belong to a single intermingling population or whether there are discrete populations in the various areas. Suda (1956) is of the belief that the albacore occurring in the North Pacific Current area are a "feeding group" and that there is a corresponding "spawning group" in the North Equatorial Current area. Furthermore, he postulates that the albacore of the Indian Ocean as well as the tropical South Pacific comprise the spawning group of another feeding group located in South Pacific temperate waters. If this is indeed the case, it may be that the Hawaiian Islands represent a portion of the spawning grounds of the northern population, and that the Sunda Islands, that of the southern population.

Our data suggest that albacore attain sexual maturity at about 90 centimeters in length (weight, 33 lbs.). This signifies that the fish exploited during the spring and summer by the Japanese and the Americans in the temperate waters of the North Pacific are largely sexually immature fish (Suda 1955, Brock 1943). The Japanese winter longline fishery in the North Pacific, on the other hand, exploits both juvenile and adult fish (Suda 1954). The gonads of these adult fish do not show any development, however. This situation is in contrast to that in the Hawaiian Islands where the catch is wholly of adult fish (fig. 7). Many of these have gonads showing considerable development. In the central equatorial Pacific, the fish are also generally large and most are adults with gonad development intermediate between North Pacific and Hawaiian Islands fish. It appears possible that the Hawaiian and central equatorial Pacific albacore are a segment of the population which, after attaining a certain size in temperate waters of the North Pacific, moves south into tropical and subtropical waters to reproduce.

SUMMARY

1. This study is based on examination of gonads of albacore taken from three general areas: the North Pacific (north of 30° N. latitude, between 180° longitude and the west coast of the United States), the Hawaiian Islands, and the central equatorial Pacific (Equator to 12° S. latitude, between 180° and 150° W. longitude, with scattered samples collected from as far east as 120° W.). Although the three areas are treated separately throughout this report, this does not infer that the fish belonged to separate stocks, or populations.

2. Gonads of both sexes were used in the study of the maturity of North Pacific albacore. Only the ovaries were used for the other two areas and the degree of maturity was determined largely from egg diameter measurements.

3. The several tests made to determine the most efficient sampling procedure indicated that mature eggs were randomly distributed throughout the length of an ovary but there were some differences in the transverse distribution. There were no differences in the distribution between the two ovaries of a pair. The adopted method of sampling was to take a random sample from the mid-section of an ovary.

4. The ovaries were classified in three stages of relative maturity: early developing, late developing, and advanced, on the basis of the most advanced eggs present. The advanced ovaries were not in a fully ripe condition.

5. The North Pacific albacore were either juveniles or sexually dormant adults with early developing gonads.

6. The Hawaiian albacore evinced varying degrees of maturity from early developing to advanced, with the bulk of the ovaries in the late developing stage. Although the samples were somewhat inadequate for a conclusive study, there was indication that spawning may occur during the summer months in the vicinity of the Hawaiian Islands. The data also indicated the possibility of a somewhat protracted spawning season.

7. The ovaries from central equatorial Pacific fish were in the early developing and late developing stages, with the early developing stage predominating.

8. The presence of egg remnants in the ovaries indicated that most of the Hawaiian fish had spawned previously. None of the ovaries from the North Pacific contained egg remnants. Of 66 central equatorial Pacific ovaries, 20 contained egg remnants. Remnants of eggs were present in ovaries in all stages of maturity from early developing through advanced.

9. The minimum size at which albacore attain sexual maturity and participate in spawning appears to be about 90 cm. (weight, 33 lbs.).

10. The size distribution of eggs within an ovary, as well as the frequent occurrences of egg remnants in advanced and late developing ovaries, indicate that albacore may undergo at least two spawnings during a spawning season.

11. Assuming that all of the eggs comprising the most advanced group within an ovary are extruded in a single spawning, the number released per spawning is about 1 to 2 million eggs per individual female albacore.

12. Ovary size is not a reliable criterion to follow in assessing the degree of maturity of an ovary. Relative ovary weight (ovary weight $\times 10^3$/virgule fish weight) is shown to be the more reliable index, particularly for segregating early developing from late developing ovaries.

13. This study shows that albacore caught by POFI vessels north of Hawaii, as well as those taken by the Japanese spring live-bait and winter longline fisheries, and those supporting the American west coast summer fishery are non-spawning fish that are either juveniles or adult fish whose gonads give no signs of incipient or past spawning. Albacore apparently do not spawn in the temperate waters of the North Pacific.

14. It appears possible that the albacore in region of the Hawaiian Islands and in the central equatorial Pacific represent a segment of the population which, after attaining a certain size in temperate waters of the North Pacific, moves south into tropical and subtropical waters to reproduce.

LITERATURE CITED

BLUNT, C. E., JR.
1954. Two mid-Pacific recoveries of California-tagged albacore. Calif. Fish and Game 40(3): 339.

BROCK, V. E.
1943. Contribution to the biology of the albacore (*Germo alalunga*) of the Oregon coast and other parts of the North Pacific. Stanford Ichthy. Bull. 2(6): 199–248.
1954. Some aspects of the biology of the sku, *Katsuwomus pelamis*, in the Hawaiian Islands. Pacific Science 8(1): 94–104.

CLARK, FRANCES N.
1929. A racial comparison of California, Hawaiian and Japanese albacore (*Germo germo*). Calif. Fish and Game 15(4): 351–353.
1934. Maturity of the California sardine (*Sardina caerulea*) determined by ova diameter measurements. Calif. Dept. Fish and Game, Fish Bull. 42: 49 p.

EGO, K., and T. OTSU.
1952. Japanese tuna-mothership expeditions in the western equatorial Pacific Ocean (June 1950 to June 1951). Com. Fish. Rev. 14(6): 1–19, U. S. Fish and Wildlife Service.

GANSSLE, D., and H. B. CLEMENS.
1953. California-tagged albacore recovered off Japan. Calif. Fish and Game 39(4): 443.

ISHII, K., and M. INOUE.
1956. Some notes on the ovary of albacore, *Germo germo*, taken from the Coral Sea. Bull. Jap. Soc. Sci. Fish. 22(2): 89–93. (Translation from the Japanese by W. G. Van Campen in the files of Pacific Oceanic Fishery Investigations Library.)

JUNE, F. C.
1950. Preliminary fisheries survey of the Hawaiian-Line Islands area. Part I. The Hawaiian long-line fishery. U. S. Fish and Wildlife Service, Com. Fish. Rev. 12(1): 1–23.
1953. Spawning of yellowfin tuna in Hawaiian waters. U. S. Fish and Wildlife Service, Fish. Bull. 54(77): 47–64.

KISHINOUYE, K.
1923. Contributions to the comparative study of the so-called scombroid fishes. Jour. Coll. Agric., Imp. Univ. Tokyo 8(3): 294–475.

OTSU, T.
1954. Analysis of the Hawaiian long-line fishery. 1948–52. U. S. Fish and Wildlife Service, Com. Fish. Rev. 16(9): 1–17.

OTSU, TAMIO, and RICHARD UCHIDA.
1959. Study of age determination by hard parts of albacore from Central North Pacific and Hawaiian Waters. U. S. Fish and Wildlife Service, Fish. Bull. 59(150):

PARTLO, J. M.
1955. Histological studies on albacore (*Thunnus alalunga*) gonads from the eastern Pacific. Jour. Fish. Res. Bd. Can. 12(1): 61–67.

SCHAEFER, M. B.
1948. Spawning of Pacific tunas and its implications to the welfare of the Pacific tuna fisheries. North American Wildlife Conference Trans. 13: 365–371.

SCHAEFER, M. B., and C. J. ORANGE.
1956. Studies of the sexual development and spawning of yellowfin tuna (*Neothunnus macropterus*) and skipjack (*Katsuwonus pelamis*) in three areas of the eastern Pacific Ocean, by examination of gonads. Inter-American Tropical Tuna Comm. Bull. 1(6): 283–320.

SHIMADA, B. M.
1951. Japanese tuna-mothership operations in the western equatorial Pacific Ocean. U. S. Fish and Wildlife Service, Com. Fish. Rev. 13(6): 1–26.

SUDA, A.
1954. Average year's fishing condition of tuna longline fisheries. 1952 edition, albacore section. Edited by Nankai Regional Fish. Res. Lab.; published by Nippon Katsuo-Maguro Gyogyokumiai Rengokai, Tokyo. (English translation) U. S. Fish and Wildlife Service, Spec. Sci. Rept.—Fish. No. 169, 131 p.

1955. Albacore studies II. Size composition of the albacore taken in the North Pacific during the period of northward movement. Bull. Jap. Soc. Sci. Fish. 21(5): 314–319. (Translation) U. S. Fish and Wildlife Service, Spec. Sci. Rept.—Fish. No. 182: 14–20.

1956. Albacore of the Pacific and Indian Oceans. Tuna Fishing No. 34, the Investigative Soc. of Tuna Fishery, Japan—Oct. 1956, p. 11–15. (Translation from the Japanese by W.G Van Campen in the files of Pacific Oceanic Fishery Investigations Library.)

UEYANAGI, S.
1955. On the ripe ovary of the albacore, *Germo germo* (Lacépède), taken from the Indian Ocean. Bull. Jap. Soc. Sci. Fish. 20(12): 1050–1053. (Translation from the Japanese by W. G. Van Campen in the files of Pacific Oceanic Fishery Investigations Library.)

VAN CAMPEN, W. G.
1952. Japanese mothership-type tuna-fishing operations in the western equatorial Pacific, June-October 1951 (Report on the seventh, eighth, and ninth expeditions). U. S. Fish and Wildlife Service, Com. Fish. Rev. 14(11): 1–9.

YUEN, H. S. H.
1955. Maturity and fecundity of bigeye tuna in the Pacific. U. S. Fish and Wildlife Service, Spec. Sci. Rept.—Fish. No. 150, 30 p.

YUEN, H. S. H., and F. C. JUNE.
1957. Yellowfin tuna spawning in the central equatorial Pacific. U. S. Fish and Wildlife Service, Fish. Bull. 57(112): 251–264.

U. S. GOVERNMENT PRINTING OFFICE: 1959 O - 485320

Blank page retained for pagination

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

GRAYLING OF GREBE LAKE, YELLOWSTONE NATIONAL PARK, WYOMING

By THOMAS E. KRUSE

FISHERY BULLETIN 149

From Fishery Bulletin of the Fish and Wildlife Service

VOLUME 59

UNITED STATES GOVERNMENT PRINTING OFFICE • WASHINGTON • 1959

For sale by the Superintendent of Documents, U. S. Government Printing Office
Washington 25, D. C. Price 35 cents

Library of Congress catalog card for this bulletin:

Kruse, Thomas E

Grayling of Grebe Lake, Yellowstone National Park, Wyoming. Washington, U. S. Govt. Print. Off., 1959.

iv, 307–351 p. illus., diagrs., tables. 26 cm. (U. S. Fish and Wildlife Service. Fishery bulletin 149)

"From Fishery bulletin of the Fish and Wildlife Service, volume 59."

Bibliography: p. 350–351.

1. Grayling. 2. Trout. 3. Grebe Lake, Wyo. (Series: U. S. Fish and Wildlife Service. Fishery bulletin, v. 59, no. 149)

[SH11.A25 vol. 59, no. 149] Int 59–18

U. S. Dept. of the Interior. Library
for Library of Congress

Library of Congress catalog card for the series, Fishery Bulletin of the Fish and Wildlife Service:

U. S. ***Fish and Wildlife Service.***

Fishery bulletin. v. 1–

Washington, U. S. Govt. Print. Off., 1881–19

v. in illus., maps (part fold.) 23–28 cm.

Some vols. issued in the congressional series as Senate or House documents.

Bulletins composing v. 47– also numbered 1–

Title varies: v. 1–49, Bulletin.

Vols. 1–49 issued by Bureau of Fisheries (called Fish Commission, v. 1–23)

1. Fisheries—U. S. 2. Fish-culture—U. S. I. Title.

SH11.A25 639.206173 9–35239 rev 2*

Library of Congress [r55e½]

CONTENTS

	Page
Introduction	307
Environment	308
Physical characters	308
Chemical factors	309
Biological features	309
History of fish in Grebe Lake	311
Recent populations in Grebe Lake	312
Population estimates	312
Factors controlling composition of the Grebe Lake population	318
Spawning of Grebe Lake fishes	318
Spawning areas	318
Time and water conditions	318
Spawning populations of grayling and hybrid trout	319
Length-frequencies	323
Sex ratios	323
Breeding	324
Mortality	326
Egg production, development, and hatching	327
Fecundity of Grebe Lake grayling and trout	327
Egg development and hatching	328
Determination of natural hatching mortality	328
Age and growth of Grebe Lake fishes	333
Problems in age assessment of Grebe Lake grayling	334
Definition and validation of the annulus	334
Failure of first annulus to appear	336
Failure of scale growth and effect on annuli	337
Growth of young grayling	338
Calculated growth rates compared	339
Problems in assessment of age in hybrid trout	340
Lack of annulus I	340
Eroded and broken scales	341
Age and growth of hybrid trout in Grebe Lake	341
Length-weight relation	342
Food analysis	343
Harvest of Grebe Lakes fishes by angling	347
Predators affecting Grebe Lake populations	348
Summary	349
Literature cited	350

ABSTRACT

This is a study of certain features of the grayling population in Grebe Lake (near the center of Yellowstone National Park) fundamental to its management as a recreational resource. Field work was done in the summers of 1952, 1953, and 1954.

Grebe Lake is an eutrophic body of water at an elevation of 8,000 feet. It has an area of 145 acres and a maximum depth of 32 feet. The lake was covered with ice 6½ months annually; the highest surface temperature recorded was 67° F. Predominant insects by volume and number were the Tendipedidae (=Chironomidae), larvae and pupae. By July 14, 1953, an oxygen deficiency in the waters below a depth of 20 feet made them unsuitable for fish life. The grayling was introduced in the lake in 1921. Rainbow trout were planted in 1907, and cutthroat trout in 1912 (only hybrid trout are present now).

In the population estimates of 1953–54 trap nets were utilized along with a mark-and-recapture method. Approximately 28,000 grayling were in the lake in 1953 and 27,000 in 1954. The population of hybrid trout was estimated at 2,000 in 1953 and 2,500 in 1954. The standing crop of fish in Grebe Lake each year approximated 81 pounds per acre of which 73 pounds per acre were grayling and 8 pounds per acre were trout.

Both the grayling and the hybrid trout spawned in all four tributaries and in the outlet of Grebe Lake between mid-May and late June. The number of grayling spawning in 1953 was 7,081 and in 1954, 7,878. Enumeration of the trout at the same times showed 674 and 405, respectively.

During 1954 the natural fry production of grayling in the tributaries of the lake was estimated as 236,500 or 2.5 percent of the estimated number of eggs produced by the spawning adults. The greatest cause of mortality during the early developmental period was attributed to dislodgment of the eggs either by subsequent spawners or by changes in water level.

The time of annulus formation for grayling younger than 3 years was prior to June 25. Accurate interpretations of age from scales of grayling after their third year was impossible because of the small annual growth both in body and scale lengths. An additional complication often resulted from an absence of a scale annulus to designate the first year of life. This occurred on fish that were too small to have had scales at the start of their second growing season. The grayling reached the legal size of 6 inches during its second summer of life and matured during its third year of life.

The hybrid trout grew slower than the grayling during its first three years, but faster after age 3. The legal size (6 inches) was attained either in the second or third year of life. Some males of age-group II had matured, but no females matured until they were 3-year-olds.

Neither the grayling nor the trout was predatory. The food of the grayling during its first year consisted of small nymphs of aquatic insects, amphipods, and *Daphnia*. The major item in the diets of adults of both kinds of fishes was found to be Diptera larvae and pupae.

Fishing pressure on Grebe Lake was light with a harvest of only 7.1 percent of the estimated population or 6 pounds per acre in 1953, and 9.9 percent or 8 pounds per acre in 1954.

The combined mortality from anglers and predators in 1954 approximated 4,200 fish or 14.2 percent of the estimated adult population of 29,500 fish.

GRAYLING OF GREBE LAKE, YELLOWSTONE NATIONAL PARK, WYO.

By Thomas E. Kruse, *Fishery Research Biologist*, BUREAU OF SPORT FISHERIES AND WILDLIFE

The holarctic grayling, *Thymallus arcticus* Pallas, is one of the rarest North American game fishes. Its localized distribution on this continent, as well as the great beauty of the fish, have focused the interest and concern of ichthyographers and sportsmen on the species.

The first specimens to be collected in America were from Winter Lake near Fort Enterprise (Northwest Territories) and were identified by Sir John Richardson who called them Back's grayling (Franklin 1823). The grayling was subsequently found in Michigan and Montana and in many streams of Alaska and Canada eastward to the western shore of Hudson Bay. This distributional pattern was evidently the result, first, of glacial action which extended the range southward, and second, of later habitat changes which left only two relict populations south of the Canadian border.

The grayling of North America is conspecific with the Asiatic form, *Thymallus arcticus* Pallas (Walters 1955; Wilimovsky 1954). Walters (1955) further recognizes for North American individuals the subspecies *signifer* (for Alaska and Canada specimens) and *tricolor* (for Michigan-Montana individuals).

In Eurasia, *Thymallus arcticus* occurs from the Ob system of western U.S.S.R. to the eastern Siberian Coast (including all streams draining into the Bering Sea and the Penzhina River draining into the Sea of Okhotsk), and south to the Baikal basin, Sea of Japan basin, and the Yellow Sea basin (Yalu River) (Walters 1955).

In Canada and Alaska the grayling is found in the Arctic Ocean drainages, and from the Bering Sea drainages and the Alsek River and Stikine system of Pacific Coast drainages, east to the western shore of Hudson Bay. The southern limit is the headwaters of the drainages concerned and south along the west shore of Hudson Bay to just north of the Nelson system in Manitoba (Walters 1955).

NOTE.—Approved for publication July 8, 1958. Fishery Bulletin 149.

In the United States, the grayling was indigenous to the following two areas: (1) the upper part of Michigan's Lower Peninsula, and in the Otter River of the Upper Peninsula (Hubbs and Lagler 1949), and (2) headwaters of the Missouri River above the Great Falls in Montana (Henshall 1902).

In Michigan, the grayling is a fish population of the past. Its disappearance has been attributed to many factors. Those most often cited are logging drives during the spawning season, competition with other species, deforestation and consequent rise in water temperatures, and fishing pressure. Streams such as the Manistee River, where the grayling was once so abundant that two men and two women were reported to have caught 3,000 individuals in 14 days and to have hauled 2,000 of them to Chicago, are now barren of the species (Creaser and Creaser 1935).

Transplantations from Montana have met with little success in distant States. Somewhat better results have been attained by stocking within the State itself. Grayling introduced into Georgetown Lake and Rogers Lake, Mont., for example, supplied for many years the majority of spawn taken for fish cultural purposes by the Montana Game and Fish Commission (Moffett 1950). However, even within Montana the range of the grayling has decreased. It is rarely observed in the Madison River drainage and is absent entirely from the Missouri River, the Gallatin River, and the main stem of the Jefferson River. The only indigenous population maintaining itself at present is in the Red Rock Lakes region of the Beaverhead drainage, where its management was studied by Nelson (1954).

Foremost among the individuals who have studied the grayling is Dr. C. J. D. Brown (1938a, 1938b, 1939, 1943) who did research on age and growth, food habits, habitat, and spawning behavior. Watling and Brown (1955) investigated the early embryology of the grayling. Moffett (1950) reported briefly on the status of the grayling in Grebe Lake.

Creaser and Creaser (1935) made a comparative analysis of age and growth of the Michigan and Montana varieties. Leonard (1939a, 1939b, 1940, 1949) recorded a number of observations in Michigan on stocks transplanted from Montana. Miller (1946), Rawson (1950), and Ward (1951) increased our knowledge of the species by life-history studies on the grayling in Canada. Wojcik (1955) also made a life-history investigation of the grayling in waters of interior Alaska.

In Yellowstone National Park, Wyo., the grayling occurred naturally in the Madison River and its tributaries, upstream to major barriers such as the Kepler Cascades on the Firehole River and Gibbon Falls on the Gibbon River. Transplants within the Park have produced varying results. Both North and South Twin Lakes provide good grayling fishing for small fish, but the population depends on regular stocking because there is no natural reproduction of the species. The most successful introductions have been those in a series of three lakes (Grebe, Ice, Wolf), formerly barren of fish life, above Virginia Cascades on the Gibbon River. Grebe and Wolf Lakes are a direct part of the Gibbon River system which drains into the Madison River, and Ice Lake is a few hundred yards from the main river on a small tributary. A fourth grayling lake, Cascade, lies close to the other three but is in the drainage of the Yellowstone River.

An alarming decline in numbers of the grayling in Grebe Lake occurred in 1948 and 1949. To rectify this, the National Park Service, responsible for preserving and maintaining the present stock of grayling in Yellowstone Park, believed that technical management measures were necessary, but basic biological data on the species and on Grebe Lake were lacking. This study, under the auspices of the U. S. Fish and Wildlife Service, was aimed at providing a scientific basis for the management of the fisheries of Grebe Lake.

I wish to thank Dr. Karl F. Lagler, Department of Fisheries, University of Michigan, for guidance during this study and for critically reviewing the manuscript. Field research was supervised by Dr. O. B. Cope, Chief of the Rocky Mountain Sport Fishery Investigations; equipment and funds were provided by the U. S. Fish and Wildlife Service.

ENVIRONMENT

PHYSICAL CHARACTERS

Grebe Lake lies at an elevation of approximately 8,000 feet on Solfatara Plateau near the center of Yellowstone National Park. This 145-acre lake is contained in a circular basin. The volcanic sand bottom is overlain by a blanket of muck (decomposed organic matter and silt) about 1 foot thick. The prevailing westerly winds have formed, through wave action, a narrow sandy beach on the eastern side of the lake. A maximum depth of 32 feet was found near the southeast shore (fig. 1). At the outlet, remnants of a beaver dam have raised the water level about 1 foot and formed a shallow curving arm 50 feet wide and 300 feet long.

Four major inlets enter Grebe Lake. These quickly break up into many small, spring-fed tributaries upstream from the lake. In addition, seepage areas contribute their flow, particularly during the moist spring and early summer. The outlet (Gibbon River) flows to the west and empties into Wolf Lake (42 acres) about 1 mile downstream from Grebe Lake. From there the stream travels 15 miles westerly to unite with the Firehole River and form the Madison River. Four miles below Wolf Lake a 50-foot cascade prevents any fish below the barrier from entering the waters above (the Grebe Lake system).

Temperatures at the surface and on the bottom of Grebe Lake were recorded continuously by a Brown thermograph (fig. 2) placed near the deepest area in the lake. Spring overturn occurred during 1953 on or about the third day after the ice completely left the lake. By July 1 the lake had stratified thermally. Maxima of average weekly surface temperatures (hourly interpretations) were reached in 1953 and 1954 between July 16 and 30 (fig. 3). Temperatures were still increasing at the bottom when the thermograph was removed from the lake on August 27, 1953.

The highest daily temperatures were 65° F. (at the 6-ft. level) on July 20, 1953, and 67° F. (1-ft. level) on July 13, 1954. Daily surface maxima occurred in the afternoons (between 1:00 and 5:00 p. m.) throughout the season. A surface minimum of 41° F. was recorded May 12, 1953. The daily range never exceeded 3° F.

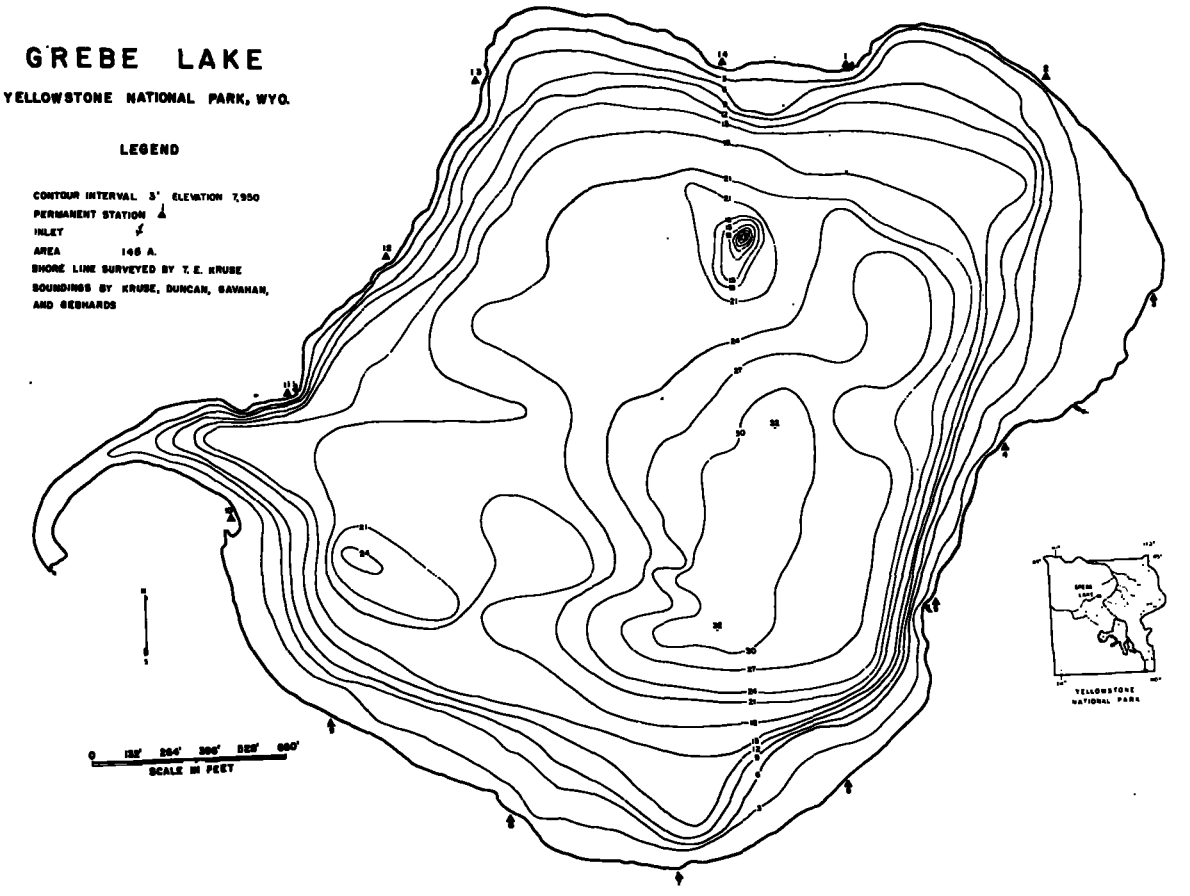

FIGURE 1.—Contour map of Grebe Lake, Yellowstone National Park, Wyo.

during 1953 (6-ft. depth) or 4° F. in 1954 (1-ft. level).

Thermal characteristics of Hatchery Creek, one of the inlets, were also recorded by a thermograph in 1953 and 1954 (fig. 4). Average weekly temperatures rose rapidly during June, then, gradually until mid-July. The maximum hourly temperature of 63° F. occurred at 3:00 p. m. on June 18, 1953. The daily peak was reached between 1:00 p. m. and 5:00 p. m. Daily minima occurred between 5:00 a. m. and 7:00 a. m. The greatest range for a 24-hour period was 23° (June 17, 18, 1953). The highest temperatures occurred in late spring and resulted from floodwater, which flowed in a shallow layer over the meadow surrounding Hatchery Creek, then drained back into the creek bed above the thermograph.

CHEMICAL FACTORS

Grebe Lake stratified both thermally and chemically during 1953 and 1954. On July 14, 1953, grayling and hybrid trout taken from trap nets set in water more than 20 feet deep were dead or in distress when the nets were lifted, but not so for those in shoal sets. The results of a water chemistry analysis made August 6, 1954, showed that the oxygen concentration in the lake at the 20-foot level contained only 4.5 p. p. m. (54.4 percent saturation) and decreased to 0.6 p. p. m. (6.8 percent saturation) at a depth of 28 feet (table 1).

Grebe Lake may be classified as an eutrophic lake with a deficiency of oxygen in its depths during the period of summer stagnation.

BIOLOGICAL FEATURES

Three species of plants dominated the vegetation within the lake. Large beds of waterlilies, *Nuphar polysepalum*, paralleled the eastern shoreline and extended into the lake up to 100 feet. On the bottom between water depths of 4 feet and 15 feet laid a nearly continuous 2-foot blanket

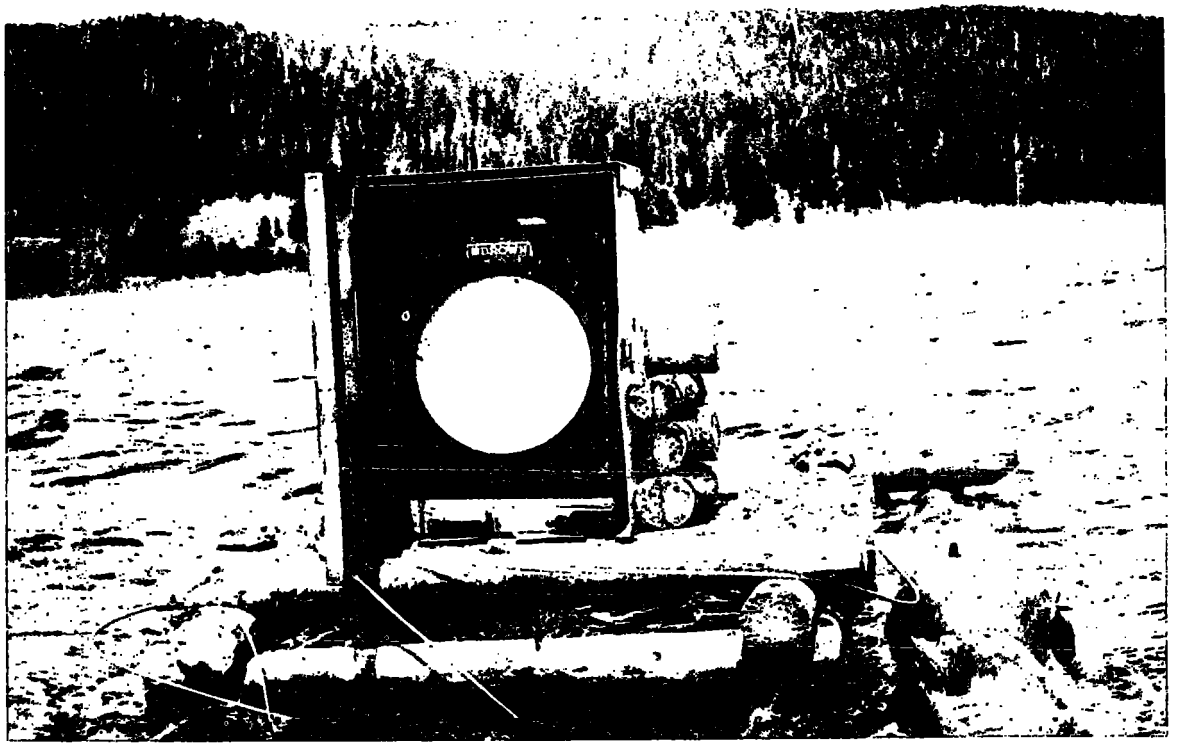

FIGURE 2.—Brown thermograph and log raft as they appeared in Grebe Lake, July 1954.

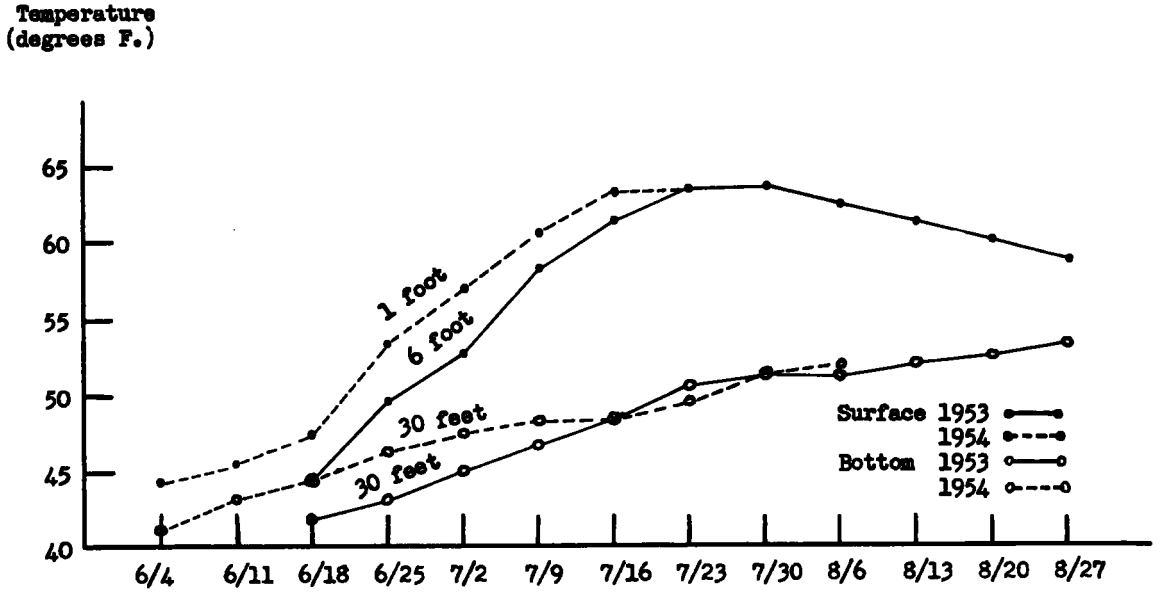

FIGURE 3.—Average weekly water temperatures (hourly observations from thermograph records) for Grebe Lake, Yellowstone National Park, Wyo., during 1953 and 1954.

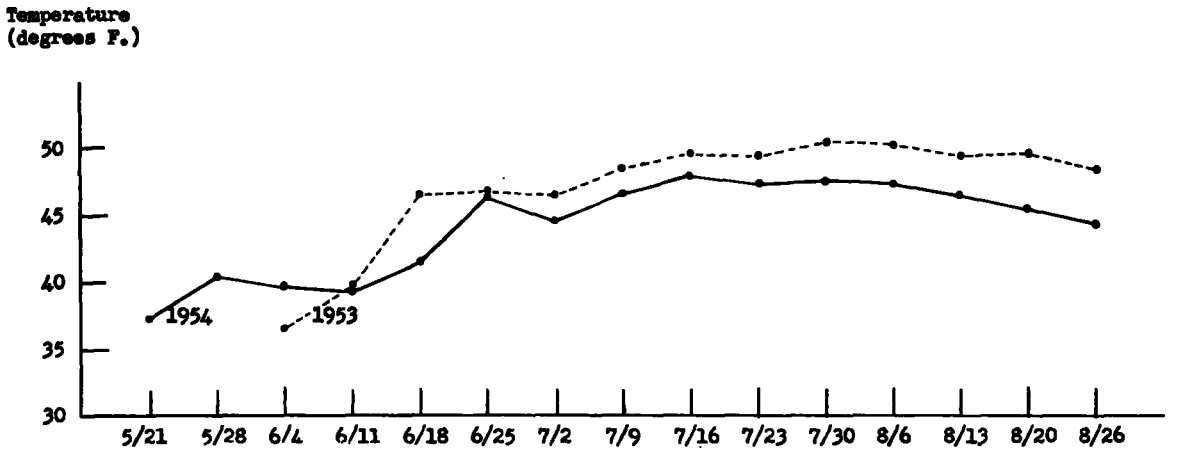

FIGURE 4.—Average weekly water temperatures (hourly interpretations from thermograph records) for Hatchery Creek, tributary of Grebe Lake, Yellowstone National Park, Wyo., during 1953 and 1954.

of *Potamogeton robinsii*. Through this dense cover grew scattered patches of another pondweed, *Potamogeton amplifolius*.

Bottom fauna was sampled with an Ekman dredge (6 ins. by 6 ins.). Standardized collections with the equipment available were possible only on bottom without a vegetative cover at depths above 15 to 18 feet. Two of the samples were collected in shallow areas less than 18 feet where only vegetation was retained by the dredge. The organisms were rinsed from the plants and enumerated for (1) general type and (2) relative abundance (table 2). Twenty-three samples from the open water of the lake were analyzed.

TABLE 1.—*Physical and chemical features of Grebe Lake on Aug. 6, 1954*

Location	Temperature (degrees F.)	Free CO_2 (p. p. m.)	pH	M. O. alkalinity (p. p. m.)	O_2 (p. p. m.)	Percent saturation
Lake surface	62	5.0	7.2	14.0	7.6	104.7
5 feet	62	4.5	7.6	18.0	7.4	102.0
10 feet	61	3.5	7.6	17.0	6.8	92.5
15 feet	60	5.0	7.2	18.0	5.4	73.4
20 feet	53	12.0	6.4	18.0	4.5	54.4
25 feet	50	21.0	6.4	17.0	1.6	19.0
28 feet	50	16.0	6.4	17.0	.6	6.8
Outlet	58	4.0	7.2	18.0	8.8	115.6

Tendipedidae (=Chironomidae) were the most important bottom organisms at all depths, both in numbers and by volume (table 2). Forbes' (1893) collections from Grebe Lake, taken before fish had been introduced, included the following forms: (from the bottom), *Chironomous*, *Gammarus*, *Pisidium*, *Diaptomus lintoni*, *Daphnia clathrata*, and *Cyclops;* (from inshore samples), *Gammarus*, *Allorchestes*, *Pisidium*, *Corisa*, *Physa*, *Chironomous*, *Spongilla*, *Nephelis*, *Clepsine*, Ephemeridae, Odonata, and *Haliplus*.

TABLE 2.—*Qualitative analysis of bottom fauna from Grebe Lake, 1952*

Organism	Depths greater than 15 feet (23 samples)			Plant rinses [1] (2 samples)		
	Number	Volume (cc per sq. ft.)	Percent volume	Number	Volume (cc per sq. ft.)	Percent volume
Nematoda	96	0.40	1.71	1	T	
Oligochaeta	1,352	2.80	11.97	25	0.05	2.38
Gastropoda	8	T		43	T	
Pelycopoda	1,056	4.00	17.09			
Hydracarina				1	T	
Ephemeroptera				3	T	
Anisoptera				1	.40	19.05
Trichoptera (case)	8	.20	.85	2	1.00	47.62
Tendipedidae (= Chironomidae)	1,744	16.00	68.38	1,736	.65	30.95

[1] Each sample was arbitrarily the amount of vegetation which filled a 2-quart jar without packing.

HISTORY OF FISH IN GREBE LAKE

In 1907, 10 cans of eggs of rainbow trout (*Salmo gairdneri*) were planted in Grebe Lake (annual reports of Superintendents of the Yellowstone National Park, 1908). In 1912, 300,000 fry of cutthroat trout (*Salmo clarki lewisi*) from Yellowstone Lake were introduced (record cards in Chief Ranger's Office, Yellowstone National Park). Since that time the two salmonid species have hybridized to such an extent that by 1952 no fish were found which were definitely pure strains

485001 O-59-2

of cutthroat or rainbow trout. The hybrids have the general appearance of rainbow trout, but with a red slash on each side of the hyoid membrane. Hyoid teeth, a cutthroat characteristic, were present in all specimens examined. Body forms range from the typical elliptical shape of the cutthroat to the blunt, stocky, high-shoulder outline of the rainbow.

TABLE 3.—*Annual removal of grayling eggs and stocking of Grebe Lake, 1931–54*

[Moffett, 1950; stocking records are in Chief Ranger's Office]

Year	Number of eggs	Eggs or fry returned to lake
1931	750,000	750,000
1932	768,000	[1] 40,000
1933	2,118,400	650,000
1934	4,443,000	735,000
1935	3,660,000	676,500
1936	4,211,140	400,000
1937	5,715,000	1,000,000
1938	5,837,000	384,635
1939	5,117,368	80,000
1940	4,660,209	1,009,410
1941	5,019,403	1,120,631
1942	4,093,589	1,021,000
1943	3,300,000	484,584
1944	1,774,784	None
1945	1,787,336	None
1946	1,746,324	153,018
1947	2,178,155	None
1948	4,217,464	None
1949	1,758,155	225,000
1950	1,653,845	500,000
1951	(2)	300,000
1952	(2)	300,000
1953	1,708,910	400,000
1954	428,800	350,000

[1] Remainder lost.
[2] Data on spawntaking activity is unavailable for these years.

Grayling were first planted in Grebe Lake in 1921, when a million eggs were brought from Anaconda, Mont. (record cards in Chief Ranger's Office, Yellowstone Park). The species was gradually established in the lake and by 1930 large spawning runs were observed in the various inlets. In 1932 a few eggs were taken artificially on an experimental basis for hatching by the U. S. Bureau of Fisheries. Results were so encouraging that a permanent hatchery was established at the lake. In 1933, more than 2 million eggs of this species were taken from Grebe Lake (Leach, 1934–35). Region II of the U. S. Fish and Wildlife Service and particularly the Park itself received most of the fish produced. The yearly take of eggs and return of eggs and fry to Grebe Lake (table 3) show how well the species established itself. An extremely low population occurred in 1949 when so few spawning fish entered Hatchery Creek weir that only a portion of the grayling egg commitments by the fish culture station could be filled. The lake was then closed to fishing; and restocking, which had been rather neglected for the previous 5 years, was undertaken vigorously.

RECENT POPULATIONS IN GREBE LAKE

Knowledge of population size and composition (year-class and species) are fundamental to the prediction of angling success. Since the Grebe Lake problem involved species interaction, knowledge of population size was particularly important.

POPULATION ESTIMATES

Populations of grayling and trout were approximated by the Schnabel (1938) formula as modified by Chapman (1952). With a population estimate of this type, fish are captured in successive time units, unmarked fish are marked, and all individuals are released. The ratio of tagged fish (s) to total captures (n) in any sample provides an estimate of the ratio between the total number of tagged fish in the population at the time of the sample (t) and the total population (N). As the numbers of marked fish in the population increase during the experiment, the ratio of s/n also increases subject to sampling errors. Schnabel used the method of maximum likelihood to combine these sequential estimates into single weighted mean such that $N=\frac{nt}{s}$.

Chapman (1952) stated that for an unbiased estimate of the true population the formula should be $N=\frac{nt}{s+1}$. With the use of either the Schnabel formula or this modification the author indicated that the confidence interval on N could be determined from the Poisson approximation given by Chapman (1948).

In 1953, the equipment used for the population study consisted of 5 impounding nets. Two were fyke nets on hoops 3½ feet in diameter; each unit was 12 feet long, was made of 1-inch mesh (mesh sizes are stretched mesh), and had two throats. Each net was also equipped with 12-foot wings but no leader. The third hoop fyke net was 4 feet in diameter, 15 feet long, and of 2-inch mesh. The wings were 50 feet in length

and were made of 2½-inch mesh. The remaining equipment consisted of 2 trap nets (much as shown by Crowe, 1950) having a pot, heart, and wings. The pot was of 1-inch mesh and the heart and wings were of 2½-inch mesh. When set, such units tapered from the wings which were 20 feet apart at their outermost end, to the pot which was 5 feet wide by 8 feet long by 3 feet deep. All the net gear was soaked in dark-green, copper naphthanate.

In 1954, four trap nets and a seine were used to capture the fish. Two trap nets were those used during 1953. Two new units were identical with the 1953 design except for a smaller mesh size (1½-ins. rather than 2½-ins.) in the wings. Leaders were not used. These new nets were preserved with light-green copper napthanate. The tied seine was 75 feet by 4 feet, with 1-inch mesh.

In the population studies, both trout and grayling were taken from depths up to 30 feet. The first sets made in deep water (more than 20 feet) killed all the fish that entered the impounding nets. Subsequently only the shallow portions of the lake (less than 20 feet deep) were fished. These shoal areas were sampled randomly by dividing a map of the lake into a grid pattern, numbering the intersections, and drawing numbered slips of paper to determine the sites. Nets were set, lifted each morning, moved to the next predetermined location, and reset. The few shallow areas where seining was possible were fished 9 times at night during the 21-day sampling period in 1954.

Captured fish were held in a floating live box attached to a boat. The seined fish were towed to the approximate center of the lake, fin-clipped, and released. Fish from nets were distributed around the lake as the boat moved from one net location to the next. The left pectoral fin was removed in 1953 and the right pelvic fin in 1954. Only grayling in their third year of life (longer than 8.4 ins.) and older, and trout more than 5 inches in length, were marked in 1954. The previous year all fish captured were marked (minimum size 4.3 inches for grayling, 3.3 inches for trout).

The period of netting extended from July 8 to August 9 (33 days) in 1953, and from July 1 to July 21 (21 days) in 1954.

To determine the most effective direction to face nets and capture grayling and hybrid trout, 30 sets were placed randomly. The results of the collections (table 4) showed that traps facing the shore were two to five times as effective as those directed toward the center of the lake or parallel to shore. An analysis of variance between numbers of fish captured during various facings indicated significance at the 5-percent level.

In the evening feeding period, the grayling and hybrid trout were evenly distributed about the lake, as judged from patterns of rises. For trout, this conclusion was substantiated by net captures. However, net locations along the outer border of the lily pads and in the shallow eastern portion (fig. 5) consistently resulted in more grayling captures than those in any of the other areas (table 5).

In 1953, the average daily catch in nets during the 33-day period was 40 fish (table 6). The trap nets were the most effective gear in this operation. These two units accounted for 983 (74.5 percent) of the 1,320 fish taken. By species, the trap nets took 21.5 percent (284) of the hybrid trout and 78.5 percent (1,036) of the grayling. Angling added 209 grayling and 67 trout to the marked population with 6 grayling and 4 trout recaptured by this means.

The greater effectiveness of trap nets over fyke nets in total catch of fish (fig. 6), and the difference in sizes of individuals captured in the two types of

TABLE 4.—*Numbers of fish captured by 30 net sets faced randomly in Grebe Lake in 1954*

Catch	Direction of net					
	Perpendicular, toward shore		Perpendicular, away from shore		Parallel to shore	
	Trout	Grayling	Trout	Grayling	Trout	Grayling
Number captured	47	256	7	25	13	102
Average catch per set	3.6	19.7	1.0	3.6	1.3	10.2
Number of sets	13		7		10	
Total catch per set (both species)	23.3		4.6		11.5	

TABLE 5.—*Fish concentrations in various parts of Grebe Lake as determined by net captures (1954 data)*

Area	Total catch		Number of sets	Catch per set		Overall average catch per set
	Trout	Grayling		Trout	Grayling	
Eastern shelf	62	254	17	3.65	14.94	18.59
South shore	29	79	10	2.90	7.90	10.80
Lily pads	72	607	36	2.00	16.86	18.86
Northwest shore	13	40	5	2.60	8.00	10.60
North shore	42	148	14	3.00	10.57	13.57
Total	218	1,128	82	2.66	13.76	16.41

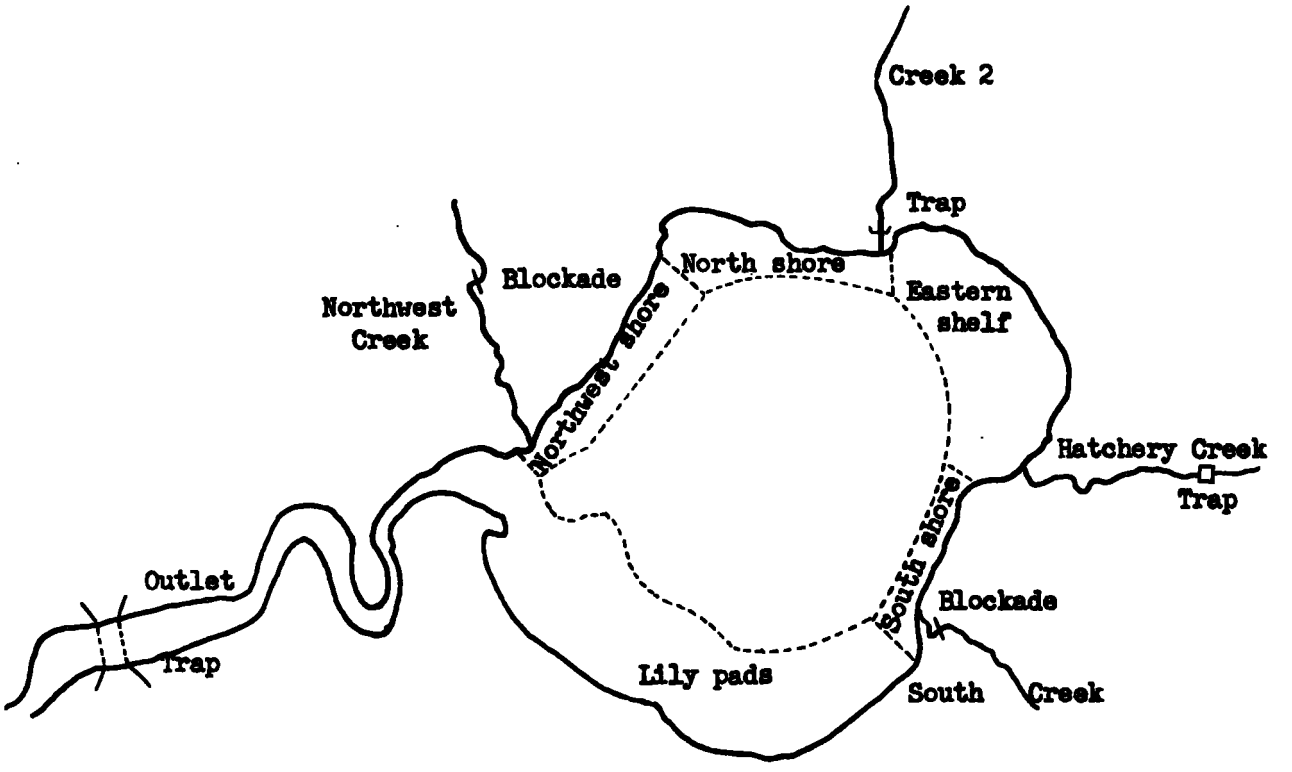

FIGURE 5.—Diagrammatic map of Grebe Lake, Yellowstone National Park, Wyo., showing tributaries, spawning barriers, and lake divisions used in netting analysis.

gear resulted in the sole use of four trap nets in 1954 plus some seining at night.

TABLE 6.—*Catch of trout and grayling in different types of nets during the Grebe Lake population study (July 8, 1953–Aug. 9, 1953, and July 1, 1954–July 21, 1954)*

Year	Species	Average daily catch [1]			Total catch		
		Trap nets	Fyke nets	Total	Trap nets	Fyke nets	Total
1953	Trout	6.8	1.8	8.6	224	60	284
	Grayling	23.0	8.4	31.3	759	277	1,036
	Combined	29.8	10.2	40.0	983	337	1,320
1954	Trout	10.4	[2] 19.3		219	174	393
	Grayling	53.9	25.0		1,132	225	1,357
	Combined	64.3	44.0		1,351	399	1,750

[1] Daily catch in various types of nets (2 trap nets, 3 fyke nets in 1953 and 4 trap nets plus seine in 1954).
[2] Daily average of the 9 days on which the seine was used.

The best results in 1954 were obtained with the two trap nets with a mesh size of 2½ inches in the wings. These two nets were 3.5 times as successful as the small-meshed units of the same design. However, the two nets with 1½-inch mesh wings were treated with a light-colored preservative (copper naphthanate); the other two were more darkly stained in the preservation process. The total catch of fish in trap nets in 1954 was 1,351 for an average daily catch of 64.3 over a 21-day period (table 6). Fish seining on nine occasions during the mark-and-recapture period took 174 trout (44 percent of total trout captures) and 225 grayling (17 percent of total grayling captures).

The population (fish more than 4.3 inches total length for grayling and 3.3 inches total length for hybrids) for Grebe Lake for 1953 was estimated to be 28,956 fish or 77.3 pounds per acre (table 7). In 1954, a comparable Schnabel-type estimate for grayling over 8.4 inches and hybrids of more than 5.7 inches was 28,430 fish or 79.2 pounds per acre.

TABLE 7.—*Population estimates for Grebe Lake, 1953, 1954*

Year	Species	Number captures	Recaptures	Estimated population	Confidence limits 95 percent [1]		Estimated weight [2] pounds per acre
					Upper	Lower	
1953	Trout	353	24	2,041	3,164	1,343	7.1
	Grayling	1,251	22	26,915	42,652	17,370	70.2
1954	Trout	393	24	2,548	3,949	1,676	8.3
	Grayling	1,357	30	25,882	38,111	17,820	[3] 70.9

[1] Confidence limits from table 1, Chapman (1948).
[2] Weight determined from length-weight relation by converting fish lengths in nets to weights of fish in nets and then assuming a proportional relation between number of fish in nets and Schnabel estimate.
[3] Pounds per acre of grayling increased in 1954 because of the larger size of fish the second year (average size 10.5 inches in 1953, 11.0 inches in 1954.).

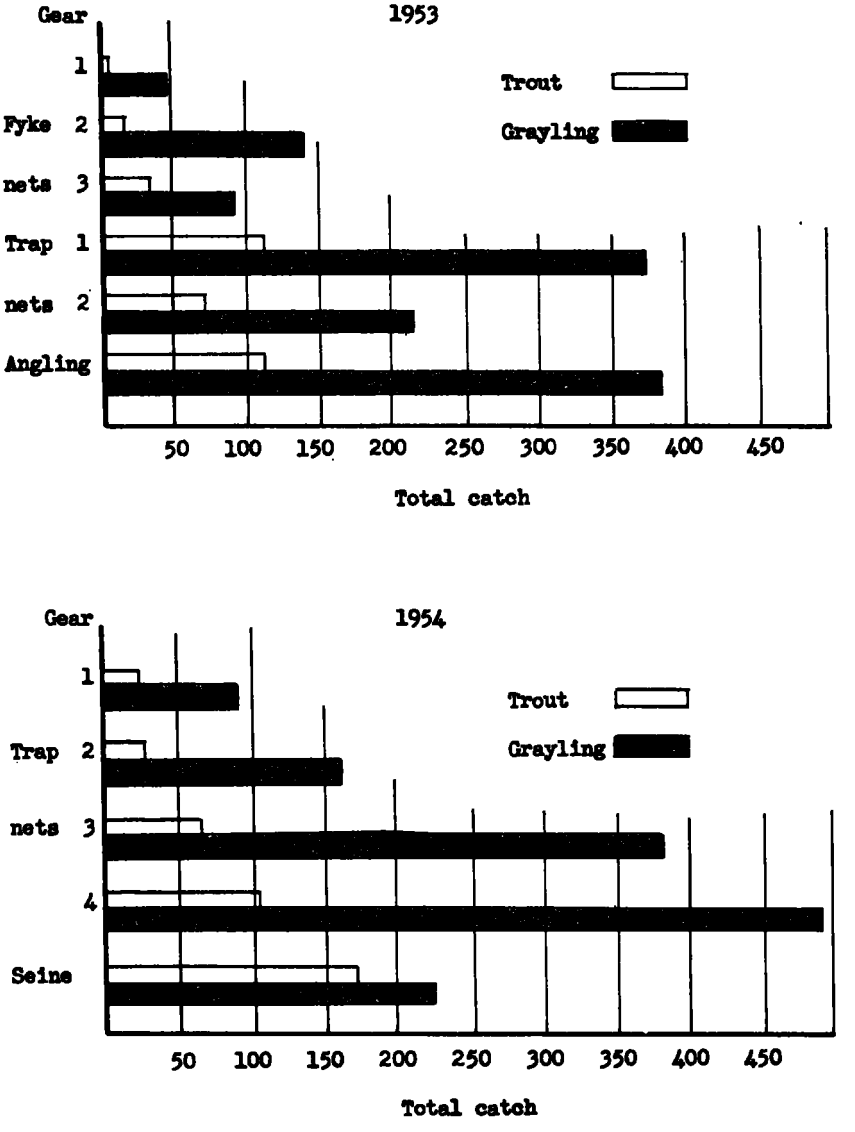

FIGURE 6.—Effectiveness of gear in capturing hybrid trout and grayling in Grebe Lake during the mark-and-recapture study, 1953 and 1954.

Methods of forming population estimates which have been used by biologists and the prerequisites necessary for the use of various methods have been adequately discussed by Ricker (1948), DeLury (1951), Cooper and Lagler (1956), and others. It is essential, however, to indicate which of these prerequisites have and have not been fulfilled by this study and hence what reliability can be placed on the estimated numbers of trout and grayling.

The first assumption of a mark-and-recapture study is that either (1) marked fish distribute themselves randomly throughout the lake, or (2) that the fish are captured by a random placement of the nets proportional to the population density in different parts of the lake. Nets in this particular study were set randomly and fish captured were redistributed in various parts of Grebe Lake to ensure randomness.

Secondly, mortality among the marked fish must not be greater than among unmarked individuals. The result of such an error would be a decrease in the marked specimens and a population estimate that is too large. Ricker (1949) was unable to demonstrate significant mortality in a population of fish from which one fin had been removed, and

no visible evidence of excessive mortality was observed by me. Frequently some fish were weakened by handling and swam near the surface in the live box. When released, these individuals remained visible from the surface and became targets for osprey after the boat left the area for the next station. Such fish, visibly weakened, were never marked. In 2 years, only one dead marked fish was found.

A third assumption is that recruitment is negligible during the time recoveries are being made. Recruitment contributed both trout and grayling to the 1953 population, biasing estimates upward. Although all grayling which were sampled during the first year were at least in their second summer of life, the smallest 2-year-olds (less than 4 inches) undoubtedly passed through the finest mesh (1½-inches), at least for the first part of the recapture period. The 1953 nettings captured no grayling between 7.4 inches (largest 2-year-olds) and 8.8 inches (smallest individual more than 2 years old). To minimize the effects of recruitment in 1954 only grayling more than 8.4 inches were marked.

Trout presented a different problem. In 1953, trout as small as 3.3 inches were marked, however, only 7 fish less than 5 inches were measured and these few trout captures were all that recruitment might have contributed to the marked population. This error was negligible. In 1954, although hybrids as small as 5 inches were to be marked, no trout less than 5.7 inches in total length were captured by the seine, or less than 6.1 inches by the nets. Since the 1954 gear would retain 5-inch hybrids, recruitment only slightly biased the 1954 estimates.

A fourth assumption is that no mortality, either natural or by fishing, acts to reduce the population during the recapture period. Grebe Lake was subject to light fishing pressure both years during the population study. Approximately 301 hybrids and 343 grayling were caught by anglers in 1953 and 275 trout and 472 grayling in 1954 during the marking period. Only four fin-clipped fish were reported by anglers in the 2 years. That some marks escaped the notice of fishermen, is probable, since of 290 fish caught by angling and marked by me in 1953 during the study, 10 of these were recaptures. Thus more than 3 percent of my captures had been marked, but only 0.3 percent were reported by anglers as fin-clipped. The result of mortality during this experiment undoubtedly increased estimates.

The fifth assumption is that there is no differential availability of marked and unmarked fish (that marked fish did not become "trap-shy" as a result of handling). A means of checking the number of recaptures by the net would be to sample the population by a means other than trap netting and compare the percentage of recaptures by the new method to results obtained from trap netting. Such samples were available in 1953 as personal angling, and during 1954 as seining. I was unable to demonstrate any significant difference between 1953 recaptures by nets and recaptures by fishing of either hybrid trout or grayling. In 1954, the ratio of marked to unmarked fish was greater in the seine than in the trap nets. A chi-square test indicated a significant difference at the 95 percent level between grayling recaptured in nets and recaptures by seining. Such evidence suggests that marked grayling avoid trap nets more frequently than unmarked individuals. The result of such differential availability in grayling was to increase the population estimate. Trout recaptures by the seine and by nets were not significant at the 95-percent level.

Of the estimated populations, 16 percent of the trout were captured in 1953 but only 4 percent of the grayling. Thus there is evidence that the trout are more susceptible to trap netting than are the grayling.

An additional error appeared in the 1953 estimate when the mean length was different for fish captured by the different types of gear (two small-mesh hoop fykes, two trap nets, and one large-mesh hoop fyke) (fig. 7). An analysis of variance (table 8) of these 1953 data indicated that this difference in mean lengths was significant at the 95 percent confidence limits. The various nets therefore sampled different parts of the population, and each did so with its own effectiveness. It was for this reason that four trap nets of a single design were used in 1954, but unfortunately all bias was not overcome because the two newer nets were preserved with a light-colored copper naphthanate and had a different mesh size in the wings.

An analysis of variance (table 9) showed that in 1954 the mean sizes of fish from the different trap nets were significantly different from one another and also from the seined sample. This

meant that, despite precautions, again in 1954 the equipment was sampling different segments of the population. Possibly this resulted from using the fish captured in the twine of the wings of the two large-meshed trap nets; this larger mesh selectively retained larger fish.

The seine proved effective when used at night close to shore. Seined grayling averaged slightly smaller than those captured by trap nets. This size difference was also significant (table 9) for this species, but such a difference could not be demonstrated for trout.

TABLE 8.—*Analysis of variance of mean lengths of fish taken in 5 nets in 1953 population study on Grebe Lake*

	Sum of squares	Degrees of freedom	Mean square	F ratio
Means	288.06	4	72.01	$F_s = \frac{72.01}{4.24} = 16.98$
Within	1,644.97	388	4.24	F05 (4,388) = 2.37

The error associated with samples stratified by size will tend to increase population estimates. Such an error is common to most problems though unrecognized when only one type of equipment is

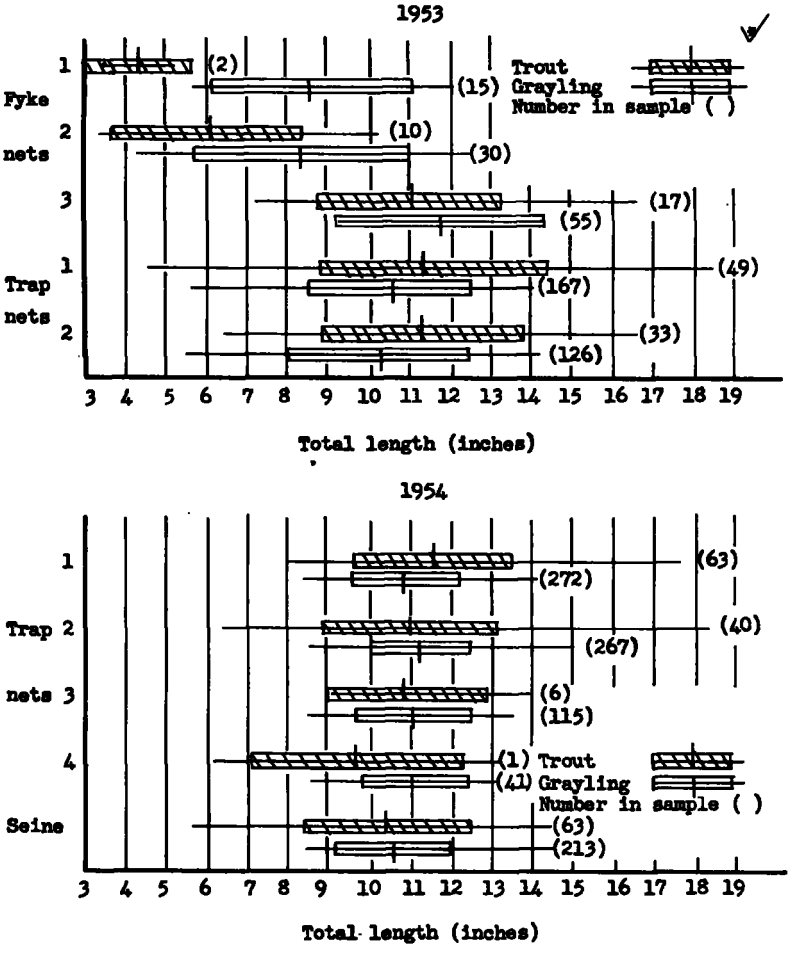

FIGURE 7.—Comparison of lengths of grayling and hybrid trout in individual nets and the seine during the 1953, 1954, population study on Grebe Lake, Yellowstone National Park, Wyo.

used. Ricker (1948) considered errors introduced through unequal vulnerability of fish of different sizes not to be serious.

TABLE 9.—*Analysis of variance of mean sizes of fish captured by various methods in 1954*

Method of capture	Species	Observed F ratio	F ratio (5-percent value)
Between 2 types of trap nets	Trout	F=2.97	F_{95} (3, 691)=2.68
	Grayling	F=3.33	F_{95} (4, 278))=2.37
Between small mesh trap nets and seine	Trout	F= .79	F_{95} (2, 177)=3.00
	Grayling	F=6.06	F_{95} (2, 366)=3.00

FACTORS CONTROLLING COMPOSITION OF THE GREBE LAKE POPULATION

SPAWNING OF GREBE LAKE FISHES

An initial determinant of fish population size is the reproductive success of its components. In the Grebe Lake system, ample spawning facilities appear to exist for both the grayling and the hybrid trout. Yet, in a search for factors limiting the abundance of the grayling (which fluctuates drastically) thought must be given to undesirable competition, and possibly to predation by trout on the spawning grounds that are shared in a very concentrated way with the grayling.

Most of the information on the spawning populations of fishes in Grebe Lake was obtained from weirs. One of these fish traps was on Hatchery Creek where grayling spawn has been collected annually since 1931. Additional weirs or blockades were installed in each of the tributaries of Grebe Lake and in the outlet (the Gibbon River) about 150 yards downstream from the lake (fig. 5).

In 1953, when the snow melted, the large volume of water from the surrounding mountains poured into the inlets, clogged the traps, and allowed many fish to bypass them. Only the installations on Hatchery Creek (fig. 8), the outlet (fig. 9), and South Creek withstood the high waters and enabled analysis of the spawning population. The weirs and blockades (fig. 10) installed in the Grebe Lake system in 1954 were more effective than those of 1953, since improvements had been made in construction and the spring runoff was spread over a longer period of time.

Spawning Areas

Grayling and trout spawn in all inlets and in the Gibbon River below Grebe Lake. The area of each waterway available for spawning was estimated by the following method. During the time of hatching and while fry were still present in the streams, the farthest upstream locations of fry were determined for each tributary. Measurements were then made from the first natural barrier above these fry to the lake. All distances were recorded by wading the creeks and measuring with a steel tape the distance traveled. On 3 of the 4 tributaries, greatest widths were taken at each 100-foot interval even to include undercut regions beneath banks. On the fourth, Northwest Creek, and on the Gibbon River, widths were measured every 357 feet.

The variability of bottom types and of currents made some sections unacceptable to spawning fish. In computing the amount of suitable spawning grounds, the sections between each width measurement station were evaluated separately and the results were combined to obtain totals (table 10). Visual estimates of suitability were based on: (1) type of bottom (best-to-worst: gravel, sand, and rubble), (2) speed of current (slow or medium current preferred to a fast velocity), and (3) general characteristic of the stream for that section (riffles attracted more spawning fish than did pools). In general, the suitability of a section corresponded to the comparative numbers of grayling seen spawning in the same or similar sections the preceding spring.

TABLE 10.—*Lengths, areas, and estimated amount of stream bottoms suitable for spawning by grayling and hybrid trout in Grebe Lake waterways (July 23–25, 1953)*

Waterways	Distance (feet) available to spawners	Total bottom area (square feet)	Grounds suitable for spawning	
			Square feet	Percentage of total area
Tributaries:				
Hatchery Creek and branches	4,030	19,727	15,053	76.3
South Creek	678	3,965	2,870	72.4
Creek 2	1,000	2,767	552	19.9
Northwest Creek	3,154	18,206	12,578	69.1
Outlet:				
Gibbon River (Wolf Lake to Grebe Lake)	8,106	93,938	42,845	45.6

Time and Water Conditions

The spawning season for both grayling and hybrid trout in Grebe Lake in 1953 and 1954 was between mid-May and late June (fig. 11). Daily average water temperatures during this interval ranged from 40° to 57° F. (tables 11 and 12). The temperatures mid-lake and just beneath the

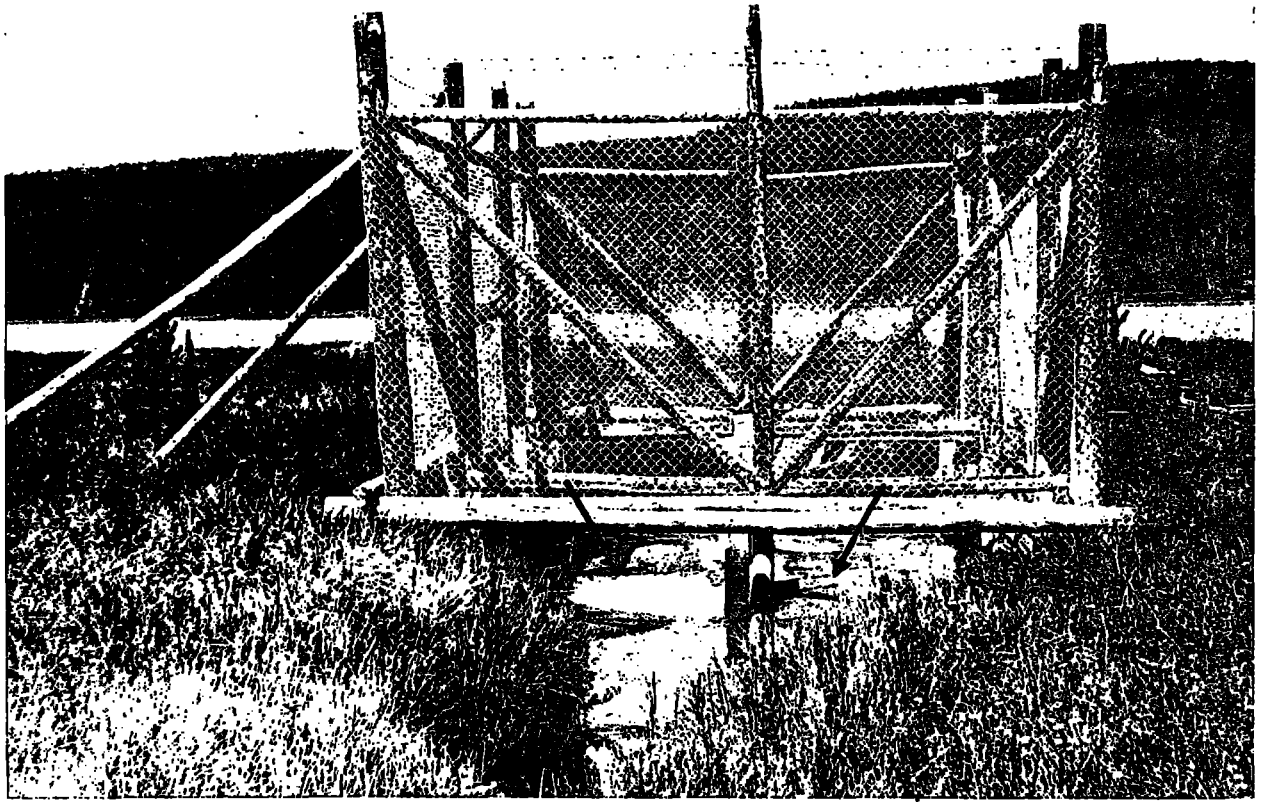

FIGURE 8.—Hatchery Creek trap (with wire-mesh superstructure to keep out bears) in August 1952 after iron rack was removed (at arrows) and fish were allowed access, looking westerly downstream with Grebe Lake in distance.

surface at this time were much like those of the streams.

Within the foregoing extremes there were behavioral differences within and between the two kinds of fishes in the lake (fig. 11). The trout did not have the definite peak of spawning migration (as reflected by movements into traps) that the grayling attained. In most streams spawning travel started 1 to 3 weeks earlier for the trout than for the grayling (tables 11 and 12), and continued at a more or less steady rate throughout the spring over the entire temperature span given above. The range of daily averages was from 40° F. to 50° F. when the grayling runs were heaviest. Temperatures near the surface of Grebe Lake were above 45° F. each year when grayling migrations were maximal (fig. 11).

Spawning Populations of Grayling and Hybrid Trout

There were 10 to 20 times more grayling than trout ascending the spawning streams in 1953 and 1954 (table 13). The actual grayling-trout ratios were 10.5 to 1 (1953) and 19.5 to 1 (1954). The difference in ratios in the 2 years might have resulted from comparing an incomplete count (possibly selective) in 1953, with a relatively complete one in 1954. In the later year, blockades on Northwest Creek, Creek 2, and South Creek seemed to have forced many spawners to accept either the outlet or Hatchery Creek as their spawning site. This may have resulted in larger counts on these two streams than would otherwise have occurred.

Records of spawntakers enumerating weir captures in years previous to 1953 showed that few

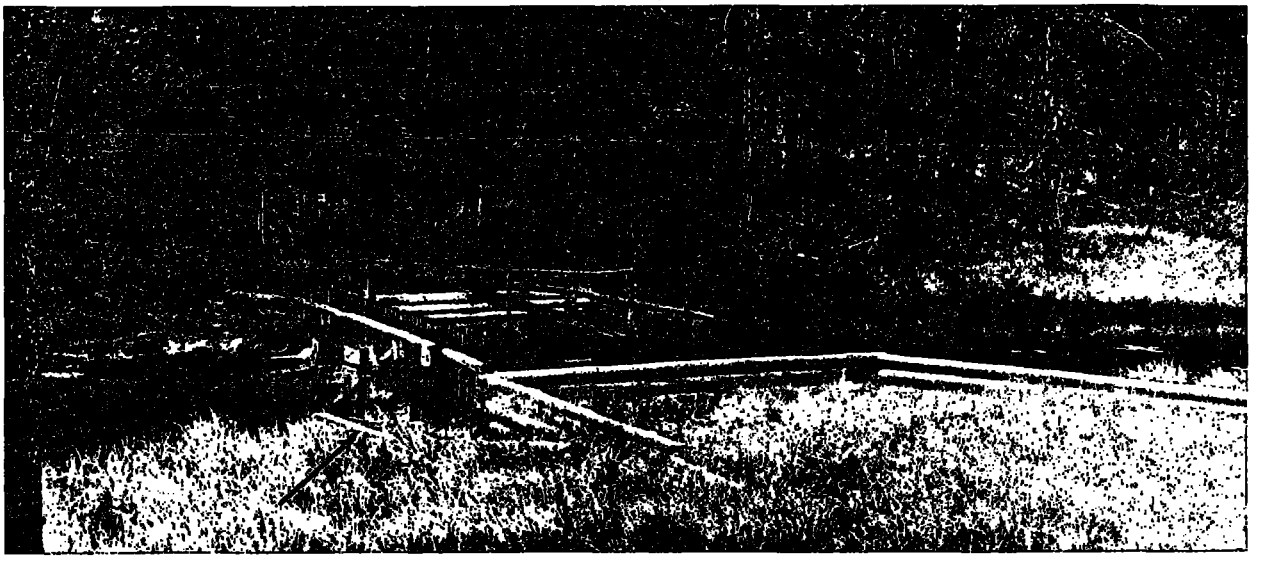

FIGURE 9.—Trap in Gibbon River outlet of Grebe Lake, showing downstream collecting pen (at arrow) July 7, 1954.

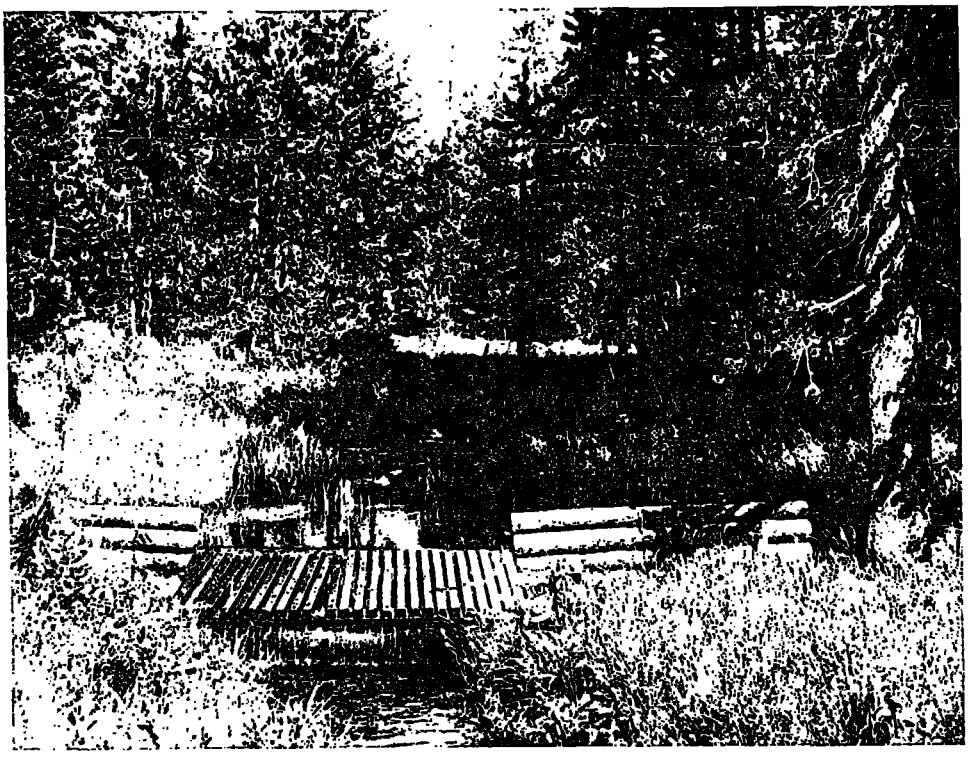

FIGURE 10.—Blockade on Northwest Creek during 1954. The picture was taken in July after the streamflow had dropped.

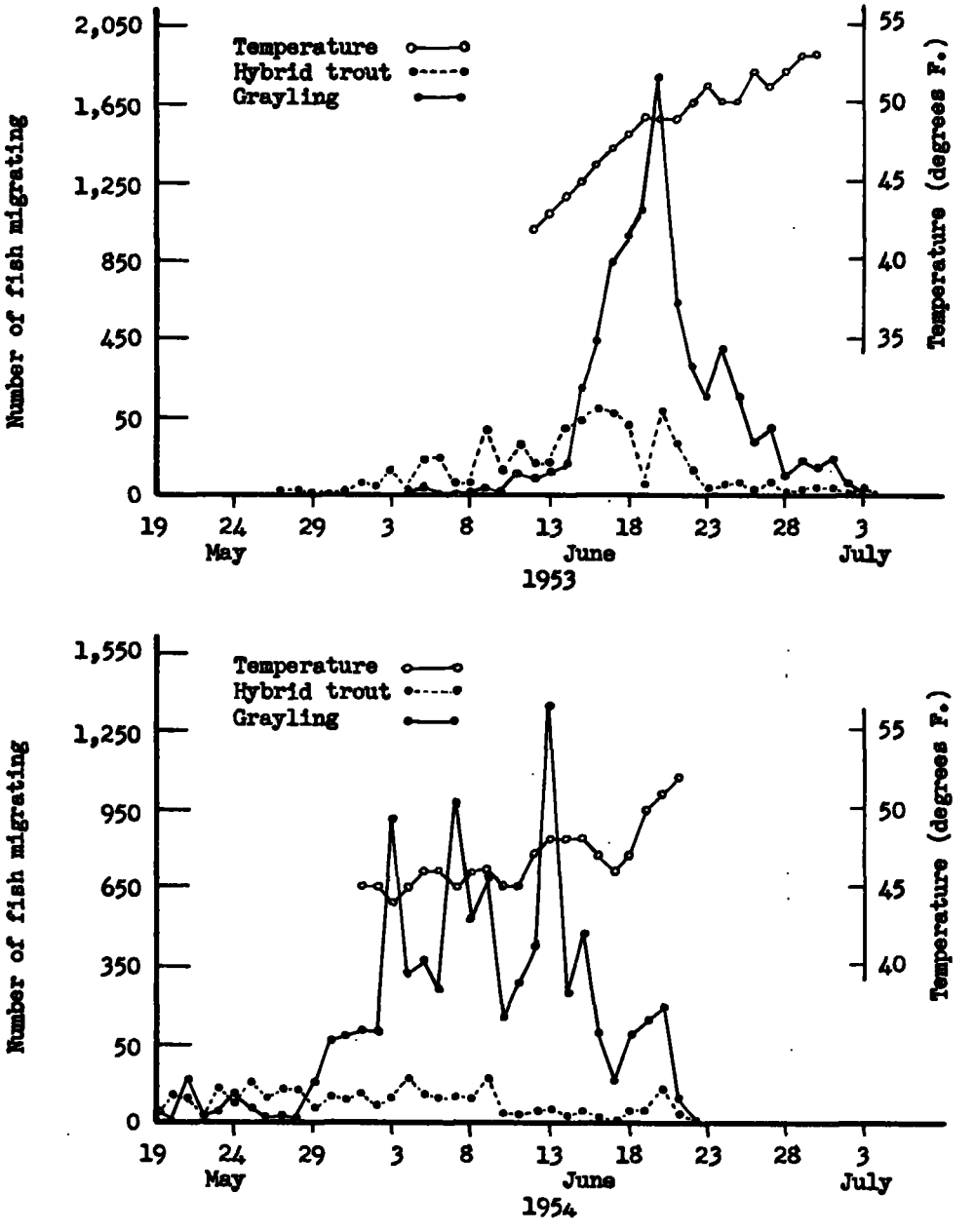

FIGURE 11.—Migration of hybrid trout and grayling into stream traps, and surface water temperatures (6-ft. depth in 1953, and 1 ft. deep in 1954) in Grebe Lake streams, 1953, 1954. Numbers of fish include only those moving to spawning grounds.

TABLE 11.—*Chronology of spawning runs and average daily water temperatures (° F.) for the Grebe Lake stream system (1953)*

Species	Movements [1]	Locations, date, temperature					
		Hatchery Creek	Creek 2	Northwest Creek	South Creek	Outlet	
						Upstream	Downstream
Grayling	First fish	June 14 (46°)	June 17 (43°)	Unknown	June 17	June 5 (36°)	June 8 (39°)
	Maximum activity	June 20 (44°)	June 24 (43°)	----------	June 21	June 18 (50°)	June 19 (50°)
	Last fish	June 26 (45°)	July 2 (47°)	----------	June 24	July 3 (36°)	June 26 (60°)
Trout	First fish	June 6 (38°)	June 1 (37°)	----------	None	June 1 (36°)	May 27 (38°)
	Last fish	June 20 (44°)	July 3 (47°)	----------	----------	July 1 (57°)	June 25 (53°)

[1] Movements recorded were upstream only in the creeks, but both directions in the outlet, as indicated.

TABLE 12.—*Chronology of spawning runs and average daily water temperatures (° F.) for Grebe Lake (1954)*

Species	Movements [1]	Locations, date, temperature					
		Hatchery Creek	Creek 2	Northwest Creek	South Creek	Outlet	
						Upstream	Downstream
Grayling	First fish	May 25 (42°)	None	June 5	June 4	May 19 (40°)	May 19 (40°)
	Maximum activity	June 3 (41°)	----------	June 13	June 12	May 21 (43°)	June 2 (45°)
		June 7 (39°)	----------	----------	----------	----------	----------
		June 13 (42°)	----------	----------	----------	----------	----------
	Last fish	June 21 (46°)	----------	June 21	June 20	June 19 (48°)	June 15 (47°)
Trout	First fish	May 24 (43°)	May 26	May 27	None	May 21 (41°)	May 19 (40°)
	Last fish	June 20 (45°)	June 21	June 21	----------	June 11 (46°)	June 21 (55°)

[1] Movements recorded were upstream only in the creeks, but both directions in the outlet, as indicated.

TABLE 13.—*Comparison of spawning migrants based on weir counts made in 1953 and 1954, Grebe Lake system*

Year and species	Weir counts								
	Outlet downstream migrants	Upstream migrants							
		Outlet	Creek 2	Hatchery Creek	Northwest Creek	South Creek	Total counted	Estimated total	Ratio grayling to trout
1953									
Grayling	263	392	403	5,416	169	438	7,081	10,984	----------
Trout	183	374	97	18	2	----------	674	960	----------
Total	446	766	500	5,434	171	438	7,755	11,944	10:5:1
1954									
Grayling	658	82	----------	5,971	754	413	7,878	7,878	----------
Trout	143	78	34	105	45	----------	405	405	----------
Total	801	160	34	6,076	799	413	8,283	8,283	19.5:1

trout spawned in Grebe Lake tributaries. However, these observations were limited to fish entering the Hatchery Creek weir. In 1953, only 18 of the 5,434 fish which entered this particular trap were hybrids. Spawning trout were relatively more numerous than this in other waterways, but no two streams gave identical indexes of relative abundance of the two species. In the outlet, the Gibbon River between Grebe and Wolf Lakes, hybrid trout comprised 41 percent (183 individuals) of the population migrating downstream in 1953 and 18 percent (143 specimens) in 1954 (table 13). Approximately 50 percent of the fish coming upstream each year were trout;

these were individuals moving toward Grebe Lake, ostensibly to spawn in its tributaries.

From the weir counts it may be concluded that: (1) currently far more grayling than trout use Grebe Lake tributaries for spawning; (2) in tributaries, competition between species for spawning facilities seems minimal; (3) the Gibbon River between Grebe and Wolf Lakes is used by trout and grayling in about equal numbers and is thus perhaps a site of active competition for reproductive locations; (4) grayling-to-trout ratios based on weir counts for any single tributary are not indicative of proportions of spawners of the two kinds in Grebe Lake.

Length frequencies

Length-frequency data were taken on samples of adult grayling trapped in both the 1953 and the 1954 seasons. Polygons of the 1953 data have two distinct modes in the female segment of spawners, and one in the male. In the 1954 material, three peaks are evident for males and two for females (fig. 12). These crests could reflect different age groups in the population. However, growth of grayling in the Grebe Lake watershed was so small in later life that age assessment was essentially impossible (see age-and-growth, p. 333).

Female grayling dominated the sizes below 11.4 inches (total length) in 1953 and below 12.2 inches in 1954. This differential size distribution of males and females is attributable to faster growth in males than in females (as reported for the grayling in Norway, Huitfeldt-Kaas, 1927).

Hybrid trout lengths were much more variable than those of the grayling. Although trout length-frequency polygons show peaks (fig. 13), the numbers of trout comprising each group were so few that the modes expressed cannot be considered as reliable indicators of modal lengths of successive age-groups. Unlike the grayling (where males grew faster than females) female hybrids were of a greater average length than males (fig. 13).

Sex ratios

The potential egg production of a system depends on the number of female spawners as well as upon their individual capabilities. Grayling in the blockaded streams were enumerated by sex as they were passed over the barriers. The males were separated from the females on the basis of the enlarged, sharply pointed, dorsal fin that reached almost to the adipose fin. This fin in the females is smaller and rounded dorsocaudally.

During the early part of the spawning season each year, males of the grayling outnumbered females in the traps on tributaries. As the runs progressed, sex ratios assumed a more nearly 1:1 ratio and ended that way. Combined data from 1953 showed 10 females for every 24 males that entered Hatchery Creek trap (table 14). That overall proportions may change from year to year is suggested by the fact that the ratio of all grayling trapped in Hatchery Creek in 1954 was inverse: 10 females to 7 males. This may have been due to an actual decrease in relative numbers of male grayling in Grebe Lake between the two seasons.

TABLE 14.—*Ratios of females to males (and sample size) for spawning migrants of the grayling in the Grebe Lake system*

Date	Upstream migrants				Downstream migrants	Combined total
	Hatchery Creek	Northwest Creek	South Creek	Outlet	Outlet	
1953	1:2.4 (1,322)	----------	----------	1:0.7 (151)	1:1.3 (87)	1:2.0 (1,460)
1954	1:0.7 (3,634)	1:1.3 (754)	1:1.1 (413)	1:0.6 (83)	1:0.9 (669)	1:0.9 (5,553)

Gustafson (1949) found a 1:1 ratio (93 females to 92 males) among 186 grayling trapped during spawning migrations from Lake Storsjö in Jämtland, Sweden. Ward (1951) reported only 1 female to 3 males on the Cold Creek (Athabaska drainage, Alberta, Canada) spawning grounds but a ratio of 5.1 females per male at the time he trapped fish for spawntaking purposes.

Correct identification of the sexes in the hybrid trout depended upon the observable presence of eggs or milt. Of 234 ripe trout captured in 1953, 80 were females and 154 were males (ratio 1:1.9). In 1954, 141 females and 164 males were identified (ratio 1:1.2).

For the grayling, age on attainment of sexual maturity was at least 3 years. In the hybrid trout, it was 2 years in the males, and 3 in females (see age-and-growth, p. 334).

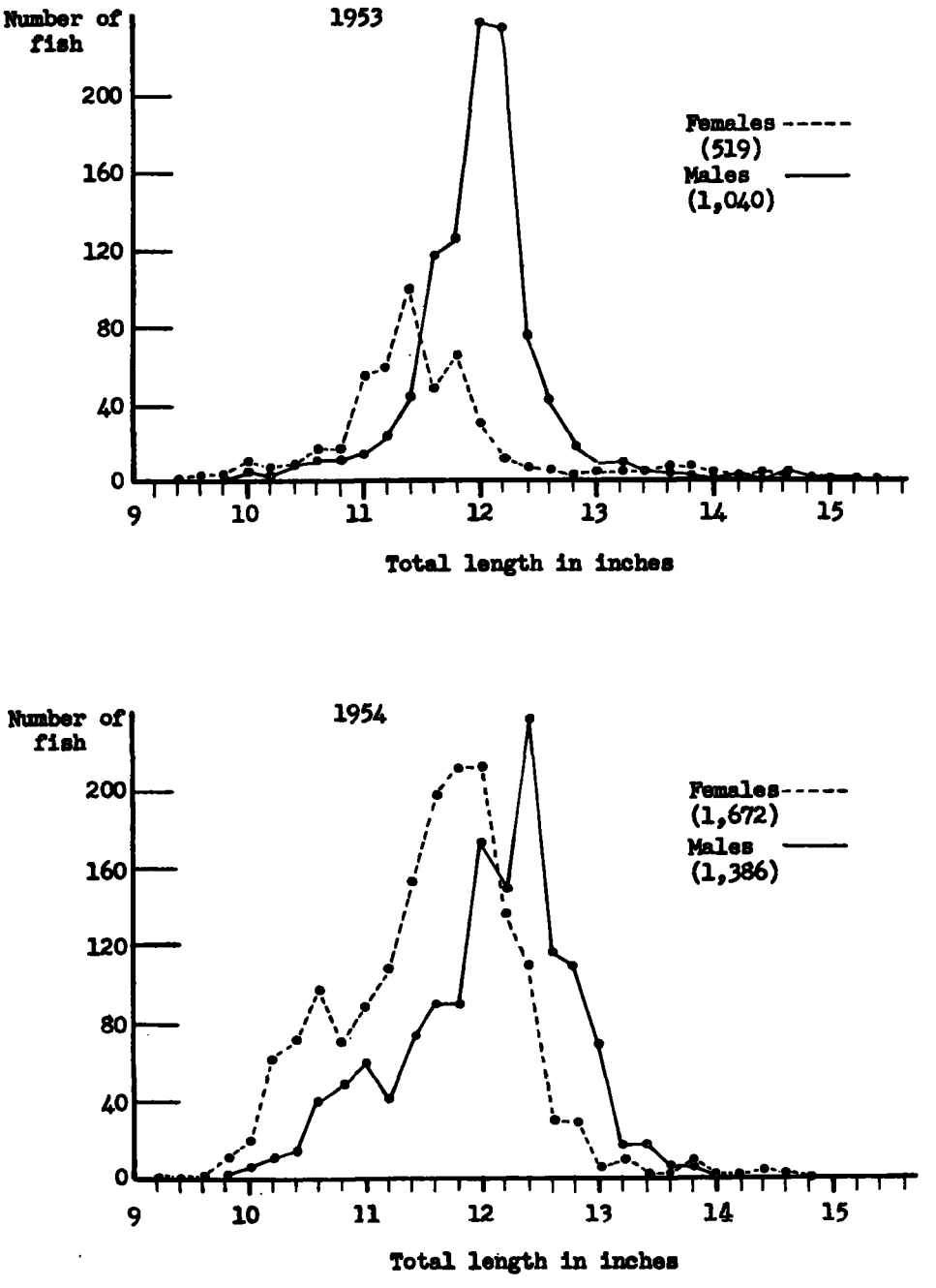

FIGURE 12.—Length-frequency diagram of Grebe Lake grayling captured during the 1953 and 1954 spawning migrations.

Breeding

Male grayling established territories on reaching suitable spawning grounds. Such areas were defended vigorously against other males. The territory varied in size with the extent of the bottom available in that immediate region. In Northwest Creek, males had territories approximately 6 inches wide and 2 feet long. In the outlet where the stream is about 8 to 10 feet wide, they were as large as 4 feet square, or approximately one-half the width of the stream at that point.

Water depth did not seem to be important in site

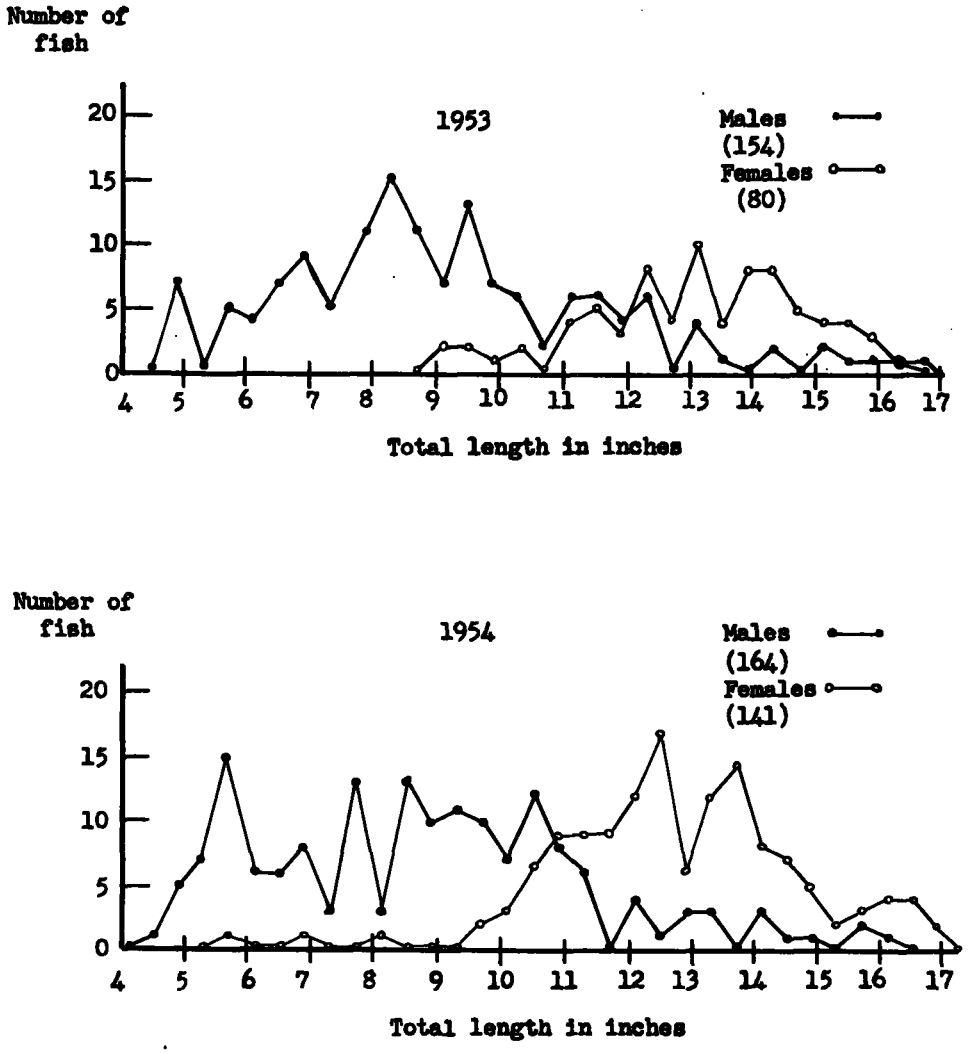

FIGURE 13.—Length-frequency diagrams of Grebe Lake hybrid trout captured during the 1953 and 1954 spawning migrations.

selection by males. Some were in water so shallow that their backs and those of the females were out of water while spawning. Tryon (1947) published a picture of a grayling on its spawning location in water so shallow its dorsal fin was emerging from the water. Other territories used for spawning were in the Gibbon River between 4 and 5 feet deep. Because of the large number of spawning fish, nearly every available location was preempted by males.

Fish on the spawning grounds became uneasy at sudden movements and shadows, but within a matter of minutes returned to spawning activities. Brown (1938) also observed that spawning grayling, though wary, were without apparent fear.

When fighting in defense of a spawning site, the mouth of the guardian male was open slightly so that the white lining inside the jaw could be seen. The dorsal fin was erect and the fish usually threatened the intruder with slightly rigid body movements, then, attacked him. After a few such passes by the aggressive guardian, the intruder would leave the area with the victor in close pursuit. Some unwanted fish were chased as far as 15 feet, after which the defending male would return to the particular part of his territory where he consistently lay.

Often two or three grayling of mixed sexes congregated below a spawning pair and appeared to be consuming eggs that drifted downstream before settling to the bottom. On one occasion a drift net (described later, figs. 17 and 18) was set below

an area (approximately 40 ft. long by 15 ft. wide) in the outlet in which several males and a few females were spawning. Three pairs of fish spawned from 3 to 40 feet above the net while it was in position. The current velocity was about 3 feet per second. Only 6 eggs were recovered by the net (4 dead and 2 fertile) and these could have been eggs from a previous spawning which were dislodged from the bottom by the spawners. Brown (1938b) also failed to collect eggs in a screen placed directly behind spawning grayling. One male and one female grayling were examined from those spawning in this area. The male's stomach contained no eggs, only caddis cases and amphipods. The female had recently swallowed a single egg and was full of dipteran larvae.

The grayling in Sweden (Fabricius and Gustafson, 1955) is mostly polygamous. Three females under observation spawned 19, 27, and 34 times, respectively, in 1 day, the first 2 with 2 different males; the third was with only a single male. The daily peak of spawning activity of these Swedish grayling was in the afternoon. Males left their territories about midnight and did not start returning until between 9 and 11 a. m. Grayling were seen spawning in Grebe Lake tributaries at all hours of the day, but no observations were made at night.

Males attempted to spawn with all females entering their territories and sometimes with other males. No females were seen to be attacked (as was noted by Fabricius and Gustafson, 1955). However, if the female was not ready to spawn, she kept moving away, and took refuge under a bank or among other fish. Often the male followed for as much as 8 feet, exhibiting courtship behavior. The male drifted repeatedly toward the female, inclining his dorsal side (particularly his extended dorsal fin) toward her. When the female was ready to spawn, the male moved closely against her to fold his dorsal fin over her back. The male then vibrated his entire body while maintaining a rigid form. The female, after 1 or 2 seconds, began to shiver. The two fish with backs arched, headed into the current, and with mouths gaping, sank to the bottom. A cloud of silt and gravel was swept upward as the vibrating caudal fins came near the bottom; eggs and milt were extruded at this time. Grayling eggs are adhesive and when first released stick to the particles that are stirred up, and also adhere to the bottom. Fabricius and Gustafson (1955) found that in *Thymallus thymallus* the male also bends his tail across that of the female. The female of *T. thymallus* curves her body and with vigorous vibrating movements works her genital opening deep into the gravel before extruding her eggs.

Brown (1938b) observed one female that spawned twice within 45 minutes (each time with a different male). He suggested that the egg laying interval lasts from 2 to 4 days per individual. I found that females placed within fenced enclosures appeared to have completely spawned on the fifth day. After completion of spawning, the grayling moved back into Grebe Lake or Wolf Lake.

Mortality

To investigate distribution of fish and natural mortality, many spawning-run individuals were marked and released in 1953 and returns sought in 1954. In 1953, plastic streamer tags were placed on 142 grayling (artificially spawned the preceding day). These fish were then released below Hatchery Creek trap. In addition, 153 individuals were similarly tagged and placed above the trap to spawn naturally. Of the 295 grayling tagged during 1953, 62 were recovered during the 1954 spawning migrations. Nineteen of these had lost their tags. Of the 43 returns still carrying their tags, 23 belonged to the naturally spawned group and 20 to the group that had been artificially spawned. It would appear that artificial spawn-taking incurred no greater mortality than natural reproduction.

Both during 1953 and 1954, fish migrating into streams other than Hatchery Creek were fin-clipped distinctively in each waterway, not only to avoid counting individuals twice, but also to identify further movements (table 15). In the outlet, fish traveling upstream (into Grebe Lake) had their right pectoral fins removed. The adipose was clipped from downstream migrants. During the 1953 population study, 1,032 grayling were further distinctively fin-clipped (left pectoral) and released.

Spawners marked in 1953 tended to return to the streams in which they had been marked the previous year, but some straying occurred (table 15).

TABLE 15.—*Number and place of fish marking in 1953, and 1954 recaptures*

Type of mark and place of release (1953)	Species	Number marked and released	Locations and numbers of recoveries (1954)						
			Outlet		Creek 2	Hatchery Creek	Northwest Creek	South Creek	Total
			Upstream	Downstream					
Adipose fin removed	Trout	183		6		1			7
Outlet downstream	Grayling	263	1	30		3			34
Right pectoral fin removed	Trout	374	8	19	1	4	1		33
Outlet upstream	Grayling	392	1	51		44	4	1	101
Left pectoral fin removed	Trout	295	1	5	2	3	1		12
Lake	Grayling	1,032	1	13		117	6	8	145
Streamer tags	Trout	7							
Hatchery Creek	Grayling	295		1		55	2	4	62

EGG PRODUCTION, DEVELOPMENT, AND HATCHING

Perhaps the most fundamental of all factors controlling populations is the annual recruitment to the breeding stock. The greatest mortality is suffered before, during, and immediately after hatching. To obtain an insight into the amount of mortality in the Grebe Lake system during these early stages of fish life it was necessary to develop experimental procedures for estimating egg production and fry returns to Grebe Lake.

Fecundity of Grebe Lake Grayling and Trout

A knowledge of potential egg production in spawning was prerequisite to later estimates of fry yield. Eggs were taken from 37 spawning grayling and counted. These 37 fish were in three total-length groups; (1) less than 11 inches, (2) between 11 and 12 inches, and (3) 12 inches and longer. The average number of eggs of females, respectively, in the foregoing length groups were: 1,889, 2,344, and 2,781 (table 16).

These values are not greatly unlike those found by other investigators. Brown (1938*b*) stated that grayling trapped at Grebe Lake in 1935 averaged 1,650 eggs per female. One 12-ounce specimen (approximately 14.5 inches total length) contained 5,563 eggs. Brown (1938*b*) also found 3 females in Georgetown Lake which averaged 32 ounces and contained 12,946, 12,642, and 8,135 eggs, respectively. Rawson (1950) reported most of the females used for spawn-taking at Reindeer Lake, Alberta, Canada, in 1948 and 1949 produced from 4,000 to 7,000 eggs apiece with a few of the largest containing more than 10,000 eggs per female.

In order to estimate potential and total egg production, females of the grayling spawning in streams were grouped in the same length intervals as above. The potential egg production for the different inlets and the outlet were computed for the 2 years (tables 17 and 18). The results showed an approximate total egg potential of 8,640,000 in 1953 and 10,600,000 in 1954.

TABLE 16.—*Number of eggs per female (based on 37 specimens of the Grebe Lake grayling 1953, 1954) by total length groupings*

Size of fish (inches)	Average size	Mean number of eggs	Range	Standard deviation	Confidence limits 95 percent	
					Upper	Lower
Below 10.95	10.5 [1] (11)	1,889	1,348–2,166	328.8	2,110	1,668
10.95 to 11.95	11.5 (13)	2,344	1,307–2,928	503.6	2,648	2,040
11.95 and over	12.4 (13)	2,781	1,836–4,166	855.8	3,298	2,264
Combined	11.5 (37)	2,362	1,307–4,166	700.6	2,596	2,128

[1] Parentheses contain number of fish in each group.

TABLE 17.—*Potential grayling egg production on various Grebe Lake waterways in 1953*

Number of females and expected egg production	Waterway					
	Outlet		Creek 2	Hatchery Creek	Northwest Creek	South Creek
	Upstream	Downstream				
Number of spawning females	350	143	192	1,677	1,127	146
Expected number of eggs	831,754	339,830	456,276	3,985,290	2,678,248	346,960
Maximum number (upper 95 percent limit)	950,488	388,342	521,411	4,554,195	3,060,571	396,489
Minimum number (lower 95 percent limit)	713,020	291,320	391,142	3,416,384	2,295,924	297,431

NOTE.—Total expected number 8,638,358; maximum, 9,871,496; minimum, 7,405,221.

TABLE 18.—*Potential grayling egg production on various Grebe Lake waterways in 1954*

Number of females and expected egg production	Waterway					
	Outlet		Creek 2	Hatchery Creek	Northwest Creek	South Creek
	Upstream	Downstream				
Number of spawning females	51	346		3,512	429	201
Expected number of eggs	122,481	830,947		8,434,349	1,030,278	482,718
Maximum number (upper 95 percent limit)	140,831	955,444		9,698,037	1,184,641	555,041
Minimum number (lower 95 percent limit)	104,130	706,449		7,170,661	875,915	410,394

NOTE.—Total expected number 10,900,773; maximum, 12,533,944; minimum, 9,267,549.

Fewer hybrid trout were collected for egg counts than grayling. The average number of eggs for each of 10 female trout (average size 12.2 inches total length; range 9.0 inches to 14.8 inches) was approximately 780 eggs (actual count). Potential egg production was derived for the entire system each year (table 19). This expected number of hybrid eggs was about 257,000 in 1953, and 143,000 in 1954.

Egg-Development and Hatching

Eggs of the grayling become fully water hardened at 24 hours and measure 3.74 to 3.85 millimeters in diameter. Hatching starts on day 16 and is completed by day 21 at an average water temperature of 51° F. (range 46°–61° F.) (Watling and Brown, 1955). At Grebe Lake, the earliest hatching is about June 25 in the outlet and the latest, about August 9 on the rest of the tributaries except South Creek (latest hatching date observed on South Creek was July 23). Although females spawn approximately in a 1½-month period, most of the eggs hatch and the fry drift into Grebe Lake within a 10-day period. Thus fry from early spawning adults apparently have little growth advantage over the fry of late-spawning adults.

TABLE 19.—*Potential trout egg production in Grebe Lake 1953–54*

Year	Approximate number of female spawners	Number of eggs per female[1]	Egg production		
			Expected	Maximum	Minimum
1953	331	775±216	256,525	328,021	185,029
1954	184	775±216	142,600	182,344	102,856

[1] Based on 10 females (average total length 12.2 inches; range 9.0 to 14.8 inches). The range of the number of eggs per female was 335–1,294.

Determination of Natural Hatching Mortality

In the Grebe Lake system two methods were used to appraise the efficiency of natural spawning of grayling in producing fry. One was by the use of traps to collect all possible fry of a known number of grayling and the other was by setting drift nets in tributaries at intervals during the time of downstream migration of newly hatched fish.

Above the intake dam for the fish cultural station, Hatchery Creek is repeatedly and naturally divided. The many individual tributaries of its system have permanent sources in springs or are of temporary derivation from melting snow. The dam at the station effectively blocks fish from further upstream migration into the tributaries above it. Although ascent may be possible during high water of some spring seasons, no adult fish were observed above the dam.

The mainstream of Hatchery Creek, 300 yards above the dam, is approximately 2½ feet wide and ½ foot deep during July and August. Since this stream is spring-fed, the temperature remains low and fairly constant in these months with mean daily values approximating 47 degrees F. One section of this creek, about 70 feet long, was separated from the remainder by ½-inch hardware cloth screens at its upper and lower ends. The bottom within this enclosure was composed largely of gravel and rubble up to 6 inches in greatest dimension. The current varied with a maximum of about 2 feet per second. Where trash accumulated along the screening at the lower barrier, a shallow pool 1 foot long and 1 foot deep was formed.

Fifty yards downstream from the lower barrier a fry trap of the inclined-plane type (Wolf 1951) was installed (fig. 14). The trap consisted of a board dam from the top of which a screen trough slanted down to the holding pen or pot below the dam. The slant of the trough was adjusted so that most of the water filtered through the screen. The overflow carrying the fry dropped into the holding pen. Screen for the entire unit (plane, trough, and pen) was 12 meshes per inch.

On June 22, 1953, five ripe female grayling and five ripe males were placed in the fenced section of the stream. The average size of the females was 11.3 inches (range, 10.4 to 12.0 ins.) and that of the males 12.0 inches (range, 11.2 to 12.3 ins.). When these fish were removed two weeks later (July 2), apparently all had spawned. The

FIGURE 14.—Inclined-plane fry trap used in Hatchery Creek, July 1954.

abdomens of the female fish were flabby and no eggs could be stripped from them. On June 29, the fry trap had been installed.

Fish first appeared in the trap on July 7, ten days after its installation. Three trout (less than 3 inches in length) entered the trap between July 7 and July 26. Grayling fry first appeared on July 25, about a month after the eggs had been spawned. A total of 177 grayling fry and three hybrid fingerlings were counted in the interval from July 7 to August 9. On August 18 electric shocks failed to yield any additional fish. The number of eggs contained by the five females stocked in the enclosure was estimated (method in table 16) to have been $11,247 \pm 1,567$ and the mortality was $11,070 \pm 1,567$, approximately 98 percent.

The previous experiment was repeated in 1954 with minor differences. The mesh size of the screen plane, trough, and pot was finer (14 per inch) and the trap was installed immediately after the spawners were placed in the fenced section. Lengths of the five females were from 10.4 to 12.1 inches and averaged 11.8 inches. The five males ranged from 11.2 to 13.2 inches in length and averaged 12.1 inches. The ripe adults were placed in the area on June 18, and removed June 23.

As a result of having the fry trap installed simultaneously with the adults, a measure of egg loss was obtained. The first eggs appeared in the pot on June 19, and the last drifted down into it on July 3. A total of 829 eggs accrued. This represented 6.8 percent of the estimated number of 12,139 eggs in the five females (based on table 16).

The first fry, three in number, entered the trap July 20. Small fish continued appearing until August 6, but only 505 fry (4.2 percent of the estimated potential number) drifted into the trap. Percentagewise this was twice that of the previous year, and probably resulted from the greater efficiency of the 14-mesh-per-inch screen used in 1954, rather than from the different chronology of events.

All of South Creek was utilized for a similar study in 1954. On June 4, 201 females of the grayling and 212 males were placed above the blockade. The fish were removed 2 weeks later. Below the blockade a dam was built to raise the water level and a Wolf-type trap was installed (fig. 15) similar to the one on Hatchery Creek.

The first fry appeared in the trapping basket July 5, and although they continued to come until July 28 most of the young had entered the trap by July 15 (fig. 16). This weir was removed August 3, when no fish could be seen in the creek. A total of 11,404 fry were actually counted. The number of eggs liberated by the 201 spawning females was approximated at $482,718 \pm 72,323$. The fry returned represented approximately 2.4 percent survival of the expected number of eggs, quite in line with the other two experiments of smaller scale.

A similar survival study with hybrid trout indicated that trout hatch much later in Grebe Lake streams than do the grayling. Although 16 female trout were used for egg production, only 12 small trout fry had been recovered by August 30 when the experiment was terminated. Some cutthroat trout in Yellowstone Lake overwinter in small tributaries (Laakso and Cope, 1956) and such an occurrence may also be common for

FIGURE 15.—The South Creek fry trap and the method of counting young fish.

Grebe Lake hybrids. Vibert-type containers (Vibert 1950) were used in Hatchery Creek for comparing development times between grayling and trout. It was found that all grayling eggs had hatched by the 19th day of incubation, but the last trout fry did not appear until the 37th day (water temperatures 39.0° F. to 48.4° F.).

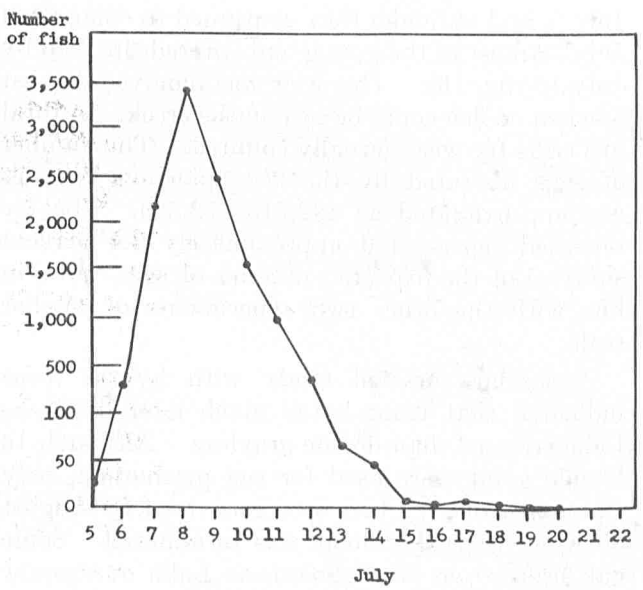

FIGURE 16.—Daily movement of fry downstream into South Creek fry trap, July 1954.

Since it was impossible to measure the actual fry production on all creeks, a method of estimation was devised utilizing drift nets. Each net was built on a rectangular frame made of ¼-inch iron rod, 2 feet wide and 1 foot high. To this frame was attached a bag of bobbinet nylon (26-mesh-per-inch), sewn to the iron rod by a strip of tent canvas (figs. 17, 18). The nylon bag was 6 feet in length to enable exhaust of large volumes of water. In Northwest Creek the following method of capturing fry with these nets was used. A board 1 by 12 by 36 inches was notched just smaller than the drift net frame opening. A ledge of wood below the notch supported the frame when it was in place. This board was placed in the creek to function as a dam. It was sealed with a sheet of canvas and both the dam and canvas were held in place with gravel. All of the streamflow ran over the notch into the nylon bag. The net itself was further supported by a rope from a stake on shore to a snap on the upper edge of the frame. Two 24-hour periods of sampling were employed. The net was placed in the stream for a 15-minute interval and removed for 30 minutes while the counts were made. The time of greatest fry movement occurred between 7:30 p. m. and 10:30 p. m. (fig. 19). Fish that hatched during the daylight hours could be seen accumulating in little

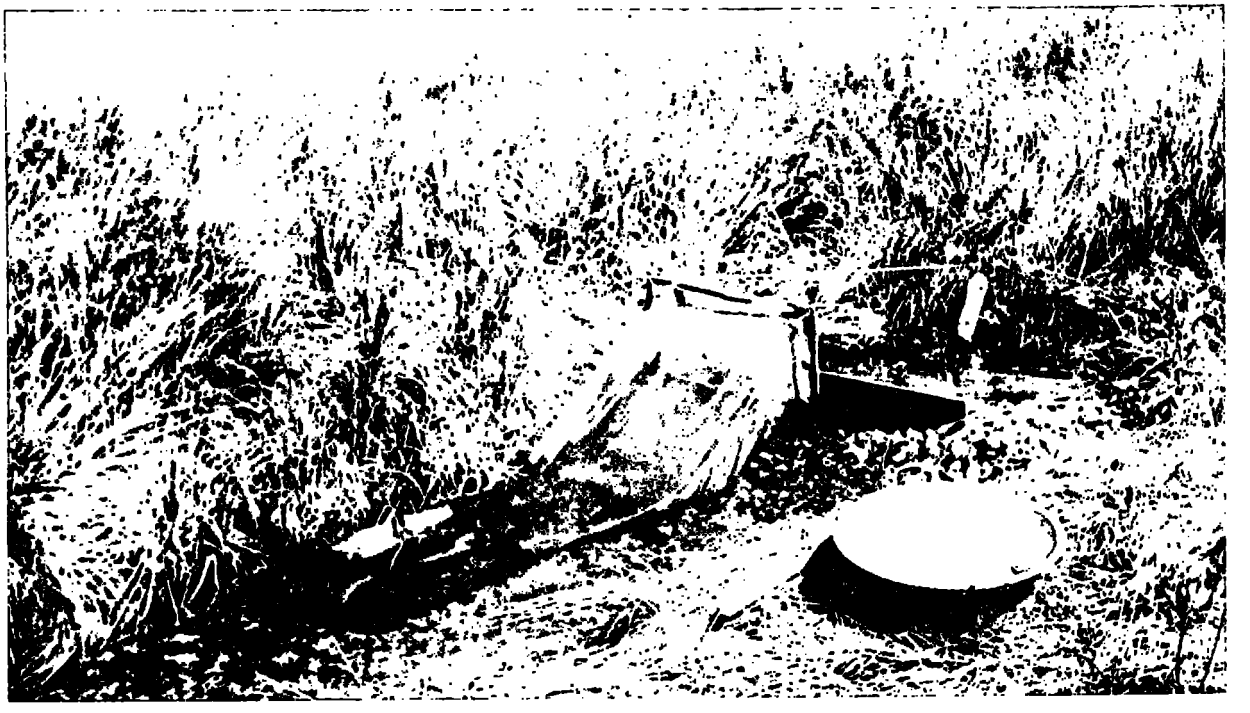

FIGURE 17.—Drift net used on Northwest Creek July 1954 looking upstream.

FIGURE 18.—View looking downstream into drift net and board dam on Northwest Creek, 1954.

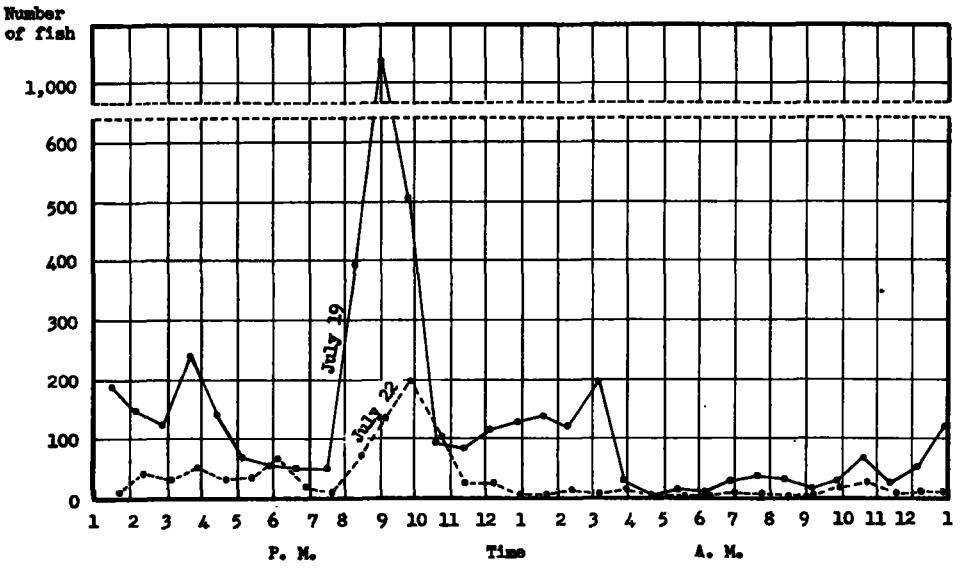

FIGURE 19.—Movement of fry into Grebe Lake over a 24-hour period as reflected by drift net captures on Northwest Creek, July 19, 22, 1954. Each dot represents a 15-minute collecting period.

quiet-water coves and in eddies along shore. These fry moved to faster water about dark, drifted downstream and entered the nets in large numbers until 10:30 p. m. Consequently, from 7:00 to 9:00 p. m. was used daily for sampling the fry production. The percentage of a day's expected total capture that would be expected between 7:00 and 9:00 p. m. was calculated from the 24-hour sets. The daily 2-hour tabulations were then expanded into total daily figures and the results combined to give an approximation of total fry production in the stream.

From the results it was estimated that 58,893 fry entered the lake from Northwest Creek in 1954. A total of 329 females and 425 males had been counted upstream. It was visually estimated that 100 more females spawned below the barricade. This total of 429 females would have an egg potential of $1{,}030{,}278 \pm 154{,}362$. The estimated number of fry represented a return of 5.7 percent (upper limit 6.7 percent; lower 5.0 percent). Although this approximation is higher than counts on other areas where all fry were captured, grayling were not confined to a particular section as in Hatchery Creek and had more spawning area available per individual than on South Creek.

The natural fry production of grayling in the Grebe Lake system in 1954 (table 20) may be approximated from the several sources available in these data as 236,448. The estimated return to the lake by Hatchery Creek is based on the 2.362-percent return found in South Creek. That for the other tributaries is founded on fry movement studies in them.

In the literature, no direct comparisons on mortality of the grayling in early life history stages in North America were available. Gustafson (1949) in his study of the grayling in Sweden captured 0.26 percent of the fry from the estimated total number of eggs laid in a stream during the spawning season. However, he reported that some grayling stayed in these streams for 4 summers, so this did not represent the true survival from eggs to fingerlings.

Foerster (1938), from three tests of natural propagation, found 1.13, 1.05, and 3.23 percent survival of sockeye salmon from estimated egg deposition to the seaward migrating smolt stage. Brasch (1949) in Wisconsin reported an 80 percent survival in five brook trout redds. Hobbs (1948) in New Zealand found a 59 percent to 87 percent survival to fry of all eggs deposited by brown trout.

The real causes of the high mortality of naturally spawned grayling eggs could not be identified with certainty. Nevertheless some possible explanations are discussed below. They lead to the conclusion that the greatest losses are due to egg dislodgment and subsequent current transport of eggs from the spawning beds.

TABLE 20.—*Spawning populations and estimated fry return to Grebe Lake of grayling in 1954*

Grayling	Hatchery [1] Creek	Northwest Creek	South Creek	Total
Female spawners	3,512	429	201	4,142
Estimated fry production	166,151	58,593	11,404	236,448

[1] Estimated fry production for Hatchery Creek based on 2.362 percent return in South Creek and expected number of eggs released by spawning females minus the 1,400,000 removed by fish cultural activities.

Low efficiency in fertilization.—Several authors have commented on the small amount of milt produced by males of the grayling (Brown 1938b; Rawson 1950). However, in nature the efficiency of fertilization seems high. In 59 naturally spawned eggs from Alberta, Canada, Ward (1951) found only two that were unfertilized. In the Grebe Lake hatchery, fertilization, as measured by fry hatch, is usually more than 90 percent.

Egg predation.—Predation on eggs often reduces the numbers available for hatching in fishes but does not seem to be important in the Grebe Lake system as shown by food studies by me, or Brown (1938a). I recovered only 37 eggs from stomachs of 13 female grayling, and none from 4 trout captured on the spawning grounds. Brown (1938a) found 137 eggs in two Grebe Lake grayling taken from spawning weirs and 35 eggs in two fish of six that he sampled in Agnes Lake, Mont. Eggs eaten at spawning apparently represent a "cleaning-up" of those that drift downstream and would therefore be lost to production. I have never observed a grayling engaged in rooting eggs on the spawning grounds.

Dislodgment of eggs during incubation.—A factor in the mortality of eggs is movement after they have been laid on the spawning grounds. Both reproductive activities of the grayling itself and environmental forces are accountable. In areas, such as the tributaries of Grebe Lake, where many adults are crowded for reproduction, it is inevitable that spawnings occur repeatedly over the same sections of stream bottom. After water hardening, eggs are not adhesive and, when dislodged by subsequent spawners, are swept downstream. Some of the embryos may be killed by water turbulence and others by sharp contact with the bottom. Still others may be deposited by the current in habitats unsuitable for development. I witnessed dislodgment many times, and Nelson (1954) found evidence of it in the eggs that he collected from pools where the grayling had not spawned. In my experiment on Hatchery Creek, 829 eggs (of a possible 12,139) drifted into the fry collecting basket. That some of these eggs were dislodged by factors other than spawning activity was shown by the fact that 125 of them entered the basket after the adult fish had been removed from the enclosure. Obviously these eggs had become separated from the substratum through agencies other than the action of adults. However, there was no observable movement after the second week of the 5-week collecting period. Slight changes in water level and current velocity seem accountable for part of the displacement which occurred.

AGE AND GROWTH OF GREBE LAKE FISHES

A knowledge of the age composition of the fish population as it relates to sexual maturity, legal size limits, and growth rates in other areas was obtained by taking scales from Grebe Lake fishes.

Scales from hybrid trout and grayling were collected in 1952, 1953, and 1954. A subsample of 15 fish in each 1½-inch size group was utilized in 1952 and 1953. In 1954, five male and five female grayling in each one-half-inch size interval were collected and used. All trout scales obtained were utilized in age and growth studies.

For use on a microprojector, imprints of grayling scales were made in plastic (0.02 inches thick) by use of a roller press. These plastic impressions were supplemented by water mounts and glycerin-gelatin slides of some scales of grayling older than age-group III when it became necessary to observe whether or not growth had been added in the posterior margin of the scale. Trout scales were cleaned and mounted on glass slides in a glycerin-gelatin medium.

For calculation of growth histories, trout scales (magnification 82.7) were measured from the focus to the anterior margin along an imaginary line bisecting the scale (fig. 20). Average scale lengths for each age group were calculated for each previous year of life. These average scale readings were then converted into average fish lengths by the formula:

$$\text{Fish length at annulus } X = \frac{(\text{Total fish length} - k)(\text{Scale radius to annulus})}{\text{Total scale radius}} + k$$

The constant (k) is a correction factor derived from the scale-body relation. In 1953 the value of

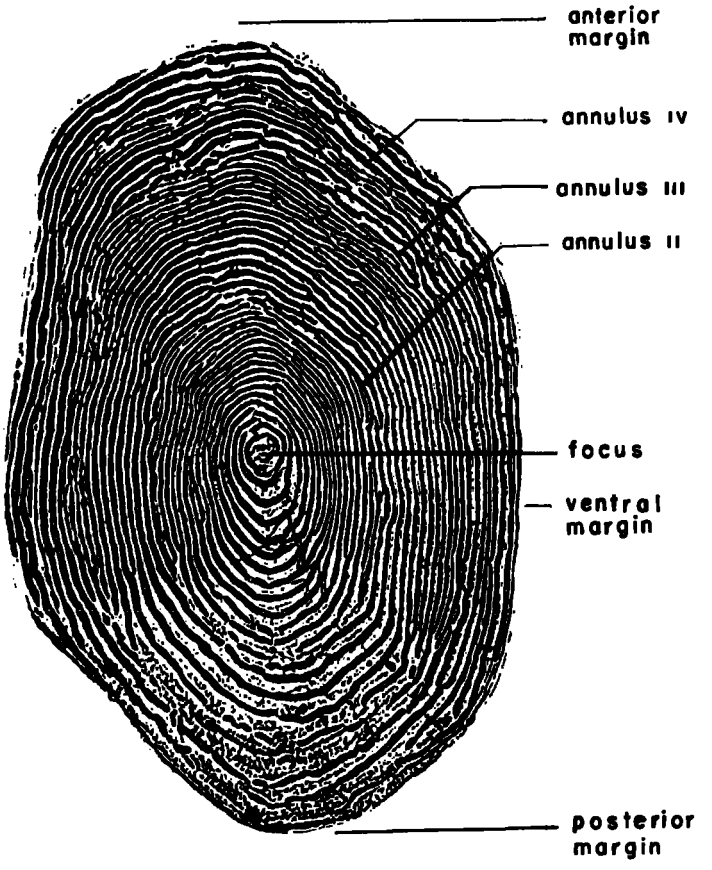

FIGURE 20.—Scale of a 4-year-old hybrid trout (total length 12.7 ins.) captured July 13, 1954, showing terminology used in identifying various regions. Fish did not have scales at the start of its second summer and annulus I is missing.

k was 2.07 and in 1954, 2.40. The procedure of averaging scale measurements follows that suggested by Van Oosten (1953).

Measurements of grayling scales (magnification 41.5) were made from the estimated center of the focus to a ventral scale margin (expressed as if in situ on the fish). Back calculations were made from scale averages using the above formula and a correction factor (k) of 0.86 in 1953 and 1.14 in 1954.

Problems in Age Assessment of Grebe Lake Grayling

Definition and validation of the annulus

The initial problem in age assessment of grayling scales is the definition and validation of the annulus. The interpretation of all of the marks on the scales of grayling collected during 1952, 1953, and 1954 from Grebe Lake was not clear even after a detailed analysis.The following information was developed during the study.

The first and second annuli on grayling scales were formed when growth resumed or accelerated in the spring (figs. 21, 22). A clear hyaline border first formed around the scale and was followed by a shadowy circulus which started near the anterolateral border and developed both in the anterior field and caudally until it was continuous around the margin. This year mark exhibited strong "cutting-over" of the outermost incomplete circuli in the posterolateral corners of the scale.

Annuli later than the first two were preceded in the anterolateral corners by a clear hyaline area and usually by broken circuli along the anterior border of the scale. Posterolaterally such year marks might cross only one or two circuli and were seldom complete in the posterior field after the third annulus.

The time of completion of annulus formation for yearlings was found to be in the third week of June, by the following procedure. In 1954, collections of grayling, which hatched the previous

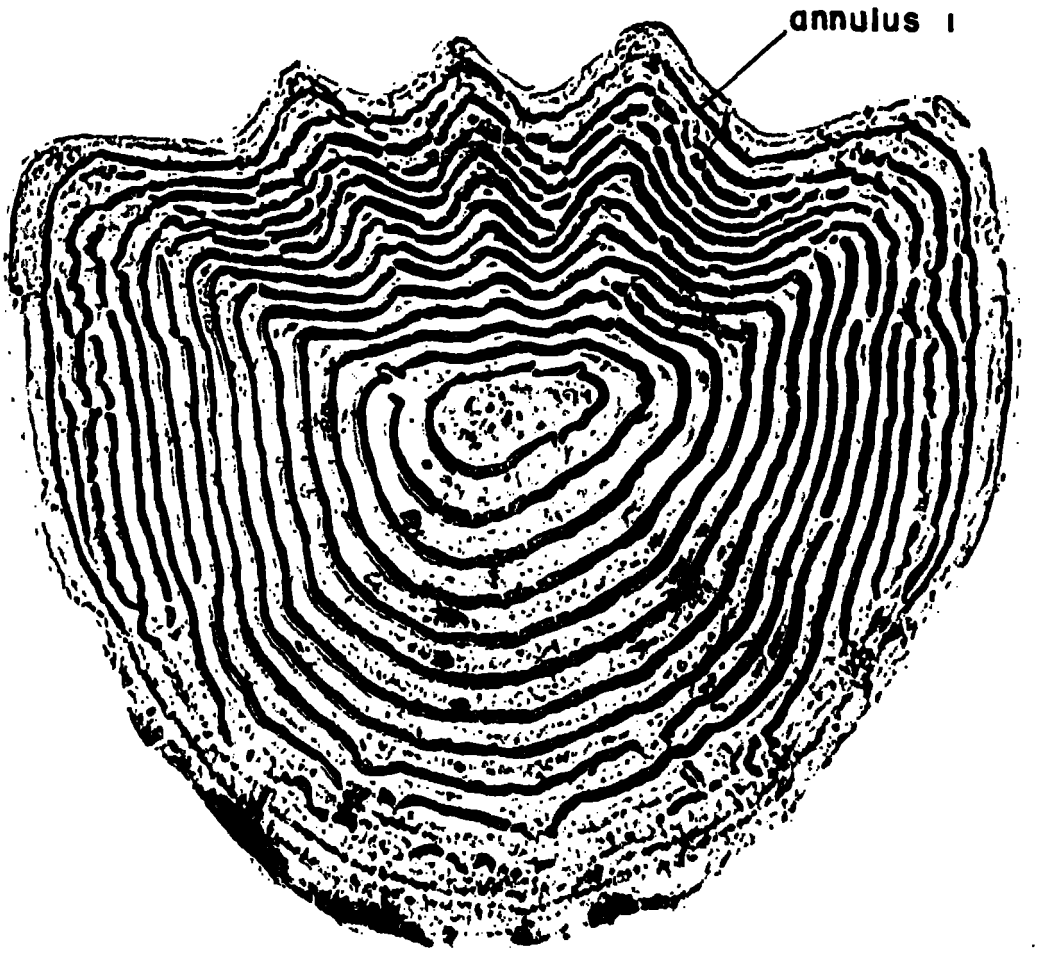

FIGURE 21.—Scale from a 1-year-old grayling (total length 5 ins.) captured June 8, 1954. Annulus has just been completed.

year, were made at intervals throughout the growing season by seining along the shore of the lake after dark. The series was started on May 24, 4 days after the ice disappeared from Grebe Lake. Lake temperatures ranged at this time from 44° F. at the 1-foot level to 41° F. at 25 feet. Hatchery Creek (the main tributary) reached a maximum of 49° F. during the day and a minimum of 34° F. at night. By June 18 when annulus formation was 94 percent complete (table 21), lake temperatures averaged 1° F. higher than each of those given above.

TABLE 21.—*Time of annulus formation in Grebe Lake—grayling entering their second summer*

Sampling date, 1954	Number of specimens	Total length, inches		Percentage with annulus started	Percentage with annulus completed	Number of new circuli beyond annulus	Number without scales [1]
		Mean	Range				
May 24	7	2.36	1.3–4.0	0	0	0	2
May 30–31	7	3.01	1.5–4.1	83	0	0	1
June 8	20	3.28	1.5–5.1	90	15	0–1	0
June 18	19	4.03	2.0–5.2	100	94	1	2
June 26	27	4.18	3.3–5.3	100	100	2–4	2
July 6 [2]	21	4.59	2.8–6.2	100	100	4–5	1
July 18 [2]	21	4.50	3.2–6.2	100	100	7–9	5
Total	122						13

[1] Number without scales at time of annulus formation.
[2] All fish smaller than 3.9 inches were examined. Of these, all specimens from 3.6 inches to 3.9 inches and larger fish randomly chosen had scales developed at time of annulus formation.

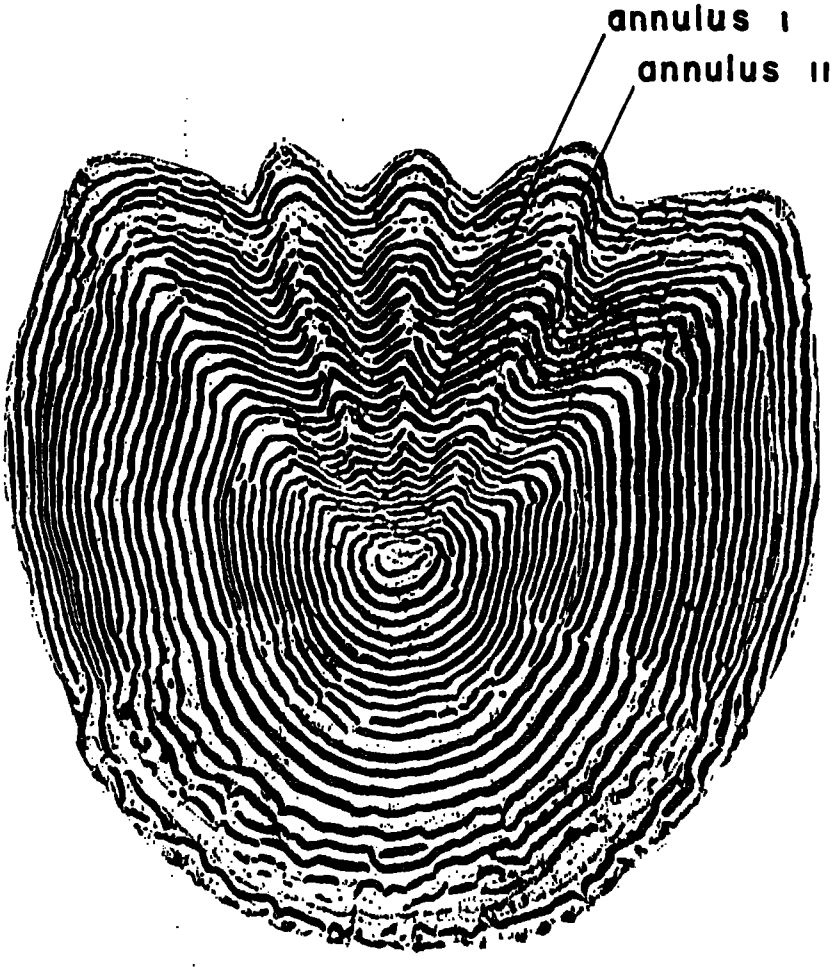

FIGURE 22.—Scale from a 2-year-old grayling (total length 9.2 ins.) captured June 10, 1954. Annulus has been completed for the present year.

Two-year-old grayling averaged very little earlier than yearlings as to time of annulus formation. All thirteen 2-year-olds collected between June 10 and 26, 1954, had a complete annulus for the current year. The first fish taken, June 10, had already added 4 to 6 new circuli beyond the second year mark.

Three-year-old grayling had a different growth pattern from younger ones. The fish of age-group III reported on here were trapped during their first spawning migration. No scales from 3-year-olds less than 13 inches in total length had an evident annulus during the current year. However, some fish longer than 13 inches showed a sub-marginal third-year mark. Consequently, 1 year was added empirically to the age of all fish 3 years old and older, when the expected year mark was not evident at or near the scale margin.

Growth subsequent to the third annulus was small and slow in both body and scale lengths. In age-group III during the remainder of the 1954 season, I found individuals in the last week of July that appeared to have just completed their third annulus. By the end of the first week of August, all specimens clearly of this age-group that were studied had deposited only one to three new circuli beyond the year mark. In years of life after the fourth, growth continued slow or ceased altogether, making further annulus recognition impossible.

Failure of first annulus to appear

A second problem in the age assessment of grayling scales was the apparent failure of annulus I to appear in certain fish and in certain years. The year 1953 was such a year in Grebe Lake.

The late breakup of ice in June 1953, with its associated retarded season, might explain the number of yearlings captured throughout the spring and summer of 1954 (table 21) which were too small to have scales at the time of annulus formation and hence lacked annulus I. The survivors of these small fish would thus occur in later years as a year older than their scale record shows. The scales of such individuals appeared to be recognizable by the great distance from the focus to the first annulus in relation to the pattern on the scales of individuals that became yearlings under conditions favoring "normal" growth and scale formation. In grayling belonging to year-classes previous to 1953 and which started growth during seasons about which I have no information concerning early spring conditions, I assumed 5½ inches to be the maximal amount of growth that could be expected of a grayling in Grebe Lake during the first year of its life. All fish calculated to have attained more than 5½ inches at the end of their first year of life were considered to be without annulus I. The data were adjusted accordingly by adding 1 year to the observed age.

Failure of scale growth and effect on annuli

The third problem of age assessment in grayling scales is that beyond the age of III (sometimes beyond age II) annulus formation is uncertain. As stated, there was little growth after 3 years of age. Furthermore, on some scales there was evident disappearance of parts of previous circuli and annuli after the third winter. Erosion of circuli in grayling has been noted previously by Brown (1943) who stated that such erosion was superficial, not peripheral, and therefore did not influence growth calculations. However, when only one or two circuli were deposited between the third and fourth year marks and erosion occurred, it sometimes became impossible to interpret the correct age of the fish.

Two sets of experimental data demonstrated the age assessment complications resulting from the failure of scale growth and resorption of scale markings in or after the third year of life. One set was from a lot of known-age grayling introduced into Grebe Lake and the other was from returns on individuals captured, scale-sampled, tagged, and released.

In 1949, the small number of grayling spawners led to the planting of 125,000 fry and 100,000 eggs for the first stocking in 3 years. The 1949 year-class appeared strongly in 1952 as 3-year-old fish (90 percent of the sampled population belonged to age-group III). In 1953, fish that dominated the samples had the following characteristics: (1) a strong third annulus, (2) some growth beyond annulus III, and (3) a circulus near the edge of the scale having all the criteria, though weakly, of a true year mark, with a little additional growth beyond. Scales from these grayling could have been assessed in one of two ways: (1) as 5 years old, by assuming the circulus near the margin which crossed one or two other circuli and was continuous through the antero-lateral corners was a true annulus, or (2) as 4 years old, by considering the mark just described as a false annulus or a check.

In 1953, 300 grayling were tagged with white plastic streamer tags (see Joeris 1953, for techniques and description) and released in Grebe Lake. Of 43 recaptures made in 1954, 38 had belonged to the age-group with the same scale picture as the fish that dominated the catch in 1953. These fish showed only one or two new circuli and no more annuli than were present the previous year. Thus the grayling tagged in 1953 and recaptured again in 1954 could have again been called 4- or 5-year-olds on the basis of their scale markings. The year's growth of these tagged individuals averaged only 0.3 inch. The circulus near the edge of the scale, which could have been interpreted as an annulus the previous year, often appeared eroded and indefinable in the recaptured fish. The tags themselves may have had a detrimental effect upon these fish as was found with the use of jaw tags on pike (Williams 1955) or trout (Alvord 1954). However, the scale morphometry of untagged grayling in 1953 and 1954 (fig. 23) was so similar to the tagged fish of approximately the same size that correct age assessment for the population older than 3 years remained in doubt. The modes of length-frequency diagrams (if valid as indicative of age-groups) suggest a growth of 0.4 inch between the fourth and fifth years of life for the males of the spawning population (fig. 12); growth in the tagged males averaged only 0.1 inch less. Scale increments related to body increments as small as this do not show growth signs that can be interpreted as annuli. Alvord (1954) found that in 69 brown trout, which added less than 0.8 inch to

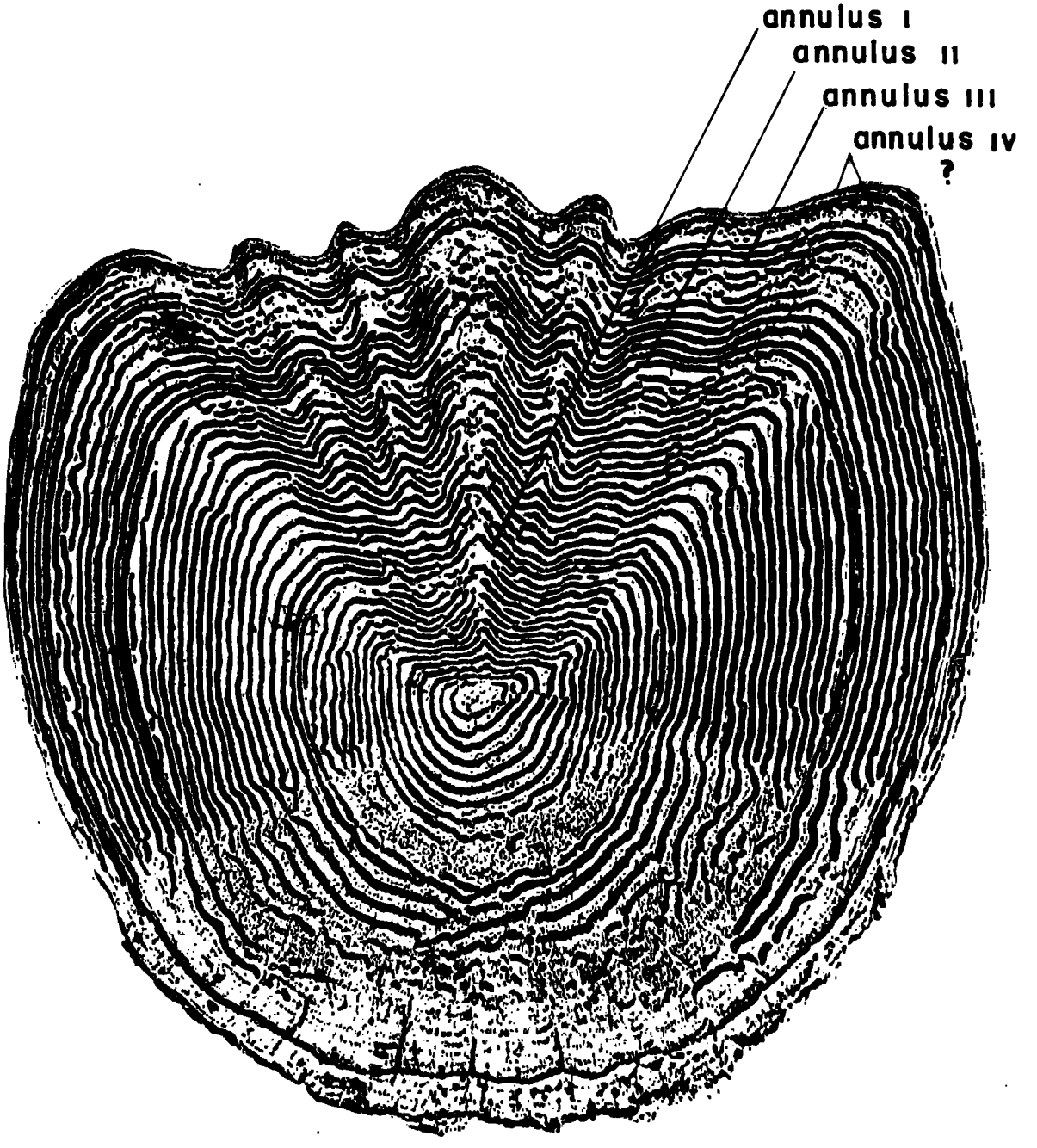

FIGURE 23.—Scale of a grayling of indeterminate age (total length 12.8 ins.) captured May 24, 1954. Fish is starting either its fourth or fifth summer.

total length during 1 year (September to September), 59.4 percent did not form a year mark.

Failure to assess age beyond III was not experienced by Brown (1943), Miller (1946), Nelson (1954), or Creaser and Creaser (1935). However, a scale photograph by Brown (1943) from a previously collected sample of Grebe Lake grayling is suggestive of a problem not unlike one presented by this study.

Growth of Young Grayling

Growth in the first 2 years was determined empirically by measurements of samples taken at intervals through the growing season until September 1, 1954. Plots of average lengths at time

of capture and time of season indicated a reasonably rapid and constant growth rate for this first year (fig. 24). Lengths of fish in their second summer (from preserved specimens) were taken from grayling captured at night when the fish moved toward the shoreline and could be seined effectively. These collections, started 4 days after the ice cover had disappeared, showed a continuing trend of growth in the fish, until the 6th of July (fig. 24). The measurements for age-group I might have tended to reflect only the smaller fish, however, since some larger yearlings had moved to deeper water as evidenced by their appearance in trap nets set during the seining period.

Calculated Growth Rates Compared

Growth rates were determined for grayling in the first 3 years by calculating the 1-year-olds and 2-year-olds separately and treating fish 3 years of age and older as a single age-group. Average total fish lengths (inches) to the first three annuli were: I, 4.4; II, 8.9; III, 11.2 (table 22).

In studies of the grayling in North America, length has been measured by different methods. Biologists in Canada (Miller 1946; Rawson 1950) and Alaska (Wojcik 1955) used the fork length measured in millimeters. In the United States, Brown (1943) took standard lengths in millimeters and total lengths in inches. Nelson (1954) and the present study have utilized total length measurements in inches.

To compare rates of growth among different study areas it was necessary to develop relationships between the various types of length measurements. Fork lengths and total lengths were determined for 17 grayling from Alaska and 33 specimens from the United States. All were in alcohol at the University of Michigan Museum of Zoology. In addition, 45 Grebe Lake grayling less than 5.5 inches total length (formalin preserved) were measured. Conversions between total and fork lengths were read directly from a

TABLE 22.—*Average calculated lengths in inches of Grebe Lake grayling for their first 3 years of life in 1953 and 1954 samples*

Date of collection	Year class	Total length at various annuli			Number fish
		I	II	III	
1953	1952	4.4			59
	1951	3.3	8.3		23
	1950 and over	4.5	8.9	11.2	134
Mean		4.4	8.8	11.2	216
1954	1953	4.1			28
	1952	4.6	8.4		24
	1951 and over	4.5	9.0	11.2	98
Mean		4.4	8.9	11.2	150

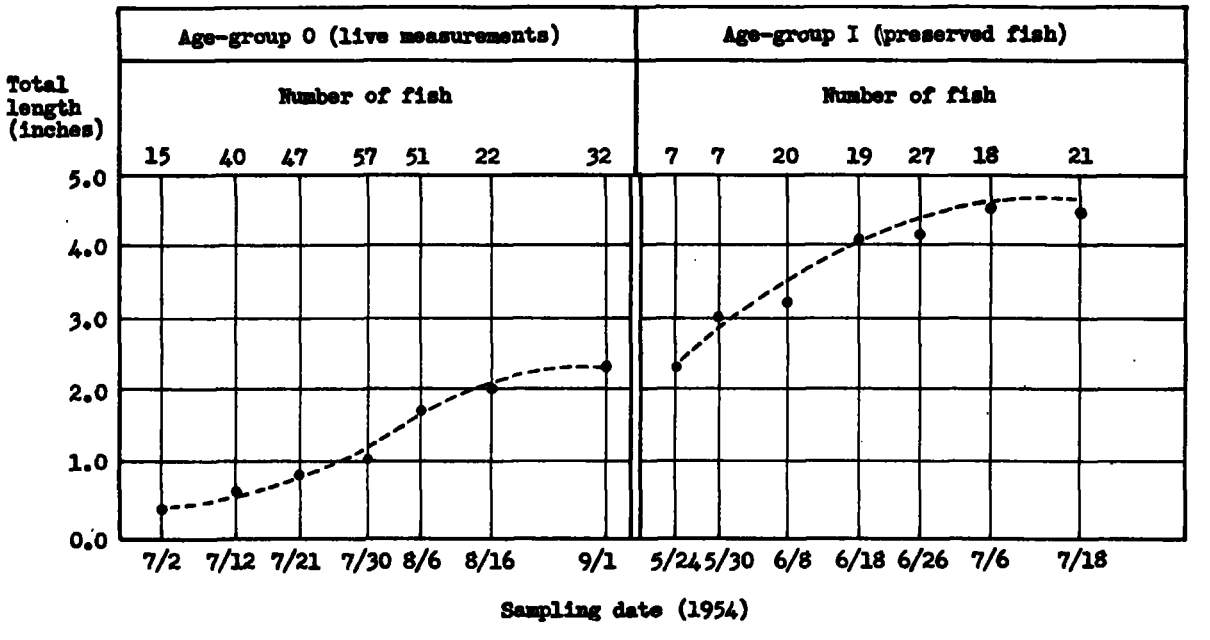

FIGURE 24.—Seasonal growth rates for grayling of age-groups O, I, during 1954.

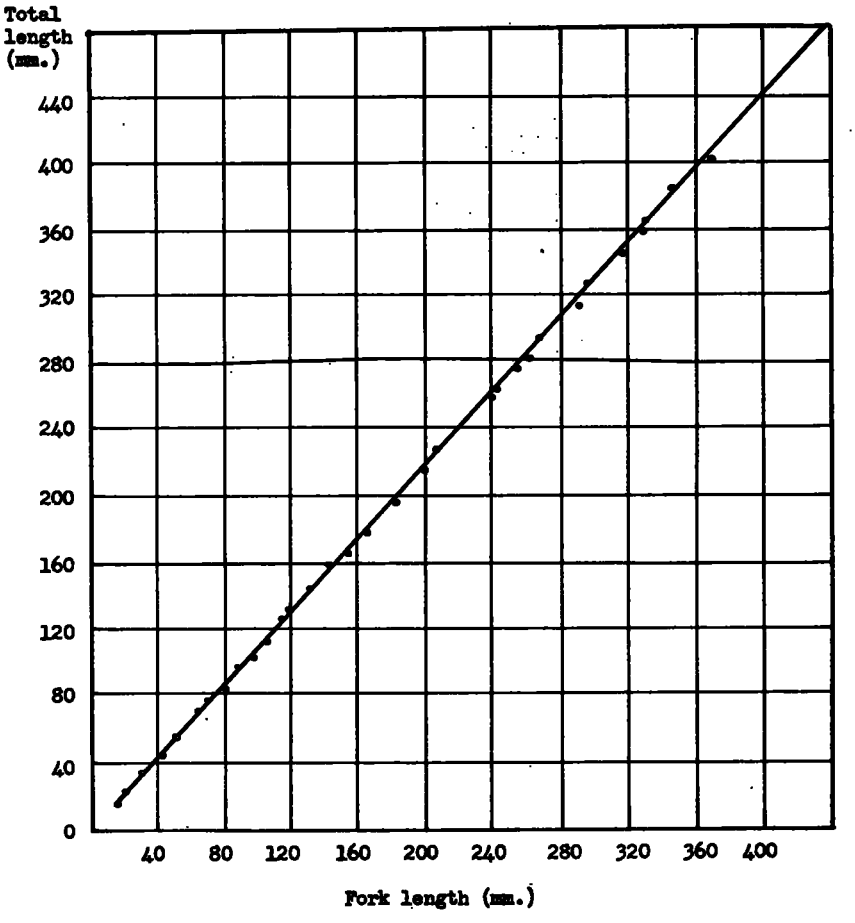

FIGURE 25.—Relation between total lengths and corresponding fork lengths of preserved grayling. Dots represent average lengths in 10 mm. total length intervals. Conversion factors for size intervals are: less than 18 mm., 1.00; from 18 mm. to 22 mm., 1.06; from 22 mm. to 400 mm., 1.097 (figures are for the conversion of fork length to total length).

line of relation of total lengths and fork lengths (fig. 25).

As one proceeds from south to north, the grayling tends to grow more slowly, mature later, live longer, and attain a greater maximum size (fig. 26). The growth of grayling in the Red Rock, Mont., area was fastest during the early years of life. However, beyond age IV the yearly increment became smaller than increments in other areas. The minimum spawning age observed by Nelson (1954) was II; the oldest fish collected belonged to age-group VI.

Grebe Lake grayling grew most nearly like those in Lake Athabaska (figures converted from Miller, 1946). The Grebe Lake fish spawned first at age III. Because of the difficulty in determining annuli beyond III in this body of water, no maximum ages are available.

Although some specimens from Great Bear Lake (Miller 1946) reached maturity during their fourth summer, the majority matured in their fifth. The oldest fish collected belonged to age-group XI.

Males of the grayling (*Thymallus thymallus* L.) in Sweden matured at an age of 2 years and females, at 3 (Gustafson 1949). The oldest individuals found were starting their eighth year of life.

Problems in Assessment of Age in Hybrid Trout

Lack of annulus I

In the trout hybrids, as in the grayling, the first year's growth often appears excessive. Because of this, and because the cutthroat trout in nearby Yellowstone Lake was sometimes without annulus I (Laakso and Cope, 1956), I established two

categories of hybrids based on the number of circuli from the focus to the first year mark. In one of these fish, which had more than 15 circuli within this area, an extra annulus was assigned (fig. 20). The first circulus from the focus was used as the first year mark. In the other category, trout with fewer than 15 circuli on the scale between the focus and the first annulus were judged to have their first year mark.

Eroded and broken scales

Many trout scales in 1953 and 1954 had broken edges, clear hyaline spots, and eroded or reabsorbed margins. Such scales were discarded as undependable for age-and-growth analyses. They made up 14.3 percent (22 fish) of the sample in 1953 and 2.5 percent (5 fish) in 1954. Some bias may have been incurred by removing these fish from the sample, because most of the individuals were more than 14 inches in total length.

Age and Growth of Hybrid Trout in Grebe Lake

Averages of calculated total lengths (inches) at various annuli for hybrid trout based on combined samples taken in Grebe Lake, 1953 and 1954, were: I, 3.7; II, 7.2; III, 10.5; IV, 12.8; V, 14.9;

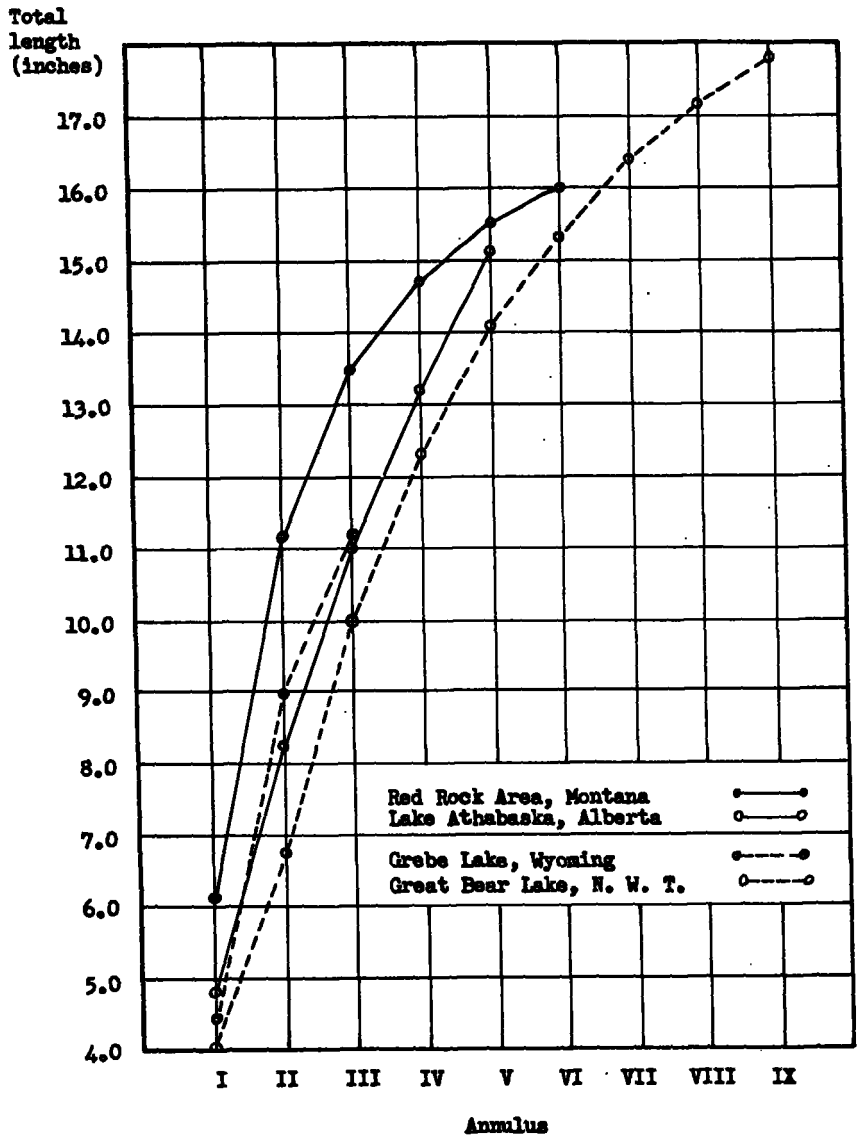

FIGURE 26.—Comparative growth rates of grayling from United States (Nelson 1954, and Kruse, present study) and Canada (Miller 1946). Fork lengths converted to total lengths.

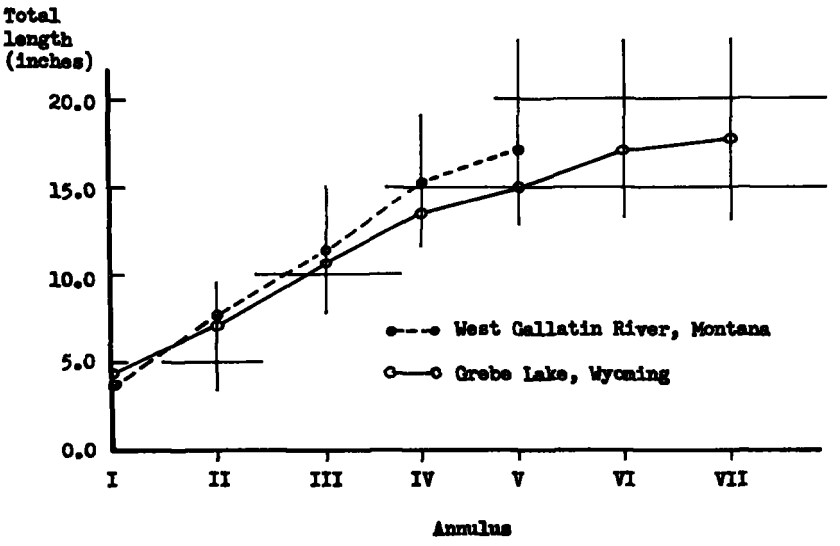

FIGURE 27.—Calculated growth rates of hybrid trout from the West Gallatin River, Mont. (data from three elevations combined, Purkett 1951) and from Grebe Lake, Wyo.

VI, 17.3; VII, 17.5 (tables 23 and 24). This was not maximal. It was slightly less than that in the West Gallatin River through the third year and markedly less than that in the fourth and fifth years (fig. 27).

Some male hybrid trout were mature in Grebe Lake at the start of their third growing season (annulus II). All female hybrids captured during the spawning season were at least 3-year-olds. Trout reached the legal size limit of 6 inches in their second or third year of life.

Female hybrid trout in Grebe Lake grew faster than did the males (table 25), and by the third year females were approximately 1.3 inches longer than the males.

TABLE 23.—*Average calculated total lengths of fish in inches at various annuli of Grebe Lake trout, 1953*

Summer of life	Year class	Calculated total fish lengths at annuli I–VI						Number of fish
		I	II	III	IV	V	VI	
2	1952	3.14						8
3	1951	3.43	6.63					17
4	1950	3.65	7.23	9.97				52
5	1949	3.66	7.41	11.00	12.69			48
6	1948	3.63	6.89	10.86	13.45	15.11		6
7	1947	4.23	8.59	12.57	15.83	16.94	17.60	2
Mean		3.60	7.22	10.53	12.88	15.57	17.60	133

TABLE 24.—*Average calculated total fish lengths in inches at various annuli of Grebe Lake trout, 1954*

Summer of life	Year class	Calculated total fish lengths at annuli I–VII							Number of fish
		I	II	III	IV	V	VI	VII	
2	1953	3.89							4
3	1952	3.99	6.99						38
4	1951	3.81	7.23	10.06					67
5	1950	3.89	7.40	10.90	12.71				61
6	1949	3.63	7.14	10.65	12.64	13.97			22
7	1948	3.88	8.27	13.42	15.39	16.76	18.19		2
8	1947	5.15	8.63	10.78	12.64	14.49	15.98	17.54	2
Mean		3.87	7.25	10.53	12.75	14.22	17.09	17.54	196

TABLE 25.—*Empirical average total lengths of fish in inches in successive years of life for 1953 and 1954 collections of male and female trout in Grebe Lake*

[Number of fish in parentheses]

Sex	Total lengths at year of life				
	2	3	4	5	6
Males	7.2 (32)	9.8 (45)	12.2 (42)	15.3 (1)	
Females		11.1 (30)	13.5 (53)	14.7 (18)	17.9 (4)

Length-Weight Relation

Length-weight relation for both the grayling and the hybrid trout were used in computing pounds of fish in Grebe Lake from length measurements. According to Hile (1936) this relation

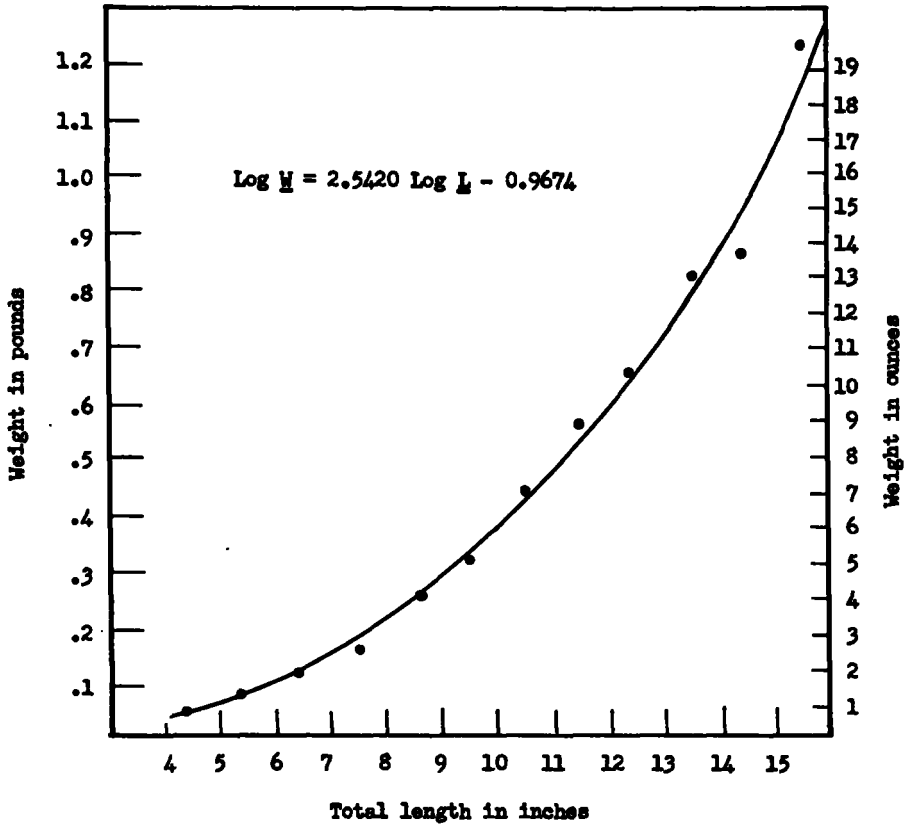

FIGURE 28.—Length-weight relation of 148 hybrid trout from Grebe Lake, Yellowstone National Park. Dots represent average weight within each 1-inch group.

can best be expressed by a parabolic curve of the form $W=cL^n$, where

W=weight of the fish,
L=length of the fish, and
c and n are constants.

Converted to logarithms, the formula becomes, log W=log c+n log L, and the constants can be determined by the method of least squares.

Paired length-weight measurements of 148 hybrid trout were from two groups of individuals. The first group was comprised of fish more than 6.0 inches long and contained both gill-net captures of August 1952, and tagged males taken during spawning runs. The second group was composed of trout under 6.0 inches in length; measurements of these were made on preserved specimens originally seined from Grebe Lake. Since only a limited number of measurements were available for the two species, both sexes were used in calculations (except no length and weights were from spawning females of either species). The 309 grayling used in computations were from gill-net captures (August 1952) (more than 6.3 inches total length) and preserved specimens (less than 6.3 inches).

The calculated curves (figs. 28 and 29) fit the empirical values very well. For the hybrid trout, the predicted weights of fish follow the formula log W=2.5420 log L−0.9674 (fig. 28). In the grayling the length-weight curve is of the form log W=2.7682 log L−1.2925 (fig. 29).

FOOD ANALYSIS

The grayling and the hybrid trout compete for food in Grebe Lake. The extent to which they do this is disclosed in part by a comparison of their stomach contents.

Stomachs were taken from 112 grayling and 24 hybrid trout during 1952 to 1954. These fish were captured with hook and line, by weirs used during the spawning season, and by nets. The stomachs were preserved in 5 percent formalin as soon as possible after collection of the fish. The total content of each was subsequently

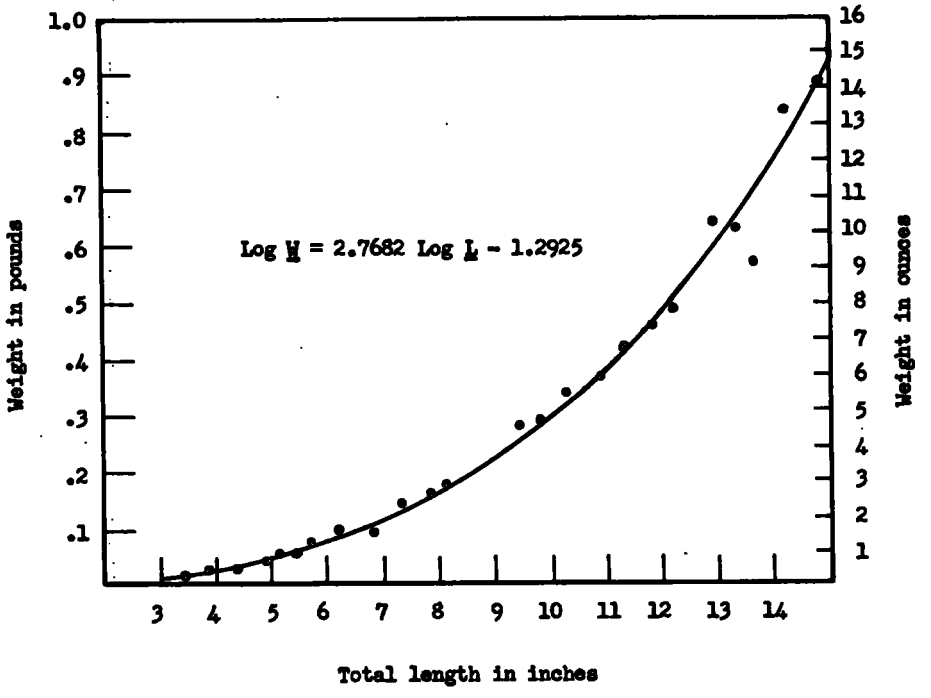

FIGURE 29.—Length-weight relation of 309 grayling from Grebe Lake, Yellowstone National Park. Dots represent unweighted average empirical weight within each ½-inch length group.

measured volumetrically by water displacement. Identifiable organisms were sorted, dried 1 to 2 minutes on blotting paper, and then measured in the same manner as the total contents. However, the small amount of material in trout from the tributaries and in the young-of-the-year grayling precluded such measurement. The organisms most commonly used as food by Grebe Lake fishes follow:

OLIGOCHAETA
- *Lumbricus terrestris*

CRUSTACEA
- Cladocera
  - *Daphnia* (probably *pulex*)
- Copepoda
  - *Cyclops* sp.
- Amphipoda
  - *Gammarus fasciatus*

INSECTA
- Plecoptera (identified by Dr. A. R. Gaufin, University of Utah)
  - *Alloperla* sp.
  - *Isoperla* sp.
  - *Pelloperla* sp.
  - *Nemoura* sp.
- Ephemeroptera (identified by Dr. George F. Edmunds, University of Utah)
  - Baetinae (possibly *Centroptilum*)
  - *Cinygmula* sp.
  - *Rhithrogena* sp.
  - *Baetis* sp. (possibly *intermedius*)
  - *Ephemeralla coloradensis* Dodds
  - *Callibaetis* sp.
  - *Caenis* sp.
  - *Ameletus* sp.
- Odonata (identified by Dr. G. H. Bick, Tulane University)
  - Zygoptera
    - *Ischnura* sp.
    - *Lestes* sp.
    - *Argia* sp.
  - Anisoptera
    - *Cordulia shurtleffi* Scudder
- Trichoptera (identified by Dr. H. H. Ross, Illinois Natural History Survey)
  - *Agrypnia deflata* Milne
  - *Limnephilus* sp.
  - *Mystacides* sp.
  - *Neothremma* sp.
  - *Molanna* sp.
  - *Agapetus* sp.
  - *Rhyacophilus* sp. (identified by Dr. H. C. Chandler, California Department of Fish and Game)
- Coleoptera (identified by Dr. H. C. Chandler)
  - Malachiidae sp.
  - Staphylinidae sp.
  - *Crenitis alticola* (Fall)
- Diptera
  - Tendipedidae (= Chironomidae)
- Hymenoptera
  - Formicidae

TABLE 26.—*Average number of each kind of food organism (and percentage frequency of occurrence) in grayling of age-groups O and I, Grebe Lake, 1954*

Date of capture (1954)	Fish average size (total length in inches)	Number of fish	Food item										
			Ephemeroptera nymphs	Ephemeroptera adults	Trichoptera larvae	Diptera larvae	Diptera pupae	Diptera adults	Amphipoda	Cladocera	Pisidium	Copepoda	Unidentifiable terrestrial insects
July 2	0.53	5					0.2 (20)						
July 12	.71	5	0.6 (40)			8.4 (100)	3.6 (80)			0.8 (60)			
July 21	.87	5							0.2 (20)	13.6 (60)			
July 30	1.12	5								17.8 (60)			
August 6	1.70	5	0.6 (40)				(1) (40)			[1] 3.0 (40)			
August 16	2.08	5	10.6 (80)	0.4 (20)				0.2 (20)				0.2 (20)	
September 1	2.48	5	[1] 10.6 (100)					0.2 (20)	1.0 (20)	20.4 (40)			
May 24	2.58	5	1.2 (60)			27.4 (80)			2.4 (40)				
May 30	2.80	5	10.2 (40)			35.4 (100)	0.2 (20)		0.2 (20)				
June 8	3.74	5	0.8 (60)		1.6 (40)	154.4 (100)	11.4 (60)		9.4 (60)		0.6 (40)	0.4 (40)	
June 26	4.26	5	0.4 (20)		8.6 (100)	15.8 (100)	49.2 (80)		2.4 (20)		1.2 (60)		0.4 (40)
July 18	4.80	5	(1) (50)		(1) (50)	(1) (100)	(1) (100)			(1) (100)			(1) (40)

[1] Food items in these fish were decomposed and could not be enumerated.

Four principal groups of fishes were sampled for food content: (1) young-of-the-year and 1-year-old grayling collected at intervals throughout 1954; (2) spawning females of grayling and of hybrid trout; (3) small trout (less than 3.4 ins. in length) inhabiting Hatchery Creek during the time the newly hatched grayling fry were descending in July 1953; and, (4) adults of both species taken from the lake proper during the 1952 to 1954 seasons.

Group 1. Grayling belonging to age-groups O and I, collected throughout the 1954 season.—Grayling in this group were taken by seining the shore of Grebe Lake at intervals between July 2 and September 1, 1954. Of all the fish in each collection, only the five that were nearest the mean length in each lot were used in the food analysis.

Young of the grayling start to feed early in life. Some individuals in a group of hatchery-reared fry began ingesting food on their fourth day and by the eighth day all individuals sampled contained food (Brown 1939). The yolk sacs of those that Brown measured averaged 0.3 inches when food was first consumed and had disappeared in most fish by the end of the second week. The smallest specimen that I found with food in it in Grebe Lake (July 2, 1954) had a yolk sac 0.1-inch in length and was probably between 1 and 2 weeks old. In this body of water, young grayling (to 1.5 inches total length) subsisted primarily on *Daphnia* and on Diptera larvae and pupae (table 26), organisms that are especially abundant in the shoal areas of Grebe Lake, which is inhabited by these small fish. Stomachs collected between July 12 and August 6 contained only *Daphnia*. From August 6 to September 1, young fish consumed mainly ephemerids (mostly Callibaetis) along with lesser amounts of Tendipedidae (=Chironomidae) larvae and pupae, *Gammarus*, *Daphnia*, and *Cyclops*. Winged insects (adult Diptera) first appeared in the diets on August 16.

The 1-year-olds collected in the spring and early summer of 1954 had eaten not only a more varied diet, but also were taking larger organisms than were the young-of-the-year. Among the food items were some Trichoptera and relatively more gammarids. The first terrestrial insects were found in stomachs on June 26 from fish averaging 4.3 inches total length. By July 18 the variety of food found in the stomachs of the 1-year-olds was nearly the same as that consumed by older fish (exceptions were the large Odonata of a size too great to be ingested by small fish).

Group 2. Spawning female trout and grayling.—Stomachs of 13 grayling and 5 hybrid trout were obtained from spawning adults collected in the streams tributary to Grebe Lake. Although these fishes readily took food in these streams, very few

kinds were available to them and feeding conditions were crowded. Consequently, more than 30 percent (5) of the grayling and 80 percent (4) of the hybrid stomachs were empty. Fish eggs were found in 8 of the 15 grayling sampled (table 27), but the greatest number from any one specimen was only 12. The fact that no sand or gravel accompanied these eggs demonstrated that they had been taken while adrift and not while attached to the substrate.

Group 3. Small trout from tributaries.—Seven small trout were taken with a fine-meshed dip net from Hatchery Creek at the time grayling fry were descending. The smallest of these was 1.8 inches in length and the largest, 3.4 inches (average, 2.3 ins.). These fish contained organisms common to the stream as well as terrestrial insects that had fallen into the water. There was no evidence of cannibalism (table 28).

TABLE 27.—*Food of 13 grayling collected from Grebe Lake tributaries during their spawning season, June 1954*

Food item	Total number	Volumetric composition (Percent)	Frequency of occurrence (Percent)
Plecoptera			
Nymphs	1	2.3	7.7
Ephemeroptera			
Nymphs	2	(1)	15.4
Odonata nymphs			
Zygoptera	20	10.5	7.7
Anisoptera	13	55.8	30.8
Trichoptera			
Larvae	10	12.0	46.2
Diptera			
Larvae	12	(1)	15.4
Pupae	129	7.0	23.1
Hymenoptera	1	(1)	7.7
Fish eggs	37	7.0	61.5
Fish scales	7	(1)	23.1
Food remains		2.3	15.4

[1] Quantity in stomachs too little (less than 0.05 ml.) to be measured volumetrically.

Group 4. Grayling and trout from Grebe Lake proper.—Although competition for food was shown by the contents of the stomachs from 40 grayling and 10 trout captured in May, July, and August, there was no evidence of predation between the two kinds of fishes. Only two grayling stomachs contained scales (table 28). The scales had belonged to two grayling more than 9 inches long and one trout over 8 inches; there was no trace of flesh or bones. Diptera larvae and pupae were the major food items in the group; these were found in 70 percent of the trout and 72.5 percent of the grayling. Fishes captured in Grebe Lake when ice was present (May and June) were subsisting primarily on amphipods and Diptera

TABLE 28.—*Stomach contents of 17 hybrid trout and 40 grayling from the Grebe Lake system, 1952 to 1954*

Food items	Grayling		Trout			
			Creek (7)		Lake (10)	
	Volumetric composition (percent)	Frequency of occurrence (percent)	Volumetric composition (percent)	Frequency of occurrence (percent)	Volumetric composition (percent)	Frequency of occurrence (percent)
Collembola			(1)	14.3		
Plecoptera						
Nymphs		5.0		28.6		
Adults			(1)	14.3		
Ephemeroptera						
Nymphs		5.0		57.1	(1)	20.0
Adults	0.9	10.0	(1)	14.3	1.0	30.0
Odonata nymphs						
Zygoptera	2.4	32.0			1.0	20.0
Anisoptera	3.1	10.0			19.2	10.0
Hemiptera						
Adults		10.0				10.0
Trichoptera						
Larvae	7.9	45.0	(1)	28.6	26.3	50.0
Pupae	1.6	12.5				
Adults	3.6	32.5			4.0	40.0
Coleoptera						
Larvae				28.6		10.0
Adults		12.5	(1)	14.3		
Diptera						
Larvae	5.4	72.5		100.0		10.0
Pupae	2.0	67.5		57.1	1.0	80.0
Adults	1.6	22.5	(1)	14.3	5.6	30.0
Hymenoptera						
Adults	.2	10.0				10.0
Amphipoda	11.2	35.0			17.2	30.0
Cladocera	4.9	42.5				30.0
Nematoda			(1)	14.3		
Aphidae			(1)	14.3		
Pisidium	.3	17.5				
Oligochaeta					2.0	10.0
Trout scales		2.5				
Grayling scales		5.0				
Fish eggs		2.5				
Food remains	53.8	87.5			22.7	70.0

[1] Quantity in stomach too little (less than 0.05 ml.) to be measured volumetrically.

larvae. Later in the season (August) their diet showed greater variety. Some individuals fed primarily on damselfly nymphs, whereas many others consumed mostly adult caddisflies. The major portion of the diet consisted of Trichoptera larvae in the early spring, and Ephemeroptera nymphs in the late spring and summer. Tendipedidae (=Chironomidae) were also taken in great numbers when available.

Previous writers (Brown 1938a; Leonard 1939, 1940; and Rawson 1950) have also found that insects, sometimes aquatic but at other times terrestrial, predominate in the food of adult grayling. Apparently the species feeds on whatever is available and shows no discernible preferences.

Although both the grayling and the hybrid trout in Grebe Lake ingested the same types of food items in approximately equal amounts, there was no apparent antagonism between the two

fishes. By way of illustration, during the evening grayling and trout rose to the surface within a few feet of one another with no gross evidence of strife in a common feeding ground. Apparently, there was sufficient food in Grebe Lake for both species, judging from the gorged condition of the digestive tracts and plumpness of the fish. The only exception was on the spawning grounds where many fish were crowded into the small streams; a relatively large number of the stomachs collected were empty.

HARVEST OF GREBE LAKE FISHES BY ANGLING

Despite the recognized limitations of a voluntary creel census it was necessary to employ such a method to obtain information on the magnitude of the sport fishery. The data gave a measure of the effect of angling on the fish population. Also, the reports made it possible to adjust the procedures of the mark-and-recapture population estimate that was in progress. A creel census form was employed to obtain records of the amount of time anglers spent in fishing, the kinds, numbers, and sizes of the fishes caught, whether or not there were identifying marks on the fish, and the types of lures used.

These creel census forms were placed in a box near the parking area, from which all fishermen had to walk the 3.5 miles to Grebe Lake. The importance of completing the creel-census records was stressed by personal contacts with the anglers.

The completeness of the voluntary returns was checked by counts of all fishing parties. In 1953, 65 of 98 groups (66 percent) filled out creel census blanks during the time of the population estimate. In 1954, the response improved slightly; 93 of 132 counted parties (70 percent) completed the forms. For the rest of the seasons in both years it was estimated that only about 50 percent of the fishermen responded.

Adjustment of the creel records on the foregoing basis enabled an approximation of the total catch each year. In the 1953 season, 780 fishermen removed 2,148 fish. Anglers increased to 818 in 1954 and caught 2,863 fish. This represented a harvest of the estimated populations that approximated 7.1 percent in 1953 and 9.9 percent in 1954.

The average size of 81 of the grayling measured from anglers' creels was 11.4 inches. Since this figure was not too different from the 11.0-inch average size of the grayling captured during the population study, I assumed the size distribution of the anglers' catch to approximate that of the trap nets during the respective years. Under these conditions the total weight of fish removed by the fishermen was 903.8 pounds in 1953 and 1,191.3 pounds in 1954.

Although grayling are approximately 10 times as numerous as trout in Grebe Lake, they comprised only 67 percent of the catch in 1953 and 75 percent of the total captures in 1954. Thus in the catch, the grayling-to-trout ratio of 3.1 to 1 in 1954 was higher than in 1953 (1.9 to 1). Personal contact with anglers indicated that most preferred to catch the hybrid trout, and that they fished primarily for it.

Results of creel-census information tabulated by monthly intervals showed a decreasing trend in fish per fisherman between July and September, 1953, but an increase during the same interval in 1954 (table 29). Fishing effort also declined rapidly after August 29 (fig. 30) However, the efficiency of the late season anglers, as reflected by the fish-per-hour rate, increased in September of both years.

TABLE 29.—*Monthly summary of fishing pressure and yield for Grebe Lake, based on 138 creel census returns in 1953, and 140 in 1954*

Item	Date of census							
	1953				1954			
	July	Aug.	Sept.	Total	July	Aug.	Sept.	Total
Number of fishermen	137	200	24	361	206	179	26	411
Number of hours	477	723	56	1,256	601	635	81	1,317
Hours per fisherman	3.5	3.6	2.3	3.5	2.9	3.5	3.1	3.2
Catch:								
Hybrid trout	131	119	12	262	211	128	11	350
Grayling	207	241	44	492	455	537	91	1,083
Unidentified	114	264	5	383	------	------	------	------
Total	452	624	61	1,137	666	665	102	1,433
Fish per fisherman	3.3	3.1	2.5	3.1	3.2	3.7	3.9	3.5
Fish per hour	0.95	0.86	1.09	0.91	1.11	1.05	1.26	1.09

The average number of fish per fisherman (3.1 in 1953, 3.5 in 1954) was good considering that the limit imposed by the National Park Service on Grebe Lake was five per angler. Some fishermen who reported limit catches often caught two or three limits and released all but five fish; others released all fish. Only trout and grayling actually removed from the lake were included in the foregoing analysis of yield. Therefore, fishing in Grebe Lake was probably better than the figures indicate. However, there was a compen-

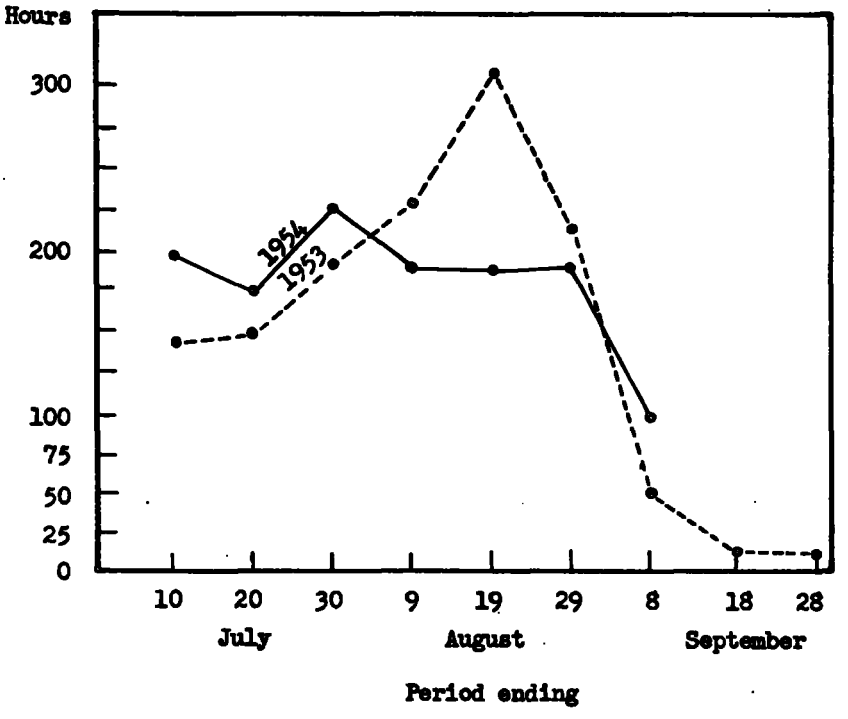

FIGURE 30.—Total number of hours (by 10-day periods) spent on Grebe Lake by fishermen during 1953 and 1954.

satory reaction on the part of fishermen to fill out forms only if they caught fish.

More fish were taken from Grebe Lake by fishermen using flies than by any other method. However, the number of fish taken by any one group of fishermen depended not so much on the type of gear they used as it did on the number of anglers in that group; the percentage of fishermen using any one lure or combination of lures agreed closely with the percentage catch by that respective method (table 30). Since tabulations are not for individual fishermen, but for parties, the combinations occurred where one person in a party would use spinners and another flies, or other lure. The average number of people per party was 2.5 in 1953 and 2.9 in 1954.

Fishing yield from Grebe Lake was low (table 29). There was a harvest of only about 6 pounds per acre in 1953 and 8 pounds per acre in 1954. In contrast, a trout lake in Oregon of similar size and also having a creel limit of five fish produced more than 50 pounds per acre of trout each year between 1945 and 1947 (Holloway 1947). In a series of trout lakes on Grand Mesa in Colorado, anglers were removing an average of 63 pounds per acre per year with two of the lakes yielding an average of 106 pounds per acre per year (Lyall 1941).

PREDATORS AFFECTING GREBE LAKE POPULATIONS

The removal of fish from Grebe Lake by predatory birds and mammals is a factor that affects the size and composition of the population. However, measurement of the effect of predation is difficult. Black bear, *Ursus americanus* Pallas, mink, *Mustela vison* Schreber, and river otter, *Lutra canadensis* Schreber, were seen on Grebe Lake between 1952 and 1954, but they were not numerous, and actual evidence of predatory activities was small. The osprey, *Pandion haliaëtus*, however, took fish throughout each season.

TABLE 30.—*Use of lures and effectiveness on Grebe Lake in 1953 and 1954*

Number of anglers	Catch by various lures						
	Flies	Spinners	Bait	Spinners and flies	Spinners and bait	Flies and bait	Spinners, flies, and bait
Number of parties (total, 305)	152	40	17	59	7	14	16
Percentage use	49.8	13.1	5.6	19.3	2.3	4.6	5.2
Catch	1,412	327	163	499	46	156	180
Percentage catch	50.7	11.7	5.9	17.9	1.7	5.6	6.5

SUMMARY

The grayling, *Thymallus arcticus*, is common both to North America and to eastern Asia. In the United States the species is highly prized by sportsmen because of its great beauty and comparative rarity. The only indigenous population maintaining itself at present in the United States is in the Red Rock Lakes region in Montana. From this center, it was introduced in other waters, including some streams and lakes in Yellowstone National Park, Wyo.

The grayling was first planted in Grebe Lake of the Park in 1921, 14 years after the rainbow trout had been introduced and 9 years after the cutthroat trout had been planted there. The two species of trout intermixed after planting and by 1952 only hybrids were found. The grayling reportedly has experienced wide fluctuations in population abundance at intervals since its introduction. One such decline in numbers in 1949 resulted in the present study on Grebe Lake. The following statements summarize the findings of my work between July 22, 1952, and September 1, 1954.

Grebe Lake is eutrophic with a well-developed thermocline during the period of summer stagnation and a deficiency of oxygen in the deep waters of 1953 and 1954. Samples of the aquatic fauna in Grebe Lake showed a predominance of Tendipedidae (=Chironomidae) both numerically and volumetrically.

Population estimates in 1953 and 1954 were obtained from trap nets and a mark-and-recapture method. About 27,000 grayling were in Grebe Lake in 1953 and 26,000 in 1954. Trout approximated 2,000 the first year and 2,500 the second. The standing crop of fish in Grebe Lake in 1953 was estimated at 77 pounds per acre: about 70 pounds per acre of grayling and 7 pounds per acre of trout. In 1954, the standing crop was approximated at 71 pounds per acre of grayling and 8.3 pounds of trout.

Both the grayling and the hybrid trout spawned in all four tributaries and in the outlet of Grebe Lake between mid-May and late June. Stream temperatures at this time ranged from 40° F. to 57° F. Weirs or blockades installed in the waterways during early May to count spawning migrants provided a means for enumeration of 7,081 grayling and 674 trout in 1953 and 7,878 and 405, respectively, in 1954.

Length-frequency polygons of the grayling spawners showed that females averaged smaller than the males. Lengths of the hybrid trout were variable and no strong modes were evident when lengths were plotted against numbers.

Males of the grayling outnumbered the females in early spawning runs each year. The ratios assumed a more nearly 1-to-1 proportion as the seasons progressed. For this species overall sex ratios in Grebe Lake during 1953 were 10 females to 24 males and, in 1954, 10 females to 9 males.

The natural fry production in Grebe Lake in 1954 was approximated as 236,500 or 2.5 percent of the estimated number of eggs produced by the spawning adults. The greatest mortality during this time was attributed to dislodgment of the eggs during the incubation period either by subsequent spawners or by changes in water level and current velocity.

Scales for age-and-growth analyses were collected from both the grayling and the hybrid trout throughout the study period. The time of annulus formation for grayling younger than 3 years was found to be prior to June 25. No scales from 3-year-olds less than 13 inches in total length had an evident annulus during the spawning season. The interpretations of scales from the grayling more than 3 years of age were considered inaccurate because of the small annual growth in body and scale lengths which in some samples either had obscured the correct interpretation of existing marks or had precluded annulus formation entirely. An additional complication often resulted from a failure of annulus I to form on individuals which had been too small to have had scales at the start of their second growing season.

None of the grayling matured before reaching age-group III. The legal size of 6 inches was attained by all during their second summer of life. Averages of the calculated total lengths in inches for the grayling at the end of their first 3 years of life were: I, 4.4; II, 8.9; III, 11.2.

Females of the trout grew faster than did the males and had matured at the start of their fourth summer of life (age-group III). Some mature males of age-group II appeared in the spawning runs. The legal size limit of 6 inches was reached either in the second or the third year of life. Some trout were also too small to have had scales at the end of their first summer and consequently lacked their first year mark. The average calculated total

lengths in inches at various annuli for the hybrid trout in 1953 and 1954 combined were: I, 3.7; II, 7.2; III, 10.5; IV, 12.8; V, 14.9; VI, 17.3; VII, 17.5.

The length-weight relation for the grayling was determined to be log weight=2.7682 log length −1.2925, and for the hybrid trout log weight= 2.5420 log length−0.9674, where weights are in hundredths of a pound and lengths are in tenths of an inch.

The food of the grayling during its first summer of life consisted of small nymphs of aquatic insects, amphipods, and *Daphnia*. By the middle of their second summer, young of the grayling were feeding on the same organisms as the adults except for some of the large Odonata of a size too great to be ingested. Diptera larvae and pupae were the major food items found in 40 of the grayling and 10 of the trout from Grebe Lake during the 1952 to 1954 seasons.

From a voluntary creel census on Grebe Lake the following estimations of fishing pressure were made. In 1953, 780 fishermen removed 2,148 fish. During 1954, 818 anglers caught 2,863 fish. The catch the first year was 3.1 fish per fisherman, the second, 3.5. Fishing pressure on Grebe Lake was light during the two seasons with a harvest of 7.1 percent of the estimated population or about 6 pounds per acre in 1953, and 9.9 percent or approximately 8 pounds per acre in 1954.

LITERATURE CITED

ALVORD, W.
1954. Validity of age determinations from scales of brown trout, rainbow trout, and brook trout. Trans. Amer. Fish. Soc., Vol. 83 (1953), pp. 91–103.

BRASCH, J.
1949. Notes on natural reproduction of the eastern brook trout (*S. fontinalis*) with a preliminary report of several experiments on the subject. Wisconsin Cons. Dept., Madison, Sect. of Fish. Biol., Invest. Rept. No. 653. Mimeo. 9 pp.

BROWN, C. J. D.
1938a. The feeding habits of the Montana grayling (*Thymallus montanus*). Jour. Wildlife Mgt., Vol. 2, No. 3, pp. 135–145.
1938b. Observations on the life-history and breeding habits of the Montana grayling. Copeia, 1938, No. 3, pp. 132–136.
1943. Age and growth of Montana grayling. Jour. Wildlife Mgt., Vol. 7, No. 4, pp. 353–364.

BROWN, C. J. D., and C. BUCK, JR.
1939. When do trout and grayling fry begin to take food? Jour. Wildlife Mgt., Vol. 3, No. 2, pp. 134–140.

CHAPMAN, D. G.
1948. A mathematical study of confidence limits of salmon populations calculated from sample tag ratios. Internat. Pac. Salmon Fish. Comm., Bull. 2, pp. 67–85.

CHAPMAN, D. G.
1952. Inverse, multiple and sequential sample censuses. Biometrics, Vol. 8, No. 4, pp. 286–306.

COOPER, G. P., and K. F. LAGLER.
1956. Appraisal of methods of fish population study. Part III. The measurement of fish population size. Trans. Twenty-first N. Amer. Wildlife Conf., pp. 281–297.

CREASER, C. W., and E. P. CREASER.
1935. The grayling in Michigan. Pap. Mich. Acad. Sci., Arts and Lett., Vol. 20, pp. 599–608.

CROWE, W. R.
1950. Construction and use of small trap nets. Prog. Fish-Cult., Vol. 12, No. 4, pp. 185–192.

DE LURY, D. B.
1951. On the planning of experiments for the estimation of fish populations. Jour. Fish. Res. Bd. Canada, Vol. 8, No. 4, pp. 281–307.

FABRICIUS, E., and KARL-JACOB GUSTAFSON.
1955. Observations on the spawning behaviour of the grayling, *Thymallus thymallus* (L.). Inst. Freshwater Res., Drottningholm, Rept. No. 36, 103 pp.

FOERSTER, R. E.
1938. An investigation of the relative efficiencies of natural and artificial propagation of sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia. Jour. Fish. Res. Bd. Canada, Vol. 4, No. 3, pp. 151–161.

FORBES, S. A.
1893. Aquatic invertebrate fauna of Yellowstone National Park, Wyoming. Bull. U. S. Fish Comm., Vol. 11, pp. 207–258.

FRANKLIN, SIR J.
1823. Narrative of a journey to the shores of the Polar Sea in the years 1819, '20, '21, '22. London, J. Murray, 768 pp.

GUSTAFSON, KARL-JACOB.
1949. Movements and growth of grayling. Inst. Fresh water Res., Drottningholm, Rept. No. 29, 44 pp.

HENSHALL, J. A.
1902. Food and game fishes of the Rocky Mountain Region. Trans. Amer. Fish. Soc., Vol. 31 (1902), pp. 74–88.

HILE, R.
1936. Age and growth of the cisco, *Leucichthys artedi* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. Bull. U. S. Bur. Fish., Vol. 48 (1935), pp. 211–317.

HOBBS, D. F.
1948. Trout fisheries in New Zealand their development and management. New Zealand Marine Dept., Fish. Bull. No. 9, 175 pp.

HOLLOWAY, R. C.
1949. Lake-management studies in Oregon. Trans. Amer. Fish. Soc., Vol. 77 (1947), pp. 105–113.

HUBBS, C. L., and K. F. LAGLER.
1949. Fishes of the Great Lakes Region. Cranbrook Inst. of Sci., Bull. No. 26, 186 pp.

HUITFELDT-KAAS, H.
1927. Studier over aldersforholde og veksttyper hos norske ferskvannsfiskar. Nationaltrykkeriet, Oslo, 358 pp.

JOERIS, L. S.
1953. Technique for the application of a streamer-type fish tag. Trans. Amer. Fish. Soc., Vol. 82 (1952), pp. 42–47.

LAAKSO, M., and O. B. COPE.
1956. Age determination in Yellowstone cutthroat trout by the scale method. Jour. Wildlife Mgt., Vol. 20, No. 2, pp. 138–153.

LEACH, G. C.
1934. Propagation and distribution of food fishes. Rept. U. S. Comm. Fish. (1933), pp. 472.
1935. Propagation and distribution of food fishes. Rept. U. S. Comm. Fish. (1934), pp. 407.

LEONARD, J. W.
1939a. The Montana grayling in Michigan. Mich. Cons., Vol. 8, No. 9, pp. 8.
1939b. Feeding habits of the Montana grayling (*Thymallus montanus* Milner) in Ford Lake, Michigan. Trans. Amer. Fish. Soc., Vol. 68 (1938), pp. 188–195.
1940. Further observations on the feeding habits of the Montana grayling (*Thymallus montanus*) and the bluegill (*Lepomis machrochirus*) in Ford Lake, Michigan. Trans. Amer. Fish. Soc., Vol. 69 (1939), pp. 244–256.
1949. The Michigan grayling. Mich. Cons., Vol. 18, No. 2, pp. 24–25.

LYALL, W. A.
1941. Problems of fish management on Grand Mesa National Forest in Colorado. Trans. Sixth N. Amer. Wildlife Conf., pp. 252–255.

MILLER, R. B.
1946. Notes on the Arctic grayling, *Thymallus signifer* Richardson, from Great Bear Lake. Copeia, 1946, No. 4, pp. 227–236.

MOFFETT, J. W.
1950. The status of Montana grayling in Grebe Lake, Yellowstone National Park. Mimeo. Rept. U. S. Fish and Wildlife Service, 12 pp.

NELSON, P. H.
1954. Life history and management of the American grayling (*Thymallus signifer tricolor*) in Montana. Jour. Wildlife Mgt., Vol. 18, No. 3, pp. 324–342.

PURKETT, C. A., JR.
1951. Growth rate of trout in relation to elevation and temperature. Trans. Amer. Fish. Soc., Vol. 80 (1950), pp. 251–259.

RAWSON, D. S.
1950. The grayling (*Thymallus signifer*) in northern Saskatchewan. Canadian Fish Cult., No. 6, 15., pp. 1–8.

RICKER, W. E.
1948. Methods of estimating vital statistics of fish populations. Indiana Univ. Sci. Ser., No. 15, 101 pp.
1949. Effects of removal of fins upon the growth and survival of spiny-rayed fishes. Jour. Wildlife Mgt., Vol. 13, No. 1, pp. 29–40.

SCHNABEL, Z. E.
1938. Estimation of total fish population of a lake. Amer. Math. Monthly, Vol. 45, pp. 348–352.

SMITH, O. R.
1947. Returns from natural spawning of cutthroat trout and eastern brook trout. Trans. Amer. Fish. Soc., Vol. 74 (1944), pp. 281–296.

TRYON, C. A., JR.
1947. The Montana grayling. Prog. Fish-Cult., Vol. 9, No. 3, pp. 136–142.

VAN OOSTEN, J.
1953. A modification in the technique of computing average lengths from the scales of fishes. Prog. Fish-Cult., Vol. 15, No. 2, pp. 85–86.

VIBERT, R.
1950. La methode "Vibert" et ses merveilleuses possibilites. Amboise, Pezon and Michel, 16 pp.

WALTERS, V.
1955. Fishes of Western Arctic America and Eastern Arctic Siberia. Bull. Amer. Mus. Nat. Hist., Vol. 106, Art. 5, pp. 290–291.

WARD, J. C.
1951. The biology of the Arctic grayling in the southern Athabaska drainage. Master of Science Thesis, Univ. Alberta, Edmonton, Canada, 71 pp.

WATLING, H., and C. J. D. BROWN.
1955. The embryological development of the American grayling (*Thymallus signifer tricolor*) from fertilization to hatching. Trans. Amer. Micro. Soc., Vol. 74, No. 1, pp. 85–93.

WILIMOVSKY, N. J.
1954. List of the fishes of Alaska. Stanford Ichthy. Bull., Vol. 4, No. 5, pp. 279–294.

WILLIAMS, J. E.
1955. Determination of age from the scales of northern pike (*Esox lucius* L.). Dissertation Abstracts, Univ. Microfilms, Ann Arbor, Mich., Vol. 15, No. 9, p. 1684.

WOJCIK, F. J.
1955. Life history and management of the grayling in interior Alaska. Master of Science Thesis, Univ. Alaska, College, Alaska, 54 pp.

WOLF, P.
1951. A trap for the capture of fish and other organisms moving downstream. Trans. Amer. Fish. Soc., Vol. 80 (1950), pp. 41–45.

U.S. GOVERNMENT PRINTING OFFICE : 1959 O—465001

Blank page retained for pagination

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

STUDY OF AGE DETERMINATION BY HARD PARTS OF ALBACORE FROM CENTRAL NORTH PACIFIC AND HAWAIIAN WATERS

BY TAMIO OTSU AND RICHARD N. UCHIDA

FISHERY BULLETIN 150

From Fishery Bulletin of the Fish and Wildlife Service

VOLUME 59

UNITED STATES GOVERNMENT PRINTING OFFICE • WASHINGTON • 1959

For sale by the Superintendent of Documents, U. S. Government Printing Office
Washington 25, D. C. - Price 15 cents

Library of Congress catalog card for this bulletin:

Otsu, Tamio.

Study of age determination by hard parts of albacore from central north Pacific and Hawaiian waters, by Tamio Otsu and Richard N. Uchida. Washington, U. S. Fish and Wildlife Service, 1959.

iv, 353-363 p. illus., diagrs., tables. 26 cm. (U. S. Fish and Wildlife Service. Fishery bulletin 150)

"From Fishery bulletin of the Fish and Wildlife Service, volume 59."

Bibliography: p. 363.

1. Tuna fish. I. Uchida, Richard N., joint author. (Series: U. S. Fish and Wildlife Service. Fishery bulletin, v. 59, no. 150)

[SH11.A25 vol. 59, no. 150] Int 59-17

U. S. Dept. of the Interior. Library
for Library of Congress

Library of Congress catalog card for the series, Fishery Bulletin of the Fish and Wildlife Service:

U. S. *Fish and Wildlife Service.*

Fishery bulletin. v. 1-

Washington, U. S. Govt. Print. Off., 1881-19

v. in illus., maps (part fold.) 23-28 cm.

Some vols. issued in the congressional series as Senate or House documents.

Bulletins composing v. 47- also numbered 1-

Title varies: v. 1-49, Bulletin.

Vols. 1-49 issued by Bureau of Fisheries (called Fish Commission, v. 1-23)

1. Fisheries—U. S. 2. Fish-culture—U. S. I. Title.

SH11.A25 639.206173 9-35239 rev 2*

Library of Congress [r55e½]

CONTENTS

	Page
Materials	353
Methods	354
Results	355
Various skeletal structures	355
Scales	355
Results of ring counts	355
Vertebrae	356
Description	356
Change in the shape of vertebrae with growth of fish	356
Criterion for an annulus	356
Results of ring counts	357
Samples from small fish	357
Determination of time of ring formation	357
Discussion	358
Summary and conclusions	360
Literature cited	363

ABSTRACT

Various hard parts of large (93–128 cm.) albacore, *Germo alalunga* (Bonnaterre), from Hawaiian waters and smaller fish (50–112 cm.) from the central North Pacific were examined for marks that could be used in determining age in this species. A cursory examination of the opercular bones and fin spines revealed no usable marks. A study of scale samples from 100 albacore showed that only one-half of them were readable, and these only with a considerable degree of subjectivity.

Several workers in other areas have reported apparent success in aging albacore by means of the rings on the vertebral centra. Their results could not be duplicated in the present study. In attempts to read the rings in the vertebrae of 212 Hawaiian and 53 central North Pacific albacore, the authors found little agreement between the counts of the different readers or even between successive counts by the same reader. Indications were seen that the rings on the vertebrae are not annuli but rather that they may be growth marks laid down randomly with time. As a clue to relative age, however, they may provide an explanation of the unbalanced sex ratio of large albacore, for they indicate the possibility that among mature fish the males grow faster than the females.

The results of this study, though largely negative, are presented for the information of those engaged at present in similar studies and for others who may work on this problem in the future.

STUDY OF AGE DETERMINATION BY HARD PARTS OF ALBACORE FROM CENTRAL NORTH PACIFIC AND HAWAIIAN WATERS

By Tamio Otsu and Richard N. Uchida, *Fishery Research Biologists*, U. S. Bureau of Commercial Fisheries

As part of the research program of the Pacific Oceanic Fishery Investigations (POFI), Fish and Wildlife Service, a study was initiated to determine the age and growth of albacore, *Germo alalunga* (Bonnaterre), occurring in the region of the Hawaiian Islands and in the central North Pacific. This study and other investigations of the albacore resources of the Pacific are conducted by POFI under Public Laws 329 (80th Congress) and 466 (Saltonstall-Kennedy Act, 83d Congress).

Several workers have reported on the age and growth of albacore as determined from surface markings on the vertebral centra. Uno (1936a, b) working with albacore taken by pole-and-line fishing in the waters east of Cape Nojima, Japan, made age determinations on 988 fish. Aikawa and Kato (1938) reported on age determinations of albacore based on 10 large fish taken near Midway Island and 5 small fish taken off northeastern Japan. Partlo (1955) studied the age and growth of the eastern Pacific albacore, utilizing the vertebrae of 531 fish taken in 1950 from offshore waters adjacent to California, Oregon, Washington, and British Columbia. Finally, Figueras (1955) reported on age determination of 67 albacore taken off the coast of Galicia in northwestern Spain.

It was our hope to extend these findings to include central North Pacific albacore and the exceptionally large fish occurring in the Hawaiian area. We assumed that methods employed in other areas to determine the age of albacore could be successfully employed in this study. Our efforts in this respect were entirely unsuccessful, however, as we were unable to verify or duplicate findings of the other workers. It was our conclusion that the markings on albacore hard parts, particularly on the vertebrae, are not true year marks, and therefore, cannot be used in the aging of these fish. The results of our study, though largely negative, are presented here for the information of those who are presently engaged in similar studies and for others who may work on this problem in the future.

NOTE.—Approved for publication Jan. 16, 1958. Fishery Bulletin 150.

MATERIALS

Scales and vertebrae were routinely collected and certain other skeletal structures such as the operculum and the fin spines were also examined. Between January 1955 and July 1956, vertebrae and scales were collected from 212 albacore taken in Hawaiian waters and 53 from the central North Pacific.

Albacore taken by the Hawaiian longline fishery from an area within 20 miles of the main islands, were generally large, ranging in length from 93 to 128 cm. (weight, 33 to 93 lbs.) (fig. 1). These fish were sampled at the two Honolulu auction markets, the Hawaii Fishing Co., Ltd., and the United Fishing Agency, Ltd., where the landings of the Honolulu-based longline vessels were sold. Albacore were obtained from the central North Pacific on POFI's exploratory fishing cruises,

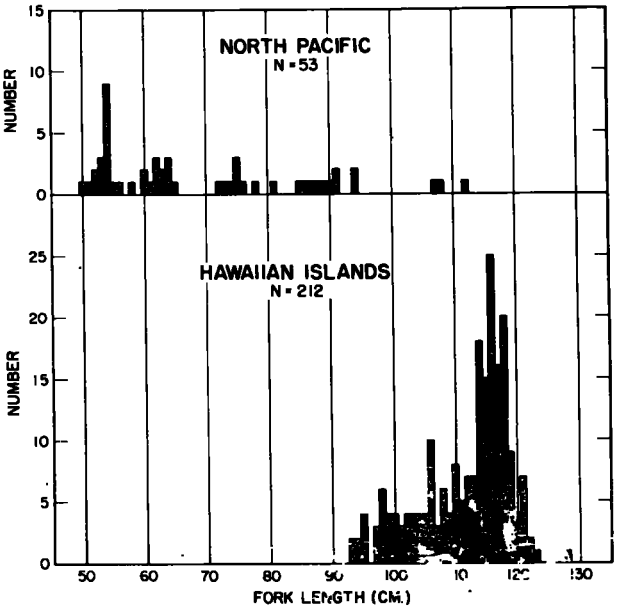

FIGURE 1.—Length frequency of albacore from which scales and vertebrae were collected.

which sampled an area between 140° W. and 180° longitude, from 30° to 50° N. latitude. These fish, taken by longline, trolling, and gill nets, were smaller, ranging in length between 50 and 112 cm. (6 to 65 lbs.) (fig. 1).

Scales were collected from the region of the body just below the second dorsal fin. The selection of this region was largely based on recommendations of researchers in California who were similarly engaged in the problem of aging the albacore, and who found scales from that region of the body "most promising" (personal correspondence). The 15th and 16th caudal vertebrae were selected for this study. While past investigators have used the thoracic vertebrae, our choice of the caudal vertebrae was based chiefly on accessibility, or the ease with which they could be acquired in the field or at the auction markets. This difference in the choice of vertebrae appears to be of little significance, since a careful examination of each of the 38 vertebrae of a single albacore revealed no notable differences in the appearance of the concentric markings.

METHODS

The scales were soaked in water overnight, after which the slime and adhering tissue were easily removed. The scales were then either dry-mounted between two glass slides or impressed on 0.030-inch thick cellulose acetate (1″ x 3″) strips, which were first softened by immersing in 95-percent ethyl alcohol for 5 minutes.

Scale images were projected on a white paper screen with a microprojector. Because of the variable sizes of the scales, the distance between the projected image and the microprojector was varied so that approximately equal-sized images could be produced. This tended to diminish to some extent the influence of the scale size in making ring counts.

In processing the vertebrae for study, the tail section, cut off at or near the 5th dorsal finlet, was boiled in water until the flesh could easily be removed from the bone. After washing, the vertebrae were sun-dried for about 2 days.

The method described by Partlo (1955) was followed in preparing the vertebrae for study. Where the 15th caudal vertebra was cut through or damaged during collection, the 16th vertebra was used. An electric jig saw was employed to cut each vertebra along a sagittal plane slightly to one side of the median line. The larger of the resulting two parts was sanded down until the center of the centrum was clearly exposed (fig. 2). Additional cleaning and accentuating of the concentric rings were done by immersing the vertebra in a 1-percent solution of potassium hydroxide for about 48 hours, followed by rinsing in fresh water and preservation in 95 percent ethyl alcohol.

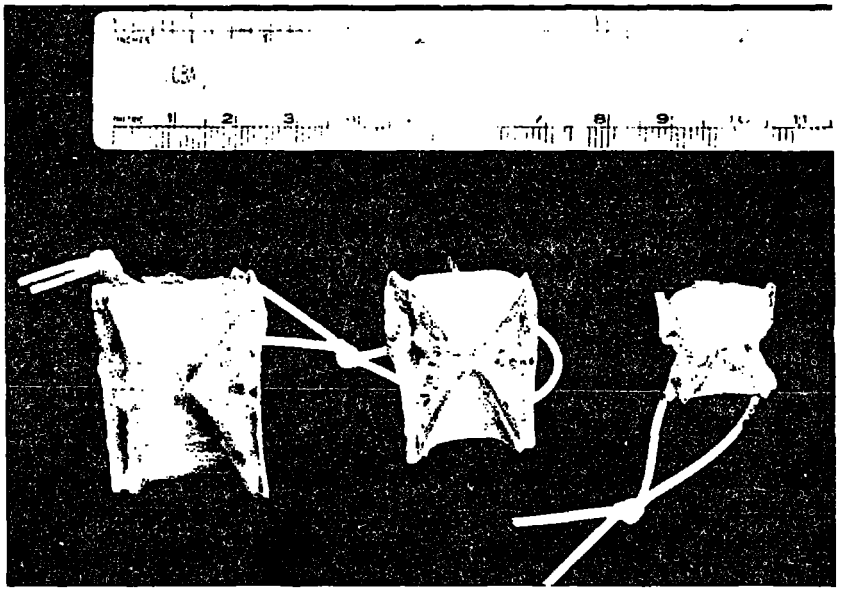

FIGURE 2.—Sectioned and prepared caudal vertebrae taken from albacore 113.9, 100.8, and 75.1 cm. long.

Measurements were made from the vertex of the cone to each ring (ring radius) and also to the outer margin of the cone (vertebral radius) along the four exposed edges. Ring radii were measured with a pair of dividers under a dissecting microscope and read off to the nearest 0.1 mm. on a ruler graduated in 0.5-mm. intervals. The anterior and posterior cone measurements were treated independently. The two corresponding ring and vertebral radii measurements of each cone were averaged.

RESULTS

Various Skeletal Structures

Cursory examination of the operculum, dorsal and pectoral fin spines, and the hypural plate produced no evidence that these structures possessed any markings which could be interpreted as "age marks." The operculum showed distinct marks only on the outer free edge; the central area was invariably thickened and devoid of any markings.

Scales

The albacore scale is cycloid and either oval or roughly rectangular in general outline. The circuli are concentric with the margin of the scale. Examination revealed that the smaller scales generally exhibited a rather distinct focus and clearly defined circuli, but that the larger scales (from fish larger than 90 cm.) were mostly characterized by obscure sculpturing and a thickened central area. Furthermore, it was noted in several instances that scales from the same specimen (usually in large fish) were of variable size and shape. A count was made of the rings on different sized scales from the same fish following the definition of an annulus as given by Nose and others (1955), who state: "The ring appears as a transparent line, near by which the circuli become fine and discontinuous . . ." Though the counts on the larger scales were necessarily somewhat subjective, because of the general opaqueness of the scales, there appeared to be some trend in the number of rings, the smaller scales having a lesser count than the larger. This would seem to indicate that the smaller scales had originated more recently than the larger ones.

Results of ring counts

Scales from 100 fish were examined. Of this total, the scales from 43 fish were considered unreadable, in large part because of opaqueness of the central area. The samples from the remaining 57 fish varied widely in the degree of readability. Despite the obvious difficulties, an attempt was made to count the rings on scales which had the greatest number of annuli for each sample. The ring counts are plotted against fish size in figure 3. There is a tendency for ring

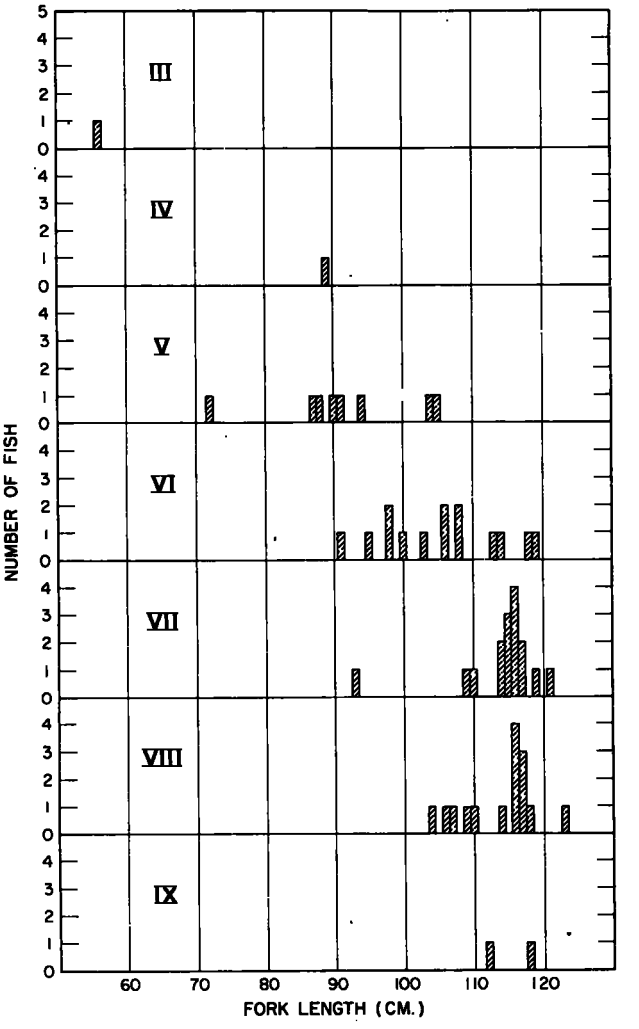

FIGURE 3.—Age of 57 albacore, determined by scale reading, plotted against fish size. (The Roman numerals represent the number of rings, or "age".)

counts to increase with increasing fish size, up to 8 rings. The size ranges of fish with 5 or more rings were broad, however, with a great amount of overlapping between successive groups.

Moore (1951) in working with Hawaiian yellowfin tuna encountered similar difficulties. He also

observed that small specimens of yellowfin, weighing about 5 pounds, had no scales except on the corselet region. He therefore concluded that scales were formed first on the anterior and later on the posterior part of the body. He stated that "if this is the case, any marks laid down in the scales would be of little value until the nature of scale formation and its relation with size and age of fish was known." The nature of scale formation on the albacore has not as yet been determined. Since it was our experience that only about half of the scales examined were considered readable, and these were read with considerable subjectivity, further work with scales was discontinued.

VERTEBRAE

Description

The albacore vertebra is amphicoelous, or concave at both ends of the centrum. A sectioned vertebra shows two cones, the vertices of which meet at or near the middle of the centrum, with their bases forming the margins of the vertebra. On the inner surface of these cones are concentric rings running parallel to the outer margin of the centrum. These rings are described by Partlo (1955) as "narrow translucent zones separated by broad, opaque zones similar to those described by Freidenfelt (1922) for *Lucioperca*. In the albacore the narrow zones were observed not only as translucent bands but also as eruptions or ridges on the centrum surface. The innermost ring differed slightly from the others but was nevertheless clearly marked." We also observed certain rings that appeared as translucent ridges on the surface of the centrum; there were other rings, however, that resembled narrow, translucent bands without any surface eruptions, and still others that were mere suggestions of lines or bands.

Change in the Shape of Vertebrae With Growth of Fish

In the course of examining a wide series of vertebrae, it was noted that while the two cones of an amphicoelous caudal vertebra were nearly the same size in small fish, the posterior cone was larger than the anterior in large fish, indicating that the vertebra changed its shape with growth of the fish. The lengths of the two cones (vertebral radii) were measured and the ratio of the two measurements was plotted against the size of the fish (fig. 4). While the ratio was nearly 1 : 1 in the smallest vertebrae examined (fish around 50 to 60 cm. long), the posterior cone was definitely larger than the anterior in the larger vertebrae. This changing proportion is described by the rectilinear regression:

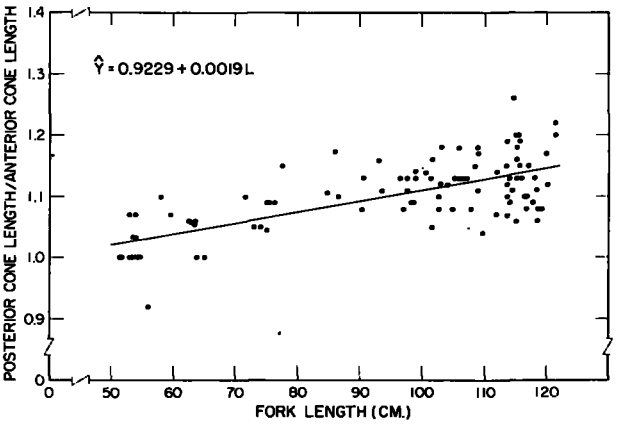

FIGURE 4.—Ratio of the average length of the posterior and anterior cones plotted against fish size to demonstrate the disproportionate growth of the two cones of the amphicoelous vertebrae of albacore.

$$\hat{Y}=0.9229+0.0019\ L$$

where $\hat{Y}$ is the ratio of the two cones and L is the fork length in centimeters. Although the two cones of a caudal vertebra grow disproportionately, each cone in itself exhibits a linear growth with growth of the fish. Thus, in working with caudal vertebrae from a wide size range of fish, it is important that any measurements of ring or vertebral radii, for the purpose of estimating the growth increments of the fish, should be confined to either the anterior or the posterior cones and not to averages of the two. By working with one cone, growth calculations can be based on the simple linear relation between size of the vertebrae and size of fish.

Criterion for an annulus

Because of the great variability in the appearance of the rings, it was extremely difficult to formulate a satisfactory criterion for an annulus. In the beginning, we followed the definition of Partlo (1955), who considered as annuli those rings which appeared as ridges on the centrum surface. However, as will be discussed, our original criterion was later expanded to include rings which appeared as translucent bands with no surface eruptions.

Results of ring counts

After deciding upon the criterion to be followed, we made a series of independent ring counts and ring-radii measurements. A total of 9 series of counts and measurements resulted in agreements between any 2 series of as low as 8 percent and as high as 45 percent. There was poor agreement not only between counts of the two readers but also between counts made by the same person. Table 1 shows the best agreement attained between readers (44.8 percent) and between sets of readings made by the same reader (38.9 percent for reader *A* and 43.9 percent for reader *B*). While most of the disagreement was by 1 ring (31 to 50 percent), discrepancies of as many as 4 rings occurred in many of the comparisons. Consistency was often not achieved even between counts of the anterior and posterior cones of the same vertebra.

TABLE 1.—*Best agreement in ring counts between two readers and between any two series of the same reader*

[The readers are designated as *A* and *B*; the numerals denote separate readings; for example, A_2 represents the second reading made by reader *A*.]

Readings compared	Percentage agreement	Percentage disagreement by:			
		1 ring	2 rings	3 rings	4 rings
A_2 vs. B_3	44.8	38.8	11.9	3.7	0.7
A_1 vs. A_2	38.9	50.5	9.8	0.8	0.0
B_3 vs. B_4	43.9	47.0	8.3	0.8	0.0

It was observed that much of the inconsistency in the counts could be attributed to the difficulty in distinguishing rings near the vertex of the cone and also at its margin. This does not mean, however, that the rings on the central portion of the cones were clear and easily distinguishable, because here also there were many inconsistencies.

Samples from small fish

Age determination by means of hard parts frequently becomes more difficult and often breaks down completely in older fish. Therefore, attempts were made to age fish less than 90 centimeters in length in order to determine whether or not the use of vertebrae from larger, older fish was the cause of the poor results. In one trial consisting of two series of counts, the agreement was 56 percent for fish less than 90 centimeters as compared with 30 percent for larger fish. The higher agreement with smaller fish is, of course, to be expected because of the fewer rings. Further trials with samples of small fish disclosed that the counts were still far too variable to be acceptable as indicators of age.

The vertebrae were examined under natural and incandescent light and also under polarized and various colored lights with no noticeable improvement in the appearance of the rings. Various types of stains were also tried, but here again the results were disappointing from the standpoint of improving the readability of the rings. Thus, we found that we could not satisfactorily duplicate ring counts and therefore could not meet the first prerequisite to the use of vertebrae for aging albacore. Our findings are in contrast to Partlo's, who reported that "counts of rings were reproducible with high consistency."

Determination of time of ring formation

In order to validate the vertebral method for aging albacore, it is necessary that some direct evidence be obtained to show that the rings on the centra are true year marks, which are laid down annually. It appears reasonable to assume that if these rings are laid down regularly once each year, rather than randomly, a study of the margins of vertebrae collected periodically throughout a year should indicate the approximate period of ring formation. The width of the margin from the last ring to the edge of the centrum (the increment of the last ring) should be at a maximum immediately before, and at a minimum just at or after the formation of the last ring. A description of such a method of analysis for the determination of time of ring formation on tuna scales is given by Nose and others (1955).

An attempt was made to obtain some indication of the time of ring formation, despite the fact that any such study would probably be futile unless the rings or annuli could first be read with assurance. Measurements were made from the mid-point of the centrum to the margin of the vertebra (vertebral radius *T*) and to the last ring (ring radius R_n). Although the last ring was carefully selected in each instance, there was a possibility of error because rings on the margins were often indistinct. The difference between the vertebral and last-ring radii was considered the increment. Figure 5 shows a plot of the relative increment (absolute increment/vertebral radius) plotted against the month of capture of the fish. The data show no indication of regularity in time

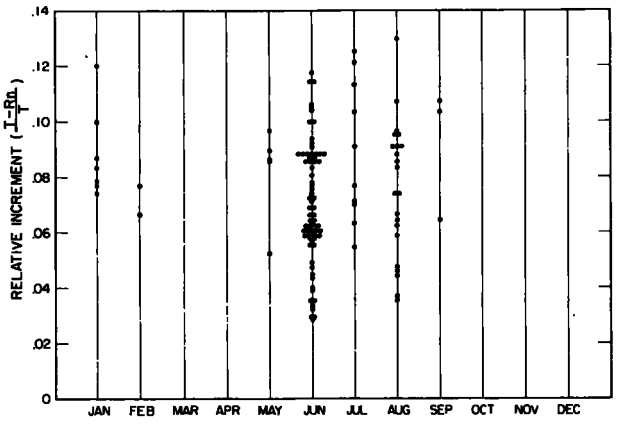

FIGURE 5.—Relative increment of the last ring plotted by month of capture of the fish.

of ring formation. Similarly, a plot of the absolute increment against time of capture resulted in a random scatter of points.

DISCUSSION

Previous investigators working on albacore age and growth have reported the presence of definite rings on the inner surface of the centrum of albacore vertebrae which, they believed, could be used as age indicators. They concluded that each of these rings represented an annulus and, therefore, assigned fish to specific age groups after making counts of these rings. Aikawa and Kato (1938) found that Uno's mean lengths (Uno 1936a, b) for age groups IV, V, and VI fell within the length range that they had established for these same age groups. Partlo (1955), on the other hand, found his ring radii values to be at variance with those observed by Aikawa and Kato, but stated that the disagreement was largely caused by the latter's not recognizing the ring closest to the vertex of the cone. Aside from this discrepancy, there was remarkable agreement between their ring radii values. Figueras (1955), who based his work largely on Partlo's technique, concluded that his results were in fair agreement with the latter.

Aikawa and Kato, Figueras, and Uno, so far as can be determined, have not satisfactorily established or presented any evidence showing that the rings on the vertebrae are age rings and annual in nature. Partlo, however, hypothesized that the rings are true year marks by the following: (1) by assuming that the length groups in the size frequencies are age groups, he found that there was acceptable agreement between the mean length of fish assigned to each vertebral ring-class and the mean length of corresponding length-groups in the sample, and (2) there was agreement between the lengths of young fish calculated from vertebral measurements of older fish and the observed lengths of young fish. For the latter, Partlo, working with a subsample of 98 fish, found that the observed lengths were consistently greater than the calculated lengths because the fish were captured some time after the last ring was formed. Partlo concluded that "from the above it seems clear that the third and subsequent vertebral rings are produced annually. It is assumed, in the absence of contrary evidence, that the inner two rings are annual also."

While Partlo's results indicated that the vertebral rings were true year marks, it was felt that more direct evidence would be desirable. One possible approach to obtaining such evidence is presented on page 357.

In this study, ring counts were not reproducible with consistency, due largely to the difficulty in formulating suitable criteria for the identification of the rings. Since it was demonstrated that there was a linear relation between the vertebral radius and the body length of the albacore (fig. 4), it was difficult to make a reading without first forming an opinion as to how many rings a certain-sized vertebra should have. Also, in making ring measurements the selection of a ring often depended on whether or not its radius fell within a certain range which encompassed all previous radii for that ring. Any extreme deviation was inadvertently questioned, and a subsequent remeasurement was made on a more "reasonable" ring, which was invariably found after closer scrutiny. For example, if the investigator measures the radius of the second ring at 5 mm. in a particular vertebra, and if all previous second-ring radii have fallen between 3 and 4 mm., he re-examines the vertebra for a second ring which he may have "missed." More often than not he will "find" the "missing" ring. In fact, it was observed that "rings" could be located at will almost anywhere on the centrum.

Aikawa and Kato (1938) state that "where the variation of the radius in comparison with other rings is very marked, the line cannot be considered an annual ring." Figueras (1955) found that in 40 percent of the specimens he examined, the first annulus as well as the succeeding annuli were lo-

cated closer to the center of the centrum than the corresponding annuli in the remaining specimens (60 percent). He therefore considered the 40 percent to belong to a different spawning season and discarded them from calculations of growth increments. From the above, it appears that these workers also experienced some difficulty in rigidly adhering to established criteria.

The fact that we have not been able to reproduce ring counts with any reasonable consistency does not in itself prove that this method of aging albacore is invalid. There are other points which should also be considered. As stated earlier, no direct evidence has yet been presented to show that the rings on the vertebral centra are "annuli." Furthermore, if we examine the results presented by some of the other workers, we find that the increments that are noted do not give either a reasonable or consistent pattern of growth. Referring to Aikawa and Kato's results, Brock (1943) stated that "it may be seen that the growth increment from the age of one to that of eight is exactly the same each year, resulting in a growth curve that is absolutely linear. This is totally at variance with what is known of growth curves in general and in all other species of fishes that have been studied. If the number of "age rings" bears this relationship to the length of the fish it is probable that they do not represent annuli and bear no direct relationship to age." Partlo's results are somewhat similar. In figure 6 we show a plot of body-length at earlier ages as calculated from 5- and 6-year fish; the data were derived from Partlo (1955: table VIII, p. 57). The calculated lengths

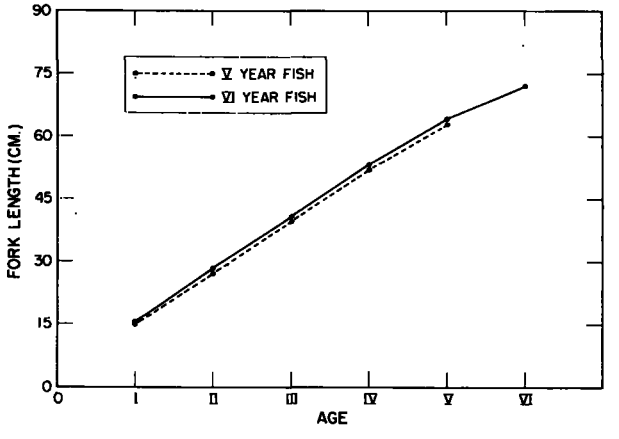

FIGURE 6.—Calculated lengths of albacore at earlier ages based on 5- and 6-year fish. (Taken from Partlo, 1955, table VIII.)

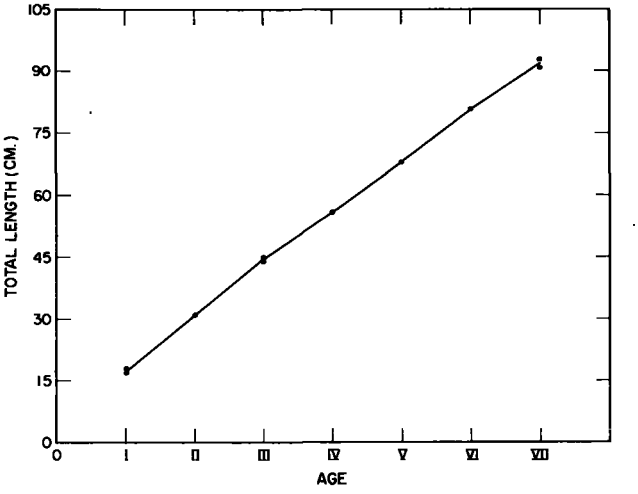

FIGURE 7.—Mean length at each age of albacore captured off northwestern Spain as reported by Figueras (1955). (Lengths given are total lengths.)

from ages 1 to 4 based on 5-year fish and the lengths for ages 1 to 5 based on 6-year fish form curves which are almost perfectly linear. The results presented by Figueras are shown in figure 7. Here again, the growth curve is remarkably linear, contrary to the general concept of growth curves.

Another consideration is that the various estimates do not appear to be consistent with growth as evidenced by tag returns. The information from this source is meager, however, and not much weight should be given it at the present time. A summary of albacore tag recoveries is given in table 2. The 5 tag recoveries which contribute information on growth are shown in figure 8.

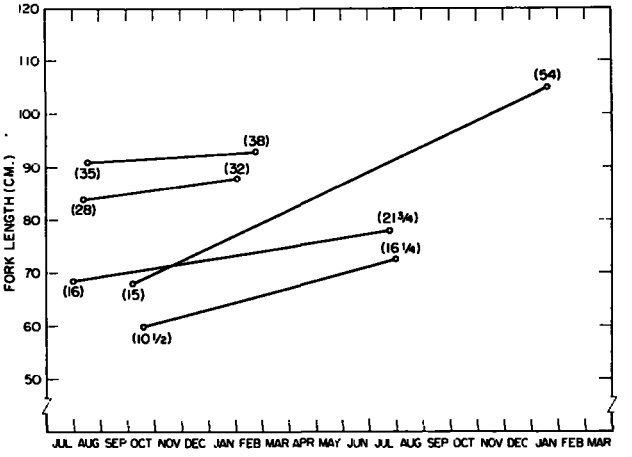

FIGURE 8.—Growth shown by 5 tagged albacore; data presented in table 2. (Body weight, in pounds, in parentheses.)

TABLE 2.—*Albacore tag recoveries reported by POFI and the California Department of Fish and Game* [1]

No.	Date of release	Locality of release	Released by	Date of recovery	Locality of recovery	Fish size	
						Release	Recovery
						cm.	*cm.*
1	Aug. 4, 1952	33°25′ N., 118°15′ W.	CF&G [2]	June 23, 1953	31°30′ N., 149°40′ E.	76	
2	Aug. 11, 1953	Guadalupe Is.	do	Feb. 2, 1954	36°40′ N., 178°12′ E.	84	88
3	Aug. 16, 1953	do	do	Feb. 23, 1954	30°10′ N., 178°54′ W.	91	93
4	Sept. 26, 1954	33°42′ N., 121°15′ W.	do	Apr. 6, 1955	31°55′ N., 143°15′ E.		
5	Oct. 4, 1954	46°30′ N., 159°18′ W.	POFI [3]	Nov. 28, 1955	35°45′ N., 157°39′ E.	78.2	
6	Oct. 5, 1954	43°31′ N., 161°16′ W.	do	Jan. 19, 1956	35°23′ N., 141°20′ E.	68	105
7	Oct. 9, 1955	42°16′ N., 147°16′ W.	do	June 24, 1956	31°54′ N., 158°37′ E.	63.4	
8	Oct. 17, 1955	44°55′ N., 144°48′ W.	do	Aug. 1, 1956	31°21′ N., 117°17′ W.	59.9	72.3 (16¼ lbs.)
9	July 31, 1956	44°31′ N., 174°55′ W.	do	July 23, 1957	30°08′ N., 119°03′ W.	68.4	78.0 (21¾ lbs.)

[1] The data for the California tag recoveries are derived from the reports of Ganssle and Clemens (1953), Blunt (1954), and Anonymous (1955).
[2] Department of Fish and Game, Sacramento, California.
[3] Pacific Oceanic Fisheries Investigations, U. S. Fish and Wildlife Service.

Variable growth is indicated, ranging from 2 cm. in about 6 months to 37 cm. in 16 months (4 to 28 cm. per year). The weights indicated in figure 8, with the exception of the last two recoveries (Nos. 8 and 9, table 2), are estimated weights based on the following length-weight relation:

$$\text{Log Weight} = -7.0239 + 2.87912 \text{ Log Length}$$ [1]

In terms of weight, a rough estimate of growth amounted to 6, 9, 27, 6, and 10 pounds per year, respectively, for the 5 fish shown from top to bottom in figure 8. Clearly, no conclusions can be drawn from these data. It is to be noted, however, that there are indications here of a moderately rapid growth rate, somewhat greater than the various estimates provided by the vertebral method of age determination.

It is possible, of course, that the rings on the centra are associated with growth but not necessarily with age of the fish. Unlike many of the fishes of the north temperate zone, it appears that albacore live under fairly uniform conditions by migrating to areas where food is available and where water temperature is suitable. They are not subject to extremes of winter and summer conditions as are certain fishes that occupy a more limited range. In the absence of any environmental extremes that might produce marked changes in the metabolic activity of the fish, it is quite possible that "winter" rings do not appear on the albacore's scales and vertebrae.

We have concluded that the rings on the vertebrae are probably not age rings which are laid-down annually or at such regular intervals that they can be used to tell the age of the fish; however, even if the rings were laid down randomly with respect to time, older fish in general would be expected to possess more rings than the younger ones. Assuming this applies to the albacore, the number of rings in relation to the size of fish might be used to differentiate rapidly growing fish from slower growing individuals. Counts of rings in albacore separated by sex show that among larger fish, the females, at a given ring count are smaller than the males (fig. 9). The number of rings in the counts ranged from 3 to 12, and the females were represented for each count up to 11 rings. Although the female albacore apparently do not grow so large as the males, having reached their maximum size at around 112 cm. (fig. 10, also Otsu and Uchida, 1959), the ring counts indicate that the largest females may be about as old as the largest males.

A great predominance of males has been noted among the larger sizes of several species of tunas (e. g. Shomura and Murphy 1955). This unequal sex ratio among the larger sizes has been attributed to "either differential mortality or differential growth, or to combinations of the two factors." Differential availability has also been suggested. For albacore there is a similar situation, but somewhat more pronounced, for the males attain a markedly larger size than females (fig. 10). Returning to figure 9, fish having 7 or more rings show growth differentiation by sex, the males being the larger for each ring class. This bit of evidence suggests that after about the seventh ring, the males have a faster growth rate than females. It is interesting to note that this apparent differentiation in growth commences when the fish attain a length of about 90 cm., which is the size at which albacore are believed

[1] Computed by POFI based on 77 fish (51–119 cm.) taken in the central North Pacific.

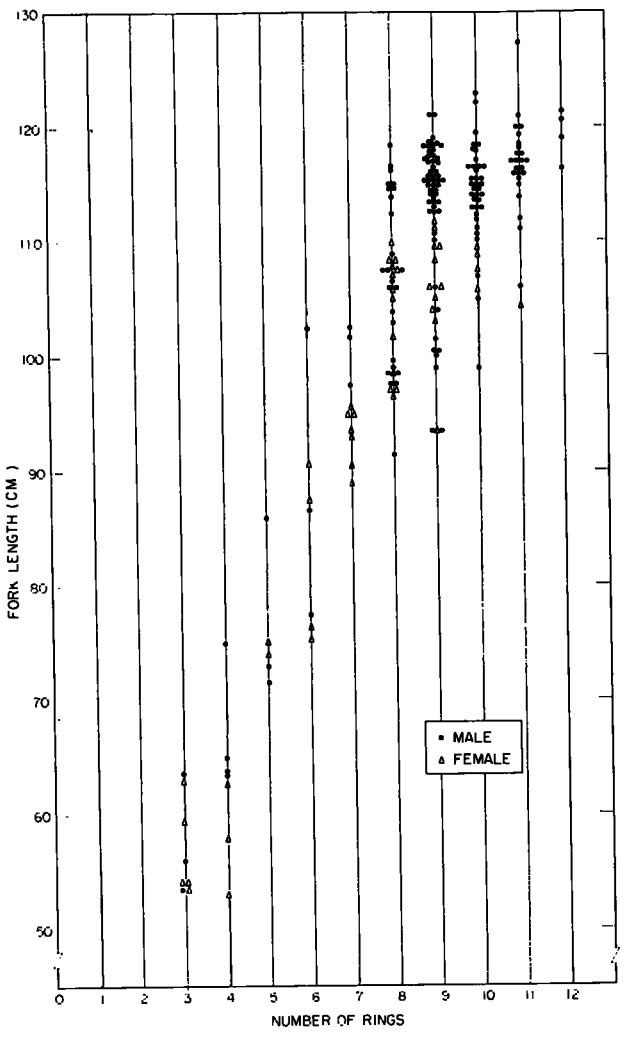

FIGURE 9.—Ring counts shown by fish size and sex for one series of anterior cone readings.

to reach sexual maturity (Otsu and Uchida, 1959; Ueyanagi 1955). Thus, as juveniles, both sexes seem to grow at about the same rate, then upon attaining sexual maturity, the males outgrow the females, so that among the larger sizes males predominate even though the larger females are just as old as the larger males. If our assumption that the rings on the vertebrae indicate "relative age" is valid, then our data suggest that this phenomenon of unbalanced sex distribution among larger albacore is due primarily to differential growth, with differential mortality or differential availability playing a possible secondary role.

It is also apparent that differential growth is not the sole factor in operation here, since size

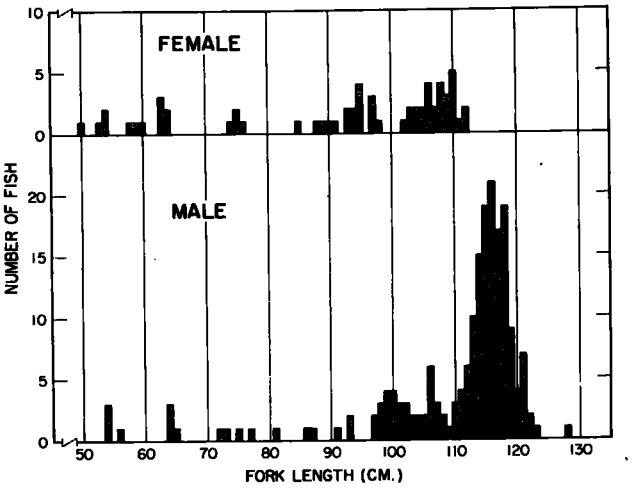

FIGURE 10.—Length and sex distribution of albacore used in this study. (The numbers of fish in smaller size classes differ from those of figure 1, which includes unsexed specimens.)

frequencies, such as in figure 10, lack a mode of large females of a magnitude comparable to the last mode of males. We would expect to find two large modes, one of females slightly to the left of that for males, in accordance with the difference in growth rates. This is not the case. Although evidence points to differential growth as being the main factor, other factors are probably acting in conjunction to cause the apparent reduction in numbers of the larger females. Here again, we must use caution in accepting any conclusions drawn from data presented in figure 9 since, ring counts could not be duplicated with any degree of consistency. Despite the questionable validity of these data, the fact that they showed the relatively smaller females to have, in general, nearly as many vertebral rings as the larger males has prompted the authors to present this discussion as a possible explanation of the puzzling phenomenon of unbalanced sex distribution encountered among the larger sizes.

SUMMARY AND CONCLUSIONS

(1) This study is based on the examination of vertebrae and scales collected from 212 Hawaiian and 53 central North Pacific albacore. In addition to scales and vertebrae, a cursory examination was made of the operculum, dorsal and pectoral fin spines and the hypural plate for possible indications of age.

(2) The sample represents fish taken by long-line, trolling, and gill nets during the period January 1955 to July 1956.

(3) None of the various structures examined revealed any markings which could be interpreted as age marks.

(4) Scales from 100 fish were examined; of these, the scales of 43 fish were considered unreadable. Samples from the remaining 57 fish varied greatly in degree of readability. A plot of the ring counts against fish size showed considerable overlapping between successive groups.

(5) Scales taken from the same fish were often of variable size. It was noted that small scales contained fewer rings than large scales, indicating that the origin of the scales was not uniform.

(6) Because of the undetermined nature of scale formation, and the fact that only about one-half of the scales were considered readable, further work with scales was discontinued.

(7) A change was observed in the shape of the caudal vertebrae with growth of the fish. Among the smaller vertebrae, from fish of about 50 to 60 cm. in length, the ratio of the length of the anterior cone to that of the posterior cone was nearly 1:1. The posterior cone was larger than the anterior in the larger vertebrae. Although the two cones of a caudal vertebra grow disproportionately, each cone in itself exhibits a linear growth with growth of the fish.

(8) In comparing independent sets of readings made by readers *A* and *B*, the highest agreement between the two readers was 44.8 percent. The best agreement between any two readings of the same reader was 38.9 percent for reader *A* and 43.9 percent for reader *B*. The most difficult rings to distinguish were those near the vertex and the margin of the cone.

(9) Although the vertebrae of small albacore were somewhat more readable than those of large albacore, it was still not possible to achieve sufficient consistency in ring counts and measurements to validate this method of age determination.

(10) The results indicated that the rings on the vertebral centra are laid down randomly with respect to time, rather than periodically. It is realized, however, that the validity of this method of analysis is questionable, since it is based on the recognition of the last ring and since the ring counts could not be duplicated with any consistency. If our results are valid, it would appear that the rings are simply growth marks rather than age marks.

(11) Considerable personal bias was inadvertently introduced into the readings and measurements. It was almost impossible to make a reading without first forming an opinion as to the number of rings that should be expected on a vertebra of a certain size.

(12) The growth increments reported by previous investigators did not appear to give either a reasonable or a consistent pattern of growth.

(13) The growth estimates of past investigators do not appear to be consistent with growth as evidenced by tag returns. Although the data derived from tagged fish are meager, they indicate that albacore have a moderately rapid growth, somewhat greater than the various estimates provided by the vertebral method of age determination.

(14) Unlike many north temperate species which occupy limited environments, the albacore appears to spend its life under fairly uniform conditions by migrating to areas of abundant food and favorable water temperature. Thus, these fish are probably not subject to the extreme summer and winter conditions which would cause "winter" marks to appear on scales and vertebrae.

(15) Although rings on the vertebrae are probably not age rings which are laid down annually or at such intervals that they could be used to tell the actual age of the fish, it was pointed out that the rings could possibly be used to assess the relative age, that is, older fish would have more rings than younger fish.

(16) Results of a series of ring counts were examined for differences between sexes. There was evidence that the unbalanced sex distribution among larger albacore, with a great predominance of males, was largely due to differential growth which sets in with the onset of sexual maturity, after which the males grow at a faster rate than the females.

LITERATURE CITED

AIKAWA, H., and M. KATO.
1938. Age determination of fish (Preliminary Report 1). Bull. Jap. Soc. Sci. Fish. 7 (1): 79–88. (English translation, U. S. Fish and Wildlife Service, Spec. Sci. Rept.—Fish. No. 20, 22 p.).

ANONYMOUS.
1955. On the recapture of an American-tagged albacore. Tuna Fishing, No. 21, p. 37 (Tokyo). (Translated from the Japanese by Wilvan G. Van Campen).

BLUNT, C. E., JR.
1954. Two mid-Pacific recoveries of California-tagged albacore. Calif. Fish and Game 40 (3): 339.

BROCK, V. E.
1943. Contribution to the biology of the albacore (*Germo alalunga*) of the Oregon Coast and other parts of the North Pacific. Stantord Ichthy. Bull. 2 (6): 199–248.

FIGUERAS, A.
1955. Renseignement sur l'âge et la Croissance du Germo (*Germo alalunga* Gmelin). Committee Meeting, International Council for the Exploration of the Sea, Committee of Scombriform Fishes, No. 24, 4 p. Mimeographed. (Translated from the French by W. G. Van Campen).

GANSSLE, D., and H. B. CLEMENS.
1953. California-tagged albacore recovered off Japan. Calif. Fish and Game 39 (4): 443.

MOORE, HARVEY L.
1951. Estimation of age and growth of yellowfin tuna (*Neothunnus macropterus* Temminck & Schlegel) in Hawaiian waters. Master of Science thesis (unpublished), University of Hawaii.

NOSE, Y., AND OTHERS.
1955. A method to determine the time of ring-formation in hard tissues of fishes, especially for the age determination of Pacific tunas. Records of Oceanographic Works in Japan 2 (3):9–18.

OTSU, TAMIO, and RICHARD N. UCHIDA.
1959. Sexual maturity and spawning of albacore in the Pacific Ocean. U. S. Fish and Wildlife Service, Fishery Bulletin 148, vol. 59, pp. 287–305.

PARTLO, J. M.
1955. Distribution, age and growth of eastern Pacific albacore (*Thunnus alalunga* Gmelin). Jour. Fish. Res. Bd. Canada 12 (1): 35–60.

SHOMURA, R. S., and G. I. MURPHY.
1955. Longline fishing for deep-swimming tunas in the Central Pacific, 1953. U. S. Fish and Wildlife Service, Spec. Sci. Rept.—Fish. No. 157, 70 pp.

UEYANAGI, S.
1955. On the ripe ovary of the albacore, *Germo germo* (Lacépède), taken from the Indian Ocean. Bull. Jap. Soc. Sci. Fish. 20 (12):1050–53. (In Japanese with English synopsis. Translated from the Japanese by W. G. Van Campen.).

UNO, M.
1936a. *Germo germo* (Lacépède) in the waters east of Nozima Promontory, Tiba Prefecture (Preliminary Report No. 1). Bull. Jap. Soc. Sci. Fish. 4 (5):307–309. (In Japanese with English synopsis translation by W. G. Van Campen.)
1936b. *Germo germo* (Lacépède) in the waters east of Nozima Promontory, Tiba Prefecture (Preliminary Report No. 2). Bull. Jap. Soc. Sci. Fish. 5 (4): 235. (In Japanese with English synopsis. Translated from the Japanese by W. G. Van Campen.)

U. S. GOVERNMENT PRINTING OFFICE: 1959 O - 489034

Blank page retained for pagination

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*
FISH AND WILDLIFE SERVICE; Arnie J. Suomela, *Commissioner*

FLUCTUATIONS IN THE POPULATION OF YELLOW PERCH, *PERCA FLAVESCENS* (MITCHILL), IN SAGINAW BAY LAKE HURON

BY SALAH EL-DIN EL-ZARKA

FISHERY BULLETIN 151
From Fishery Bulletin of the Fish and Wildlife Service
VOLUME 59

UNITED STATES GOVERNMENT PRINTING OFFICE • WASHINGTON • 1959

For sale by the Superintendent of Documents, U. S. Government Printing Office
Washington 25, D. C. - Price 40 cents

Library of Congress catalog card for this bulletin:

el-Zarka, Salah el-Din, 1922–

Fluctuations in the population of yellow perch *Perca flavescens* (Mitchill), in Saginaw Bay, Lake Huron. Washington, U. S. Govt. Print. Off., 1959.

iv, 365–415 p. map, diagrs., tables. 26 cm. (U. S. Fish and Wildlife Service. Fishery bulletin 151)

"From Fishery bulletin of the Fish and Wildlife Service, volume 59."

Bibliography: p. 413–415.

1. Perch. 2. Animal populations. I. Title. (Series: U. S. Fish and Wildlife Service. Fishery bulletin, v. 59, no. 151)

[SH11.A25 vol. 59, no. 151] Int 59–56

U. S. Dept. of the Interior. Library
for Library of Congress

Library of Congress catalog card for the series, Fishery Bulletin of the Fish and Wildlife Service:

U. S. *Fish and Wildlife Service.*
Fishery bulletin. v. 1–
Washington, U. S. Govt. Print. Off., 1881–19

v. in illus., maps (part fold.) 23–28 cm.

Some vols. issued in the congressional series as Senate or House documents.
Bulletins composing v. 47– also numbered 1–
Title varies: v. 1–49, Bulletin.
Vols. 1–49 issued by Bureau of Fisheries (called Fish Commission, v. 1–23)

1. Fisheries—U. S. 2. Fish-culture—U. S. I. Title.

SH11.A25 639.206173 9–35239 rev 2*

Library of Congress [r55e1]

CONTENTS

	Page
Introduction	365
Materials and methods	366
Collection of samples	366
Records for individual fish	366
Determination of age	366
Preparation and examination of scales	366
Age analysis	367
Commercial fishery for yellow perch	368
General trends of the fishery, 1891–1955	368
Catch by gear	370
Seasonal distribution of the catch	370
Age composition and year-class strength	371
Annual and seasonal differences of age distribution	371
Relative strength of year classes	374
Size at capture	377
Length distribution of samples	377
Length distribution of age groups	378
Change in length between 1929–30 and 1943–55	379
Length-weight relation	380
General length-weight relation	381
Weight in relation to condition of gonads	382
Seasonal change in weight	382
Comparison with length-weight relation in 1929–30 and with other Great Lakes populations	383
Calculated growth	384
Body-scale relation	384
Key scales below the lateral line	384
Key scales above the lateral line	386
Comparison of length calculated from different scales of the same fish	386
Implications as to procedure in calculation of growth	387
Growth in length	387
Growth in length of age groups	387
General growth rate	390
Annual fluctuation of growth in lengths	391
Fluctuations in first-year growth	392
Fluctuation in growth in later years of life	393
Growth in weight	394
Growth in weight of the age groups: general growth	394
Annual fluctuation of growth in weight	396
Difference in growth rate in 1929–30 and 1943–55 and comparison with growth from other Great Lakes waters	398
Probable factors of the decrease in growth rate	400
Possible factors of fluctuations in year-class strength and growth rate	404
Environmental factors and fluctuation in year-class strength	405
Environmental factors and fluctuation in growth rate	406
First-year growth	406
Growth in later years of life	407
Sex and maturity	408
Size at maturity	408
Sex ratio	409
Sex ratio of individual samples	409
Change of sex ratio with increase in age	410
Summary	411
Literature cited	413

ABSTRACT

The average annual commercial production of Saginaw Bay yellow perch dropped from 1,961,309 pounds in 1891–1916 to 499,938 pounds in 1917–55. Since 1938 (1939–55), the catch has exceeded 500,000 pounds in only 3 years. The small catches of 1939–55 do not reflect scarcity of yellow perch. The catch of legal-sized fish per unit-of-effort has tended to increase, but fishing intensity has decreased sharply.

This paper is written around two major themes: Comparison of perch collected in 1929–30 with specimens collected in 1943–55, as to growth rate, age composition, size distribution, length-weight relation, and sex ratio; description and inquiry into the causes of fluctuations in the strength of the year classes of 1939–52, and of the growth rate during 1942–54.

The growth in length and weight of Saginaw Bay yellow perch in 1943–55 was the slowest yet reported from any Great Lakes waters. The decrease in growth rate in Saginaw Bay was believed to have resulted from a more than sevenfold increase in the population density. A "space factor" rather than competition for food may account for the decline in growth rate. Fish of the 1943–55 samples gave no evidence of a scarcity of food; on the contrary, they were heavier for their length than fish caught in 1929–30.

The weight of yellow perch in the 1943–55 samples increased as the 3.262 power of the length. Seasonal changes in the length-weight relation were small. Females lost 12.3 percent of their weight at spawning.

Age determination and growth calculation were based on the scales of 4,285 fish, 3,407 of them collected during the spawning seasons of 1943–55 and the remainder at other seasons in 1955. The average age of fish in impounding-net samples collected in the spring increased between 1929–30 (3.8 years) and 1943–55 (4.3 years), and growth declined sharply. Saginaw Bay yellow perch of the 1929–30 samples reached legal length (8½ inches) in 3 years but those taken in 1943–55 required more than 5 years to attain the same size. At the same time the modal length dropped from 8.5–8.9 to 6.5–6.9 inches and the percentage of legal-sized fish from 74 to 11 percent. In both periods, the females averaged larger than the males and grew more rapidly.

Males were relatively more plentiful in 1943–55 (62 percent) than in 1929–30 (25 percent). The percentage of males decreased with increase of age in 1929–30 but increased in 1943–55. Both males and females attained sexual maturity at a small size (nearly all males were mature at 5.0–7.5 inches; 80 percent of females at 7.0–7.4 inches).

The strongest year classes were those of 1939 and 1952. The weakest were those of 1941 and 1945. Year-class strength was correlated significantly with production 4, 5, and 6 years later, but it was not correlated with the abundance of legal-sized fish in the year of hatching or with temperature, precipitation, water level, and turbidity.

The annual fluctuation of growth (length) in the first and in later years of life were dissimilar. First-year growth was poorest in 1942 but tended strongly to improve in subsequent years. First-year growth was correlated negatively with turbidity in June but was not correlated with year-class strength or other factors investigated. Fluctuations of growth in later years of life were largely without trend. Growth in these years was not correlated with the abundance of legal-sized fish, temperature, precipitation, or turbidity, but varied inversely with the water level for May to October.

FLUCTUATIONS IN THE POPULATION OF YELLOW PERCH, *PERCA FLAVESCENS* (MITCHILL), IN SAGINAW BAY, LAKE HURON

By Salah El-Din El-Zarka, University of Michigan[1]

The yellow perch, *Perca flavescens* (Mitchill), is one of the most important and widely distributed food fishes of the northeastern United States and southeastern Canada. It inhabits the Great Lakes, inland lakes, and large streams but is never plentiful in Lake Superior. Because of this wide distribution and its frequent great abundance, the yellow perch has become important to both commercial fishermen and anglers in many localities. The commercial fishery statistics for 1954 from the United States and Canada indicate that the yellow perch fishery contributed 16,230,000 pounds or 13 percent of the total production of the lake fisheries. It was surpassed only by the lake herring which formed 18 percent of the total catch. In United States waters of the Great Lakes, the yellow perch together with the chubs and lake herring formed the largest percentage of the catch (lake herring 25.6 percent, chubs 13.5 percent, and yellow perch 10.0 percent). Statistics are not available on the sport fishery of the Great Lakes, but it is well known that in many localities the anglers annually remove more yellow perch than do the commercial fishermen. Despite the wide range of the species, the commercial production of yellow perch is mostly concentrated in Lake Erie (especially the western part of the lake), Green Bay in Lake Michigan, and Saginaw Bay in Lake Huron.

Few studies had been done on yellow perch in the Great Lakes. Jobes (1952) published a detailed account of the life history of yellow perch in Lake Erie and Hile and Jobes (1942) issued a small paper on the growth in Wisconsin waters of Green Bay and northern Lake Michigan. In Saginaw Bay, a most important center of yellow perch production in the State of Michigan, only one small paper has been published (Hile and Jobes 1941) reporting the age composition and the growth rate of fish collected in 1929 and 1930.

Since 1943 the annual visits to Saginaw Bay by the United States Fish and Wildlife Service employees indicated that the yellow perch population was undergoing a definite change in its size structure. The fish were much smaller than in previous years and the percentage of legal-sized fish (8½ inches) likewise was low. Thus, because of the apparent threat to this valuable fishery and hence to the economy of Saginaw Bay commercial fishermen, it was decided to collect materials that would permit the determination of possible changes in the perch stocks since earlier observations and would also throw light on various aspects of the biology not previously explored. The collections of materials which were started by the Fish and Wildlife Service staff in 1943 formed the basis of the present study. From these data it has been possible to describe the general status of the population and follow the changes in age composition, growth, and other biological characters.

This study of yellow perch in Saginaw Bay was made possible by a cooperative arrangement between the Department of Fisheries, School of Natural Resources, University of Michigan, and Great Lakes Fishery Investigations, Fish and Wildlife Service, United States Department of the Interior. I am grateful to Dr. Karl F. Lagler, Chairman of the Department of Fisheries, for recommending me to the Fish and Wildlife Service and to Dr. James W. Moffett, Chief of Great Lakes Fishery Investigations, for accepting me temporarily in his research group. As a de facto member of the Great Lakes staff I was permitted the use of past collections of fish, given

[1] Present address Alexandria Institute of Hydrobiology and Fisheries, Kayet Bay, Alexandria, Egypt.

Note.—Approved for publication October 23, 1957. Fishery Bulletin 151.

assistance in the collection of additional materials, and granted access to all facilities necessary to the proper conduct of my research.

John E. Bardach, Chairman of my doctoral committee, planned and supervised my schedule of graduate training; Dr. Ralph Hile directed my research and the preparation of this dissertation; other members of my committee gave most useful advice and assistance.

Various staff members of the Fish and Wildlife Service were helpful in the field and laboratory. Leonard S. Joeris in particular assisted greatly when I was making a start on the preparation and examination of scales. Howard J. Buettner transferred various kinds of data to punch cards and prepared tabulations of length frequencies and length-weight records. All collections before the spring of 1955 were made by Service employees.

Cecil C. Craig, Director, Statistical Research Laboratory, University of Michigan, advised in problems of multiple correlation and regression analysis. Glenn W. Graves of the laboratory staff programmed the materials for IBM processing.

Reeve M. Bailey, Curator, Fish Division, Museum of Zoology, University of Michigan, supplied small Saginaw Bay perch from the Museum collections for the study of the body-scale relation.

Field work was greatly furthered by the cooperation of: A. J. Neering, Michigan Department of Conservation; Henry Engelhard, Bay Port Fish Co.; and John Gillingham, R. L. Gillingham Fishing Co.

MATERIALS AND METHODS

Collection of Samples

The study of the Saginaw Bay yellow perch population has been based on the determination of age and the calculation of the growth histories of 4,285 fish, 3,407 of them collected during the spawning seasons of 1943–55 (no fish were collected in 1945 and 1952). The term spawning-run sample has a degree of elasticity in its application to the 1955 collections; some tabulations included the samples of April 18, May 18, and June 7, whereas others included only the sample of May 18, the one taken nearest the height of the spawning season. The samples through 1954 were gathered by the U. S. Fish and Wildlife Service as part of a continuing study of the Saginaw Bay fisheries. In addition to the spawning-run samples, the 1955 collections included data from months outside the spawning period (table 1). All fish were caught by commercial trap nets in the Bay Port area. The actual location of the trap nets ranged from Fish Point to Charity Island (fig. 1), but most lifts were nearer Bay Port. Because no evidence of subpopulations was found, the samples all are considered to have been drawn from the same general stock.

TABLE 1.—*Collections of scales from Saginaw Bay yellow perch*

Date of collection	Number of fish	Date of collection	Number of fish
May 4, 1943	333	May 12, 1954	427
May 3, 1945	99	Apr. 18, 1955	230
June 3, 1946	155	May 18, 1955	184
May 28, 1947	199	June 7, 1955	328
May 15, 1948	200	June 22, 1955	509
May 10, 1949	263	Oct. 19, 1955	369
May 18, 1950	320		
May 1, 1951	371	Total	4,285
May 5, 1953	298		

Records for Individual Fish

The total length of fish (from tip of the head to tip of the tail, with lobes compressed to give the maximum measurement) was determined by a measuring board to the nearest 0.1 inch.

Weights were recorded either to the nearest gram or to the nearest 0.1 ounce depending on the kind of balance. Two types of balances were used: A dietary platform balance calibrated by 2-gram intervals (weight was estimated to the nearest gram); a spring balance calibrated by 0.2-ounce intervals (weight recorded to the nearest 0.1 ounce).

The sex and state of gonads were recorded for all fish except the collections of 1950 and June 7, 1955, for which information is available only on sex.

All samples of the 1943–55 period for which length and weight were recorded (4,285 fish) were used in the study of the length-weight relation.

Determination of Age

Preparation and examination of scales

Scales for age and growth studies were collected from all fish (except the 1954 collection) from below the lateral line on the left side. For the 1954 sample, scales were taken from above the lateral line. Because of this inconsistency as

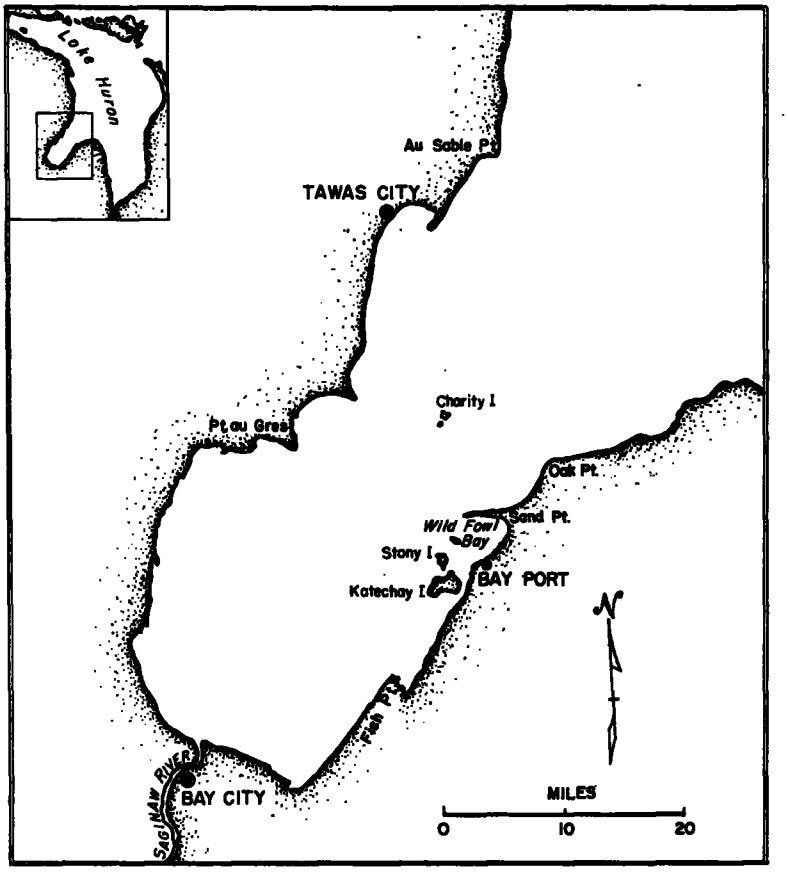

FIGURE 1.—Saginaw Bay.

to the point of scale collection, two body-scale curves were required for the calculation of growth.

The two body-scale curves were based on "key" scales taken from above and from below the lateral line of: Fish collected from trap nets on June 22, 1955 (386 fish); 80 selected (large and small) fish captured in November 1955; and 84 young-of-the-year and yearlings (caught on various dates) from the collections of the Fish Division, Museum of Zoology, University of Michigan.[2] Each key scale from below the lateral line was taken from the third row below the line on the left side of the fish and directly beneath the sixth spine of the dorsal fin. The key scale from above the lateral line also was removed from the left side and came from the second row above the line and below the insertion of the first dorsal spine. The locations of the key scales were chosen to be near the centers of the areas from which routine samples were taken.

[2] The total length of these museum specimens was increased by 2 percent for shrinkage.

Some scales (about 1,400) were mounted on glass microscope slides in a glycerin-gelatine medium described by Van Oosten (1929). The remaining scales were impressed on cellulose acetate, 0.020 or 0.040 inch thick, by a roller press similar to that described by Smith (1954). Butler and Smith (1953), demonstrated that method of preparation does not affect the measurements of scales. The examinations and the measurements of scales were made by means of a microprojector similar to the apparatus described by Van Oosten, Deason, and Jobes (1934) at the magnification × 43. The length of each scale and the distance from the focus to each annulus were measured along the interradial space most nearly collinear with the focus and recorded to the nearest millimeter.

Age analysis

Ages were determined by counting the annuli and are given in terms of completed years of life. They are expressed by Roman numerals corresponding to the number of annuli. Thus

fish with one annulus belong to age group I, those with two annuli to age group II, * * *. (Young-of-the-year are assigned to age group 0.) Hile (1948) recommended for convenience and for the consistency in the relation of year of origin, year of capture, and age, that each fish be considered to pass into the next higher age group on January 1. Under this convention a "virtual" annulus is credited at the edge of the scale from January 1 until the new annulus is actually formed in spring or early summer. Year classes, identified by the year of hatching, thus can be determined by subtracting the age from the year of capture; for example, a fish of age group IV captured in 1955 belongs to the 1951 year class.

COMMERCIAL FISHERY FOR YELLOW PERCH

General Trends of the Fishery, 1891–1955

Statistics of the production of yellow perch in Saginaw Bay were available for the years 1891–1908 and 1916–55 (table 2 and fig. 2). Although production always has varied widely, almost erratically, two intervals (1891–1916 and 1917–55) can be established within which these variations showed no definite trend. The first period (1891–1916) was one of high production. The annual catch varied from 3,379,200 pounds in 1901 to 1,085,788 pounds in 1908. The average yield for the whole period (19 years) was 1,961,309 pounds. On the other hand, in the second period (1917–55), the commercial catch was far below that of the early years. The annual production was above a million pounds in only two years (1919 and 1936) and the average catch for the whole period (499,938 pounds) was 74 percent below that of the early interval. This percentage did not differ much from 72 percent recorded by Hile and Jobes (1941) for the 1917–38 period. Since 1938 (1939–55) the commercial catch has been below 500,000 pounds except in 1943, 1944, and 1945. The highest yield was in 1943 (883,087 pounds) and the lowest was reached in 1947 (250,570 pounds).

Hile and Jobes (1941) believed the low production of 1917–38 was due to a less dense yellow perch population in Saginaw Bay that had resulted from overfishing. Data for recent years (the relatively small catches of 1939–55) suggest that the yellow perch recently might have become even scarcer and hence need protection even more than in 1938 and earlier. However, the records of fishing pressure and availability or abundance (table 3) show that after 1938 (1939–55), fluctuations in the abundance of yellow perch (fig. 3) were irregular but with a definite upward trend.[3] On the other hand, fishing intensity was declining though with some irregularities. The decrease of intensity was great enough that the

TABLE 2.—*Annual commercial production of Saginaw Bay yellow perch in 1891–1908 and 1916–55*

Year	Production (pounds)	Year	Production (pounds)	Year	Production (pounds)
1891	1,102,650	1920	803,725	1942	459,527
1892	1,801,600	1921	659,254	1943	883,087
1893	1,691,600	1922	461,111	1944	536,318
1894	2,013,500	1923	572,817	1945	353,102
1895	1,754,300	1924	444,064	1946	281,022
1896	1,577,300	1925	414,137	1947	250,570
1897	1,539,000	1926	314,848	1948	640,044
1898	2,197,650	1927	112,711	1949	447,456
1899	2,804,200	1928	192,008	1950	322,412
1900	3,452,800	1929	441,373	1951	306,650
1901	3,379,200	1930	611,679	1952	422,404
1902	2,394,500	1931	655,542	1953	394,454
1903	2,069,200	1932	587,532	1954	432,628
1904	1,529,200	1933	330,877	1955	488,209
1905	1,571,700	1934	398,555		
1906	1,747,900	1935	836,784		
1907	1,935,000	1936	1,073,861		
1908	1,085,877	1937	351,382	Average, 1891–1916	1,961,309
1916	1,637,691	1938	326,824		
1917	642,840	1939	440,512	Average, 1917–55	499,938
1918	769,287	1940	441,201		
1919	1,018,292	1941	331,486		

TABLE 3.—*Abundance, production, and fishing intensity for Saginaw Bay yellow perch fishery in 1929–55*

[Expressed as percentages of the 1929–43 average]

Year	Abundance	Production	Fishing intensity
1929	105	81	79
1930	105	112	109
1931	94	120	131
1932	115	108	96
1933	68	61	92
1934	86	73	87
1935	123	154	128
1936	130	197	155
1937	65	65	101
1938	72	60	85
1939	91	81	91
1940	92	81	90
1941	86	61	72
1942	115	84	75
1943	153	162	109
1944	115	98	88
1945	79	65	84
1946	75	52	7[illegible]
1947	86	46	5[illegible]
1948	186	118	65
1949	152	82	55
1950	109	59	56
1951	102	56	57
1952	126	78	63
1953	121	72	61
1954	143	79	57
1955	173	90	53

[3] Indices of abundance given in table 3 were derived from data on the catch per unit of effort (table 4) by the method described by Hile (1937); the method of computing the intensity index was described by Hile and Jobes (1941).

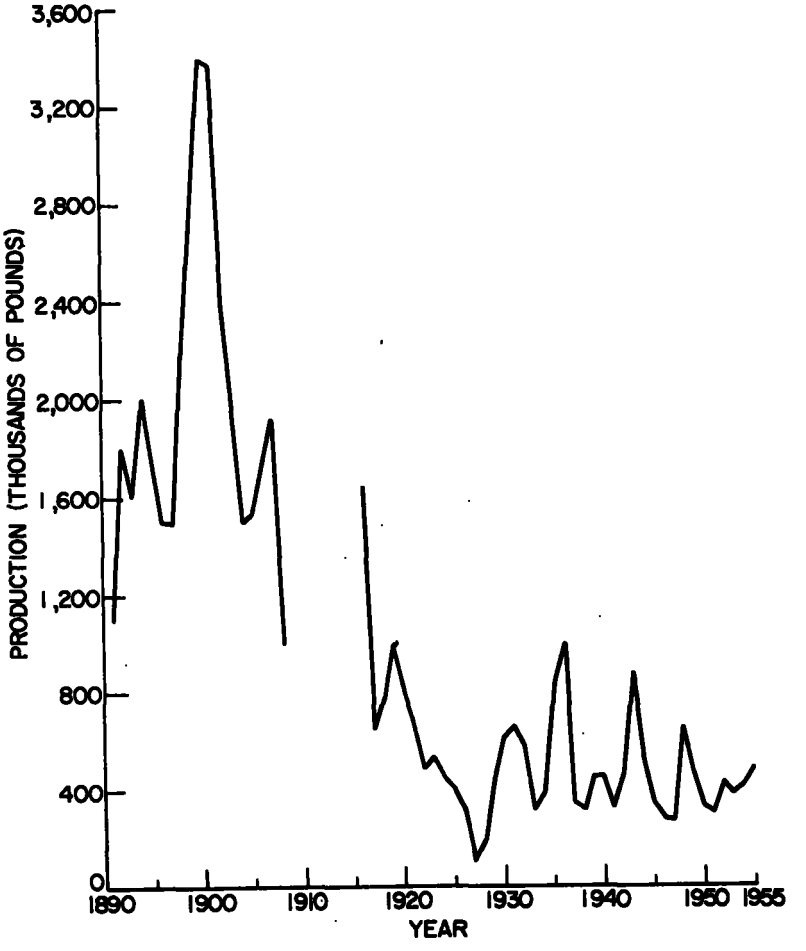

FIGURE 2.—Annual commercial production of yellow perch in Saginaw Bay, 1891–1955.

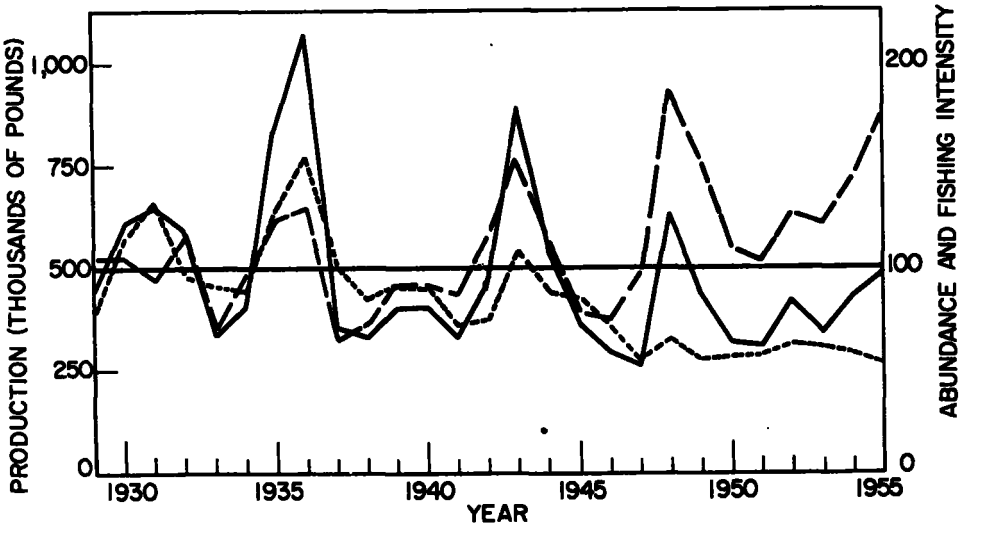

FIGURE 3.—Annual fluctuations in the production (solid lines), abundance (long dashes), and fishing intensity (short dashes), of Saginaw Bay yellow-perch fishery. Production in pounds; abundance and intensity, expressed as percentages of 1929–43 average.

489035 O—59——2

TABLE 4.—*The catch of yellow perch per unit of fishing effort of 5 gears in Saginaw Bay over the period 1929–55*

[The units of effort are: Small-mesh gill nets, lift of 1,000 linear foot; pound, shallow trap, and fyke nets, lift of 1 net; seines, 1 haul of a 100-rod seine]

Year	Catch (pounds) per unit of effort in gear				
	Small-mesh gill net [1]	Pound net [1]	Shallow trap net	Fyke net	Seine
1929	46	6	18	6	30
1930	15	7	18	10	22
1931	10	7	16	10	22
1932	16	7	19	12	20
1933	9	3	12	7	15
1934	8	4	15	6	27
1935	12	4	24	12	52
1936	16	5	26	7	42
1937	5	3	11	9	44
1938	4	4	12	7	34
1939	5	5	15	8	44
1940	11	8	15	10	25
1941	6	10	13	12	38
1942	20	15	17	18	35
1943	26	100	23	20	57
1944	13	8	18	17	39
1945	6	18	12	11	26
1946	----------	13	12	8	15
1947	----------	19	14	11	18
1948	11	32	31	19	48
1949	11	33	24	20	21
1950	6	26	18	15	36
1951	9	----------	17	11	16
1952	9	43	21	12	13
1953	20	15	19	14	27
1954	23	18	23	18	28
1955	22	----------	28	24	68

[1] Based on limited data in some years; no usable data in a few years.

upward trend of abundance was more than counterbalanced, so that the annual production continued to be low. The relatively high catches of 1943 and 1948 were mainly due to high abundance and a slight increase in fishing intensity in these two years.

Catch by Gear

The trap net is the principal gear for catching yellow perch in Saginaw Bay (75.9 percent of the yellow-perch catch by trap nets; table 5). Second to this gear, the fyke net contributed 10.5 percent to the commercial yield. All other gears (small-mesh gill nets, pound nets, seines, * * *) contributed a minor percentage of the catch.

Seasonal Distribution of the Catch

The seasonal production of Saginaw Bay yellow perch (table 6; fig. 4) is concentrated in the fall; 75 percent of the catch is made in September, October, and November. The peak was reached in October (207,425 pounds; 42.9 percent of average annual total). Then followed November (91,867 pounds, 19.0 percent) and September (63,214 pounds, 13.1 percent). The catch in the

TABLE 6.—*Average monthly commercial production (pounds) of Saginaw Bay yellow perch in 1929–55*

Month	Production	Percentage
January	15,382	3.2
February	7,003	1.5
March	16,113	3.3
April	26,820	5.6
May	3,603	.7
June	13,641	2.8
July	10,133	2.1
August	13,030	2.7
September	63,214	13.1
October	207,425	42.9
November	91,867	19.0
December	14,935	3.1

TABLE 5.—*Commercial production of yellow perch in Saginaw Bay, 1929–55, according to gear*

Year	Production (pounds) by gear						Total
	Small-mesh gill net	Pound net	Shallow trap net	Fyke net	Seine	All others [1]	
1929	25,689	54,985	269,132	46,524	27,241	17,802	441,373
1930	74,171	51,262	383,059	63,104	37,332	2,751	611,679
1931	74,277	47,358	431,454	68,492	29,784	4,177	655,542
1932	28,351	22,754	439,539	64,695	16,269	15,924	587,532
1933	10,855	16,651	264,937	28,466	8,625	1,343	330,877
1934	7,096	17,665	335,623	16,499	10,965	10,707	398,555
1935	122,473	17,266	627,040	35,990	22,305	11,710	836,784
1936	256,970	15,766	743,668	25,704	24,307	7,446	1,073,861
1937	23,696	4,929	254,792	41,231	25,414	1,320	351,382
1938	4,787	4,963	266,076	33,490	16,574	934	326,824
1939	6,173	8,932	362,429	42,242	20,551	185	440,512
1940	24,183	11,070	361,969	34,578	9,226	175	441,201
1941	4,026	11,893	259,511	35,743	20,262	51	331,486
1942	20,019	4,913	348,857	72,400	13,338	----------	459,527
1943	197,647	8,096	541,270	108,329	23,840	3,905	883,087
1944	22,777	479	394,408	95,842	17,981	4,831	536,318
1945	14,200	253	273,507	45,901	13,857	5,384	353,102
1946	3,919	1,064	229,513	34,444	9,762	2,320	281,022
1947	1,539	3,343	208,950	32,903	3,218	617	250,570
1948	5,964	1,754	534,247	76,469	20,504	1,106	640,044
1949	1,634	3,236	371,006	66,918	4,628	34	447,456
1950	5,506	3,065	271,001	38,577	4,263	----------	322,412
1951	10,236	49	249,699	44,532	2,003	131	306,650
1952	5,906	5,462	348,222	60,920	933	961	422,404
1953	2,912	4,588	323,782	60,624	2,548	----------	394,454
1954	4,830	480	373,696	51,094	2,528	----------	432,628
1955	8,956	----------	433,523	41,447	4,187	96	488,209
Average	35,881	11,936	366,700	50,636	14,461	3,478	493,166
Percentage	7.4	2.5	75.9	10.5	3.0	0.7	----------

[1] Includes catches made by: Large-mesh gill nets, deep trap nets, spears, set-hooks, and handlines. Includes also a small poundage for which gear of capture is unknown.

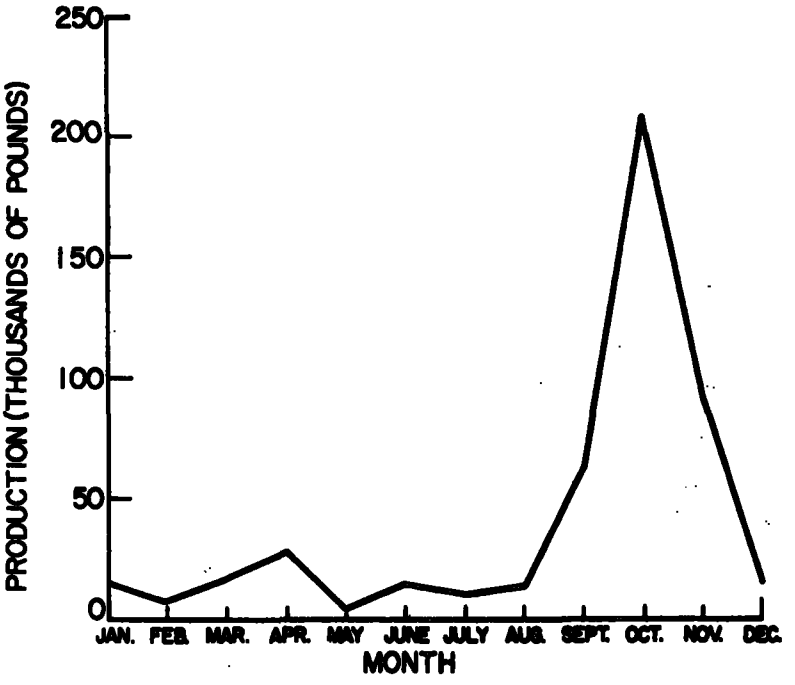

FIGURE 4.—Average monthly commercial production of yellow perch in Saginaw Bay, 1929–55.

9 other months constituted 25 percent of the perch production, varying from 0.7 percent in May to 5.6 percent in April. The take in late spring and early summer would have been greater had not closed seasons been in effect. The dates of these seasons in various years have been: 1927–33, April 15–June 15; 1933–37, April 15–May 15; 1937–47, April 15–June 1; 1947–56, April 15–May 10.

AGE COMPOSITION AND YEAR-CLASS STRENGTH

Annual and Seasonal Differences of Age Distribution

The age composition of yellow perch caught by commercial trap nets in Saginaw Bay in May or early June varied considerably from year to year (table 7; fig. 5). Because these samples came from the spawning run, they probably were biased by segregation on the basis of maturity. Hile and Jobes (1942) held that during this period the younger, immature fish were usually not highly represented. Nevertheless, samples collected in the same season throughout the whole period of study (1943–55) will, despite their bias, bring out annual changes of age distribution. Effects of gear selectivity likewise were reduced by using only fish from trap nets.

The dominant age varied between age group III and age group V. Age group III dominated the catch in only 1 year (1951) and the V group was dominant in 4 years (1945, 1948, 1949, and 1954). Age group IV dominated in the remaining 6 years (1943, 1946, 1948, 1950, 1953, and 1955). In 2 years (1949 and 1954) the percentage representations of the two most plentiful age groups (IV and V) were nearly equal (1949, 40.3 and 38.4 percent; 1954, 43.6 and 44.7 percent). The representation of other age groups, i. e., age groups II and VI–IX, during this 11-year period was consistently less than 10 percent except for the 1945 when age group VI formed 16.2 percent of the sample. In the combined 1943–55 collections age group IV constituted 48.6 percent of the total, followed by age group V (29.9 percent) and age group III (15.9 percent). The remaining age groups (II and VI–IX) together contributed only 5.6 percent.

The year-to-year change in age composition of spawning-run samples is reflected in fluctuations of the average age. The oldest fish were caught in 1945 (average age 5.1 years) and the youngest in 1951 (3.8 years). The mean age was below 4 years in 1946 and 1947 also, but in the remaining years ranged between 4.0 (1950) and 4.6 (1948). The mean of the averages for the 11 spawning-run samples was 4.3 years.

Information on the seasonal fluctuation in age composition of yellow perch from Saginaw Bay

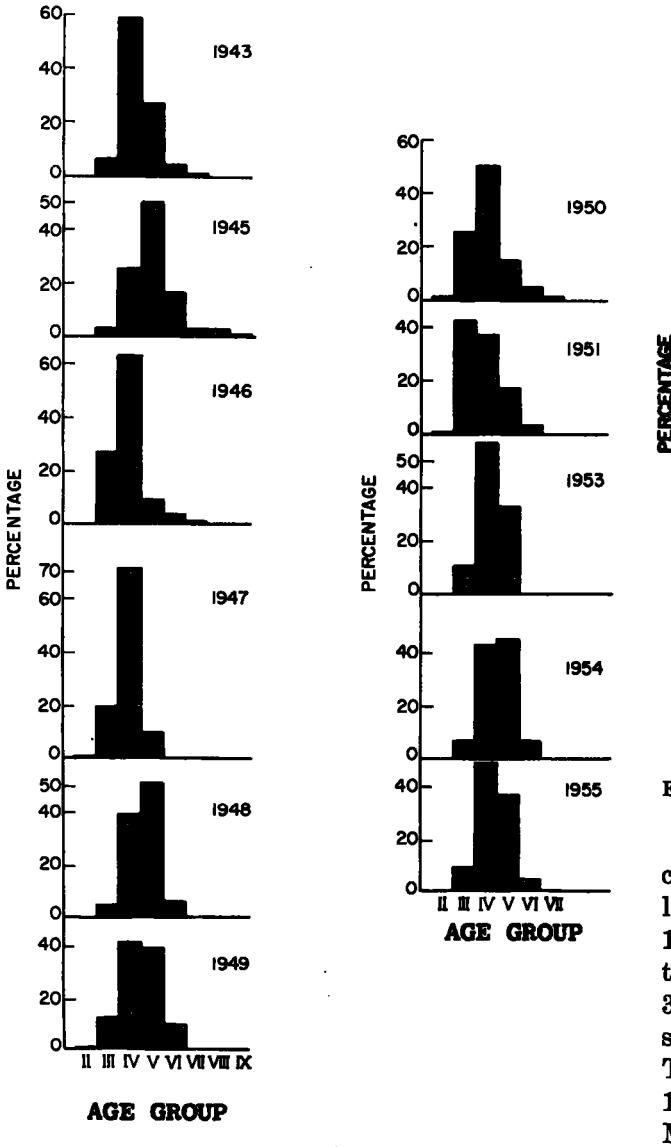

FIGURE 5.—Age composition of the spawning-run collections of Saginaw Bay yellow perch, 1943–55.

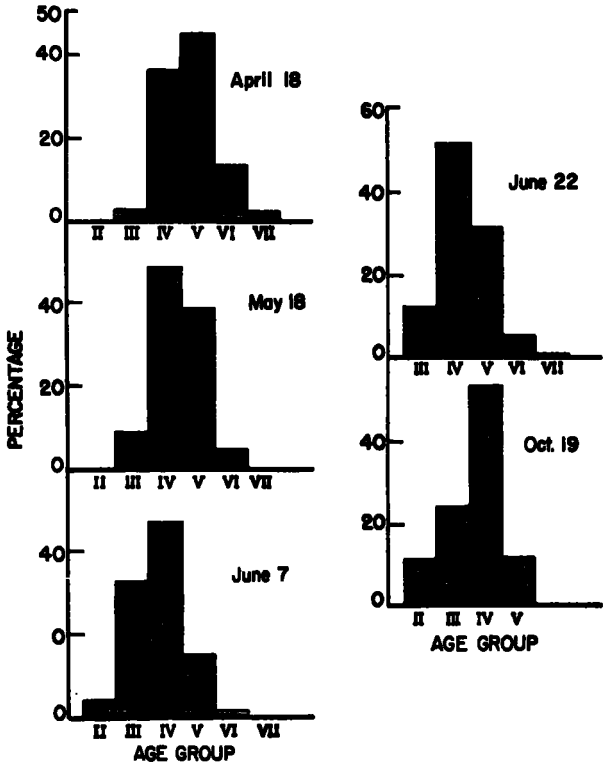

FIGURE 6.—Age composition of Saginaw Bay yellow perch on different dates in 1955.

is limited to 1955 when collections were made on April 18, May 18, June 7, June 22, and October 19 (table 8; fig. 6). The data indicate no clear-cut seasonal change of age composition and average age.[4] The average age decreased from 4.8 on April 18 to 4.4 on May 18 and to 3.8 on June 7, then increased to 4.3 on June 22. On October 19, the average age decreased again to 3.7. This change in average age was accompanied by a shift in the dominance of age groups. Age group V was strongest on April 18 (45.6 percent), whereas age group IV dominated the collections of May 18, June 7, June 22, and October 19 (48.4, 47.2, 51.9, and 53.1 percent, respectively). Age group III composed as much as 32.6 and 23.8 percent, of June 7 and October 19 samples, and as little as 2.6 percent (April 18). The representation of the VI group ranged from 13.5 percent (April 18) to 1.2 percent (June 7). Members of age groups II and VII were scarce or lacking in all samples except on October 19 when age group II constituted 11.1 percent of the sample.

In comparing Saginaw Bay perch with other yellow perch populations, consideration must be given only to those fish caught in similar seasons, since age composition varies within the year. A comparison of Saginaw Bay perch during the present period of study (April, May, and June collections) with those of 1929–30 (spring and early summer) discloses greater age in more recent years (table 9). In 1929–30 age groups III and IV were best represented; each made up about 39 percent of the total collection. During the 1943–55 period, age groups IV and V constituted 48.6 and 29.9 percent, respectively, of the

[4] Records in table 8 are for the sexes combined since males and females exhibited similar seasonal trends.

TABLE 7.—*Age distribution of yellow perch in May or early June collections*

[Percentages in parentheses. Asterisks indicate dominant age groups]

Date of capture	Number of fish	Number and percentage in age group								Average age [1]
		II	III	IV	V	VI	VII	VIII	IX	
May 4, 1943	333	----	21 (6.3)	*199 (59.8)	93 (27.9)	15 (4.5)	5 (1.5)	----	----	4.4
May 3, 1945	99	----	3 (3.0)	23 (25.6)	*50 (50.5)	16 (16.2)	3 (3.0)	3 (3.0)	1 (1.0)	5.1
June 3, 1946	155	----	38 (24.5)	*97 (62.6)	13 (8.4)	6 (3.9)	1 (0.6)	----	----	3.9
May 28, 1947	199	1 (0.5)	39 (19.6)	*140 (70.4)	19 (9.5)	----	----	----	----	3.9
May 15, 1948	200	----	9 (4.5)	77 (38.5)	*102 (51.0)	12 (6.0)	----	----	----	4.6
May 10, 1949	263	1 (0.4)	29 (11.0)	*106 (40.3)	*101 (38.4)	26 (9.9)	----	----	----	4.5
May 18, 1950	320	3 (0.9)	83 (25.9)	*165 (51.6)	50 (15.6)	16 (5.0)	3 (0.9)	----	----	4.0
May 1, 1951	371	1 (0.3	*157 (42.3)	139 (37.5)	63 (16.9)	11 (2.9)	----	----	----	3.8
May 5, 1953	298	----	31 (10.4)	*168 (56.4)	99 (33.2)	----	----	----	----	4.2
May 12, 1954	427	----	26 (6.1)	*182 (42.6)	*191 (44.7)	28 (6.6)	----	----	----	4.5
May 18, 1955	184	----	16 (8.7)	*89 (48.4)	71 (38.6)	8 (4.3)	----	----	----	4.4
Total	2,849	6 (0.2)	452 (15.9)	*1,385 (48.6)	852 (29.9)	138 (4.8)	12 (0.4)	3 (0.1)	1 [2] (0.1)	[3] 4.3

[1] Average number of annuli.
[2] Actually, less than 0.05.
[3] The unweighted mean and the weighted mean of the averages for the individual samples are the same.

TABLE 8.—*Age distribution of yellow perch on different dates in 1955*

[Percentage in parentheses. Asterisks indicate dominant age groups]

Date of capture	Number of fish	Number and percentage in age groups						Average age [1]
		II	III	IV	V	VI	VII	
Apr. 18	230	----	6 (2.6)	83 (36.1)	*105 (45.6)	31 (13.5)	5 (2.2)	4.8
May 18	184	----	16 (8.7)	*89 (48.4)	71 (38.6)	8 (4.3)	----	4.4
June 7	328	13 (4.0)	107 (32.6)	*155 (47.2)	49 (14.9)	4 (1.2)	----	3.8
June 22	509	----	61 (12.0)	*264 (51.9)	158 (31.0)	25 (4.9)	1 (.2)	4.3
Oct. 19	369	41 (11.1)	88 (23.8)	*196 (53.1)	44 (11.9)	----	----	3.7

[1] Average number of annuli. Unweighted mean of averages for individual samples is 4.2.

TABLE 9.—*Age distribution of yellow perch in Lake Michigan, Lake Erie, and Saginaw Bay*

[Sources of data: Lake Erie, Jobes (1952); southern Green Bay and northern Lake Michigan, Hile and Jobes (1942); Saginaw Bay 1929–30 samples, Hile and Jobes (1941); Saginaw Bay 1943–55 samples, present study. Percentage in parentheses]

Locality and season	Number and percentage in age groups									Total and average age [1]
	I	II	III	IV	V	VI	VII	VIII	IX	
Saginaw Bay (1929–30) spring and early summer	----	25 (3.0)	317 (38.7)	318 (38.8)	138 (16.8)	17 (2.1)	5 (0.6)	----	----	820 (3.8)
Saginaw Bay (1943–55):										
April, May, and June	----	6 (0.2)	452 (15.9)	1,385 (48.6)	852 (29.9)	138 (4.8)	12 (0.4)	3 (0.1)	1 (0.03)	2,849 (4.2)
October	----	---- (11.1)	41 (23.8)	88 (53.1)	196 (11.9)	44	----	----	----	369 (3.7)
Lake Erie: [2]										
April	----	2 (1.5)	98 (73.7)	33 (24.8)	----	----	----	----	----	133 (3.2)
Late summer and fall	392 (13.5)	1,634 (56.3)	797 (27.4)	75 (2.6)	5 (0.2)	----	----	----	----	2,903 (2.2)
Southern Green Bay: [3]										
Spring	----	28 (9.1)	44 (14.3)	144 (46.8)	63 (20.4)	20 (6.5)	4 (1.3)	4 (1.3)	1 (0.3)	308 (4.1)
Fall	2 (0.9)	92 (42.2)	99 (45.4)	21 (9.6)	4 (1.8)	----	----	----	----	218 (2.7)
Northern Lake Michigan [4] fall	----	25 (9.1)	98 (35.5)	118 (42.7)	27 (9.8)	8 (2.9)	----	----	----	276 (3.6)

[1] Average number of annuli.
[2] Fish caught in commercial and experimental trap nets.
[3] Fish caught in fyke nets, pound nets, and 2¾-inch-mesh gill nets.
[4] Fish caught in 2½-inch-mesh gill nets.

catch. This shift in age composition between the two periods of study in Saginaw Bay is marked by a similar change in the average age. The average age was raised from 3.8 in 1929–30 to 4.3 in 1943–55.

The Saginaw Bay yellow perch averaged older than fish of other Great Lakes stocks for which records of age have been published. The average age of Lake Erie perch was 3.2 years in April. In southern Green Bay the average age of 4.1 years in the spring was nearly equal to the average of 4.3 for Saginaw Bay in 1943–55.

The fall collection from Green Bay (average age 2.7 years), northern Lake Michigan (3.6 years), and Lake Erie (2.2 years) were likewise younger than those caught from Saginaw Bay in October 1955 (3.7 years). It should be mentioned that in all three localities from which both spring and fall collections were obtained the spring fish were considerably the older.

The effects of gear selection on the estimation of average age cannot be judged precisely. Catches of impounding nets (pound, trap, and fyke nets) are probably comparable. The fall samples from northern Lake Michigan, taken in 2⅝-inch-mesh gill nets, almost certainly were biased by selection toward the older age groups.

Relative Strength of Year Classes

Near the turn of the century, shortly after the discovery and validation of the scale method of determining the age of fish, investigators became aware of wide variations from year to year in the success of reproduction. As studies were continued on individual stocks and expanded to include new ones, it became increasingly apparent that the fluctuations in the strength of the year classes are major factors in the determination of the yield of the fisheries. It follows then that an understanding of the extent and the factors in these fluctuations can contribute fundamentally to the development of a scientific system of exploitation and management of fishery resources.

Despite the overriding importance of the subject and the considerable attention it has received, the gaining of information on the magnitude of fluctuations and the development of understanding of their causes have been painfully slow. The sampling requirements are rigorous, the analytical procedures are difficult, and the factors that must be considered are numerous and complex. Seemingly we must approach understanding through a process of slow accretion in which each new bit of evidence, though not conclusive in itself, must be welcomed.

Fishery investigators in the Great Lakes mostly have lacked the facilities for continuing studies that are so essential for inquiries into the degree and causes of fluctuations. Instead they have had to content themselves with calling attention to the occurrence of year classes of exceptional strength or weakness. Observations of this type have been made in Lake Erie for: yellow perch (Jobes 1933, 1952); walleyes, blue pike, and saugers (Deason 1933); sheepshead (Van Oosten 1938); white bass (Van Oosten 1942); whitefish (Van Oosten and Hile 1949); cisco (Scott 1951); all of the species just listed (Van Oosten 1948). In other Great Lakes waters, information on year-class strength was recorded for: South Saginaw Bay lake herring (Van Oosten 1929); Saginaw Bay yellow perch (Hile and Jobes, 1941); Saginaw Bay (Lake Huron) lake trout (Fry 1953); Green Bay walleyes, whitefish, and lake herring (Hile 1950); Green Bay lake herring (Smith 1956). In a 1954 paper, Hile attempted the ranking of 12 consecutive year classes of the Saginaw Bay walleye and commented on the strength or weakness of others.

Despite severe limitations and defects in the data (small numbers of fish in some samples; lack of collections in 1944 and 1952) it was believed that data on the age composition of yellow perch in the present study have warranted an attempt at a more precise estimate of the relative strength of year classes than has been attempted previously for Great Lakes stocks. It had been hoped originally that these estimates might be made through the application of sample data to the statistical records on catch per unit of effort in trap nets in the various years of capture, but the scarcity (even lack) of legal-sized fish in the samples forced abandonment of the idea. It was then decided to use an adaptation of the procedure employed by Hile (1941) for the estimation of annual fluctuations in growth rate. It is based on a series of comparisons in which the abundance of each year class is estimated in terms of the strength of the preceding one. From these comparisons a sequence of positions is established for each year class in the series. The procedure can be illustrated by the comparison of year classes 1943 and 1944 (table 10). The 1943 year

class appeared in the collections at various ages contributing to the samples in different calendar years as follows: 1946, III group, 24.5 percent; 1947, IV group, 70.4 percent; 1948, V group, 51.0 percent; 1949, VI group, 9.9 percent; 1950, VII group, 0.9 percent. The sum of the percentages is 156.7. The 1944 year class appeared as follows: 1947, III group, 19.6 percent; 1948, IV group, 38.5 percent; 1949, V group, 38.5 percent; 1950, VI group, 5.0 percent; 1951, VII group, 0.0 percent; sum of percentages, 101.5.

The 2 sums of percentages contributed to annual samples by the 2 year classes under comparable sampling conditions are taken as representative of their relative strengths (table 11). The change of year-class strength from 1943 to 1944 is computed as

$$\frac{2\,(101.5 - 156.7)}{101.5 + 156.7} \times 100 = -42.8$$

(The use of the mean of the two percentage totals rather than the total for the earlier year as a base for the estimation of the change is essential if systematic bias is to be avoided. See Hile 1941, p. 253, footnote 23.)

TABLE 10.—*Age composition and year classes of Saginaw Bay yellow perch in 1943–55*

Date of capture	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	Average age and total
May 4, 1943:																		
Age group	VII	VI	V	IV	III													4.4
Number of fish	5	15	93	199	21													333
Percentage	(1.5)	(4.5)	(27.9)	(59.8)	(6.3)													
May 3, 1945:																		
Age group	IX	VIII	VII	VI	V	IV	III											5.1
Number of fish	1	3	3	16	50	23	3											99
Percentage	(1.0)	(3.0)	(3.0)	(16.2)	(50.5)	(25.6)	(3.0)											
June 3, 1946:																		
Age group				VII	VI	V	IV	III										3.9
Number of fish				1	6	13	97	38										155
Percentage				(0.6)	(3.9)	(8.4)	(62.6)	(24.5)										
May 28, 1947:																		
Age group							V	IV	III	II								3.9
Number of fish							19	140	39	1								199
Percentage							(9.5)	(70.4)	(19.6)	(0.5)								
May 15, 1948:																		
Age group							VI	V	IV	III								4.6
Number of fish							12	102	77	9								200
Percentage							(6.0)	(51.0)	(38.5)	(4.5)								
May 10, 1949:																		
Age group								VI	V	IV	III	II						4.5
Number of fish								26	101	106	29	1						263
Percentage								(9.9)	(38.4)	(40.3)	(11.0)	(0.4)						
May 18, 1950:																		
Age group								VII	VI	V	IV	III	II					4.0
Number of fish								3	16	50	165	83	3					320
Percentage								(0.9)	(5.0)	(15.6)	(51.6)	(25.9)	(0.9)					
May 1, 1951:																		
Age group										VI	V	IV	III	II				3.8
Number of fish										11	63	139	157	1				371
Percentage										(2.9)	(16.9)	(37.5)	(42.3)	(0.3)				
May 5, 1953:																		
Age group													V	IV	III			4.2
Number of fish													99	168	31			298
Percentage													(33.2)	(56.4)	(10.4)			
May 12, 1954:																		
Age group													VI	V	IV	III		4.5
Number of fish													28	191	182	26		427
Percentage													(6.6)	(44.7)	(42.6)	(6.1)		
May 18, 1955:																		
Age group														VI	V	IV	III	4.4
Number of fish														8	71	89	16	184
Percentage														(4.3)	(38.6)	(48.4)	(8.7)	

TABLE 11.—*Data employed in the determination of year-class fluctuation of Saginaw Bay yellow perch*

Year classes compared	Age groups included	Sum for 1st year	Sum for 2d year	Mean	Difference	Percentage difference between years
1939–40	VI, VII	16.8	3.9	10.4	−12.9	−124.0
1940–41	V, VI	54.4	8.4	31.4	−46.0	−146.5
1941–42	IV, V, VI	34.0	78.1	56.1	44.1	78.4
1942–43	III, IV, V, VI, VII	81.1	156.7	118.9	75.6	63.6
1943–44	III, IV, V, VI, VII	156.7	101.5	129.1	−55.2	−42.8
1944–45	II, III, IV, V, VI	101.5	63.8	82.6	−37.7	−45.6
1945–46	II, III, IV, V	60.9	79.5	70.2	18.6	26.5
1946–47	II, III, IV	62.6	63.8	63.2	1.2	1.9
1947–48	II, III, VI	26.3	49.8	38.0	23.5	61.8
1948–49	II, V, VI	40.7	49.3	45.0	8.6	19.1
1949–50	IV, V	101.1	81.2	91.2	−19.9	−21.8
1950–51	III, IV	53.0	54.5	53.8	1.5	2.8
1951–52	III	6.1	8.7	7.4	2.6	35.1

To obtain the relative positions of all year classes, the 1939 year class is given arbitrarily a value of 0.0 and the positions of succeeding year classes are determined by the successive addition of the "percentage" differences in the right hand column of table 11. The series so obtained is then adjusted to a mean of 0.0 to give the final ranking (table 12; fig. 7).

The year-class strength dropped from 147.4 in 1939 (highest recorded value) to −123.1 in 1941 (lowest value). The position or index value increased until it reached 18.9 in 1943 and dropped to −69.5 in 1945. From 1945 to 1952 the trend was strong toward improvement in year-class strength (only exception in 1950). The indices remained below average until 1947. From 1948 to 1952 the year-class strength was above average, reaching a value of 55.9 in 1952 (second highest value).

If the fluctuations of year-class strength are substantial, it is to be expected that their effects will be felt in later years in the abundance of fish and in the production of the commercial fishery. To test this point for Saginaw Bay yellow perch, coefficients of correlation r were computed between year-class strength and the abundance and production (see section on the commercial fishery) 4 to 6 years later (table 13; see also fig. 8). These intervals and combinations of intervals were chosen because few perch

TABLE 13.—*Correlation between estimated strength of year classes and later abundance and production of yellow perch in the commercial fishery*

Years after hatching	Coefficient of correlation		Degrees of freedom	Value of r at	
	Abundance	Production		p=0.05	p=0.01
4	0.380	0.630	11	0.553	0.684
5	.345	.658	10	.576	.708
6	−.044	.653	9	.602	.735
4 and 5	.438	.799	10	.576	.708
4, 5, and 6	.333	.904	9	.602	.735

TABLE 12.—*Index values of year-class strength of Saginaw Bay yellow perch, 1939–52*

[Adjusted to a 1939–52 mean of 0.0]

	Year class													
	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
Deviation from mean	147.4	23.4	−123.1	−44.7	18.9	−23.9	−69.5	−43.0	−41.1	20.7	39.8	18.0	20.8	55.9

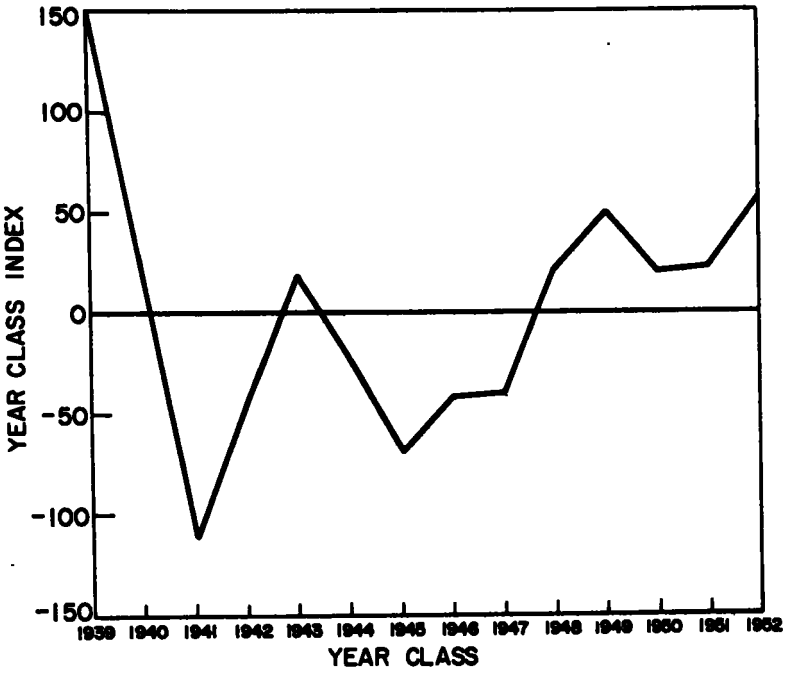

FIGURE 7.—Fluctuation in the relative strength of year classes 1939 to 1952 of Saginaw Bay yellow perch.

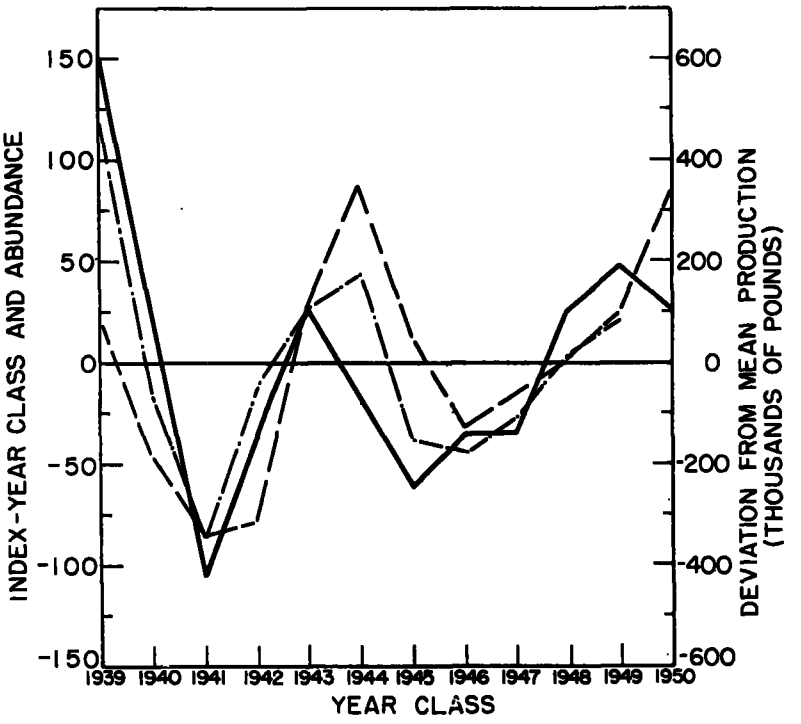

FIGURE 8.—Relation between year-class strength (solid line) and the abundance after 4 and 5 years (dashes) and production (dots and dashes) 4, 5, and 6 years later.

reach legal size in less than 4 years and fish older than the VI group are rare.

Except for the 6-year interval all coefficients of correlation between year-class strength and abundance as estimated from records of catch per unit effort were positive, but all of them were far below significant values. Correlations between year-class strength and later production, on the other hand, were all significant, three of them at the 5-percent and 2 at the 1-percent level.

Discussion of possible factors of fluctuation in year-class strength is given in a later section along with the treatment of factors of fluctuations in growth rate.

SIZE AT CAPTURE

Length Distribution of Samples

The length-frequency distribution of Saginaw Bay yellow perch during the 1943–55 period (table 14) was typically unimodal. The 1945 collection showed some tendency toward bimodality but this might be due to the accidental capture of some large fish and to the small number in the sample (only 97 fish). With the exception of 1943 and 1945, the modal lengths lay within the range of 6.0–6.9 inches total length. Most common was at 6.5–6.9 inches. In 2 years only (1947 and 1955), the modal lengths were at 6.0–6.4 inches. In 1943 and 1945, on the other hand, the modes were 7.5–7.9 and 8.0–8.4 inches. This annual variation in the length may be attributed largely to fluctuations in the age composition of the stock and to the change of growth from year to year (these fluctuations are discussed in earlier and later sections). Differences from year to year in the percentage of males and females also had a certain effect on this variation. Jobes (1952) included the selectivity of the different kinds of nets among the causes of annual variation of length. The effect of gear selectivity was minimized in the present study because all samples came from one kind of net (trap net).

The percentage of legal-sized yellow perch (total length 8½ inches or longer) of the combined samples was 11.0. This percentage varied considerably, however, from year to year. The highest value was recorded in 1945 (66 percent). In 1948 the sample included no legal-sized fish. Although it is not to be concluded that the legal-sized perch were unavailable in Saginaw Bay during that year, it is obvious that in the early season the fisherman must have had to do tedious sorting to find a marketable catch.

TABLE 14.—*Length-frequency distribution of Saginaw Bay yellow perch from the spawning-run samples according to year of capture*

[Modes designated by asterisks]

Total length interval (inches)	Mid-point	Year of capture											Total
		1943	1945	1946	1947	1948	1949	1950	1951	1953	1954	1955	
4.5–4.9	4.7											4	4
5.0–5.4	5.2			5	3		1	1	1	1	1	46	59
5.5–5.9	5.7	7	1	24	47	5	7	19	20	7	31	144	312
6.0–6.4	6.2	12	3	31	*64	49	33	54	60	32	66	*162	566
6.5–6.9	6.7	30	1	*42	37	*55	*81	*101	*103	*53	*94	135	*732
7.0–7.4	7.2	62	4	28	26	45	71	57	99	45	*94	69	600
7.5–7.9	7.7	*71	4	12	20	39	34	49	52	*60	83	42	466
8.0–8.4	8.2	58	*20	9	1	7	18	27	24	46	35	47	292
8.5–8.9	8.7	35	6	1	1		6	10	6	23	8	41	137
9.0–9.4	9.2	25	10	2			3	1	4	15	9	28	97
9.5–9.9	9.7	14	*11				3			5	3	16	52
10.0–10.4	10.2	10	8	1			3	1	1	7	1	7	39
10.5–10.9	10.7	8	12				2		1	2	1	1	27
11.0–11.4	11.2		3						1	1	1		6
11.5–11.9	11.7	1	2				1			1			5
12.0–12.4	12.2		2								1		3
12.5–12.9	12.7		2										2
13.0–13.4	13.2		5										5
13.5–13.9	13.7		2										2
14.0–14.4	14.2												
14.5–14.9	14.7		1										1
Number of fish		333	97	155	199	200	263	320	372	298	428	742	3,407
Average length		7.97	9.59	6.72	6.46	6.91	7.17	7.00	7.02	7.60	7.12	6.80	7.16
Percentage legal		27.9	66.0	2.6	.5	0	6.8	3.8	3.5	18.1	5.6	12.5	11.0

Many of the undersized fish are destroyed in the sorting and handling. Jobes (1952) indicated that 14 percent of illegal perch taken by trap nets in Lake Erie were dead when the nets were lifted. Van Oosten (1936) also concluded that trap nets destroyed more small fish than did other kinds of nets.

The length-frequency distribution not only varies from year to year but also in the different seasons of the year (table 15). A distinct trend

TABLE 15.—*Length-frequency distribution of Saginaw Bay yellow perch on different dates in 1955*

Total length (inches)	Apr. 18	May 18	June 7	June 22	Oct. 19
4.5–4.9			4		
5.0–5.4			46	2	4
5.5–5.9	9	8	127	74	21
6.0–6.4	34	45	83	220	37
6.5–6.9	45	48	42	118	43
7.0–7.4	25	34	10	53	63
7.5–7.9	8	29	5	27	72
8.0–8.4	27	16	4	9	55
8.5–8.9	36	4	1	3	34
9.0–9.4	24		4	1	19
9.5–9.9	14		2	1	14
10.0–10.4	7			1	3
10.5–10.9	1				3
11.0–11.4					1
Number of fish	230	184	328	509	369
Average length	7.7	7.0	6.1	6.5	7.6
Percentage legal	35.6	2.2	2.1	1.2	20.0

in the length-frequency distribution and average size of yellow perch caught in 1955 (sexes combined) can be seen. The average length dropped from 7.7 inches on April 18 to 6.1 inches on June 7. Then the length increased to 6.5 inches in early summer (June 22) and 7.6 inches in the fall (October 19). The October fish were still 0.1 inch shorter than those of the April 18 sample. Over the April 18–October 19 period the modal intervals ranged from 5.5–5.9 inches (June 7) to 7.5–7.9 inches (October 19).

The percentage of legal-sized yellow perch also varied seasonally. On April 18 this percentage was 35.6, but fishermen did not benefit from the relatively high value because fishing for perch is not allowed at that time (closed season, April 15–May 10). The proportion of legal-sized perch subsequently fell to barely 2 percent on May 18 and June 7 and less than 2 percent on June 22. In the fall (October 19) the percentage increased again to 20.0. This increase is due in some measure to the presence of a large number of females that typically attain larger size than males.

Length Distribution of Age Groups

In the compilation of data on the length-frequency distribution of the age groups (table 16), fish of the same age and sex in all the spawning-run samples were combined. Because of a certain amount of year-to-year variation in the length distribution, these combinations increased the range and dispersion for the individual age groups. The data serve, nevertheless, to show the general distribution and the range of length over which fish of a particular age can be expected to vary. In well-represented age groups, the range for the males varied from 4 inches in age group III to 5½ inches in age group V. The females had a slightly wider range of 4 inches

TABLE 16.—*Length-frequency distribution of spawning-run collections of Saginaw Bay yellow perch, 1943–55, according to age groups and sex*

[Modal intervals are designated by asterisks. M = male; F = female]

Total length (inches)	Age group														Grand total			Percentage		
	II		III		IV		V		VI		VII		VIII							
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	Both	M	F	Both
4.5– 4.9		2	1	1											1	3	4	0.03	0.09	0.12
5.0– 5.4	3	*11	23	11	10		1								37	22	59	1.1	.6	1.7
5.5– 5.9		2	*94	66	118	19	13								225	87	312	6.6	2.5	9.2
6.0– 6.4		1	91	61	251	94	56	11	1						399	167	566	11.7	4.9	16.6
6.5– 6.9			53	*67	*289	*128	161	22	12						*515	*217	732	15.1	6.4	21.5
7.0– 7.4			14	48	173	120	*205	22	17	1					409	191	600	12.0	5.6	17.6
7.5– 7.9			6	20	77	113	149	58	*40	1	2				274	192	466	8.0	5.6	13.7
8.0– 8.4			2	5	31	93	64	*60	32	2	*3				132	160	292	3.9	4.7	8.6
8.5– 8.9				1	10	42	31	34	16	2	1				58	79	137	1.7	2.3	4.0
9.0– 9.4					5	28	16	35	7	6					28	69	97	.8	2.0	2.8
9.5– 9.9					2	11	5	23	3	*7	1				11	41	52	.3	1.2	1.5
10.0–10.4						7	3	16	4	6	2	1			9	30	39	.3	.9	1.2
10.5–10.9						3	2	12	1	5	2	2			5	22	27	.15	.6	.8
11.0–11.4						1		4		1						6	6		.18	.2
11.5–11.9								3		2						5	5		.15	.2
12.0–12.4									1	2					1	2	3	.03	.06	.09
12.5–12.9										2						2	2		.06	.06
13.0–13.4										2		2		1		5	5		.15	.15
13.5–13.9												1		1		2	2		.06	.06
14.0–14.4																				
14.5–14.9														1		1	1		.03	.03
Total	3	16	284	280	966	659	706	300	134	39	11	6		3	2,104	1,303	3,407	61.8	38.2	
Average length	5.2	5.3	6.1	6.5	6.7	7.4	7.3	8.4	8.0	10.2	9.1	12.0		13.9	6.9	7.5	7.2			
Percentage legal	0	0	0	.03	1.8	14.0	8.1	42.3	23.9	89.7	54.5	100.0		100.0	5.3	20.3				
Percentage legal (both sexes)	0		0-02		7.9		25.2		56.8		72.8		100.0		11.0					

in age group III to 6 inches in age group VI. The widest ranges were mostly confined to age groups IV, V, and VI. The younger and older age groups (groups II, III, and VII) had the narrower range (in part, probably, because of the limited numbers of fish and for the young fish the inability of the nets to hold the smaller members of the age groups).

This range of length of age groups together with the distinctly slow growth led to an extensive overlap. Consequently the length of Saginaw Bay yellow perch at these ages is a poor index of age. A fish of a particular length might belong to 2 to 5 age groups (mostly 4 age groups).

The percentage of legal-sized yellow perch was nil or small at the lesser ages but increased with growth. In well-represented groups (age groups IV, V, and VI), the percentage (sexes combined) ranged from 7.9 to 56.8 percent. These three age groups are the main contributors to the commercial yellow perch fishery in Saginaw Bay. The percentage of legal-sized males was always less than that of the females. For males the value ranged from 1.8 percent for fish of age group IV to 54.5 percent in age group VII. The percentage of legal-sized females, on the other hand, rose from 14.0 percent in age group IV to 100 percent in age group VII.

Change in Length Between 1929–30 and 1943–55

The length-frequency distributions of spring collections of yellow perch from impounding nets in 1929–30 and 1943–55 (table 17; fig. 9) indicate an enormous shift in the length composition. In 1929–30 the modal length was at 8.5–8.9 inches, whereas in 1943–55 this mode was 6.5–6.9 inches, a loss of 2 inches in the modal length of the fish (2.3 inches in the mean length). In the

TABLE 17.—*Length-frequency distribution of the early-season collections of Saginaw Bay yellow perch, 1929–30 and 1943–55*

Total length (inches)	1929–30 [1]		1943–55	
	Number of fish	Percentage	Number of fish	Percentage
4.5–4.9			4	0.12
5.0–5.4			59	1.7
5.5–5.9	3	0.4	312	9.2
6.0–6.4	4	.5	566	16.6
6.5–6.9	9	1.1	732	21.5
7.0–7.4	10	1.2	600	17.6
7.5–7.9	47	5.8	466	13.7
8.0–8.4	90	11.2	292	8.6
8.5–8.9	139	17.3	137	4.0
9.0–9.4	109	13.6	97	2.8
9.5–9.9	105	13.1	52	1.5
10.0–10.4	111	13.8	39	1.2
10.5–10.9	101	12.6	27	.8
11.0–11.4	39	4.8	6	.2
11.5–11.9	20	2.5	5	.15
12.0–12.4	9	1.1	3	.09
12.5–12.9	7	.9	2	.06
13.0–13.4			5	.15
13.5–13.9			2	.06
14.0–14.4				
14.5–14.9			1	.03
Total or average	803	9.4	3,407	7.2

[1] Data adapted from table 7, Hile and Jobes (1941).

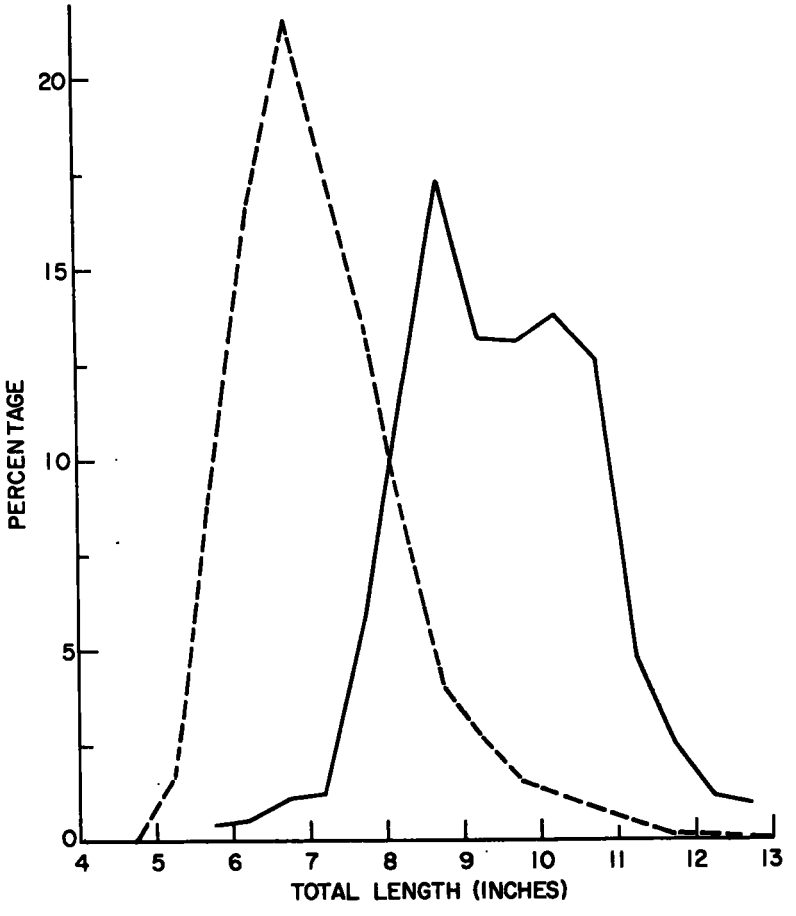

FIGURE 9.—Length-frequency distribution of Saginaw Bay yellow perch in 1929–30 (solid lines) and 1943–55 (short dashes).

two periods the mesh size of the fishing gears did not change appreciably, if at all, and thus the effect of net selectivity could be excluded.

This change of length is reflected in the percentage of legal-sized fish (8½ inches) in the two periods. In 1929–30 the legal-sized yellow perch comprised 73.9 percent of the catch. In 1943–55 this percentage dropped to only 11.0 percent.

LENGTH-WEIGHT RELATION

The length-weight relationship of fish has sometimes been described by the "cube law," $W = CL^3$ (where W = weight, C = a constant, and L = length). This law, however, can be applied only if the form and the specific gravity of fish remain constant throughout life. These requirements are so rarely met, that the more general equation $W = cL^n$ (c and n are determined empirically) is usually the more suitable in the study of length-weight relationship. Hile (1936) demonstrated that the exponent n can vary widely (he showed values from 1.34 to 3.68 for various samples and stocks of ciscoes). Hile (1936) and Le Cren (1951) discussed many of the questions and controversies involved in the application of this relationship. The cube relationship serves best in the study of "condition" since the value of C, the condition factor, measures "plumpness" or degree of well-being regardless of the actual length-weight relationship. Some have advocated the use of c in $W = cl^n$ in the study of condition, but this application is beset with many difficulties (Hile 1936).

The equation $W = cL^n$ was proved by several authors to describe the general length-weight relationship of yellow perch adequately (Hile and Jobes, 1941 and 1942; Jobes 1952; and Le Cren 1951 for the European perch).

General Length-Weight Relation

The determination of the length-weight relationship of Saginaw Bay yellow perch of 1943–55 collections was based on the combined data for all fish regardless of time of capture, sex, and state of maturity (table 18). This procedure gives the most practical curve for conversions between length and weight. The fitting of a straight line (by least squares) to the logarithms of lengths and weights of table 18 led to the equation: $\log W = -2.3982 + 3.2620 \log L$, where W = weight in ounces and L = total length in inches. This equation may be written also in the form $W = 3.9975 \times 10^{-3} L^{3.2620}$.

In the graphical representation of the length-weight relation (fig. 10) the smooth curve represents the calculated weights and the dots the empirical ones. The agreement of the calculated and empirical weights (table 18) was satisfac-

TABLE 18.—*Length-weight relationship of Saginaw Bay yellow perch of the combined collections of 1943–55*

Number of fish	Total length (inches)	Weight (ounces)		Standard length (millimeters)	Calculated weight (grams)
		Empirical	Calculated		
1	4.6	0.70	0.58	100	16
2	4.8	.70	.66	102	19
1	4.9	.60	.76	105	22
7	5.0	.76	.76	108	22
10	5.1	.84	.81	111	23
18	5.2	.86	.86	113	24
15	5.3	.91	.98	114	28
15	5.4	.99	.98	116	28
57	5.5	1.03	1.04	119	29
38	5.6	1.12	1.10	121	31
97	5.7	1.13	1.20	123	34
99	5.8	1.21	1.23	124	35
116	5.9	1.26	1.31	127	37
156	6.0	1.35	1.38	129	39
144	6.1	1.44	1.46	132	41
184	6.2	1.54	1.54	135	44
176	6.3	1.59	1.62	136	46
163	6.4	1.67	1.70	138	48
194	6.5	1.78	1.79	140	51
171	6.6	1.88	1.88	143	53
191	6.7	1.91	1.98	144	56
168	6.8	2.02	2.08	145	59
169	6.9	2.16	2.18	148	62
165	7.0	2.29	2.28	151	65
131	7.1	2.39	2.39	154	68
170	7.2	2.54	2.50	156	71
130	7.3	2.56	2.62	157	74
120	7.4	2.74	2.74	159	78
144	7.5	2.90	2.86	162	81
122	7.6	3.09	2.98	164	84
97	7.7	3.01	3.12	166	88
116	7.8	3.25	3.25	168	92
86	7.9	3.30	3.39	170	96
98	8.0	3.59	3.53	172	100
81	8.1	3.72	3.68	178	104
74	8.2	3.97	3.82	180	108
51	8.3	3.87	3.82	183	108
52	8.4	4.26	4.14	185	117
36	8.5	4.50	4.30	187	122
42	8.6	4.56	4.47	189	127
31	8.7	4.69	4.64	191	132
36	8.8	5.06	4.82	194	137
29	8.9	5.01	5.00	196	142
39	9.0	5.27	5.18	198	147
26	9.1	5.83	5.37	200	152
19	9.2	5.85	5.57	202	158
13	9.3	5.72	5.77	205	164
20	9.4	6.17	6.00	207	170
24	9.5	6.23	6.18	209	175
12	9.6	6.69	6.40	211	181
6	9.7	6.50	6.62	213	188
16	9.8	6.62	6.84	216	194
9	9.9	6.98	7.07	218	200
13	10.0	7.38	7.31	220	207
6	10.1	7.87	7.55	222	214
10	10.2	7.66	7.79	224	221
5	10.3	8.76	8.05	227	228
9	10.4	8.50	8.30	229	235
12	10.5	8.92	8.57	231	243
5	10.6	8.58	8.84	233	251
6	10.7	9.25	9.11	235	258
3	10.8	8.60	9.39	240	266
4	10.9	9.38	9.68	243	274
3	11.0	10.23	9.97	245	283
1	11.1	10.90	10.27	247	291
1	11.2	11.10	10.58	249	300
1	11.3	10.80	10.89	252	309
1	11.4	9.00	11.09	254	314
4	11.5	11.40	11.52	256	327
1	11.6	12.20	11.87	258	336
1	12.0	13.50	13.23	267	375
1	12.1	12.50	13.61	269	386
1	12.3	14.00	14.35	274	407
1	12.5	16.10	15.13	278	429
1	12.6	13.50	15.53	281	440
1	13.0	15.80	17.19	290	487
1	13.1	17.50	17.64	292	500
2	13.2	17.40	18.08	294	512
1	13.3	18.50	18.54	296	526
1	13.6	21.00	19.92	303	565
1	13.8	28.80	20.90	307	592
1	14.9	24.50	26.84	332	761

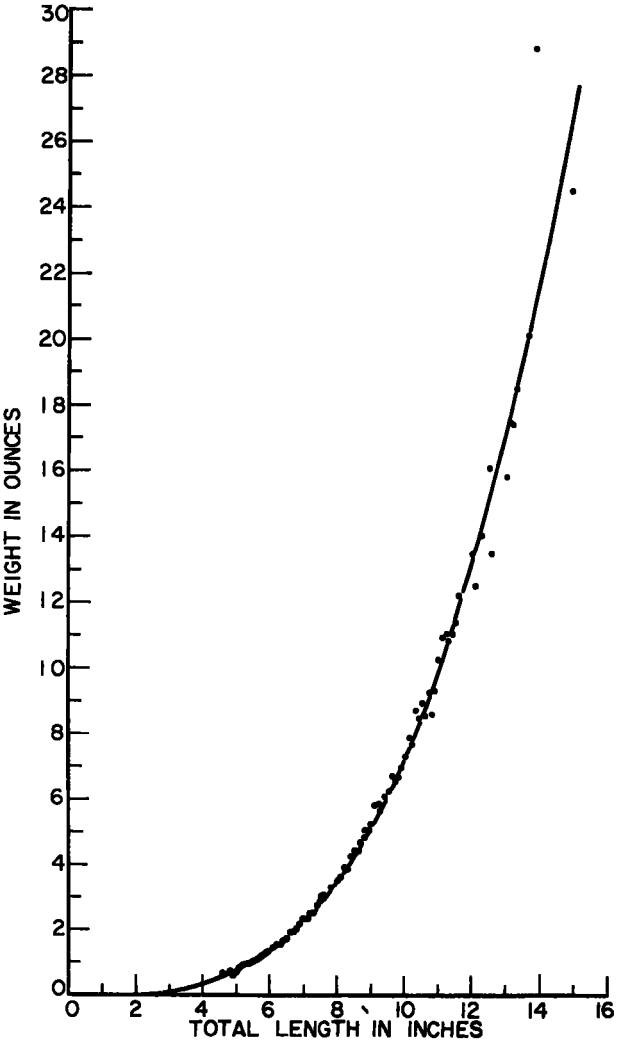

FIGURE 10.—Length-weight relation. The smooth curve represents the calculated weights and the dots represent the empirical weights.

tory. The discrepancies were more pronounced among larger fish, but on the whole, distribution of the disagreements had no particular trend. Jobes (1941) noticed that disagreements were very large for Lake Erie perch beyond 11.8 inches total length, but attributed them to the small number of fish. In addition, the heterogenity of the sample must be considered as the cause of some disagreements because collections of different years were combined in the determination of the length-weight relation.

Weight in Relation to Condition of Gonads

Information on the state of the gonads was, unfortunately, not available for all the spawning-run samples. For this reason, only those for 1949, 1951, 1953, 1954, and 1955 could be used for the study of the relation of weight to the condition of the gonads. Annual variations of weight in the 5 years were so small among fish of the same length, sex, and the state of the organs that the data were combined in the preparation of table 19. The insignificant difference of weight between ripe and spent males justified their combination as adult males. On the other hand, the differences between ripe and spent females indicated a large percentage loss of weight at spawning. The loss exhibited no clear-cut trend with increase of length. This observation agreed with the finding of Jobes (1952) that no relation exists between the percentage loss of weight and the length of fish.

The loss of weight of females at spawning varied between 8.5 and 22.2 percent (a gain was indicated at 5.5–5.9 inches but the comparison was based on only 2 fish). Over the length interval in which both unspent and spent fish were represented by 9 or more fish in each comparison (6.5–9.4 inches) the values ran from 8.5 to 16.7. The average percentage loss for the whole sample was 12.3 percent, much less than the 16.1 percent recorded by Jobes (1952) for Lake Erie yellow perch.

The weights of the immature fish of both sexes, of adult males, and of spent females all were closely similar, and as noted, substantially below those of ripe females of corresponding length.

Seasonal Change in Weight

Information on seasonal variation in weight can be studied only for 1955, the 1 year with collections outside the spawning season. Because of their relatively greater weight, ripe females are listed separately in the data on the length-weight relation of spawning-run fish (table 20). In later collections, however, the difference in weight between the sexes was too small to warrant separate presentation.

TABLE 19.—*Length-weight relation of Saginaw Bay yellow perch according to sex and state of organ*

[Based on spawning-run collections of 1949, 1951, 1953, 1954, and 1955. Number of fish in parentheses]

Total length (inches)	Male		Female				
	Immature	Adult [1]	Immature	Ripe or nearly ripe [2]	Spent	Loss at spawning	Percentage loss
5.0–5.4		0.8	0.9				
		(2)	(2)				
5.5–5.9		1.2	1.2	1.3	1.5	−0.2	−15.4
		(64)	(7)	(1)	(1)		
6.0–6.4	1.5	1.5	1.5	1.8	1.4	.4	22.2
	(5)	(192)	(22)	(2)	(5)		
6.5–6.9	1.7	1.9	1.9	2.4	2.0	.4	16.7
	(6)	(284)	(46)	(18)	(18)		
7.0–7.4	2.4	2.4	2.4	2.7	2.4	.3	11.1
	(2)	(248)	(16)	(28)	(32)		
7.5–7.9		3.0	3.0	3.3	2.9	.4	12.1
		(155)	(12)	(26)	(40)		
8.0–8.4		3.7	3.5	4.2	3.7	.5	11.9
		(74)	(1)	(27)	(47)		
8.5–8.9		4.5		5.2	4.6	.6	11.5
		(35)		(9)	(35)		
9.0–9.4		5.4		5.9	5.4	.5	8.5
		(17)		(11)	(27)		
9.5–9.9		6.1		7.1	6.2	.9	12.7
		(5)		(3)	(17)		
10.0–10.4		7.4		9.2	7.6	1.6	17.4
		(2)		(2)	(13)		
10.5–10.9		8.4		9.8	8.8	1.0	10.2
		(1)		(1)	(4)		
Total or average	13	1,079	106	128	239		[3] 12.3

[1] All mature fish combined (nearly ripe fish omitted).
[2] Ripe and nearly ripe fish combined.
[3] In the computation of this average, each percentage was weighed by the sum of the number of fish in the 2 groups whose weights were compared to obtain the percentage.

TABLE 20.—*Length-weight relation of Saginaw Bay yellow perch in the different seasons of 1955*

[Number of fish in parentheses]

Total length (inches)	Spawning season [1]			June 22 [3]	Oct. 19 [3]
	Males and spent females [2]	Ripe females	All fish		
5.0–5.4				1.1 (2)	1.1 (3)
5.5–5.9	1.2 (11)	2.1 (2)	1.3 (13)	1.2 (74)	1.3 (15)
6.0–6.4	1.4 (39)	1.7 (1)	1.4 (40)	1.5 (219)	1.7 (31)
6.5–6.9	2.0 (47)	3.6 (2)	2.1 (49)	1.9 (118)	2.1 (40)
7.0–7.4	2.4 (29)	2.5 (1)	2.4 (30)	2.4 (53)	2.6 (61)
7.5–7.9	2.9 (9)	3.0 (4)	2.9 (13)	3.0 (27)	3.1 (69)
8.0–8.4	3.7 (23)	3.8 (10)	3.7 (33)	4.0 (9)	3.8 (54)
8.5–8.9	4.5 (30)	4.8 (9)	4.6 (39)	4.8 (3)	4.7 (33)
9.0–9.4	5.5 (17)	5.8 (9)	5.6 (24)	6.5 (1)	5.6 (19)
9.5–9.9	6.1 (11)	7.1 (3)	6.3 (14)	8.0 (1)	6.7 (13)
10.0–10.4	6.6 (4)	9.2 (2)	7.5 (6)	9.5 (1)	7.1 (3)
10.5–10.9	8.4 (1)		8.4 (1)		8.5 (3)
11.0–11.4					11.6 (1)

[1] Based on samples of Apr. 18 and May 18. The June 7 sample was excluded because of the lack of records as to the state of gonads in some fish.
[2] Ripe and spent males and spent females combined; no immature fish.
[3] Mature fish, sexes combined.

The differences in weight among the different seasons were so slight that it is not possible to speak of a seasonal trend. Nevertheless, some differences could be detected. The males and spent females of the spawning-run sample, for example, usually were lighter than perch caught June 22 and October 19, and ripe females had a somewhat weaker tendency to be heavier than fish caught later in the year. The fall fish (October 19) were a little heavier than the June 22 sample for lengths between 5.0 and 7.9 inches, but for larger sizes (8.0 to 10.4 inches) yellow perch tended to be heavier in summer. In his study of the length-weight relation of Lake Erie perch, Jobes (1952) found the fish to be lighter in June than later in the season. He recorded the following coefficients of conditions for different months: June, 1.80; July, 1.97; August, 1.98; September, 1.92; October, 1.87. No other studies have been made of the seasonal trends of weight in perch in the Great Lakes.

Comparison with Length-Weight Relation in 1929–30 and with other Great Lakes Populations

Data on the length-weight relation (table 21) of the yellow perch from Green Bay, Lake Michigan, Lake Erie, and Saginaw Bay (1929–30) are from records published by Hile and Jobes (1941, 1942) and Jobes (1952). The table was arranged to facilitate the comparison of weights of fish of the same length in the different Great Lakes populations. The following length-weight equations from which weights were derived will clearly show the different degrees of deviation from the cube relationship between weight and length.

TABLE 21.—*Length-weight relation of yellow perch populations in the different Great Lakes waters*

[Data adapted from publications as follows: Green Bay and Lake Michigan' Hile and Jobes (1942); Lake Erie, Jobes (1952); Saginaw Bay in 1929–30, Hile and Jobes (1941)]

Total length (inches)	Calculated weights (ounces)				
	Green Bay	Lake Michigan	Lake Erie	Saginaw Bay (1929–30)	Saginaw Bay (1943–55)
5.0	0.7	1.0	0.8	0.8	0.8
5.5	1.0	1.4	1.1	1.0	1.0
6.0	1.4	1.8	1.4	1.3	1.4
6.5	1.7	2.2	1.9	1.6	1.8
7.0	2.2	2.7	2.3	2.0	2.3
7.5	2.8	3.4	2.9	2.7	2.9
8.0	3.4	4.0	3.5	3.4	3.5
8.5	4.1	4.8	4.1	4.0	4.3
9.0	4.9	5.6	5.0	4.9	5.2
9.5	5.8	6.6	6.1	6.1	6.2
10.0	7.0	7.7	7.0	7.2	7.3
10.5	8.1	8.9	8.3	8.1	8.6
11.0	9.4	10.1	9.4	9.5	10.0
11.5	10.8	11.4	10.9	11.0	11.5
12.0	12.2	12.8	12.3	12.5	13.2
12.5	13.9	14.4	14.1	13.3	15.1
13.0	15.8	16.0	15.8	16.0	17.2
13.5	17.8	17.9	17.6	17.8	19.4
Exponent value (n)	3.133	2.811	3.015	3.117	3.262

Lake Erie:

$$W = 1.766 \times 10^{-5} L^{3.015}$$

Green Bay:

$$W = 0.9319 \times 10^{-5} L^{3.133}$$

Lake Michigan:

$$W = 5.8405 \times 10^{-5} L^{2.811}$$

Saginaw Bay (1929–30):

$$W = 0.9826 \times 10^{-5} L^{3.1174}$$

In all the above equations W = weight in grams and L = standard length in millimeters.

The length-weight relations (weights calculated from length-weight equations) of the different Great Lakes yellow-perch populations (table 21) did not differ greatly. Most important differences, perhaps, were in the values of the exponent n which measures the ratio of the instantaneous rates of increase in weight and length. The value of n in the equation for Saginaw Bay samples of 1943–55 (3.262) shows the most rapid rate of increase in weight with increase in length yet reported for a Great Lakes stock of perch. Thus these Saginaw Bay perch, though substantially lighter than Lake Michigan fish at the shorter lengths, were able to overtake

and then surpass in weight the Lake Michigan population at greater lengths. On the other hand, although Lake Michigan yellow perch had the lowest exponent value (2.811), they were so heavy at the shorter lengths that the other Great Lakes populations (Green Bay, Lake Erie, and Saginaw Bay 1929–30) were unable to reach their weights even at the greatest lengths.

The unusually low value of n (2.811) in the equation for yellow perch of northern Lake Michigan probably can be attributed to the selective action of the commercial gill nets (2⅝-inch mesh) by which they were captured. Gill nets have been shown to take the relatively heavier of the shorter fish and the relatively lighter of the longer ones (Farran 1936; Deason and Hile, 1947; Le Cren 1951).

The rapid rate of increase of weight with length in Saginaw Bay collections of 1943–55 also gave them a weight advantage over fish collected in 1929–30. Differences between the two groups were nil or slight at the shorter lengths, but among larger fish the 1943–55 collections had substantially greater weights. At 10.5 to 13.5 inches the advantage ranged from 0.5 to 1.6 ounces.

CALCULATED GROWTH

Body-Scale Relation

Most workers who have published on the growth of yellow perch have given only the average size of age groups, or, if they published calculated lengths have assumed that the body-scale ratio is constant at all lengths of fish. Studies have been made, however, of the body-scale relation of perch in Saginaw Bay (Hile and Jobes, 1941), Lake Erie (Jobes 1952) and Lake of the Woods (Carlander 1950). Particulars on the findings for the two Great Lakes stocks are given later in this section. Carlander described the body-scale relation in yellow perch of Lake of the Woods by two conic-section parabolas, one fitted to data for fish 50 to 150 mm. long and the other to data for smaller (down to 19 mm.) and larger (up to 289 mm.) fish.

Inasmuch as the curve of regression of fish length on the radius of the key scale below the lateral line, presented by Hile and Jobes (1941), was based on plentiful materials, its use in the present study for the calculation of growth from measurements of scales from the same general area of the body could be considered valid. Through a misunderstanding on the part of the field collectors, however, the scale samples of the 1954 collections were removed from above the lateral line, which made necessary a study of the body-scale relation for scales from that part of the body. Because the assembling of materials for a body-scale study was necessary it was decided to extend the study and make a redetermination of the relation for the key scale below the lateral line. This extension permitted the comparison of two regression lines determined independently for the same key scale and also the comparison of the growth of the same fish as estimated independently by regression lines for scales from two positions on the body. (The exact positions of both key scales are stated in the section on materials and methods.)

Key scales below the lateral line

The graphic presentation of the body-scale data from below the lateral line (fig. 11) indicated that for fish over 70-mm. standard length the body-scale relation could be represented by a

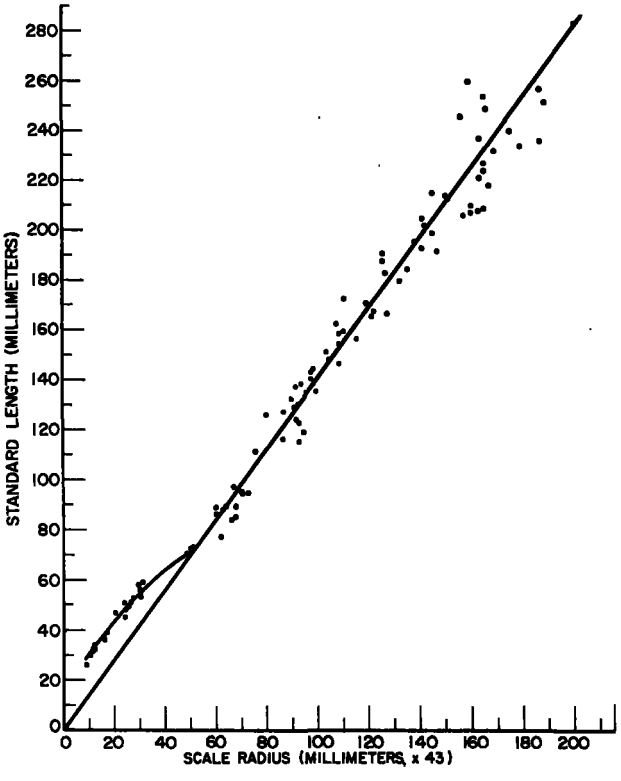

FIGURE 11.—Relation between body length and scale length of Saginaw Bay yellow perch (key scales from below the lateral line).

straight line passing through the origin. This view was supported by the fact that the values of the body-scale ratio, L/S (table 22), did not show any trend with change of length. The straight line of figure 11, therefore, was drawn through the origin at a slope equal to the average L/S value of 1.40. For these lengths above 70 mm., the direct-proportion computations were valid as calculated. For lengths less than 70 mm., however (body-scale curve drawn freehand in fig. 11) the direct-proportion calculation always gave an underestimate of length. The amount of correction required at a particular length can be obtained by measuring the vertical distance between the straight line and the empirical curve. Table 23 was set up to show the correction for each direct-proportion calculated length.

Similar body-scale relations were determined for the same key scale by Hile and Jobes (1941) for Saginaw Bay and by Jobes (1952) for Lake Erie. In both studies the relation for the larger fish could be described by a straight line through the origin but direct-proportion calculations gave underestimates at the smaller lengths. The amount of correction differed, however, between Lake Erie and Saginaw Bay and between the Hile and Jobes sample and the recent one from Saginaw Bay. Without exception the corrections determined in the present study were smaller than those published for Saginaw Bay by Hile and Jobes; furthermore, the 1955 samples indicated no need for corrections beyond 70 mm. whereas Hile and Jobes listed corrections through 101 mm. Differences between corrections at corresponding lengths averaged 4.5 mm. over the range, 38–101 mm. The corrections of direct-proportion calculations at the smaller lengths of fish for Lake Erie yellow perch were greater at most lengths than those given by Hile and Jobes for Saginaw Bay perch and were much larger than those determined in the present study. The average differences in the two comparisons were

TABLE 22.—*Relation between body length (L) and the anterior interradial measurement (S) of key scales of yellow perch from above and from below the lateral line*

Standard length interval	Number of fish	Average standard length	Average scale radius (x43)		Average L/S ratio	
			Below lateral line	Above lateral line	Below lateral line	Above lateral line
25–30	5	28.4	8.8	4.6	3.23	6.17
31–35	13	32.3	11.4	6.6	2.83	4.89
36–40	6	37.2	16.2	9.6	2.30	3.88
41–45	2	43.0	22.2	14.2	1.94	3.03
46–50	11	48.0	23.9	15.5	2.01	3.10
51–55	8	52.2	27.8	17.7	1.88	2.95
56–60	5	57.0	30.3	18.6	1.88	3.06
61–65	4	63.5	39.5	21.1	1.61	3.01
66–70	8	67.6	44.4	23.0	1.52	2.94
71–75	8	73.2	49.8	28.2	1.47	2.60
76–80	1	77.0	61.5	34.5	1.25	2.23
81–85	3	84.0	65.8	36.0	1.28	2.33
86–90	8	87.6	63.4	37.2	1.38	2.35
91–95	1	95.0	69.5	38.5	1.37	2.47
96–100	1	97.0	67.0	41.0	1.45	2.36
111–115	2	113.0	84.8	52.8	1.33	2.14
116–120	4	116.8	89.2	71.6	1.31	1.63
121–125	22	122.7	88.5	61.4	1.39	2.00
126–130	19	128.3	89.7	59.4	1.43	2.16
131–135	14	133.3	92.8	65.3	1.44	2.04
136–140	40	138.2	94.3	64.4	1.46	2.14
141–145	22	143.4	98.2	70.5	1.46	2.03
146–150	17	147.3	106.3	71.6	1.38	2.06
151–155	30	152.5	106.4	76.2	1.43	2.00
156–160	45	157.6	112.1	76.6	1.40	2.06
161–165	30	163.2	113.8	78.1	1.43	2.09
166–170	48	167.5	124.0	79.9	1.35	2.10
171–175	19	172.0	110.6	79.8	1.56	2.16
176–180	7	179.0	132.9	89.7	1.35	2.00
181–185	35	182.4	128.8	90.9	1.42	2.01
186–190	14	188.5	126.0	84.0	1.50	2.24
191–195	21	192.0	144.7	95.0	1.33	2.02
196–200	7	198.0	145.8	99.1	1.36	2.00
201–205	11	203.1	149.7	105.2	1.36	1.93
206–210	9	208.3	160.6	112.4	1.30	1.85
211–215	8	212.8	150.8	108.5	1.41	1.96
216–220	6	218.5	166.0	115.7	1.32	1.90
221–225	2	223.0	165.5	118.8	1.35	1.88
226–230	9	227.0	165.5	125.6	1.37	1.81
231–235	9	232.6	177.2	133.5	1.31	1.74
236–240	4	238.2	173.0	141.5	1.38	1.68
241–245	3	245.0	157.0	107.9	1.56	2.27
246–250	2	248.0	166.8	127.0	1.49	2.00
251–255	4	252.0	178.2	133.0	1.41	1.89
256–260	2	257.5	173.8	135.0	1.48	1.91

TABLE 23.—*Amount of correction to be added to direct-proportion calculated standard lengths of yellow perch from Saginaw Bay and Lake Erie*

[Scales from below the lateral line]

Direct-proportion calculated length (millimeters)	Amount to be added (millimeters)		
	Saginaw Bay (1955)	Saginaw Bay [1] (1929–30)	Lake Erie [2]
15–21	16		
22–30	15		
31–35	14		
36	14		19
37	13		18
38–39	13	16	18
40	12	16	18
41–42	12	15	18
43–45	11	15	17
46–47	11	14	17
48–49	10	14	17
50	10	13	16
51–53	9	13	16
54–56	8	12	15
57	8	12	14
58	7	12	14
59	7	11	14
60	6	11	14
61	6	10	13
62–63	5	10	13
64	4	10	13
65	4	9	12
66–67	3	9	12
68	2	8	12
69	1	8	12
70	0	8	11
71–72	0	8	10
73–75	0	7	9
76–78	0	6	8
79	0	6	7
80	0	5	7
81–83	0	5	6
84–86	0	4	5
87	0	4	4
88	0	4	3
89	0	3	3
90–91	0	3	2
92	0	2	2
93–95	0	2	1
96–101	0	1	0

[1] Data taken from table 5 of Hile and Jobes (1941).
[2] Data adapted from table 4 of Jobes (1952.)

1.9 mm. (absolute values employed) and 7.2 mm.

It is not possible at this time to state to what extent the difference between the Hile and Jobes curve and the one determined in the present study represent a true change in the population or to what extent they reflect random variation. Unpublished data on body-scale curves derived from different samples of Great Lakes fish (from a single lake) do indicate a considerable sample-to-sample variability, but the possibility of a real change is not to be discounted. At any rate, it was obviously proper to apply the more recently derived curve to the 1943–55 collections.

Key scales above the lateral line

The graph of body-scale data (fig. 12) indicated a linear relation between the standard length and the scale radius for fish longer than 75 mm. The straight line fitted by least squares to data for fish longer than 75 mm. had the equation:

$$L = 30.5 + 1.63\ S$$

where

L = standard length in mm.,

and

S = scale radius (×43) in mm.

For practical use the intercept was taken to be 30 mm.

Calculated lengths greater than 75 mm. were computed by the formula:

$$L_n = 30 + \frac{(L_t - 30)}{S_t} S_n,$$

where

L_n = calculated length at the end of n years,

L_t = standard length at capture,

S_n = scale radius to the nth annulus,

and

S_t = total scale radius.

Calculated lengths less than 75 mm. obtained by this formula are overestimates. Corrections for these overestimates (table 24) were determined from the body-scale curve (fig. 12). They are the vertical distance between the empirically fitted body-scale curve for fishes below 75 mm. and the extension of the straight line.

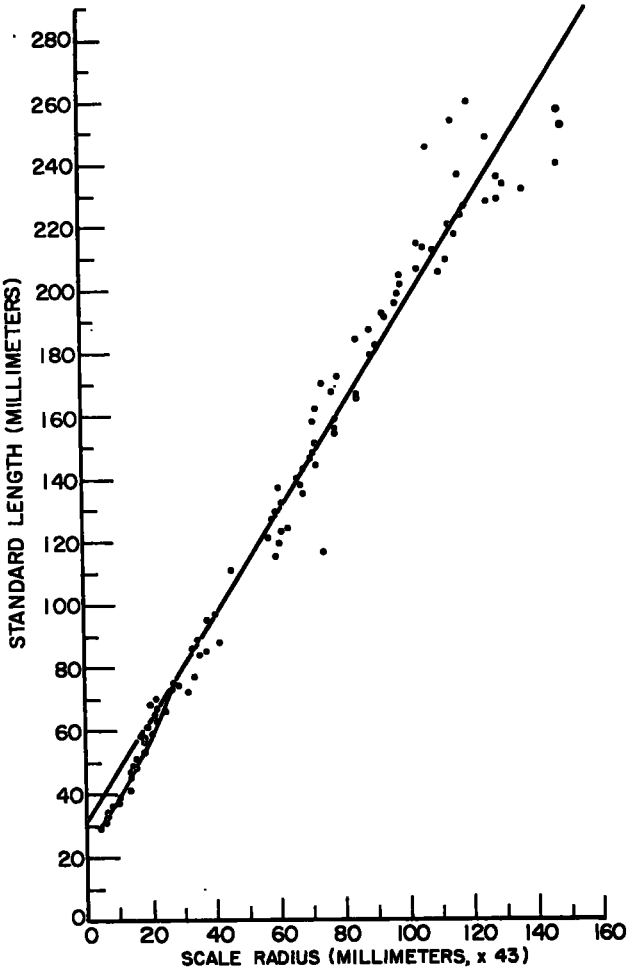

FIGURE 12.—Relation between body length and scale length of Saginaw Bay yellow perch (key scales from above the lateral line).

TABLE 24.—*Correction to be subtracted from standard lengths of Saginaw Bay yellow perch calculated by formula*

[Scales from above the lateral line]

Calculated length interval (millimeters)	Correction to be subtracted (millimeters)	Calculated length interval (millimeters)	Correction to be subtracted (millimeters)
29–45	9	66–67	4
46–53	8	68–70	3
54–61	6	71–73	2
62–65	5	74	1

Comparison of lengths calculated from different scales of the same fish

Inasmuch as the two body-scale curves were determined from selected or key scales it should be expected that nearly identical estimates of growth of fish in the sample would be obtained from the two sets of scales. The comparison of the growth histories of the same fish as computed from measurements of scales from above and below the lateral line (table 25) supports this expectation with the exception of calculated lengths at the end of the second year of life. At this age the scales above the lateral line consistently gave the higher calculated lengths; the

discrepancies ranged from 1 to 6 mm. and averaged 3.6 mm. There is no information now from which to determine the cause of this bias. Fortunately, the discrepancies affect principally a single year of life and are not excessive.

Implications as to procedure in the calculation of growth

The differences in body-scale relation between stocks and between two scale positions on the body of the same fish emphasize the importance of an exact knowledge of the body-scale relation of the population under study and a high degree of consistency in the field as to the point from which scale samples are removed. Not only must the body-scale relation be known for a particular key area; routine samples of scales must be taken from that area.

Even with these precautions, precision may not be so great as would be desired. The differences between the body-scale curves derived for Saginaw Bay perch by Hile and Jobes (1941) and in the present study, and discrepancies between lengths calculated for the same fish from measurement of scales above and below the lateral line indicate a certain amount of variability that cannot yet be explained.

TABLE 25.—*Calculated standard length (millimeters) of the same yellow perch from key scales above and below the lateral line*

Age group and position of scales	Number of fish	Calculated length at end of year					
		1	2	3	4	5	6
Male:							
Age group III	10						
Above		61	111	[1] 142			
Below		61	110	142			
Discrepancy		0	1	0			
Age group IV	30						
Above		58	94	115	[1] 133		
Below		59	90	114	133		
Discrepancy		1	4	1	0		
Age group V	58						
Above		57	92	115	132	[1] 151	
Below		58	88	113	132	151	
Discrepancy		1	4	2	0	0	
Age group VI	12						
Above		59	86	104	124	142	[1] 160
Below		61	92	109	127	143	160
Discrepancy		2	6	5	3	1	0
Female:							
Age group III	31						
Above		63	110	[1] 155			
Below		60	109	155			
Discrepancy		3	1	0			
Age group IV	58						
Above		63	103	134	[1] 169		
Below		62	100	134	169		
Discrepancy		1	3	0	0		
Age group V	138						
Above		59	93	119	144	[1] 175	
Below		60	88	119	145	175	
Discrepancy		1	5	0	1	0	
Age group VI	32						
Above		58	92	112	134	156	[1] 181
Below		60	87	109	133	157	181
Discrepancy		2	5	3	1	1	0

[1] Size of fish at capture.

Growth in Length

Growth in length of the age groups

In the presentation of average calculated lengths for yellow perch collected from Saginaw Bay during the spawning season of 1943–55 (tables 26 and 27) sexes are kept separate because of the more rapid growth of the females. Data for the calculated growth histories of age groups from different years are combined to give a best estimate of average conditions.

The calculated lengths of the males and females through age group VI for the different years of life show a definite tendency to decrease as the fish grow older. This discrepancy in calculated length is more pronounced in the later years of life, particularly after the second year. Among the first-year calculated lengths the values for different age groups beyond the II group are nearly the same.

TABLE 26.—*Calculated total length at the end of the different years of life for male yellow perch collected during the spawning seasons of 1943–55*

[The figures in this table were rounded from original records carried to the nearest 0.01 inch, hence the discrepancy between the 5th-year grand average increment and the 4th- and 5th-year lengths derived from summation of the increments. Increments in parentheses]

Age group	Number of fish	Length (inches) at end of year						
		1	2	3	4	5	6	7
II	3	3.1	5.1					
			(2.0)					
III	284	2.7	4.6	6.2				
			(1.9)	(1.6)				
IV	963	2.6	4.2	5.5	6.7			
			(1.6)	(1.3)	(1.2)			
V	706	2.6	4.0	5.4	6.3	7.3		
			(1.4)	(1.4)	(.9)	(1.0)		
VI	134	2.6	3.9	5.2	6.2	7.1	8.0	
			(1.3)	(1.3)	(1.0)	(.9)	(.9)	
VII	6	2.5	3.5	4.7	6.0	7.0	8.0	8.8
			(1.0)	(1.2)	(1.3)	(1.0)	(1.0)	(.8)
Grand average calculated length		2.6	4.2	5.5	6.5	7.3	8.0	8.8
Increment of average		2.6	1.6	1.3	1.0	.8	.7	.8
Grand average increment of length		2.6	1.6	1.4	1.1	1.0	.9	.8
Sum of average increments		2.6	4.2	5.6	6.7	7.6	8.5	9.3

TABLE 27.—*Calculated total length at the end of the different years of life for female yellow perch collected during the spawning seasons of 1949–55*

[Increments in parentheses]

Age group	Number of fish	Length (inches) at end of year								
		1	2	3	4	5	6	7	8	9
II	15	2.9	5.0							
			(2.1)							
III	281	2.7	4.5	6.6						
			(1.8)	(2.1)						
IV	660	2.7	4.3	5.8	7.5					
			(1.6)	(1.5)	(1.7)					
V	300	2.6	4.1	5.6	7.0	8.3				
			(1.5)	(1.5)	(1.4)	(1.3)				
VI	39	2.7	4.1	5.5	7.3	8.6	10.0			
			(1.4)	(1.4)	(1.8)	(1.3)	(1.4)			
VII	6	2.9	4.7	6.6	8.2	9.8	10.8	11.8		
			(1.8)	(1.9)	(1.6)	(1.6)	(1.0)	(1.0)		
VIII	3	3.2	5.3	7.7	9.6	10.8	12.4	13.3	13.9	
			(2.1)	(2.4)	(1.9)	(1.2)	(1.6)	(.9)	(.6)	
IX	1	2.5	4.8	8.1	10.5	12.4	13.2	13.7	14.1	14.5
			(2.3)	(3.3)	(2.4)	(1.9)	(.8)	(.5)	(.4)	(.4)
Grand average calculated length		2.7	4.3	5.9	7.4	8.4	10.3	12.4	14.0	14.5
Increment of average		2.7	1.6	1.6	1.5	1.0	1.9	2.1	1.6	.5
Grand average increment of length		2.7	1.6	1.6	1.6	1.3	1.4	.9	.6	.5
Sum of average increments		2.7	4.3	5.9	7.5	8.8	10.2	11.1	11.7	12.2

Most of the calculated lengths of age groups VII–IX of the females, on the other hand, were greater than the corresponding calculated lengths of younger age groups. That these discrepancies can be attributed to erroneous interpretation of the difficult scales of old fish seems unlikely since the trend toward higher calculated lengths among the older perch is present in the earlier as well as in the later years of life. Ordinarily the first 3 or 4 annuli are easy to locate and measure even on the scales of old fish. Inasmuch as age groups VII–IX were represented by only 10 fish it can hardly be concluded that the survivors to advanced ages are regularly the more rapidly growing individuals, but the possibility of such a selective survival should not be ignored.

The discrepancies shown in tables 26 and 27, for yellow perch other than the older females, exhibit a different pattern from that of "Lee's phenomenon of apparent decrease in growth rate" as defined by that author (Lee 1920). In Lee's phenomenon the discrepancies among calculated lengths are greatest in the early years of life and become less and less in later years. In the Saginaw Bay perch, on the contrary, the disagreements affect the later years of life most severely. A similar situation has been reported earlier for Saginaw Bay by Hile and Jobes (1941) and also for perch of Lake Erie (Jobes 1952) and Green Bay (Hile and Jobes 1942) and for certain species of deep-water ciscoes (Jobes 1949a, 1949b, and 1943; Deason and Hile 1947).

A change in calculated lengths occurred also between samples of the same age group caught in spring and fall (tables 28 and 29). Among males the disagreements were generally smaller between the calculated lengths of any age group caught in the fall and the next higher age group caught in the spring than were the differences

TABLE 28.—*Calculated lengths of spring and fall samples of 3 age groups of male yellow perch, 1955*

Age group and time of capture	Number of fish	Length (inches) at end of year					
		1	2	3	4	5	6
III							
Spring	72	2.9	4.8	[1]6.0			
Fall	30	2.7	4.2	5.3	[1]6.2		
IV							
Spring	179	2.7	4.1	5.4	[1]6.3		
Fall	58	2.7	4.1	5.2	6.1	[1]7.0	
V							
Spring	149	2.6	3.9	5.1	6.1	[1]7.1	
Fall	12	2.7	4.0	4.8	5.8	6.6	[1]7.4

[1] Size at capture.

TABLE 29.—*Calculated lengths of spring and fall samples of 3 age groups of female yellow perch, 1955*

Age group and time of capture	Number of fish	Length (inches) at end of year					
		1	2	3	4	5	6
III							
Spring	57	2.8	4.6	[1]6.3			
Fall	58	2.9	4.6	6.2	[1]7.8		
IV							
Spring	148	2.7	4.1	5.8	[1]7.3		
Fall	139	2.8	4.1	5.5	6.7	[1]8.0	
V							
Spring	76	2.6	4.0	5.0	6.3	[1]7.7	
Fall	32	2.8	4.0	5.0	6.2	7.3	[1]8.2

[1] Size at capture.

between members of the same age group. Although the same observation does not hold well for the females the data offer evidence that much of the disagreement among calculated lengths of different age groups is established between the spring and fall during the time of active growth in length and when fishing intensity is high.

Jobes (1952) discussed the possible causes of these discrepancies among calculated lengths in full detail. The present comments will be limited, therefore, to those factors believed to be most important in Saginaw Bay perch.

Much of the disagreement in calculated lengths of Saginaw Bay perch can be attributed to biased samples and to the progressive elimination of the more rapidly growing individuals from the population. These two sources of discrepancy are interrelated.

Selection according to legal size: Although this factor was mentioned in the preceding paragraph, it is given a special listing because of its great importance. The mortality of legal-sized fish caught in commercial nets is 100 percent. Inasmuch as the commercial fishery is supported principally by age groups whose length distributions cross the legal minimum of 8½ inches this selective destruction, particularly if the fishery is intensive, has a profound effect on the growth characteristics of the survivors.

Selective action of gears: The mesh sizes of the commercial trap nets by which the samples were taken (about 2½ inches, extension measure) were large enough to permit the escape of the smaller individuals of the younger age groups (the older the fish the higher the percentage held by the nets). As a result, the size at capture and calculated lengths of the younger age groups were overestimates of their growth.[5] Furthermore, these larger members of the younger age groups, as a result of being caught, were subjected to certain mortality hazards. The few that had reached legal size (8½ inches) all were killed. Those shorter than 8½ inches were returned to the water but they experienced some mortality from handling and sorting (nearly all fish are dead in gill nets). The extent of the mortality of small fish is not known, but Jobes (1952) estimated that in Lake Erie 14 percent of the perch were dead when the trap nets were lifted. This selective destruction of the more rapidly growing fish surely affects the growth characteristics of samples from the same year classes taken in subsequent years at older ages.

Selection due to segregation by sexual maturity and size: Segregation according to maturity can be significant in the present study since the principal samples were taken in the spawning season during which time small, immature fish tend to avoid the spawning grounds. Data from our samples (see Size at Maturity, p. 408) gave no evidence of this type of segregation, although other investigators have reported it frequently. A scarcity of immature fish can mean a segregation according to size because the fast-growing individuals usually mature earlier. Selective destruction of the mature fish during the spawning season is of limited consequence since most or all of the spawning is covered by the closed season during which all perch must be returned to the water.

Segregation according to sex and size can lead to biased sampling and selective mortality at all times of year. Evidence is strong for a segregation of sexes in various months outside the spawning season (Eschmeyer 1937, Weller 1938, Jobes 1952). It is well known also that perch of different size inhabit different regions of a lake, but the nature of this segregation apparently differs among populations (Hile and Juday, 1941). Data are lacking for a description of segregation by sex and by size in Saginaw Bay, but undoubtedly it occurs. This segregation can lead both to biased samples and selective mortality since fishermen can be expected to concentrate their efforts on grounds occupied by the larger fish.

Greater natural mortality rate for fish with rapid growth: Hile (1936) found a higher natural mortality rate among the rapidly growing ciscoes of Silver Lake (northern Wisconsin) than among the slow-growing ones. Whether a similar differential mortality occurs in the Saginaw Bay yellow perch is not known. Indeed, it would be most difficult to obtain information on the question in view of the known selective destruction of rapidly growing individuals in the fishery.

Evidence that the discrepancies of calculated lengths among the age groups of Saginaw Bay yellow perch are of the type that would result from the selective mortality of fish with the more rapid growth is given in table 30 which contains

[5] The selective action of such other gears as pound nets, fyke nets, and seines is similar to that of trap nets. Gill nets are even more selective as both the smallest and largest fish escape capture.

TABLE 30.—*Effect of the elimination of fish with the more rapid growth on the determination of the calculated lengths of female yellow perch of group IV, collected on Oct. 19, 1955*

[Age group V is included for comparison]

Age group	Sample	Number of fish	Length at capture	Calculated length (inches) at end of year					
				1	2	3	4	5	6
IV	All fish included	138	8.0	2.8	4.1	5.5	6.7	[1]8.0	----
IV	Fish longer than 7.9 inches excluded.	68	7.3	2.8	4.0	5.3	6.3	[1]7.3	----
V	All fish included	32	8.2	2.8	4.0	5.1	6.2	7.3	[1]8.2

[1] Size at capture.

three sets of calculated lengths (all for fish collected Oct. 19, 1955): Age group IV, entire sample; age group IV, with the more rapidly growing fish excluded; age group V. It is seen that exclusion of the larger IV-group fish results in a growth curve closely similar to that of the full sample of age group V.

From the previous discussion it is apparent that various factors bias sampling and change the growth characteristics of yellow perch in Saginaw Bay but that it is not possible to rank these factors as to their relative importance. The factors doubtless operate together to bring about these consistent discrepancies among the calculated lengths of the different age groups.

General growth rate

Two estimates of general growth are given in the bottom section of tables 26 and 27. One is based on the grand average calculated lengths and the second on the summation of the grand average annual increments of length. The grand average calculated lengths serve best to show the regression of size on age in an exploited stock, and the sum of the increments is believed to indicate approximately the average growth that yellow perch might have if the stock were not subjected to selective destruction of individuals with the more rapid growth. The present discussion is based on the sums of increments since this curve is held to be the more descriptive of biological growth potential. The selection of these data was mainly due to the discrepancies in calculated length of the age groups. This view agrees with that of earlier investigators who made similar use of average annual increments to show the general growth of yellow perch in Saginaw Bay (Hile and Jobes, 1941), Green Bay (Hile and Jobes, 1942) and Lake Erie (Jobes 1952). Comments on general growth and a comparison of the growth of the sexes are best made from table 31 which was prepared from data of tables 26 and 27 (see also fig. 13).

The lengths of the sexes were closely similar in the first and second years of life (a difference of 0.1 inch). Then, the curves started to diverge (with the females the longer). The advantage of the females increased from 0.3 inch at the end of the third year to 1.8 inches at the end of the seventh (no males older than age-group VII in

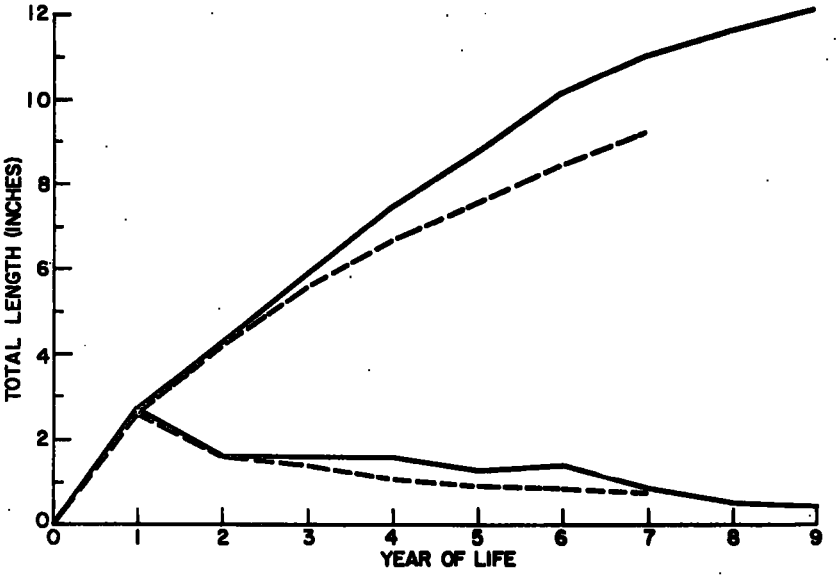

FIGURE 13.—General growth in length and annual increments in length of Saginaw Bay yellow perch of the 1943–55 spawning-run samples. Males, broken line; females, solid line.

TABLE 31.—*Calculated total lengths (inches) and length increments of male and female yellow perch of Saginaw Bay in different years of life*

[Data from tables 26 and 27]

Year of life	Males		Females		Size advantage of females
	Calculated length	Increment	Calculated length	Increment	
1	2.6	2.6	2.7	2.7	0.1
2	4.2	1.6	4.3	1.6	.1
3	5.6	1.4	5.9	1.6	.3
4	6.7	1.1	7.5	1.6	.8
5	7.6	[1] 1.0	8.8	1.3	1.2
6	8.5	.9	10.2	1.4	1.7
7	9.3	.8	11.1	.9	1.8
8			11.7	.6	
9			12.2	.5	

[1] See caption of table 29.

the samples). This difference in growth rate between male and female fish affected the age at which the legal size (8½ inches) was reached. The male perch took 6 years to reach this legal size and the female more than 4½ years.

The greatest increase in length for both sexes took place during the first year of life (2.6 inches for the males and 2.7 inches for the females). The amount of growth dropped sharply during the second year (1.6 inches for both sexes). The decrease continued for the males through the seventh year but the females made nearly the same amount of growth every year (1.3 inches to 1.6 inches) through the sixth year of life. After the sixth year annual growth increments dropped continuously.

A divergence of growth curves of the sexes surely is characteristic of the yellow perch and may be of the perch family. It has been observed in the three Great Lakes stocks of perch that have been studied and was reported for the Saginaw Bay walleye by Hile (1954).

Annual fluctuation of growth in length

Data on the annual fluctuation of growth in length of Saginaw Bay yellow perch (tables 32 and 33) are so arranged as to facilitate the comparison of the growth increments. The growth in a particular year of life in the different calendar years can be read from the horizontal rows. The columns show the increments for the different years of life in a particular calendar year. The growth histories of individual age groups can be traced from the diagonal rows. Records are given separately by sex and age because of sex differences in growth and systematic discrepancies among calculated lengths of fish of different ages. Age groups represented by fewer than 10 fish have been omitted from the tables.

It is readily apparent from tables 32 and 33 that growth increased or decreased sharply in some years, whereas for other years no trend can be detected. A comparison of the growth of males in 1945 and 1946, for example, reveals a consistent increase of the increments from 1945 to 1946 for all the years of life for the different age groups (table 32). On the other hand, the

TABLE 32.—*Annual increments of growth in length of male Saginaw Bay yellow perch, spawning-run collections of 1948–55*

[Each diagonal gives the growth history of an age group, belonging to the year class indicated by the year of 1st-year growth and captured in the spring of the calendar year following the one for which the last increment is given. Number of fish in sample of each age group in parentheses immediately below 1st-year increment]

Age groups and years of life	Increment of standard length (millimeters) in calendar years																
	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954
Age group VI:																	
6										19	20	23	24			19	20
5									20	18	15	18			16	20	
4								20	24	20	18			21	23		
3							22	26	27	23			26	30			
2						23	22	24	32				35	29			
1					55	55	53	57			55	55					
Number of fish					(12)	(17)	(16)	(10)			(27)	(34)				(27)	(34)
Age group V:																	
5					29		28	22	24	18	25	24	22		19	20	21
4				26		33	30	24	24	22	23	20		27	21	22	
3			34		33	33	22	28	29	23	24		33	26	24		
2		32		28	27	31	26	27	30	35		29	38	30			
1	58		56	58	55	54	54	55	58		55	54	55				
Number of fish	(32)		(14)	(10)	(14)	(66)	(85)	(41)	(56)		(56)	(183)	(149)				
Age group IV:																	
4					37			24	26	28	30	24	27		25	22	20
3				32			26	30	31	28	33	25		31	24	27	
2			32			35	27	28	32	33	38		35	39	31		
1		61			58	54	53	56	56	59		56	56	58			
Number of fish		(112)			(48)	(75)	(51)	(77)	(102)	(98)		(70)	(146)	(179)			
Age group III:																	
3					45				33		43	36	40		30	31	26
2				36				34		36	46	41		42	40	40	
1			55				58		59	58	58		57	58	63		
Number of fish			(14)				(17)		(18)	(50)	(73)		(10)	(17)	(72)		

TABLE 33.—*Annual increments of growth in length of female Saginaw Bay yellow perch, spawning-run collections of 1943–55*

[Each diagonal gives the growth history of an age group, belonging to the year class indicated by the year of 1st-year growth and captured in the spring of the calendar year following the one for which the last increment is given. Number of fish in sample of each age group in parentheses immediately below 1st-year increment]

Age groups and years of life	Increment of standard length (millimeters) in calendar years																
	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954
Age group VI																	
6							28										
5						38											
4					57												
3				38													
2			37														
1		60															
Number of fish		(10)															
Age group V																	
5					31		31			19	26				33		31
4				31		52			29	23				37		27	
3			34		44			33	34				39		22		
2		31		34			24	28				30		39			
1	62		55			54	54				56		56				
Number of fish	(61)		(36)			(36)	(16)				(43)		(76)				
Age group IV																	
4					48		41	31	34	25	37	33	38		37	37	35
3				34		50	27	32	35	30	39	27		38	27	35	
2			32		45	34	26	34	34	33	42		42	38	30		
1		60		59	58	55	55	58	58	61		56	59	58			
Number of fish		(87)		(18)	(49)	(65)	(26)	(29)	(63)	(41)		(98)	(36)	(148)			
Age group III								41	38		57	42	48		47		37
3								36		32	47	42		39		39	
2							34										
1						55	56		57	59	60		58		60		
Number of fish						(29)	(22)		(11)	(33)	(84)		(21)		(57)		

growth in 1944 was less than that of 1943. In 1948 and 1949 change of growth was irregular for the different age groups. In 1949, growth of all years of life of age group VI were higher than that of 1948, whereas in age groups V, IV, and III growth was less than that of 1948. Similar comparisons for the females can be made from table 33.

The comparison of growth increments in tables 32 and 33 is instructive but gives only a rough quantitative picture of the changes that occurred. Hile (1941) suggested the use of the actual percentage changes in growth to obtain more precise data on growth fluctuations. This method has been applied to several fish populations (Hasler and Farner, 1942; Carlander 1945a and 1945b; Van Oosten and Hile, 1949; Jobes 1952; Hile 1954). Procedural details for estimating the percentage changes in growth are not discussed here since a complete account was given by Hile (1941).

The percentage deviations of growth from average for the first year and for later years of life (tables 34 and 35) indicate dissimilar growth fluctuations during the two periods. A like situation was noticed by Hile (1941) for the rock bass and by Van Oosten (1929) for the Saginaw Bay lake herring. In the Saginaw Bay walleye, on the contrary, the fluctuations of growth in the first and in the later years were closely similar (Hile 1954).

Fluctuation in first-year growth

Although the range of percentage deviations of first-year growth from the 1942–51 average was much greater for females than for males, the trends were similar (table 34). The coefficient of correlation between the annual deviations of the sexes was highly significant ($r = 0.850$). Therefore, the unweighted means of the percentages for the sexes (bottom row of table 34) can

TABLE 34.—*Percentage deviation of growth in length for the 1st year of life of Saginaw Bay yellow perch from the 1942–51 average*

Sex	Percentage deviation from average growth in calendar year									
	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951
Male	−1.9	−4.9	−6.7	−1.8	0.9	2.6	2.6	1.5	2.6	5.2
Female	−16.5	−11.2	−10.6	−5.3	−.5	3.7	[1] 5.4	8.8	14.0	12.3
Average	−9.2	−8.1	−8.6	−3.6	.2	3.2	4.0	5.2	8.3	8.8

[1] Percentage obtained by linear interpolation.

describe the fluctuations in first-year growth very satisfactorily.

The poorest first-year growth (9.2 percent below average) was made in 1942 (fig. 14). In subsequent years a strong trend toward improvement of growth is apparent. The first-year growth in length remained below average until 1946. From 1946 to 1951 growth was continually above average reaching the maximum of 8.8 percent in 1951.

Fluctuation of growth in later years of life

The data used in the analysis of fluctuations of growth of later years of life covered the 1944–54 period only. The records for earlier calendar years, particularly those for females, are believed to be inadequate. In the later years of life, as with first-year growth, the annual percentage deviations of sexes (table 35) agreed very well (coefficient of correlation, 0.942) and thus the average percentage was used to describe the fluctuation of growth. Data for the two periods agreed further in showing a greater range of fluctuations in the females.

Contrary to the first-year growth which exhibited a consistent trend, fluctuations in growth in the later years of life were largely without trend, indeed were almost erratic (fig. 15). Growth in years later than the first was slightly below average in 1944 (–1.4 percent). Growth improved to 2.2 percent above average in 1945 and 8.2 percent above in 1946, dropped to 4.2 percent below average in 1947, and then jumped to the 11-year maximum of 16.8 in 1948. Following a drop in 1949 (to 0.3) and an increase in 1950 (12.4, second highest value) 2 sharp decreases carried the percentage to the 11-year minimum (–16.2) in 1952. Growth improved in 1953 (–8.4 percent) but 1954 was the second poorest year of the period (–14.0 percent).

The difference in growth fluctuations between the first year of life and those for later years was discussed by past investigators. Van Oosten (1929) showed that lake herring in their first year of life spend a larger part of the growing season inside Saginaw Bay than do older fishes (which seem to move into Lake Huron) and thus are affected more by any changes that might happen in the Bay. Hile (1941) explained this difference in the Nebish Lake rock bass on the basis that conditions controlling the first year of growth and that of later years are not the same. In the Saginaw Bay perch, the factors that determine first-year and later growth obviously are dissimilar. In 1948, for example, first-year growth was only slightly above average (4.0 per-

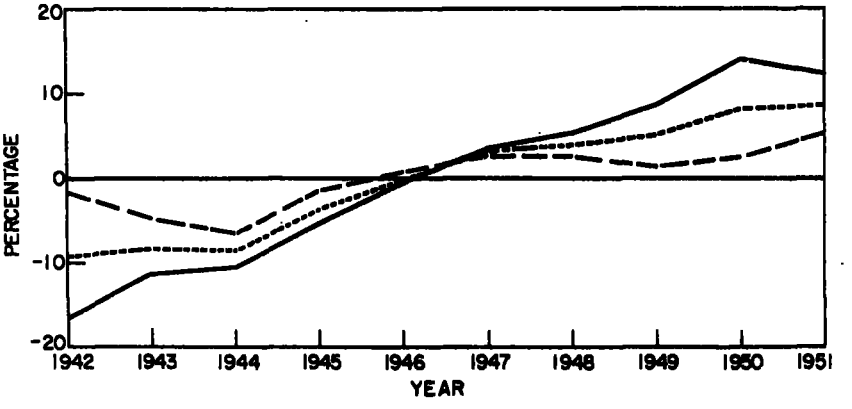

FIGURE 14.—Annual fluctuations in the growth in length of Saginaw Bay yellow perch in the first year of life. Males, broken line; females, solid line; both sexes, dots and dashes.

TABLE 35.—*Percentage deviation of the growth in lengths in the 2d and later years of life of Saginaw Bay yellow perch from the 1944–54 average*

Sex	Percentage deviation from average growth in calendar year										
	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954
Male	–4.0	–2.6	7.2	–0.2	10.2	–0.6	9.8	4.4	–8.8	–4.9	–10.5
Female	1.1	6.9	9.2	–8.1	23.4	1.2	14.9	3.9	–23.7	–11.9	–17.5
Average	–1.4	2.2	8.2	–4.2	16.8	.3	12.4	4.2	–16.2	–8.4	–14.0

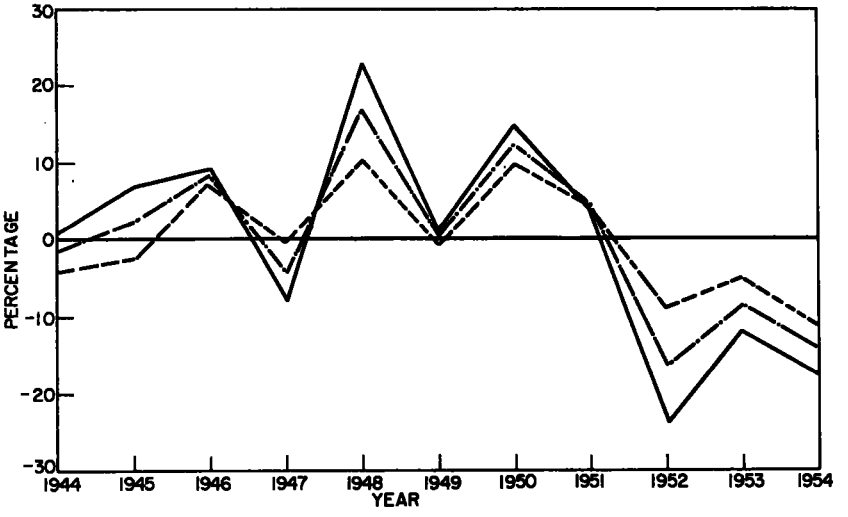

FIGURE 15.—Annual fluctuations in the growth in length of Saginaw Bay yellow perch in the second and later years of life. Males, broken line; females, solid line; both sexes, dots and dashes.

cent) whereas that in later years of life was at the maximum (16.8 percent). Other calendar years show similar disagreements; furthermore, the trends were entirely different (cf. figs. 14 and 15).

Growth in Weight

Growth in weight of the age groups: general growth

Data on calculated growth in weight (tables 36 and 37) were obtained by applying the calculated lengths of tables 26 and 27 to the length-weight equation. Thus the length and weight at a particular age derived by this equation are exactly comparable. (The mean weight of a group of fish in which both length and weight vary is higher than the normal weight of a fish of average length.)

The discrepancies among the calculated weights of the different age groups are so similar to those previously described for the calculated lengths that they may be summarized briefly and with very little comment. Among the males and in age groups III–VI of the females growth rate generally decreased with increase of age. The discrepancies were small in the earlier years of life, but became larger with increase in the year of life for which the calculations were made. In age-groups VII–IX of the females this downward trend of growth rate was reversed and growth in weight was relatively fast. The previous discussion of factors of discrepancies in calculated lengths applies, of course, to the calculated growth in weight.

With growth in weight as with growth in length, the general growth (table 38; fig. 16) is based on the sums of the grand average incre-

TABLE 36.—*Calculated weights at the end of the different years of life for male yellow perch collected during the spawning season of 1943–55*

[Increments in parentheses]

Age group	Number of fish	Weight (ounces) at end of year						
		1	2	3	4	5	6	7
II	3	0.16	0.78 (.62)					
III	284	.11	.68 (.57)	1.56 (.88)				
IV	963	.13	.42 (.29)	1.05 (.63)	2.01 (.96)			
V	701	.08	.37 (.29)	.90 (.53)	1.65 (.75)	2.68 (1.03)		
VI	134	.08	.34 (.26)	.88 (.54)	1.60 (.72)	2.39 (.79)	3.55 (1.16)	
VII	6	.08	.24 (.16)	.67 (.43)	1.46 (.79)	2.32 (.86)	3.65 (1.33)	5.37 (1.72)
Grand average calculated weight		0.11	0.43	1.06	1.84	2.63	3.55	5.37
Increment of average		.11	.32	.63	.78	.79	.92	1.82
Grand average increment of weight		.11	.33	.62	.86	.99	1.17	1.82
Sum of average increments		.11	.44	1.06	1.92	2.91	4.08	5.90

TABLE 37.—*Calculated weights at the end of the different years of life for female yellow perch collected during the spawning seasons of 1943–55*

[Increments in parentheses]

Age group	Number of fish	Weight (ounces) at end of year								
		1	2	3	4	5	6	7	8	9
II	12	0.13	0.82 (.69)							
III	281	.11	.58 (.47)	1.90 (1.32)						
IV	660	.10	.45 (.35)	1.28 (.83)	2.94 (1.66)					
V	300	.10	.39 (.29)	1.09 (.70)	2.36 (1.27)	4.23 (1.87)				
VI	39	.10	.40 (.30)	1.08 (.68)	2.76 (1.68)	4.89 (2.13)	7.69 (2.80)			
VII	6	.18	.70 (.52)	2.01 (1.31)	4.08 (2.07)	6.60 (2.52)	10.55 (3.95)	13.82 (3.27)		
VIII	3	.18	.98 (.80)	3.12 (2.14)	6.51 (3.39)	9.53 (3.02)	14.93 (5.40)	18.54 (3.61)	21.14 (2.60)	
IX	1	.08	.71 (.63)	3.75 (3.04)	8.18 (4.43)	14.74 (6.56)	18.08 (3.34)	20.65 (2.57)	22.42 (1.77)	24.85 (2.43)
Grand average calculated weight		.10	.47	1.37	2.78	4.42	8.70	15.91	21.46	24.85
Increment of average		.10	.37	.90	1.41	1.64	4.28	7.21	5.55	3.39
Grand average increment of weight		.10	.36	.91	1.56	1.93	3.11	3.30	2.39	3.39
Sum of average increments		.10	.46	1.37	2.93	4.86	7.97	11.27	13.66	17.05

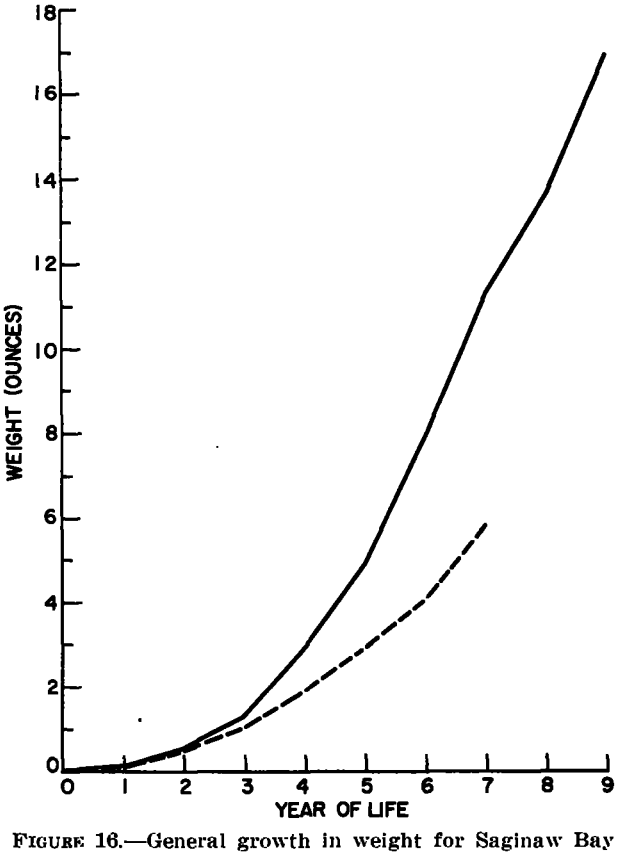

FIGURE 16.—General growth in weight for Saginaw Bay yellow perch of the 1943–55 spawning-run samples. Male, broken line; female, solid line.

ments. The calculated weights of the females were higher than those of the males in all years of life except the first. At the end of their second year the females were only a little heavier than the males (a difference of 0.02 ounce) but

TABLE 38.—*Calculated weights (ounces) and weight increments of male and female yellow perch of Saginaw Bay in different years of life*

[Data from tables 36 and 37]

Year of life	Males		Females		Growth advantage of females		
	Calculated weight	Increment	Calculated weight	Increment	Difference in weight	Ratio of weight	Ratio of increments
1	0.11	0.11	0.10	0.10	−0.01	0.91	0.91
2	.44	.33	.46	.36	.02	1.04	1.09
3	1.06	.62	1.37	.91	.31	1.29	1.47
4	1.92	.86	2.93	1.56	1.01	1.53	1.81
5	2.91	.99	4.86	1.93	1.95	1.67	1.95
6	4.08	1.17	7.97	3.11	3.89	1.95	2.66
7	5.90	1.82	11.27	3.30	5.37	1.91	1.81
8			13.66	2.39			
9			17.05	3.39			

in subsequent years the weights of the sexes were widely separated. The growth advantage of females can be clearly shown from the ratios of weights of females to those of males (table 38). These ratios increased steadily from the second to later years of life (slight decrease in seventh year). At the end of the sixth and seventh years the weights of the females were nearly double those of the males (ratios 1.95 and 1.91 for the sixth and seventh years, respectively).

The annual increments of weight for both sexes increased almost continuously after the first year of life (only exception, eighth year of life of females). The females attained their greatest advantage in annual increase over the males in the sixth year when they had added more than 2½ times the weight gained by the males (ratio 2.66). The sharp drop in growth increment in the eighth year of life might be due to the inadequacy of the sample.

Annual fluctuation of growth in weight

The annual increments of growth in weight (tables 39 and 40) are arranged in the same manner as those of length presented in an earlier section. Likewise, the percentage deviations of the growth in weight for the first and later years of life (tables 41 and 42) were determined separately because of the different pattern of growth in the two periods. The fluctuations of growth of males and females during their later years of life agreed well except for 1944; if that year is excluded, the coefficient of correlation for the percentages is 0.867. For the first year of life agreement between males and females was poor ($r = 0.113$); here the percentages for the sexes were arbitrarily combined for the sake of consistency with the treatment of other data on growth.

Since the calculated weights were based on the calculated lengths, it was to be expected that the trends of the annual fluctuation of growth in weight would show certain similarities to those of growth in length (figs. 17 and 18). However,

TABLE 39.—*Annual increment of growth in weight of male Saginaw Bay yellow perch, spawning-run collections of 1948–55*

[See table 32 for explanation of arrangement]

Age groups and years of life	Increment of weight (ounces) in calendar years																
	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954
Age group VI:																	
6										0.94	0.97	1.13	1.37			1.19	1.10
5									0.67	0.77	0.52	0.81			0.60	0.84	
4								0.49	0.60	0.56	0.56			0.76	0.68		
3							0.32	0.45	0.45	0.44			0.56	0.64			
2						0.18	0.18	0.19	0.32			0.34	0.26				
1					0.08	0.18	0.07	0.10			0.08	0.08					
Number of fish					(12)	(17)	(16)	(10)			(27)	(34)				(27)	(34)
Age group V:																	
5					1.54		0.45	1.21	0.97	0.77	1.16	1.02	1.08		0.94	1.06	0.88
4				1.01		1.22	1.14	0.66	0.70	0.68	0.66	0.65		0.97	0.73	0.68	
3			0.85		0.67	0.69	0.39	0.48	0.48	0.39	0.55		0.67	0.58	0.42		
2		0.32		0.25	0.25	0.29	0.20	0.22	0.29	0.36		0.26	0.35	0.28			
1	0.10		0.09	0.10	0.08	0.08	0.08	0.08	0.10		0.08	0.08	0.08				
Number of fish	(32)		(14)	(10)	(14)	(66)	(85)	(41)	(56)		(56)	(183)	(149)				
Age group IV:																	
4					1.57			0.91	0.85	0.93	1.12	0.98	1.03		1.03	0.78	0.64
3				0.80			0.61	0.51	0.51	0.63	0.75	0.63		0.69	0.49	0.58	
2			0.31			0.36	0.22	0.23	0.29	0.31	0.41		0.32	0.43	0.30		
1		0.12			0.10	0.08	0.07	0.09	0.09	0.11		0.09	0.09	0.10			
Number of fish		(112)			(48)	(75)	(51)	(77)	(102)	(98)		(70)	(146)	(179)			
Age group III:																	
3					1.13				0.85		1.18	1.08	1.14		0.82	0.86	0.67
2				0.33				0.32		0.41	0.61	0.46		0.46	0.46	0.57	
1			0.08				0.10		0.11	0.10	0.10		0.10	0.10	0.14		
Number of fish			(14)				(17)		(18)	(50)	(73)		(10)	(17)	(72)		

TABLE 40.—*Annual increment of growth in weight of female Saginaw Bay yellow perch, spawning-run collections of 1948–55*

[See table 32 for explanation of arrangement]

Age groups and years of life	Increment of weight (ounces) in calendar years																
	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954
Age group VI:																	
6							3.40										
5						3.57											
4					3.11												
3				1.06													
2			0.44														
1		0.12															
Number of fish		(10)															
Age group V:																	
5					1.79		2.74			0.95	1.31				2.05		1.58
4				1.37		2.72			0.98	0.76				1.59		0.78	
3			0.85		1.10			0.55	0.67				0.90		0.39		
2		0.33		0.32			0.18	0.23				0.28		0.28			
1	0.13		0.08			0.08	0.08				0.09		0.09				
Number of fish	(61)		(36)			(36)	(16)				(43)		(76)				
Age group IV:																	
4					2.33		2.48	1.21	1.27	1.00	1.59	1.48	1.83		1.99	1.57	1.45
3				0.84		1.63	0.61	0.58	0.85	0.72	0.97	0.71		0.98	0.69	0.85	
2			0.31		0.60	0.36	0.20	0.30	0.33	0.31	0.59		0.47	0.43	0.28		
1		0.12		0.11	0.10	0.08	0.08	0.10	0.10	0.12		0.09	0.11	0.10			
Number of fish		(87)		(18)	(49)	(65)	(26)	(29)	(63)	(41)		(98)	(36)	(148)			
Age group III:																	
3								1.02	0.99		1.71	1.37	1.57		1.46		1.06
2							0.32	0.34		0.32	0.65	0.54		0.42		0.44	
1						0.08	0.09		0.10	0.11	0.12		0.10		0.12		
Number of fish						(29)	(22)		(11)	(33)	(84)		(21)		(57)		

TABLE 41.—*Percentage deviation of the growth in weight for the 1st year of life of Saginaw Bay yellow perch from the 1942–52 average*

Sex	Percentage deviation from average growth in calendar year										
	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
Male	−13.9	12.8	−30.0	−9.2	1.9	2.4	2.4	2.4	2.4	2.9	26.2
Female	21.0	−1.2	.8	−23.0	−23.0	−0.4	[1] −8.5	1.9	21.9	20.9	----------
Average	3.6	5.8	−14.6	−16.1	−10.6	−3.5	−3.0	2.2	12.2	11.9	----------

[1] Percentage obtained by linear interpolation.

TABLE 42.—*Percentage deviation of the growth in weight in the 2d and later year of life of Saginaw Bay yellow perch from the 1944–54 average*

Sex	Percentage deviation from average growth in calendar year										
	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954
Male	−17.3	−5.5	−3.5	−3.0	10.6	7.5	15.9	17.5	−5.8	−0.10	−16.8
Female	27.7	−7.3	4.2	−16.3	26.8	8.6	26.2	17.3	−19.6	−29.8	−37.8
Average	5.2	−6.4	.4	−9.6	18.7	8.0	21.0	17.4	−12.7	−15.0	−27.3

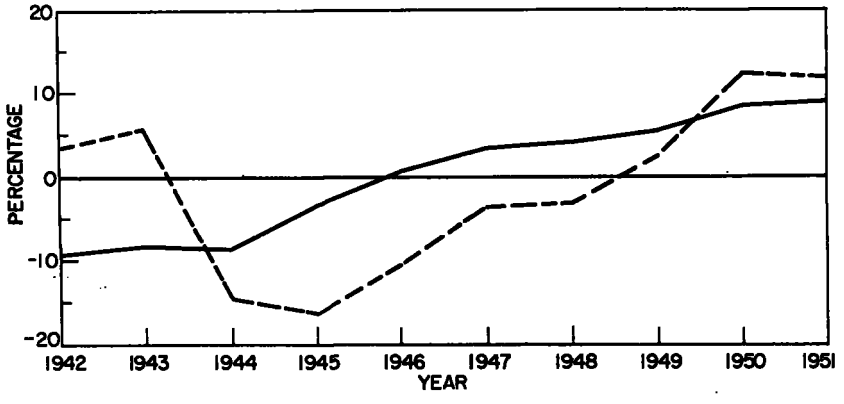

FIGURE 17.—Annual fluctuations of growth in length (solid line) and growth in weight (broken line) in the first year of life of Saginaw Bay yellow perch (sexes combined).

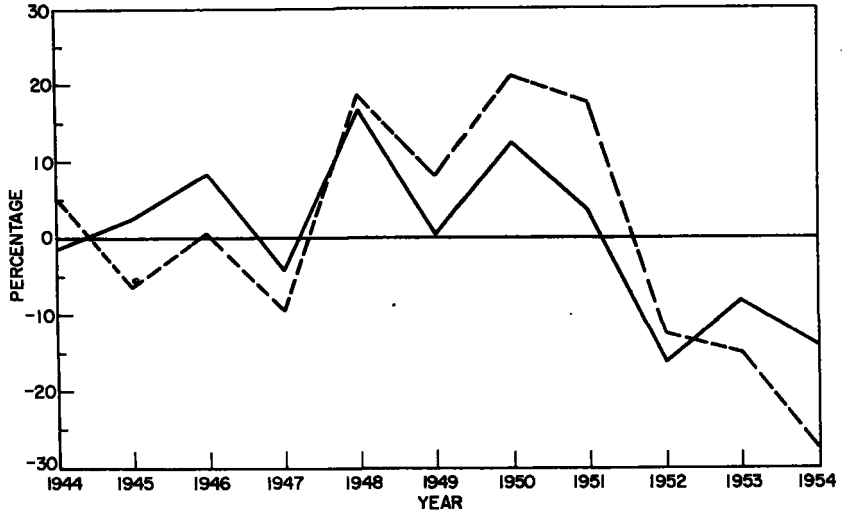

FIGURE 18.—Annual fluctuations of growth in length (solid line) and growth in weight (broken line) in the second and later years of life of Saginaw Bay yellow perch (sexes combined).

the range of fluctuation of annual increments in weight was greater than that of length and the curves disagree in certain details. Hile (1954) showed a similar situation in the fluctuation of growth of the walleye in Saginaw Bay. This difference between the annual fluctuations of growth in length and weight depends partly on the nature of the length-weight relation (weight varies approximately as the cube of the length). Thus the growth in weight in a particular year varies both according to the amount of increase in length made in that year and with the actual length of the fish at the time the increase is made. In other words, when two groups of fish in a particular year of life have equal increments of length, their weight increments will differ if the lengths were not equal at the start of that year of life. This influence of length when the growth is made on the value of weight increments can be shown clearly in the fluctuation of first-year growth of Saginaw Bay perch. Here, the growth in weight, as that of length, followed the same strong trend toward improvement in 1942–51 (fig. 17). Yet the slow growth in length during the years 1942–45 had reduced the length of perch to an extent that the improved growth in length (1946–51) did not bring growth in weight above average until 1949.

The annual fluctuations of growth in weight in later years of life followed those of length more closely than did those for the first year (fig. 18). Here again, however, the slow growth in length in 1947 reduced the size of the fish enough to delay the attainment of the maximum growth in weight. Although the maximum growth in length was attained in 1948, the highest value for weight was reached in 1950.

Still another factor contributing to the discrepancies between curves of fluctuations of growth in length and in weight in the second and later years is the difference in the years of life that predominate in controlling the course of the curves. A curve of fluctuation of growth in length (especially for males) is influenced most strongly by the data for the earlier years of life when growth in length is most rapid. Curves of fluctuation of growth in weight, on the other hand, are affected most by the data for later years when growth in weight is most rapid. Although no differences of trend of annual fluctuations in growth could be detected beyond the first year, the percentage changes in different years of life were not identical. Only random variation in these changes can be a source of discrepancy between curves of fluctuations of growth in length and weight.

Difference in Growth Rate in 1929–30 and 1943–55 and Comparison with Growth from other Great Lakes Waters

Hile and Jobes (1942) and Jobes (1952) offered detailed comparisons of the growth rate of Saginaw Bay yellow perch (collected in 1929–30) with that of perch in Lake Erie, southern Green Bay, and northern Lake Michigan. Since this previous discussion need not be repeated, the present section emphasizes the changes that occurred in the growth of Saginaw Bay yellow perch population between the 1929–30 and 1943–55 collections.

The calculated lengths (table 43, fig. 19) reveal a pronounced change in the growth of Saginaw Bay perch between 1929–30 and 1943–55. Saginaw Bay yellow perch of the 1929–30 samples were second longest or longest for their age, but those collected in 1943–55 had the slowest growth in length yet reported from the Great Lakes. The legal size (8½ inches) which was reached by 1929–30 fish during the fourth growing season was not attained by 1943–55 perch until the sixth growing season.

The change in growth of Saginaw Bay perch between 1929–30 and 1943–55 is shown even more

TABLE 43.—*Growth in length of yellow perch from different localities of the Great Lakes*

[Sources of data: Lake Erie, Jobes (1952); southern Green Bay and northern Lake Michigan, Hile and Jobes (1942); Saginaw Bay 1929–30 samples, Hile and Jobes (1941); Saginaw Bay 1943–55 samples, present study]

Locality and sex	Average calculated length (inches) at end of year						
	1	2	3	4	5	6	7
Lake Erie:							
Male	3.6	6.6	8.4	9.4	10.1	------	------
Female	3.7	6.7	8.6	9.8	10.7	------	------
Sexes combined [1]	3.6	6.6	8.5	9.6	10.4	------	------
Southern Green Bay:							
Male	2.9	4.6	6.0	7.4	8.4	9.6	10.3
Female	2.8	4.6	6.4	8.0	9.0	10.4	11.3
Sexes combined [1]	2.8	4.6	6.2	7.7	8.7	10.0	10.8
Northern Lake Michigan [2]	2.8	4.4	5.9	7.1	8.3	9.6	------
Saginaw Bay (1929–30):							
Male	3.0	5.3	7.7	9.3	10.6	11.6	12.3
Female	3.0	5.4	8.1	9.6	10.7	12.1	13.2
Sexes combined [1]	3.0	5.4	7.9	9.4	10.6	11.8	12.8
Saginaw Bay (1943–55):							
Male	2.6	4.2	5.6	6.7	7.6	8.5	9.3
Female	2.7	4.3	5.9	7.5	8.8	10.2	11.1
Sexes combined [1]	2.6	4.2	5.8	7.1	8.2	9.4	10.2

[1] Unweighted means.
[2] No data for sexes separately.

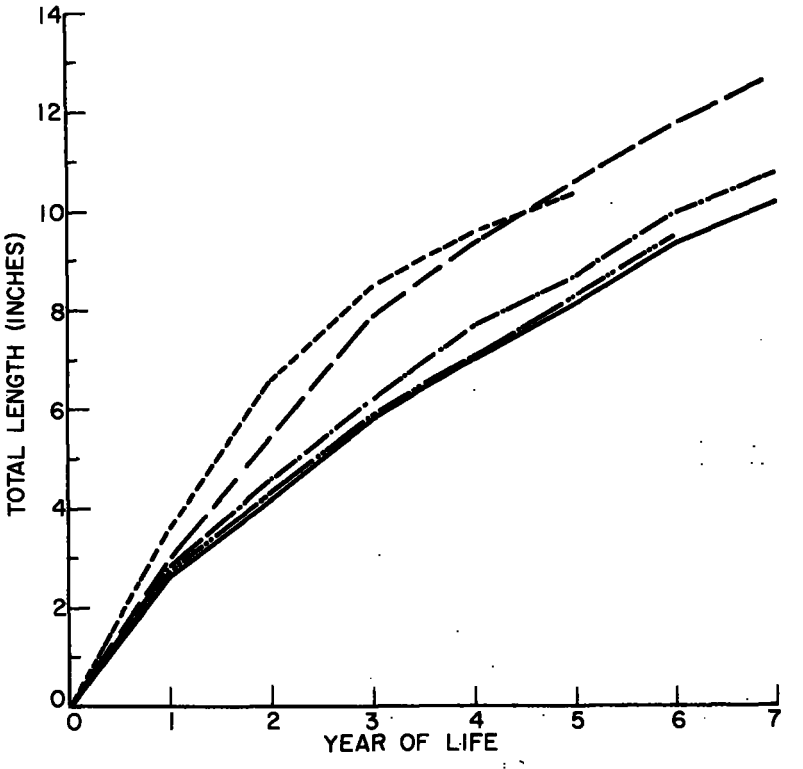

FIGURE 19.—Average calculated lengths at the end of each year of life for yellow perch from different Great Lakes waters (sexes combined). Lake Erie, short dashes; Green Bay, dots and dashes; northern Lake Michigan, two dots and dashes; Saginaw Bay, 1929–30, long dashes; Saginaw Bay, 1943–55, solid line.

forcefully by the comparison of calculated weights for the various samples (table 44, fig. 20). The growth of the earlier collection of Saginaw Bay perch, for weight as well as length, ranked second or first among the Great Lakes stocks. It was surpassed by the Lake Erie perch during the first 4 years of life, but in the fifth and later years (no data for Lake Erie beyond the fifth year), Saginaw Bay perch were the heaviest for their age of all perch populations. In the 1943–55 period, the situation was completely reversed; the growth of Saginaw Bay perch was inferior to that of all other Great Lakes perch populations. This sharp drop in the growth in weight affected all years of life. The ratios of calculated weights of 1929–30 fish to those of perch collected in 1943–55 follow:

TABLE 44.—*Growth in weight of yellow perch from different localities of the Great Lakes*

[Sources of data: Lake Erie, Jobes (1952); southern Green Bay and northern Lake Michigan, Hile and Jobes (1942); Saginaw Bay 1929–30 samples, Hile and Jobes (1941); Saginaw Bay 1943–55 samples, present study]

Locality and sex	Average calculated weight (ounces) at end of year						
	1	2	3	4	5	6	7
Lake Erie:							
Male	0.28	1.98	3.98	5.64	7.20	------	------
Female	.32	2.08	4.41	6.70	8.68	------	------
Sexes combined [1]	.30	2.03	4.20	6.17	7.94	------	------
Southern Green Bay:							
Male	.14	.60	1.38	2.57	4.16	6.28	7.90
Female	.14	.60	1.62	3.39	5.08	8.01	10.83
Sexes combined [1]	.14	.60	1.50	2.98	4.62	7.14	9.36
Northern Lake Michigan [1 2]	.21	.78	1.73	2.93	4.73	7.16	------
Saginaw Bay (1929–30):							
Male	.14	.88	2.89	5.50	8.22	11.57	13.93
Female	.14	.95	3.35	6.10	8.64	13.16	17.00
Sexes combined [1]	.14	.92	3.12	5.80	8.43	12.36	15.46
Saginaw Bay (1943–55):							
Male	.09	.43	1.10	1.98	2.98	4.30	5.77
Female	.10	.46	1.31	2.86	4.82	7.79	10.27
Sexes combined [1]	.10	.44	1.20	2.42	3.90	6.04	8.02

[1] Unweighted means.
[2] No data for sexes separately.

Year of life	Ratio	Year of life	Ratio
1	1.4	5	2.2
2	2.1	6	2.0
3	2.6	7	1.9
4	2.4		

From these ratios, it is apparent that in most years Saginaw Bay yellow perch caught in 1929–30 were more than twice as heavy as those in the 1943–55 samples.

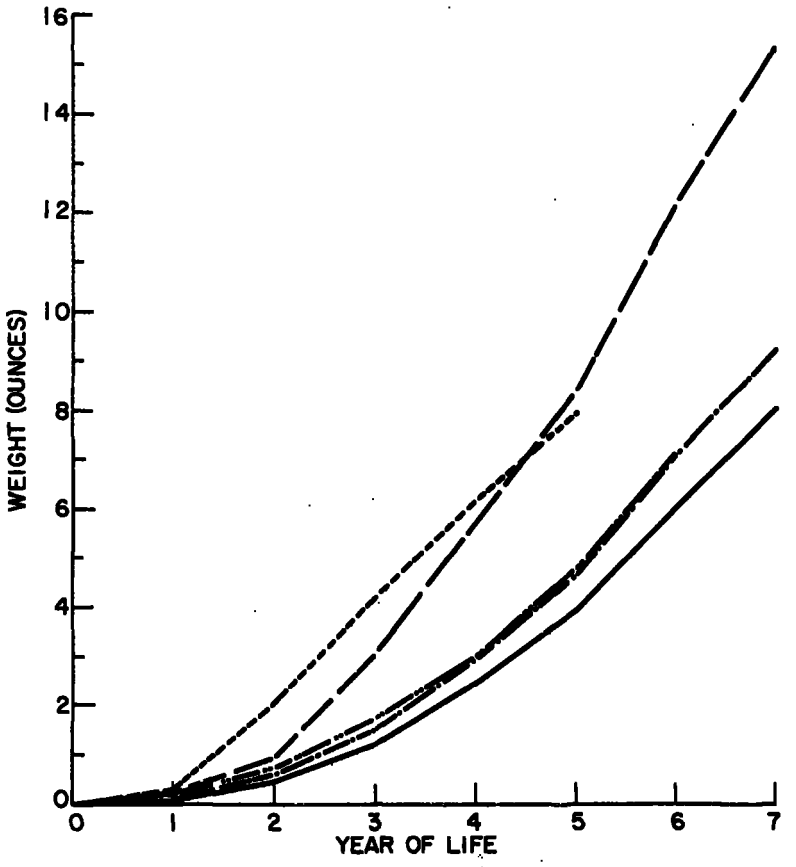

FIGURE 20.—Average calculated weights at the end of each year of life for yellow perch from different Great Lakes waters (sexes combined). Lake Erie, short dashes; Green Bay, dots and dashes; northern Lake Michigan, two dots and dashes; Saginaw Bay, 1929–30, long dashes; Saginaw Bay, 1943–55, solid line.

Probable Factors of the Decrease in Growth Rate

The extensive decrease in the growth rate of the Saginaw Bay yellow perch as indicated by the records for the 1929–30 and 1943–55 samples offers convincing evidence that the species is living now in a greatly changed situation. Many factors might contribute to this change: Limnological conditions including production of food; pollution; meteorological conditions; changes within populations of associated species and of the yellow perch itself.

Limnological factors are omitted in this study because of lack of data. The first limnological observations on Saginaw Bay of consequence were made in 1956.

With pollution also we are in poor position to offer quantitative estimates of differences between the periods. Even if we had full knowledge of sources, kinds, and quantities of pollutants, interpretation would be difficult because of the wide variety of substances and their equally varied and largely unknown effects on the several species of fish and fish-food organisms. (For a survey of conditions in 1935 and 1936, see the Saginaw Valley Report, Adams 1937.) Although changes in the pollution situation in Saginaw Bay cannot be described quantitatively, it appears most probable that conditions in recent years are less adverse than formerly. Construction of sewage-disposal plants in cities and great advances in the treatment of industrial wastes surely have decreased the total load. Evidence of lessening of industrial pollution comes from the decrease in complaints about tainted fish.

Although certain meteorological conditions appear to show a degree of correlation with limited annual fluctuations in growth rate (p. 404) there is no evidence for a major climatic change of the proportions that would have to be postulated if the large drop in growth rate were to be attributed to weather.

The changes within the populations of fish in Saginaw Bay are somewhat better understood,

and for some species quantitative estimates of annual abundance are available from the statistics of the commercial fishery. Before these changes are discussed, however, comments are needed on the "degree of association" between perch and other species in Saginaw Bay.

According to the experimental trawling from the research vessel *Cisco* in the summer and fall of 1956 the two species taken in greatest numbers along with yellow perch were smelt (*Osmerus mordax*) and the alewife (*Pomolobus pseudoharengus*). The *Cisco* was able to do only limited fishing in the shallow inner part of the Bay, which includes many of the more productive commercial grounds. On the outer, deeper grounds where bottom suitable for trawling was not extensive, association among the three species seems to be well established. In the larger-meshed commercial gears which take relatively few smelt or alewives the principal species captured along with perch are suckers (most of them *Catostomus commersoni*, a few *C. catostomus* and some *Moxostoma* spp.), catfish (*Ictalurus punctatus*), walleye (*Stizostedion v. vitreum*), and carp (*Cyprinus carpio*). The preceding have been arranged in the estimated order of degree of association as judged from records of commercial catch and from observations of lifts. With all species the degree of association is subject to seasonal variation. Walleyes, for example, move farther offshore in summer than do perch, whereas carp and catfish remain in relatively shallower waters. Still another important component of the catch in Saginaw Bay, the lake herring (*Coregonus artedi*) is rarely taken in quantity in the same nets as yellow perch. Lake trout (*Salvelinus namaycush*) and whitefish (*Coregonus clupeaformis*), two formerly plentiful species in the Saginaw Bay area, taken mostly in the outer Bay and in immediately adjacent waters of Lake Huron, likewise were little associated with perch.

The commercial fishery for smelt, one of the two principal associates of the yellow perch in Saginaw Bay has been too limited and too erratically prosecuted to provide quantitative information on the development and fluctuations of the stock. Yet, interest in the species as a sport fish has been such that a fairly dependable account can be offered. The first record of the capture of a smelt in Saginaw Bay is for 1928 (Van Oosten 1937). The population developed during the 1930's, reaching a high level toward the end of that decade and in the early 1940's. In the fall of 1942 an epidemic all but exterminated the entire stock (Van Oosten 1947). Smelt were extremely scarce during the next few years, and no significant catch was listed until 1950 when the take was 112,000 pounds. In the next 5 years the catch ranged from 138,000 to 218,000 pounds.

Possibly some idea of the rate of recovery of the smelt stock in Saginaw Bay can be gained by statistics on the stock of northern Green Bay where a brisk commercial fishery has existed since the late 1930's. The Green Bay population was nearly destroyed in the late winter of 1943 by the same epidemic that had struck Saginaw Bay the preceding fall (Van Oosten 1947). According to records of the catch of smelt per unit effort (gill nets and pound nets) published by Hile, Lunger, and Buettner (1953) smelt were extremely scarce in 1944–46 and despite steady improvement the catches did not approach the "premortality" level until 1949 and 1950.

The information on the smelt in Saginaw Bay leads to two important conclusions. First, smelt were too scarce to have been of any consequence in the ecology of the fast-growing yellow perch collected in 1929–30. Second, they were present throughout the period covered by growth data for the 1943–55 samples, but the abundance varied enormously. Smelt were plentiful up to the mortality of 1942, then were scarce for several years and finally became abundant again about 1950. The growth of perch of the 1943–55 samples, despite certain annual fluctuations, was consistently below that of the 1929–30 samples regardless of the abundance of smelt. An assumption that the addition of smelt to the fish fauna of the Bay was the cause of the poor growth of perch in the later years, therefore, cannot be supported.

Even though the smelt cannot be established as a causative agent in the slow growth of yellow perch of the 1943–55 collections, the mere fact of their close association dictates that the two species should have effect on each other. Formal studies of the food of smelt and perch have not been made in Saginaw Bay, but such information as is available on the feeding habits in other Great Lakes waters (Allin 1929, Ewers 1933, Schneberger 1927, Turner 1920) suggests that they are food competitors at the smaller sizes.

The opening of stomachs of the larger Saginaw perch in samples of the present study indicated smelt to be an important, possibly the principal, item of diet. Perch sometimes take smelt of surprising size (often the tail of the smelt protrudes from the perch's mouth).

Total length of perch (inches)	Total length of smelt (inches)
6.6	5.0
7.3	5.0
7.7	5.8
8.9	6.2

The alewife can be dismissed as a significant factor in the slow growth of yellow perch of the 1943–55 samples because it has become plentiful too recently. The current great abundance of alewives in Saginaw Bay is new. It is to be questioned whether alewives were present in consequential numbers before 1954 or even 1955. Should alewives continue to be plentiful, they could supply additional forage for the larger perch. The degree of food competition with small perch is not known.

The abundance indices for other associates of the yellow perch in Saginaw Bay (table 45) are based on records of the commercial catch per unit of fishing effort and were computed by the procedure described by Hile (1937); the base of 100 is the mean abundance for 1929–43. It should be understood that the indices are based on the catch of only the legal- or marketable-sized fish and that they have been biased to some degree by changes of regulations. In the most recent years the abundance of suckers and carp probably was underestimated because of the failure of fishermen to land their entire catch (weak market conditions). Despite their defects, these indices are our best information on the changes in population level of the several species, except perch for which additional information is given later.

TABLE 45.—*Average abundance and production of yellow perch and associated species in Saginaw Bay in 1929–30 and 1943–55*

Species	1929–30		1943–55		Ratio of indices
	Abundance index	Production [1]	Abundance index	Production [1]	
Yellow perch	105	526	125	443	1.19
Sucker	128	1,440	152	881	1.19
Catfish	89	124	146	271	1.64
Walleye	60	818	44	383	.73
Carp	52	598	200	1,267	3.85
Lake herring	52	2,552	104	988	2.00

[1] In thousands of pounds.

The mean abundance index of yellow perch and of all its associates except the walleye increased from 1929–30 to 1943–55. The average index for perch in 1943–55 was 1.19 times that for 1929–30. For the other species the ratio ranged from 0.73 (walleyes—only value below 1.00) to 3.85 (carp). These changes of the index, the addition of smelt as an important member of the population, and the recent great abundance of alewives all point toward a substantial rise in the fish population of Saginaw Bay.

The records of sizes of yellow perch in random samples from commercial gear in 1929–30 and 1943–45 makes possible a more discriminating estimate of the change in the population density of that species. The nature of the computations can be illustrated with the data for 1929–30. From the length-frequency distribution published by Hile and Jobes (1941) and from their length-weight equation it was determined first that the 640 legal-sized fish (then 9 inches or longer) in their sample had a total weight of 239.5 pounds. In the same 2 years the average catch of yellow perch per lift of one trap net was 17.83 pounds. It is then calculated that the lifting of 100 trap nets in 1929–30 yielded $640 \times \frac{17,830}{239.5}$ or 4,765 legal-sized fish. The same sample, however, contained also 302 undersized perch which correspond to a rate of capture of 2,248 per 100 lifts. The same procedure applied to the size distribution of all samples and the average catch per trap net for 1943–55 leads to an estimated take of 5,062 legal (now 8½ inches or longer) and 42,502 undersized perch per 100 trap nets.

The comparison of the estimates of numbers of legal- and undersized yellow perch taken per 100 trap-net lifts in 1929–30 and 1943–55 (table 46) brings out the enormous change that has

TABLE 46.—*Estimated numbers of legal-sized and undersized yellow perch captured in Saginaw Bay per lift of 100 shallow trap nets in 1929–30 and 1943–55*

[Minimum legal size: 1929–30, 9 inches; 1943–55, 8½ inches]

Years	Legal-sized	Undersized	Total
1929–30	4,765	2,248	7,013
1943–56	5,062	42,502	47,564
Ratio	1.06	18.91	6.78

taken place in the yellow perch population of Saginaw Bay. The numbers of legal-sized perch in the two periods were closely similar but this similarity is largely the result of the decline in growth rate that permitted so few perch to reach 8½ inches in 1943–55. In total numbers of fish taken, the rate of capture in 1943–55 was nearly 7 (6.78) times that of 1929–30. The actual increase in numbers was surely even higher than the ratio indicates. Because of their slow growth rate many fish of the 1943–55 population could escape from the nets at ages which were adequately sampled in 1929–30. A ratio of 10 rather than 6.78 might be much nearer the truth.

Despite the possibility that other factors may have been of some consequence, it is believed that the increase in population density of Saginaw Bay yellow perch is in itself sufficient to explain the observed decrease of growth rate.

The status of rate of growth of fish as a density-dependent variable is too well established to require presentation of argument or any extensive review of the voluminous literature on the subject. Evidence in the matter has come mainly from two sources: Changes in growth following transplantation from densely to thinly populated areas; changes in growth accompanying change of population density within a stock. Changes of population density that have been accompanied by change of growth rate have included fluctuations resulting from fluctuations in rate of exploitation or in the strength of year classes, from destruction of a considerable portion of the stock by a catastrophe, such as an epidemic or a winterkill, and by a deliberate, experimental destruction of the stock. A single example of each type of observation should provide adequate illustration.

The classic example of results from moving fish from crowded to thinly populated grounds is provided by plaice (*Pleuronectes platessa*) of the North Sea area. These experiments started early in the present century. Borley (1912) reported on the improved growth of plaice transferred from inshore waters to the Dogger Bank in 1904–08. These and later studies proved benefits to growth to be so substantial that the Danes developed an economically profitable enterprise in the transfer of young from the crowded nursery grounds to the broads of the Limfjord. A comprehensive review of the plaice transplantation experiments was published by Blegvad (1933).

The plaice also provided an early clear-cut illustration of change of growth rate with fluctuation in the density of the stocks. Prior to World War I excessive exploitation had greatly thinned the stock but during the war the drastic curtailment of operations permitted a substantial accumulation of fish on the grounds, and with it came not only an increase of average age but also a sharp decline in growth rate. The resumption of heavy fishing in post-war years led in turn to a thinning of the plaice, a decrease of average age, and an increase in growth rate. A thorough discussion of various aspects of the problem of population density and growth, centered largely about observations on plaice, was given by Bückmann (1932), Russell (1932), and other contributors to volume 80 of Rapports et Procès-Verbaux, Conseil Permanent International pour l'Exploration de la Mer.

Evidence on the effects of destruction of a large segment of the population by catastrophe was provided by Beckman's (1950) study of the growth of fishes in four Michigan Lakes that suffered severe winterkill in early 1945. With the exception of a single species in a single lake, all stocks exhibited an immediate marked improvement of growth. The rapid growth was soon lost, however, as reproduction restored population density to a high level.

The effects of an experimental reduction of population size was demonstrated by Beckman (1941 and 1943) for the rock bass (*Ambloplites rupestris*) of Standard Lake (Mich.). The destruction of the entire stock of fish in one basin of this hourglass-shaped lake in 1937 produced an immediate sharp improvement in growth. This good growth was still largely maintained at least as late as 1942, the year of the last sampling.

Critical reviews of the literature and references to publications on the relation between population densities and growth rates of fishes have been given by Hile (1936), Van Oosten (1944), and Watt (1956).

Changes of growth rate with increase or decrease of population density have mostly been related to the availability of food. In many situations, as notably with the plaice, evidence in support of this view is good. Some authors have suggested, however, that space available per

individual may in itself affect growth, independently of food conditions. The possibility of an influence of space on growth was recognized many years ago. Semper (1880) demonstrated a strong positive correlation between water volume per individual and the growth of snails (*Lymnaeus stagnalis*) reared from the same batch of eggs. Willer (1929) applied the term "Raumfaktor" to this influence of space on growth and offered the view that it is important in determining growth rate in natural populations as well as under experimental conditions. Numerous authors since have mentioned the space factor as of possible importance in observed correlations between growth rate and population density, but have not been able to separate its effects from those of food competition (see Hile 1936).

The sevenfold or greater increase from 1929–30 to 1943–55 in the numbers of yellow perch in Saginaw Bay suggests at once that competition for food has greatly increased, for we can hardly assume that food production has increased in a corresponding ratio. On the other hand, we are quite without evidence that an actual scarcity of food for perch has existed in recent years. Furthermore, the fish give no indication of starvation. They lack altogether, the large-headed, thin-bodied appearance of the stunted perch described and figured by Eschmeyer (1937), but, on the contrary, appear plump and healthy. This impression as to the well-being of fish of the 1943–55 samples is supported by the facts, for the earlier data on the length-weight relation proved them to be heavier, length for length, than the rapidly growing perch of the 1929–30 samples. The evidence, then, supports the conclusion that crowding in itself, not a scarcity of food, was the principal factor in the decline in growth.

POSSIBLE FACTORS OF FLUCTUATIONS IN YEAR-CLASS STRENGTH AND GROWTH RATE

The literature on the relation between environmental factors and the fluctuation of year-class strength and growth in fishes is extensive. No general review of this subject is undertaken here since excellent and detailed reviews were given by Hile (1936 and 1941), Van Oosten (1944), and more recently by Watt (1956).

Evidence from the literature suggests that factors not only vary, but conditions that control growth and success of reproduction are not the same for any particular species in different waters. It appears also that under natural conditions, the year classes and growth rate are not controlled by single factors, but by a number of interacting ones, some of which may be beneficial while others are harmful. The interrelations among these complex factors are unknown and indeed it is to be suspected that some important factors have not been discovered or tested. Most work done on this subject has been only exploratory.

The present inquiry is also exploratory and not conclusive. It is limited to possible effects of population density and to certain environmental factors about which information was available; temperature, precipitation, water level, and turbidity. The study is restricted also to growth in length. More intensive study must await the accumulation of information covering a greater span of calendar years.

Data on precipitation and on monthly air temperatures at Bay City (Mich.) published by the United States Weather Bureau, were taken as indicative of fluctuations of rainfall and the water temperature of the Bay itself. Doan (1942) showed a significant correlation between average temperatures of the air and water for Lake Erie. Similar correlations were determined between average air temperature and the temperature of water, for April through October 1939 to 1950. The data were collected at the intake (3,400 feet from shore) of the Bay City filtration plant. The values of r for the different months are as follows:

Month	r	Month	r
April	0.748	August	0.607
May	.887	September	.640
June	.846	October	.781
July	.699		

The preceding values of r are statistically significant at the 1-percent level except for July, August, and September which are significant at the 5-percent level.

Data on the average monthly turbidity were obtained from the Bay City water plant for the years 1939–52 (after 1952 the intake was changed to a different location) and expressed as parts per million (table 47).

TABLE 47.—*Turbidity of the raw water from the intake of the municipal water plant Bay City, Mich.*

Month	Turbidity (p. p. m.) in year													
	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
January	5	5	7	8	24	5	5	15	5	5	7	43	7	2.3
February	5	5	3	3	7	6	5	6	5	5	7	11	8	1.5
March	11	5	4	17	42	18	7	27	6	61	7	15	15	4
April	7	14	6	62	79	73	22	26	78	94	43	81	21	27
May	15	16	17	32	57	20	30	26	39	32	20	43	38	16
June	12	21	18	38	59	27	39	16	21	15	14	13	15	10
July	14	12	21	23	40	25	27	17	24	17	31	16	16	10
August	13	19	21	15	29	25	18	15	35	17	40	25	20	15
September	14	11	13	23	22	25	20	8	21	21	13	23	20	[1] 24
October	11	12	16	13	27	19	22	9	19	11	21	17	22	17
November	10	31	16	23	14	14	22	5	12	10	15	22	19	17
December	10	18	25	16	9	13	13	5	7	8	13	14	7	12

[1] New intake.

Records of water level were taken from charts and from monthly report sheets issued by United States Lake Survey, Army Corps of Engineers.

Environmental Factors and Fluctuation in Year-Class Strength

The first environmental factor checked as possibly having an effect on the strength of the year classes was the density of the population. The coefficients of correlation between the indexes of abundance and production of Saginaw Bay yellow perch and the year-class strength for the period 1939–52 had insignificant values (r = 0.321 and 0.272 for abundance and production, respectively). This result indicates that the number of legal-sized fish did not affect the brood strength.

The correlation coefficients of table 48 also did not indicate any significant relation between year-class strength and the environmental factors. The coefficients for precipitation in April (r = 0.462) and September (r = 0.492) although moderately high, were far from significant. Likewise the different multiple correlations (table 49) failed to reveal any relation between the year-class strength and environmental factors. No values of R^2 or of the regression coefficients were significant. Jobes (1952) similarly failed to establish a relation between certain environmental factors and year-class strength of Lake Erie yellow perch.

TABLE 48.—*Coefficients of correlation between year-class strength and temperature precipitation, water level, and turbidity*

[Values of r at the 5-percent and 1-percent levels of significance are: 0.532 and 0.661]

Month	Temperature	Precipitation	Water level	Turbidity
April	−0.377	0.462	0.063	−0.045
May	.233	−.364	.135	−.116
June	.319	.158	.125	−.298
July	.290	.030	.143	−.282
August	.004	−.230	.199	−.092
September	−.167	−.493	.196	.010
October	−.202	−.255	.138	−.115

TABLE 49.—*Coefficients in regression equation and R^2 in the study of the relation between environmental factors and year-class strength of Saginaw Bay yellow perch*

[When regression coefficient is not given, that variable was not considered in the determination of the equation]

Number of variables and *months*	Constant term (a)	Temperature (b_1)	Precipitation (b_2)	Water level (b_3)	Turbidity (b_4)	R^2
4 variables:						
April–June	−6608.35	0.42	9.92	11.35	−0.86	0.060
May–June	−10857.47	9.03	12.38	17.73	−1.70	.186
April–May	−4481.54	−6.30	−8.59	9.23	−.47	.064
May	−5989.02	.28	−13.68	10.38	−.13	.154
June	−15540.36	10.85	23.82	25.47	−3.02	.476
3 variables:						
Various [1]	−16469.42	−9.35	17.09	29.05		.323
Various [2]	−9024.83	−7.28	−51.36	16.17		.184
Various [3]	−4913.22	−6.39	5.27	9.07		.093
Various [4]	−1569.80	−8.27	1.14	3.52		.080
2 variables:						
Various [5]	−6454.96		8.39	11.08		.046
Various [6]	−2385.52		.25	4.11		.004
Various [7]	−8115.53		8.94	13.94		.059
Various [8]	−4183.38		−.53	7.22		.010
April	−6739.39	−6.75		12.16		.172
Various [9]	−8003.88	−6.82		14.35		.183

[1] Temperature, April; precipitation, June; water level, April.
[2] Temperature, April; precipitation, July; water level, April.
[3] Temperature, September–October; precipitation, June; water level, April–May.
[4] Temperature, September–October; precipitation, July; water level, April–May.
[5] Precipitation, June; water level, April.
[6] Precipitation, July; water level, April.
[7] Precipitation, June; water level, April–May.
[8] Precipitation, July; water level, April–May.
[9] Temperature, April; water level, April–May.

Failure to establish a relation between the year-class strength and the abundance of yellow perch or any of four environmental factors is not surprising. Unquestionably, we shall need a much broader and more detailed knowledge of limnological conditions within Saginaw Bay before we can hope for even a modest measure of success. We need particularly to know conditions during embryological development, at hatching, and during the early larval stages. It has long been believed that the strength of a year class is determined very early in its history (Hjort 1914), and many feel that the success of reproduction is determined by conditions over

a very brief period of time. For the yellow perch Jobes (1952) and Pycha and Smith (1954) agreed that the availability and kind of food organisms had an important effect on the survival of newly hatched fish.

Environmental Factors and Fluctuation in Growth Rate

In the attempt to uncover possible relations between the four environmental factors and the fluctuations of growth special emphasis was placed on the environmental factors in the months April to October. The months include and probably exceed the growing season for Saginaw Bay yellow perch. In samples collected on June 7 and June 22, the percentages of individuals exhibiting new (current-season) growth were 28.4 percent and 42.6 percent, respectively. Jobes (1952) found that 15 percent of the total growth of Lake Erie perch had taken place in June. In the present study, although little or no growth occurs before June, the months of April and May were included because it is possible that the conditions in these two months might have some influence on the growth of fish later in the season. There are no good data on the time the growing season ends in Saginaw Bay but Jobes (1952) showed that in Lake Erie growth appeared nearly to have ceased toward the end of September (his 1927 data indicated that growth was still active in October). Accordingly, to take into account any exceptional growth later in the season, environmental conditions in October were included in the present study.

As a matter of general procedure simple correlations first were computed between annual fluctuations in growth rate and each of the 4 environmental factors for each month in the 7-month period considered, and for certain arbitrarily selected combinations, a number of multiple correlations were computed to evaluate the importance of combinations of the factors on growth.

First-year growth

In view of repeated observations on the relation between population density and growth rate (see preceding section on factors of change in growth rate from the 1929–30 to the 1943–55 collections), it is logical to assume that first-year growth may be good in years producing weak year classes and poor in years producing strong year classes. The coefficient of correlation between the year-class strength and the fluctuation in the first-year growth of Saginaw Bay yellow perch for the years 1942–51 ran contrary to such an assumption. The relatively high value of the correlation coefficient ($r = 0.507$; $r = 0.632$ at the 5-percent level) suggests that good growth and a strong year class occur in the same calendar year.

The correlation coefficients of table 50 indicate no correlation between the annual fluctuations in growth rate and the fluctuations of different environmental factors except for turbidity in June ($r = -0.799$). The value was fairly high for July also ($r = -0.555$) but was not significant. Other values of r were very low except those for rainfall in May (−0.617) and temperature in October (0.565). The possible association between first-year growth and turbidity in June and July was further indicated from the several multiple correlations shown in table 51. Although no multiple correlation involving turbidity and 2 or 3 other factors was significant, all that involved 1 other factor were significant when turbidity in June (or June and July) was included. The regression coefficients for turbidity likewise were significant in three of these two-factor equations. The only other indication of significance lay in the regression coefficient for precipitation in the combination: Temperature, July and August; precipitation, May. The multiple correlation, however, was not significant. Thus it appears that among the environmental factors an argument can be made for turbidity alone as possibly influencing first-year growth.

It is difficult to judge the effects of turbidity on ecological conditions in Saginaw Bay or the manner in which turbidity might affect the first-year growth of yellow perch. The literature on

TABLE 50.—*Coefficients of correlation between annual fluctuation of growth in the first year of life and temperature, precipitation, water level, and turbidity*

[Asterisk indicates significance at the 5-percent level. Absolute values for r at 5- and 1-percent levels of significance are: 0.632 and 0.765]

Month	Temperature	Precipitation	Water level	Turbidity
April	−0.159	0.313	−0.096	−0.126
May	.013	−.617	.012	.015
June	−.226	−.297	−.175	*−.799
July	−.092	.258	−.138	−.555
August	−.274	−.338	−.105	.217
September	.080	−.042	−.080	−.288
October	.565	−.124	−.091	−.097

TABLE 51.—*Coefficients in regression equation and R^2 in the study of the relation between environmental factors and growth in length in the first year of life of Saginaw Bay yellow perch*

[When regression coefficient is not given, that variable was not considered in the derivation of the equation. Values significant at the 5-percent level are indicated by an asterisk]

Number of variables and months	Constant term (a)	Temperature (b_1)	Precipitation (b_2)	Water level (b_3)	Turbidity (b_4)	R^2
4 variables:						
May–October	175.24	−0.45	−1.60	−0.23	−0.38	0.219
June–September	286.70	−.52	−.21	−.41	−.60	.381
July–August	532.63	−1.51	−1.78	−.72	.05	.125
April–May	925.18	−.89	−2.76	−1.50	−.01	.197
3 variables:						
Various [1]	−7.35	.31	−.66		−.27	.663
Various [2]	39.48	−.39	−.39		−.43	.581
Various [3]	73.18	−.88	−.80		−.29	.688
2 variables:						
Various [4]	10.15		−.50		−.33	*.646
Various [5]	13.08		−1.00		−.39	*.610
Various [6]	57.32	−.68			*−.35	*.667
Various [7]	−5.12	.25			*−.33	*.650
Various [8]	61.98	−.74			*−.36	*.670
Various [9]	−35.11	.79	−2.05			.541
Various [10]	107.71	−1.38	*−2.63			.493

[1] Temperature, October; precipitation, May; turbidity, June.
[2] Temperature, June–August; precipitation, May–June; turbidity, June–July.
[3] Temperature, July–August; precipitation, May; turbidity, June.
[4] Precipitation, May; turbidity, June.
[5] Precipitation, May; turbidity, June–July.
[6] Temperature, June–August; turbidity, June.
[7] Temperature, October; turbidity, June.
[8] Temperature, July–August; turbidity, June.
[9] Temperature, October; precipitation, May.
[10] Temperature, July–August; precipitation, May.

relations between turbidity and fish is voluminous, controversial, and inconclusive. Arguments have been particularly lively as to effects on fish of turbidities at levels encountered in the Great Lakes, especially Lake Erie. Langlois (1941) held that siltation and turbidity resulting from land erosion in the watershed were the cause of the decreasing abundance of the more choice species of fish in Lake Erie, and Doan (1942) supported the same general view. Van Oosten (1948), however, held the Langlois "turbidity theory" to be invalid and offered extensive data and detailed argument in support of his belief. He pointed out in particular that: Recent trends of turbidity in Lake Erie had been downward, not upward as Langlois had argued; turbidity levels encountered in Lake Erie and other Great Lakes waters are too low to have a significant effect on fish; no relation can be established for Lake Erie species between annual fluctuations of turbidity and of growth or year-class strength. Van Oosten (1948) included an exhaustive review of the literature on turbidity.

If the observed negative correlation between turbidity and the first-year growth of yellow perch in Saginaw Bay is accepted as a cause-and-effect relation, three possible explanations suggest themselves: The reduced light penetration may affect the photosynthetic action in phytoplankton and thus lower the biological productivity; lowered visibility in the water may impede the feeding activities of the small perch; under turbid conditions the availability of food may be lessened by the concentrations of zooplankton near the surface (Doan 1942) while perch remain near the bottom.

Growth in later years of life

The first approach to the study of factors affecting growth beyond the first year was the determination of correlations between the fluctuation of growth and of abundance and production of yellow perch in the same year (p. 368). Both values of the coefficient were insignificant (r = 0.049 and 0.112 for abundance and production, respectively). This result indicates that growth was not affected by fluctuations in the numbers of legal-sized fish within the range of variation of the stock during the present study.

The coefficient (r) of table 52 show no correlation between the annual fluctuation in growth rate and the different environmental factors in single months except for water level. The coefficients for water level were negative and significant for May to October, but insignificant for April. It is to be noticed also that the values of r had an upward trend during the season. Other moderately high but insignificant correlation coefficients were those for turbidity in April (r = 0.405), May (r = 0.555), and October (r = −0.429) and temperature in June (r = −0.498).

TABLE 52.—*Coefficients of correlation between annual fluctuation of growth in the second and later years of life and temperature, precipitation, water level, and turbidity*

[Asterisk indicates significance at the 5-percent level. Absolute value for r for turbidity at 5- and 1-percent levels of significance are 0.666 and 0.798; for temperature, precipitation, and water level they are 0.602 and 0.735]

Month	Temperature	Precipitation	Water level	Turbidity
April	−0.050	−0.127	−0.589	0.405
May	−.001	−.007	*−.612	.555
June	−.498	−.004	*−.664	−.017
July	−.260	−.234	*−.681	.015
August	−.293	.091	*−.681	−.132
September	−.080	.022	*−.710	−.258
October	.103	−.210	*−.701	−.429

The possible relation between growth in the second and later years of life and water level was further revealed from the selected multiple correlations in table 53. When all the variables were included in the regression equation, only

TABLE 53.—*Coefficient in regression equation and R^2 in the study of the relation between environmental factors and growth in length in the second and later years of life of Saginaw Bay yellow perch*

[When regression coefficient is not given that variable was not considered in the derivation of the equation. Values significant at the 5-percent level are indicated by an asterisk]

Number of variables and months	Constant term (a)	Temperature (b_1)	Precipitation (b_2)	Water level (b_3)	Turbidity (b_4)	R^2
4 variables:						
May–October	4145.74	−8.06	−13.48	6.23	1.21	0.766
June–September	4102.51	−2.89	−3.20	−6.69	.40	.668
July–August	5984.74	−.63	−2.10	−10.18	.84	.735
Various [1]	1436.48	*−3.06	*−5.51	−2.08	.20	*.891
Various [2]	2225.78	−.98	−2.56	−3.72	.45	.782
3 variables:						
Various [3]	3246.18	−1.29		−5.44	.32	.619
Various [4]	2148.65	−2.62		−3.39	.26	.679
May–October	4759.44	−4.63	−6.59	*−7.65		*.707
June–September	3917.67	−3.74	−5.35	*−6.27		*.671
July–August	4343.16	−1.30	−.28	−7.31		.511
June–August	4086.74	−2.30	−1.28	−6.75		.603
Various [5]	4256.61	−1.32	−.81	−7.16		.550
2 variables:						
Various [6]	212.55	−3.12			.339	.611
June–September	4147.70	−1.89		*−6.92		*.554
July–August	4372.78	−1.29		*−7.37		*.511
Various [7]	4365.95	−1.36		*−7.35		*.535

[1] Temperature, June–Aug.; precipitation, July–Aug.; water level, June–Aug.; turbidity, April–May.
[2] Temperature, July–Aug.; precipitation, July; water level, June–Sept.; turbidity, May.
[3] Temperature, July–Aug.; water level, June–Sept.; turbidity, May.
[4] Temperature, July–Aug.; water level, July–Aug.; turbidity, April–May.
[5] Temperature, July–Aug.; precipitation, July; water level, June–Sept.
[6] Temperature, July–Aug.; turbidity, April–May.
[7] Temperature, July–Aug.; water level, June–Sept.

one combination was significant (temperature, June–Aug.; precipitation, July–Aug.; water level, June–Aug.; turbidity, April–May). In this combination, regression coefficients were not significant for water level and turbidity, but were significant for both temperature and precipitation. When three variables were used in the multiple correlation, only two combinations, neither of which included turbidity, gave significant correlation (temperature, precipitation, and water level for May–Oct., and for June–Sept.). In these two regressions, the only significant regression coefficients were those of water level. With 2 variables, 2 of the 3 correlations that included water level were significant (temperature and water level for June–Sept.; temperature for July–Aug., and water level for June–Sept.), and all three regression coefficients for water level also were significant. In the combination, temperature and water level for July and August, the regression coefficient for water level was significant but the multiple correlation was not.

These correlations offer strong evidence that the growth of Saginaw Bay yellow perch in the second and later years of life has fluctuated inversely with the water level. Despite this apparent relation, it is not possible to offer an ecological explanation as to how water level might affect growth. Possibly the adverse effects of deeper water over the usual shallows is greater than beneficial effects from the creation of new shallows along the shore. Limnological studies are needed on the food production of inshore areas.

The regressions also provide some but much less convincing evidence that growth has been correlated negatively with temperature in June through August and with precipitation in July and August. Jobes (1952) showed a similar negative but insignificant correlation between fluctuation in growth and the combined temperature of June to August for Lake Erie yellow perch.

SEX AND MATURITY

Size at Maturity

The spawning-run samples are considered by many investigators as almost entirely mature fish. Van Oosten (1929) showed that immature fish were not represented in the spawning-run collection of Saginaw Bay lake herring and hence concluded that these samples were not suitable for the estimation of size at first sexual maturity. A similar conclusion was expressed in studies on Great Lakes yellow perch (Hile and Jobes, 1941, 1942; Jobes 1952).

In the present investigation, the comparison of the spawning-run samples for the period 1943–55 with the 1955 collections made outside the spawning season (summer and fall) revealed no significant difference in the percentage of mature yellow perch at corresponding lengths. Consequently, the data on the percentage of mature fish in the collections from all seasons were combined in the preparation of table 54 (in the collections of 1950 and June 7, 1955, records of maturity were not available).

TABLE 54.—*Relation between length and sexual maturity of Saginaw Bay yellow perch in 1943–55*

[All perch longer than those recorded in the table were mature]

Total length (inches)	Male			Female		
	Immature	Mature	Percent mature	Immature	Mature	Percent mature
5.0–5.4		10	100	7		0
5.5–5.9	7	165	96	45	35	44
6.0–6.4	8	393	98	70	170	71
6.5–6.9	8	430	98	86	174	67
7.0–7.4	2	376	99	46	183	80
7.5–7.9		247	100	29	182	86
8.0–8.4		120	100	8	179	96
8.5–8.9		57	100	2	100	98
9.0–9.4		27	100	1	84	99
9.5–9.9		9	100		55	100

Nearly all the males were mature including the smallest size captured (100 percent at 5.0–5.4 inches; 96 to 99 percent at lengths of 5.5–7.4 inches). All males more than 7½ inches long were mature.

Females attain sexual maturity at a slightly greater length than do males. No females were mature at 5.0–5.4 inches and fewer than half (44 percent) were mature at 5.5–5.9 inches. At all greater lengths, however, the majority of the females were mature. The 80-percent level was reached at 7.0–7.4 inches and the 95-percent figure passed at 8.0–8.4 inches. All females more than 9 inches long were mature.

The evidence in table 54 on the small size of Saginaw Bay yellow perch at first maturity indicates that the protection of immature fish to preserve a spawning stock needs little consideration in the management of the fishery. The present size limit of 8½ inches permits the capture of almost no immature fish and destruction of nonspawners would be unimportant even at 7 inches. The double protection from the 8½-inch size limit and a closed season during spawning seems unnecessary. Indeed, under present fishing conditions the imposition of either a size limit or a closed season must be justified on economic grounds.

The size at first maturity of Saginaw Bay yellow perch in 1943–55 appears to be closely similar to that in the same stock in 1929–30 and in Green Bay. Hile and Jobes (1941) published no details on the state of the gonads of the perch in their Saginaw Bay samples, but their comment that 96 percent of their specimens were mature and the published length frequencies give strong evidence of maturity at small size. For Green Bay perch Hile and Jobes (1942) stated that males were predominantly mature down to a length of 5 inches. A majority of females were immature at lengths below 7 inches but 59 percent were mature at 7–7½ inches and all were mature at lengths above 7½ inches.

Yellow perch mature at a greater length in Lake Erie than in Saginaw Bay and Green Bay. The 50-percent level of maturity is first exceeded by the males in Lake Erie at 6½–7 inches and by the females at 8½–9 inches (Jobes 1952).

Sex Ratio

The present study of the sex composition of Saginaw Bay yellow-perch population has served principally to confirm the findings of earlier investigators concerning the extreme variability of the sex ratio in samples of the species (Schneberger 1935; Weller 1938; Eschmeyer 1937, 1938; Hile and Jobes 1941, 1942; Jobes 1952; Alm 1946, European perch). Jobes (1952) showed that the sex ratio of Lake Erie yellow perch varied erratically even in day-to-day collections. He concluded that the best estimate of the sex ratio in the population could be obtained from the unweighted means of the percentages of males and females, determined for several individual samples.

Eschmeyer (1938) attributed this wide sample-to-sample fluctuation in the sex ratio to a persistent segregation of the sexes in nonspawning fish and during the spawning season. He based his conclusion on the stomach contents of fish that had been killed in the poisoning of an entire population. Females had consumed items characteristic of the surface and of shallow water, whereas males had eaten deep-water forms.

Sex ratio of individual samples

The data on sex ratio of Saginaw Bay yellow perch from the spawning runs in 1943–55 (right column, table 55) show pronounced year-to-year variability. The percentage of males varied from 26 percent in 1945 to 87 percent in 1954. In 4 years (1943, 1946, 1947, 1953) the sexes were nearly equally represented. For all the collections combined, the males were more abundant than the females (62 percent males).

Wide fluctuation in the sex composition was observed not only from year to year but also in collections of the same year (table 56). The males were most plentiful at the beginning and at the end of spawning season (April 18, 70 percent; June 7, 65 percent). On the other hand, females predominated strongly in the collections of June 22 (33 percent males) and October 19 (30 percent males). Males and females were represented equally in the remaining sample (May 18).

A high percentage of males in spawning-run samples has been observed commonly and among many species of fish. Different explanations of the phenomenon have been offered. Numerous investigators believe that males ripen sooner, move to the spawning grounds earlier, and remain there longer than do females. Deason and Hile (1947) showed that this explanation did

TABLE 55.—*Sex composition of Saginaw Bay yellow perch in spawning-run samples of 1943–55, expressed as percentage of males*

[Number of fish in parentheses, males at left, females at right]

Date of capture	Percentage of males in age group								All ages
	II	III	IV	V	VI	VII	VIII	IX	
May 4, 1943		67 (14–7)	56 (112–87)	34 (32–61)	40 (6–9)	40 (2–3)			50 (166–167)
May 3, 1945		33 (1–2)	22 (5–18)	28 (14–36)	37 (6–10)	0 (0–3)	0 (0–3)	0 (0–1)	26 (26–73)
June 3, 1946		24 (9–29)	49 (48–49)	77 (10–3)	100 (6–0)	100 (1–0)			48 (74–81)
May 28, 1947	0 (0–1)	44 (17–22)	54 (75–65)	74 (14–5)					53 (106–93)
May 15, 1948		33 (3–6)	66 (51–26)	65 (66–36)	100 (12–0)				66 (132–68)
May 10, 1949		62 (18–11)	73 (77–29)	84 (85–16)	65 (17–9)				75 (197–65)
May 18, 1950	0 (0–3)	60 (50–33)	62 (102–63)	82 (41–9)	100 (16–0)	100 (3–0)			66 (212–108)
May 1, 1951	0 (0–1)	46 (73–84)	70 (98–41)	89 (56–7)	91 (10–1)				64 (237–134)
May 5, 1953		32 (10–21)	42 (70–98)	71 (56–43)					46 (136–162)
May 12, 1954		65 (17–9)	80 (146–36)	96 (183–8)	96 (27–1)				87 (373–54)
Apr. 18, May 18, and June 7, 1955	23 (3–10)	56 (72–57)	55 (179–148)	66 (149–76)	79 (34–9)	100 (5–0)			61 (442–300)
Total	17 (3–15)	50 (284–281)	59 (963–660)	70 (706–300)	77 (134–39)	85 (11–6)	0 (0–3)	0 (0–1)	[1] 62 (2,101–1,305)

[1] The unweighted mean for the collections is 58.

TABLE 56.—*Sex composition of Saginaw Bay yellow perch in different seasons of 1955, expressed as percentage of males*

[Number of fish in parentheses, males at left, females at right]

Date of capture	Percentage of males in age group						All ages	Average age of females
	II	III	IV	V	VI	VII		
Apr. 18		50 (3–3)	66 (55–28)	70 (74–31)	77 (24–7)	100 (5.0)	70 (161–69)	4.2
May 18		12 (2–14)	25 (22–67)	58 (41–30)	88 (7–1)		50 (72–112)	4.2
June 7	23 (3–10)	63 (67–39)	66 (103–53)	69 (34–15)	75 (3–1)		65 (210–118)	3.6
June 22		29 (18–43)	30 (79–185)	38 (61–98)	32 (8–17)		33 (166–343)	4.2
Oct. 19	24 (10–31)	34 (30–58)	30 (58–138)	27 (12–32)			30 (110–259)	3.7

not hold for their data on the sex ratio of kiyi (*Coregonus* [*Leucichthys*] *kiyi*) and suggested that the great activity of males during spawning led to their capture in numbers out of proportion to their true abundance. Possibly both the actual abundance and differential activity affect the estimates of the sex ratio of spawning-run samples of perch.

Change of sex ratio with increase in age

The tendency toward a decrease in the percentage of males with advancing age has been repeatedly shown for many species. Hile (1936) who reviewed the subject of change of the sex ratio with age concluded with the suggestion that this condition might be characteristic among fish. A decrease in the percentage of males with increase of age has been observed also in a number of yellow perch populations (Schneberger 1935; Weller 1938; Hile and Jobes 1941, 1942; Jobes 1952). Exceptions to this trend were recorded, however, by Eschmeyer (1937 and 1938) and by Alm (1946) for populations of stunted perch. Thus the possibility suggests itself that the change in growth rate of Saginaw Bay yellow perch from 1929–30 to 1943–55 may be associated with a reversal in the change of the sex ratio with age. In the earlier years males grew scarcer with increasing age whereas in most of the 1943–55 samples (tables 55 and 56) the percentage of males increased with age (oldest age groups excepted).

In all of the 1943–55 samples, except for the spawning-run collections of 1943 and 1945 and the sample of June 22, 1955, the males became more plentiful with increase of age. This trend toward increase was so strong in some years (1948, 1950, 1954) that fish in age group VI

were almost all males. Beyond age group VI, the change in the sex ratio could not be considered as descriptive because of the small number of fish. In the 1943 collection, the females were more plentiful in age group V–VII than in age groups III–IV and in the 1945 data and the June 22, 1955, sample no trend is apparent. For all spawning-run collections combined (bottom of table 55), the percentage of males increased continuously from 17 percent in age group II to 77 percent in age group VI and then dropped slightly to 65 in the VII group. The 4 older fish were all females.

It is difficult to judge the degree to which the trends of tables 55 and 56 are actually descriptive of the sex ratio of the Saginaw Bay stock of yellow perch. Samples of perch from commercial gear are biased, and this bias, in turn, leads to differential destruction in the fishery. Because of sex differences of growth rate (more rapid growth of females), the younger males are much less easily captured than are females. Even before fish of either sex attain legal size, this differential rate of capture leads to a greater mortality of females since numbers of undersized fish are killed in the handling and sorting of the catch. As the fish reach legal size this differential destruction is intensified, since females grow to 8½ inches in about 4½ years, as compared with 6-years for males.

SUMMARY

(1) The yellow perch is an important fish for both commercial fishermen and anglers because of its wide distribution and its frequent great abundance.

(2) In Saginaw Bay, the average commercial catch of yellow perch has decreased from 1,961,309 pounds in 1891–1916 to 499,938 pounds in 1917–55. Since 1938 the commercial production of yellow perch has been below 500,000 pounds except in 1943, 1944, and 1945. Statistics of the commercial fishery prove that the recent low output has resulted from reduced fishing intensity, not from a scarcity of fish.

(3) The trap net is the principal gear for catching yellow perch in Saginaw Bay (75.9 percent of the catch). Production is concentrated in the fall (75 percent of the catch in September, October, and November).

(4) The present study of age and growth was based on the determination of age and the calculation of growth histories of 4,285 fish, 3,407 of them collected during the spawning seasons of 1943–55 (no collections, 1945 and 1952). In 1955 additional collections were made outside the spawning periods.

(5) In the combined 1943–55 spawning-run collections, age group IV contributed 48.6 percent of the total, followed by age group V (29.9 percent) and age group III (15.9 percent). The remaining age groups (II and VI–IX) together contributed only 5.6 percent. The mean of the average ages for the 1943–55 spawning-run samples was 4.3 years.

(6) In 1955 the age composition changed seasonally. Average ages on various dates were: April 18, 4.8 years; May 18, 4.4 years; June 7, 3.8 years; June 22, 4.3 years; October 19, 3.7 years.

(7) Saginaw Bay yellow perch collected in 1943–55 averaged older than fish from the same Bay collected in 1929–30 and from other Great Lakes stocks (southern Green Bay, northern Lake Michigan, and Lake Erie).

(8) The estimation of year-class strength for 1939–52 was based on a series of comparisons of the percentage representation at various age groups. The strongest year classes were those of 1939 and 1952. The weakest were those of 1941 and 1945. The estimated year-class strength was correlated significantly with production 4, 5, and 6 years later, but the corresponding correlation with later commercial availability was not significant.

(9) It was not possible to establish a relation between year-class strength and the abundance of legal-sized fish in the year of hatching or with temperature, precipitation, water level, and turbidity.

(10) Length frequencies of the spawning-run samples were typically unimodal. The modal lengths (½-inch intervals) fluctuated from year to year but mostly lay within the range 6.0–6.9 inches, total length. The length-frequency distribution also varied seasonally in 1955. From April 18 to October 19 the modal intervals ranged from 5.5–5.9 inches (June 7) to 7.5–7.9 inches (October 19).

(11) The length distributions of successive age groups overlapped extensively. Fish of a particular length might belong to 2 to 5 age groups (mostly 4 age groups). The overlap made the length of Saginaw Bay perch a poor index of age.

(12) The length composition of the spring collections of Saginaw Bay yellow perch changed enormously between 1929–30 (modal length 8.5–8.9 inches) and 1943–55 (mode at 6.5–6.9 inches). At the same time the percentage of legal-sized fish (8½ inches and more) dropped from 73.9 percent in 1929–30 to 11.0 percent in 1943–55.

(13) The relation between the total length in inches (L) and the weight in ounces (W) of the 4,285 Saginaw Bay yellow perch in the combined collections was described satisfactorily by the equation:

$$W = 3.9975 \times 10^{-3} L^{3.260}$$

The value of the exponent in this equation was greater than that determined for Saginaw Bay fish in 1929–30 or for any other Great Lakes stock of perch.

(14) The annual variations of weight were so small among fish of the same length, sex, and condition of the gonads that the data for different years were combined in the study of the relation between weight and sexual condition. No significant difference of weight existed between ripe and spent males. On the other hand, the females showed an average loss of 12.3 percent of their weight at spawning.

(15) The seasonal differences of weight were so slight that it is not possible to speak of a seasonal trend. The males and spent females of the spawning-run sample usually were lighter than fish caught on June 22 and October 19. Ripe females had a somewhat weaker tendency to be heavier than fish caught later in the year.

(16) Because in 1954 scales were taken from above the lateral line rather than from below, as in other collections, it was necessary to establish two body-scale curves for the calculation of growth. These curves were based on "key" scales from above and below the lateral line of 520 fish.

(17) For scales collected from below the lateral line, the direct-proportion method was valid for the calculation of growth to the end of various years of life for standard lengths of 70 mm. and greater. Direct-proportion calculated lengths below 70 mm. were underestimates and had to be corrected on the basis of the empirical body-scale curve.

(18) The relation between fish length (standard length in millimeters) and the scale radius for scales above the lateral line was a straight line with a 30-mm. intercept on the length axis. Lengths computed from this relation were overestimates at values of 75 mm. and shorter. Corrections were determined from the empirical body-scale curve.

(19) Growth histories of the same fish as computed from measurements of scales from above and from below the lateral line were nearly identical except for the calculated lengths at the end of second year of life (discrepancies at this age averaged 3.6 mm.).

(20) The calculated lengths for a particular year of life tended to decrease as the fish grew older. These discrepancies in calculated length were most pronounced in the later years of life, particularly after the second year. They differed from "Lee's phenomenon" of apparent decrease in growth rate in which earlier years are affected most.

(21) The principal causes of discrepancies among calculated lengths are: Biased sampling from selective action of gears and from segregation by sexual maturity and size; higher mortality of the faster growing fish in the fishery. A higher natural mortality rate in faster growing fish also may be possible.

(22) The lengths of the sexes were similar in the first and second year of life. In later years the females were the longer; 0.3 inch at the end of the third year of life to 1.8 inches at the end of the seventh. The annual increments of growth in length decreased progressively with age among males and irregularly among females. Males reached the legal length of 8½ inches in about 6 years and females in a little more than 4½ years.

(23) The annual fluctuations of growth in length the first year and in the later years of life were dissimilar.

(24) The poorest first-year growth (9.2 percent less than the 1942–51 average) was made in 1942. In subsequent years a strong trend toward improvement of growth was apparent. The best first-year growth was 8.8 percent above average in 1951.

(25) No correlation could be demonstrated between first-year growth and: Year-class strength in year of growth; temperature; precipitation; water level. Significant negative correlation was found between first-year growth and turbidity in June (and possibly July). Possible explanations

of apparent effects of turbidity on fluctuation of growth were given.

(26) Fluctuations in growth in the later years of life were largely without trend. The maximum value (1948) was 16.8 percent above the 1944–54 average and the minimum (1952) was 16.2 percent below average.

(27) Little or no evidence was discovered of a correlation between growth in the second and later years of life and: Commercial production; abundance of legal-sized fish; temperature; precipitation; turbidity. Evidence was strong that growth had fluctuated inversely with the water level for May to October. No ecological explanation could be offered as to how water level might affect growth.

(28) The calculated weights of the females were higher than those of the males in all years of life except the first year where the increments were nearly equal. At the end of the second year of life and in subsequent years, the females were consistently heavier than the males. In the sixth and seventh years of life the weights of the females were nearly double those of males.

(29) The annual increments of weight for both sexes increased throughout life. The females attained their greatest advantage in annual increase over the males in the sixth year of life when they added more than 2½ times the weight gained by the males.

(30) The annual fluctuations of growth in weight were similar to those of growth in length but covered a wider range.

(31) The Saginaw Bay yellow perch collected in 1943–55 had grown much more slowly than fish collected from the Bay in 1929–30 and from other Great Lakes waters. Possible factors of the decrease in growth rate in Saginaw Bay were discussed. It was concluded that the increase in population density (about sevenfold or greater) was probably the cause.

(32) Male yellow perch in Saginaw Bay matured at a smaller size than females. Nearly all the males were mature at the length of 5.0 to 7.5 inches. All males more than 7½ inches long were mature. Among females 44 percent were mature at 5.5–5.9 inches, 80 percent at 7.0–7.4 inches; 95 percent at 8.0–8.4 inches. All females more than 9 inches long were mature.

(33) The sex ratio of Saginaw Bay yellow perch from the spawning runs in 1943–55 varied widely from year to year. The percentage of males ranged from 26 percent in 1945 to 87 percent in 1954. For all the collections combined the males constituted 62 percent. The sex ratio also varied seasonally (from 70 percent males on April 18 to 30 percent on October 19 in the 1955 samples).

(34) In 1929–30 the males grew scarcer with increasing age whereas in most of the 1943–55 samples the percentage of males increased with age. For the combined spawning-run collections the percentage of males rose from 17 percent in age group II to 77 percent in age group VI and then dropped to 65 percent in the VII group. The 4 older fish, however, were all females. The fact that a rise in the percentage of males with increase of age has been shown by other authors for populations of stunted perch suggests that the change in growth rate of Saginaw Bay yellow perch in recent years was also the cause of this reversal in the changes of the sex ratio with age.

LITERATURE CITED

ADAMS, MILTON P.

1937. Saginaw Valley report. Mich. Stream Control Comm., 104 pp.

ALLIN, A. E.

1929. Seining records and food of the intermediate stages of Lake Erie fishes. Bull. Buffalo Soc. Nat. Sci., (1928), vol. 14, no. 3, pp. 188–194.

ALM, GUNNAR.

1946. Reasons for the occurrence of stunted fish populations with special regard to the perch. Medd. Kungl. Lantbruksst. nr. 25, 146 S.

BECKMAN, WILLIAM C.

1941. Increased growth rate of rock bass, *Ambloplites rupestris* (Rafinesque), following reduction in the density of the population. Trans. Am. Fish. Soc., vol. 70 (1940), pp. 143–148.

1943. Further studies on the increased growth rate of the rock bass, *Ambloplites rupestris* (Rafinesque), following the reduction in density of the population. Trans. Am. Fish. Soc., vol. 72 (1942), pp. 72–78.

1950. Changes in growth rates of fishes following reduction in population densities by winterkill. Trans. Am. Fish. Soc., vol. 78 (1948), pp. 82–90.

BLEGVAD, H.

1933. Plaice transplantations. Jour. du Cons., Cons. Perm. Internat. Exp. Mer, vol. 8, pp. 161–180.

GORLEY, J. O.

1912. Report on the experimental transplantation of plaice to the Dogger Bank carried out by the Marines Biological Association in the years 1904–8. Internat. Fish. Invest., Rep. 4 (Southern Area Cd. 6125), pp. 1–79.

BÜCKMANN, ADOLF.

1932. Die Frage nach der Zweckmässigkeit des Schutzes untermässiger Fische und die Voraussetzungen für ihre Beantwortung. Rapp. et Procès-Verb., Cons. Perm. Internat. Exp. Mer, vol. 80, 16 pp.

BUTLER, ROBERT L., and LLOYD L. SMITH, JR.

1953. A method for cellulose acetate impressions of fish scales, with a measurement of its reliability. Prog. Fish-Cult., vol. 15, pp. 175–178.

CARLANDER, KENNETH D.

1945a. Age, growth, sexual maturity, and population fluctuations of the yellow pike-perch, *Stizostedion vitreum vitreum* (Mitchill), with reference to the commercial fisheries, Lake of the Woods, Minnesota. Trans. Am. Fish. Soc., vol. 73 (1943), pp. 90–107.

1945b. Growth, length-weight relationship and population fluctuations of the tullibee, *Leucichthys artedi tullibee* (Richardson), with reference to the commercial fisheries, Lake of the Woods, Minnesota. Trans. Am. Fish. Soc., vol. 73 (1943), pp. 125–136.

1950. Growth rate studies of saugers, *Stizostedion canadense canadense* (Smith) and yellow perch, *Perca flavescens* (Mitchill) from Lake of the Woods, Minnesota. Trans. Am. Fish. Soc., vol. 79 (1949), pp. 30–42.

DEASON, HILARY J.

1933. Preliminary report on the growth rate, dominance, and maturity of the pike-perches (*Stizostedion*) of Lake Erie. Trans. Am. Fish. Soc., vol. 63, pp. 348–360.

DEASON, HILARY J., and RALPH HILE.

1947. Age and growth of the kiyi, *Leucichthys kiyi* Koelz, in Lake Michigan. Trans. Am. Fish. Soc., vol. 74 (1944), pp. 88–142.

DOAN, KENNETH H.

1942. Some meteorological and limnological conditions as factors in the abundance of certain fishes in Lake Erie. Ecol. Mono., vol. 12, pp. 293–314.

ESCHMEYER, R. WILLIAM.

1937. Some characteristics of a population of stunted perch. Pap. Mich. Acad. Sci., Arts, and Lett., vol. 22 (1936), pp. 613–628.

1938. Further studies of perch populations. Pap. Mich. Acad. Sci., Arts, and Lett., vol. 23 (1937), pp. 611–631.

EWERS, LELA A.

1933. Summary report of Crustacea used as food by the fishes of the western end of Lake Erie. Trans. Am. Fish. Soc., vol. 63, pp. 379–390.

FARRAN, G. P.

1936. On the mesh of herring drift-nets in relation to the condition factor of the fish. Jour. du Cons., Cons. Perm. Internat. Exp. Mer, vol. 11, pp. 43–52.

FRY, F. E. J.

1953. The 1944 year class of lake trout in South Bay, Lake Huron. Trans. Am. Fish. Soc., vol. 82 (1952), pp. 178–192.

HASLER, ARTHUR D., and D. S. FARNER.

1942. Fisheries investigation in Crater Lake, Oregon, 1937–40. Jour. Wildlife Man., vol. 6, pp. 319–327.

HILE, RALPH.

1936. Age and growth of the cisco, *Leucichthys artedi* (Le Sueur), in the lakes of the northeastern highlands, Wisconsin. Bull. U. S. Bur. Fish., vol. 48, pp. 211–317.

1937. The increase in the abundance of the yellow pike-perch, *Stizostedion vitreum* (Mitchill), in Lakes Huron and Michigan, in relation to the artificial propagation of the species. Trans. Am. Fish. Soc., vol. 66 (1936), pp. 143–159.

1941. Age and growth of the rock bass, *Ambloplites rupestris* (Rafinesque), in Nebish Lake, Wisconsin. Trans. Wis. Acad. Sci., Arts, and Lett., vol. 33, pp. 189–337.

1948. Standardization of methods of expressing lengths and weights of fish. Trans. Am. Fish. Soc., vol. 75 (1945), pp. 157–164.

1950. Green Bay walleyes. A report on the scientific investigation of the marked increase in abundance of walleyes in Green Bay. The Fisherman, vol. 18, no. 3, pp. 5–6.

1954. Fluctuations in growth and year-class strength of the walleye in Saginaw Bay. Fish. Bull., U. S. Fish and Wildlife Service, vol. 56, pp. 7–59.

HILE, RALPH, and FRANK W. JOBES.

1941. Age, growth, and production of the yellow perch, *Perca flavescens* (Mitchill), of Saginaw Bay. Trans. Am. Fish. Soc., vol. 70 (1940), pp. 102–122.

1942. Age and growth of the yellow perch, *Perca flavescens* (Mitchill), in the Wisconsin waters of Green Bay and northern Lake Michigan. Pap. Mich. Acad. Sci., Arts, and Lett., vol. 27 (1941), pp. 241–266.

HILE, RALPH, and CHANCEY JUDAY.

1941. Bathymetric distribution of fish in lakes of the northeastern highlands, Wisconsin. Trans. Wis. Acad. Sci., Arts, and Lett., vol. 33, pp. 147–187.

HILE, RALPH, GEORGE F. LUNGER, and HOWARD J. BUETTNER.

1953. Fluctuations in the fisheries of State of Michigan waters of Green Bay. Fish. Bull., U. S. Fish and Wildlife Service, vol. 54, pp. 1–34.

HJORT, JOHAN.

1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. et Procès-Verb., Cons. Perm. Internat. Exp. Mer, vol. 20, 288 pp.

JOBES, FRANK W.

1933. Preliminary report on the age and growth of the yellow perch (*Perca flavescens* Mitchill) from Lake Erie, as determined from a study of its scales. Pap. Mich. Acad. Sci., Arts, and Lett., vol. 17 (1932), pp. 643–652.

1943. The age, growth, and bathymetric distribution of Reighard's chub, *Leucichthys reighardi* Koelz, in Lake Michigan. Trans. Am. Fish. Soc., vol. 72 (1942), pp. 108–135.

JOBES, FRANK W.—continued
1949a. The age, growth, and bathymetric distribution of the bloater, *Leucichthys hoyi* (Gill), in Lake Michigan. Pap. Mich. Acad. Sci., Arts, and Lett., vol. 33 (1947), pp. 135–172.
1949b. The age, growth, and distribution of the longjaw cisco, *Leucichthys alpenae* Koelz, in Lake Michigan. Trans. Am. Fish. Soc., vol. 76 (1946), pp. 215–247.
1952. Age, growth, and production of yellow perch in Lake Erie. Fish. Bull., U. S. Fish and Wildlife Service, vol. 52, pp. 205–266.

LANGLOIS, THOMAS H.
1941. Two processes operating for the reduction in abundance or elimination of fish species from certain types of water areas. Trans. Sixth N. Am. Wildlife Conf., pp. 189–201.

LE CREN, E. D.
1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatalis*). Jour. Animal Ecol., vol. 20, pp. 201–219.

LEE, ROSA M.
1920. A review of the methods of age and growth determination in fishes by means of scales. Min. Agric. and Fish., Fish. Invest., ser. II, vol. 4, no. 2, pp. 1–32.

PYCHA, RICHARD L., and LLOYD L. SMITH, JR.
1955. Early life history of the yellow perch, *Perca flavescens* (Mitchill), in the Red Lakes, Minnesota. Trans. Am. Fish. Soc., vol. 84 (1954), pp. 249–260.

RUSSELL, E. S.
1932. Is the destruction of undersized fish by trawling prejudicial to the stock? Rapp. et Procès-Verb., Cons. Perm. Internat. Exp. Mer, vol. 80, pp. 2–13.

SCHNEBERGER, EDWARD.
1935. Growth of the yellow perch (*Perca flavescens* Mitchill) in Nebish, Silver and Weber Lakes, Vilas County, Wisconsin. Trans. Wis. Acad. Sci., Arts, and Lett., vol. 29, pp. 103–130.
1937. The biological and economic importance of the smelt in Green Bay. Trans. Am. Fish. Soc., vol. 66 (1936), pp. 139–142.

SCOTT, W. B.
1951. Fluctuations in abundance of the Lake Erie cisco (*Leucichthys artedi*) population. Royal Ont. Mus. Zool., Contrib., no. 32, 41 pp.

SEMPER, KARL.
1880. Die natürlichen Existenzbedingungen der Thiere. Erster Theil. F. A. Brockhaus, Leipzig, x + 299 S.

SMITH, STANFORD H.
1954. A method of producing plastic impressions of fish scales without the use of heat. Prog. Fish-Cult., vol. 16, pp. 75–78.
1956. Life history of lake herring of Green Bay, Lake Michigan. Fish. Bull., U. S. Fish and Wildlife Service, vol. 57, pp. 87–138.

TURNER, CLARENCE L.
1920. Distribution, food and fish associates of young perch in the Bass Island region of Lake Erie. Ohio Jour. Sci., vol. 20, pp. 137–152.

VAN OOSTEN, JOHN.
1929. Life history of the lake herring (*Leucichthys artedi* Le Sueur) of Lake Huron as revealed by its scales, with a critique of the scale method. Bull. U. S. Bur. Fish., vol. 44 (1928), pp. 265–428.
1936. The mortality of fish in Lake Erie. Great Lakes Fisherman, vol. 1, no. 4, pp. 2–3.
1937. The dispersal of smelt, *Osmerus mordax* (Mitchill), in the Great Lakes region. Trans. Am. Fish. Soc., vol. 66 (1936), pp. 160–171.
1938. The age and growth of the Lake Erie sheepshead, *Aplodinotus grunniens* Rafinesque. Pap. Mich. Acad. Sci., Arts, and Lett., vol. 23 (1937), pp. 651–668.
1942. The age and growth of the Lake Erie white bass, *Lepibema chrysops* (Rafinesque). Pap. Mich. Acad. Sci., Arts, and Lett., vol. 27 (1941), pp. 307–334.
1944. Factors affecting the growth of fish. Trans. Ninth N. Am. Wildlife Conf., pp. 177–183.
1947. Mortality of smelt, *Osmerus mordax* (Mitchill), in Lakes Huron and Michigan during the fall and winter of 1942–1943. Trans. Am. Fish. Soc., vol. 74 (1944), pp. 310–337.
1948. Turbidity as a factor in the decline of Great Lakes fishes with special reference to Lake Erie. Trans. Am. Fish. Soc., vol. 75 (1945), pp. 281–322.

VAN OOSTEN, JOHN, H. J. DEASON, and FRANK W. JOBES.
1934. A microprojection machine designed for the study of fish scales. Jour. du Cons., Cons. Perm. Internat. Exp. Mer, vol. 9, pp. 241–248.

VAN OOSTEN, JOHN, and RALPH HILE.
1949. Age and growth of the lake whitefish, *Coregonus clupeaformis* (Mitchill), in Lake Erie. Trans. Am. Fish. Soc., vol. 77 (1947), pp. 178–249.

WATT, KENNETH E. F.
1956. The choice and solution of mathematical models for predicting and maximizing the yield of a fishery. Jour. Fish. Res. Bd. Canada, vol. 13, pp. 613–645.

WELLER, THOMAS H.
1938. Note on the sex ratio of the yellow perch in Douglas Lake, Cheboygan County, Michigan. Copeia 1938, no. 2, pp. 61–64.

WILLER, ALFRED.
1929. Untersuchungen über das Wachstum von Fischen. Verh. intarnat. Verein. theoret. und angewandte Limnol., Bd. 4, S. 668–684.

Blank page retained for pagination

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

YOUNG JACK CREVALLES (*CARANX* SPECIES) OFF THE SOUTHEASTERN ATLANTIC COAST OF THE UNITED STATES

BY FREDERICK H. BERRY

FISHERY BULLETIN 152

From Fishery Bulletin of the Fish and Wildlife Service

VOLUME 59

UNITED STATES GOVERNMENT PRINTING OFFICE • WASHINGTON • 1959

For sale by the Superintendent of Documents, U. S. Government Printing Office, Washington 25, D. C.
Price 65 cents

Library of Congress catalog card for this bulletin:

Berry, Frederick Henry.

Young jack crevalles (*Caranx* species) off the southeastern Atlantic coast of the United States. Washington, U. S. Govt. Print. Off., 1959.

iv, 417–535 p. illus., maps, diagrs., tables. 26 cm. (U. S. Fish and Wildlife Service. Fishery bulletin 152)

"From Fishery bulletin of the Fish and Wildlife Service, volume 59."

Bibliography: p. 526–532.

1. Caranx. I. Title. (Series: U. S. Fish and Wildlife Service. Fishery bulletin, v. 59, no. 152)

[SH11.A25 vol. 59, no. 152] Int 59–55

U. S. Dept. of the Interior. Library
for Library of Congress

Library of Congress catalog card for the series, Fishery Bulletin of the Fish and Wildlife Service:

U. S. *Fish and Wildlife Service.*

Fishery bulletin. v. 1–

Washington, U. S. Govt. Print. Off., 1881–19

v. in illus., maps (part fold.) 23–28 cm.

Some vols. issued in the congressional series as Senate or House documents.

Bulletins composing v. 47– also numbered 1–

Title varies: v. 1–49, Bulletin.

Vols. 1–49 issued by Bureau of Fisheries (called Fish Commission, v. 1–23)

1. Fisheries—U. S. 2. Fish-culture—U. S. I. Title.

SH11.A25 639.206173 9–35239 rev 2*

Library of Congress [r55e½]

CONTENTS

	Page
Introduction	417
Methods	418
Definitions	419
Key to Western Atlantic species of *Caranx*	424
Comparison of species	426
Description of species	441
Caranx crysos	441
Caranx ruber	458
Caranx bartholomaei	472
Caranx sp. ("*latus* and/or *hippos*")	487
Caranx latus	491
Caranx hippos	503
Caranx dentex	521
Caranx lugubris	523
Hemicaranx fasciatus	525
Uraspis heidi	526
Literature cited	526
Addenda	532

ABSTRACT

The young of five species of jack crevalles (*Caranx*) commonly occur off the Atlantic coast of the United States: *Caranx crysos*, *C. ruber*, *C. bartholomaei*, *C. latus*, and *C. hippos*. Morphometric, meristic, and morphological characters, and serial illustrations are presented for each of these species from the smallest larval or early juvenile sizes available into the better-known juvenile and adult stages. Development of certain body parts is defined and discussed, and comparisons are made for the species. The smallest available specimens of *C. dentex* and *C. lugubris*—species which occur in the Western Atlantic, but have not been reliably reported from inshore waters of the United States—are briefly compared with the five common species. Nomenclatorial problems are discussed; several identification and distribution records are corrected; and a key to the seven species is given.

Apparently the five common species have an offshore larval existence. Off the southeastern Atlantic coast of the United States the larval stage occurs in association with the offshore waters of the Gulf Stream. *C. latus* and *C. hippos* lose their preopercular spines (a larval character persisting into the juvenile stage) at about 20 mm standard length—at a smaller body size than occurs in the other three common species—and they tend to migrate inshore at about this size. *C. crysos*, the relatively most-abundant young *Caranx* in this area, apparently does not migrate inshore before its late juvenile stage; *C. bartholomaei* occurs inshore only occasionally as a juvenile or adult; and *C. ruber* has an apparent tendency to remain offshore. As late juveniles or adults, all these species may return to more southern areas.

The following suppositions are made regarding spawning of the five common species: Spawning tends to occur in offshore waters, at least partially in association with major current systems, and extends from about February into September. *C. bartholomaei* probably spawns off the southeastern Atlantic coast of the United States, and the other four common species do spawn there; but the major spawning areas for these species are to the south of this area.

The time and place of spawning and the larval and early juvenile forms are unknown for *C. dentex* and *C. lugubris*. Their juvenile and adult habitats are apparently in offshore waters and in association with offshore islands.

The smallest, definitely identified specimens available for study were, in standard length, *C. crysos*, 5.4 mm.; *C. ruber*, 12.4 mm.; *C. bartholomaei*, 8.1 mm.; *C. latus*, 16.1 mm.; *C. hippos*, 15.3 mm.; *C. dentex*, 87 mm.; and *C. lugubris*, 242 mm. A series of specimens, 5.4 to 8.3 mm., identified only as *Caranx* sp. ("*latus* and/or *hippos*") includes either one or both of these species.

The affinity of *Hemicaranx fascialus* (Cuvier) and *Uraspis heidi* Fowler to the genus *Caranx* is briefly discussed.

YOUNG JACK CREVALLES (*CARANX* SPECIES) OFF THE SOUTHEASTERN ATLANTIC COAST OF THE UNITED STATES

By FREDERICK H. BERRY, *Fishery Research Biologist*
BUREAU OF COMMERCIAL FISHERIES

The family Carangidae is noted for the diversity of body form of its species. Certain of these species undergo an ontogenetic change of form in having a deep-bodied larval stage and an elongated adult shape that is inverse to the development of many other fishes in which the larvae are narrow-bodied forms and the depth generally increases as the fish mature.

The genus *Caranx* has cosmopolitan distribution in tropical and subtropical waters, and extends into more temperate waters. The young jack crevalles furnish food for many surface-feeding carnivores, and the adults are themselves predatory on other fishes. In some areas they are utilized as food fish or for bait, and everywhere are recognized as respectable game fish.

Five species of *Caranx* commonly occur in waters off the Atlantic coast of the southeastern United States: *C. latus* Agassiz, *C. hippos* (Linnaeus), *C. bartholomaei* Cuvier, *C. ruber* (Bloch), and *C. crysos* (Mitchill). Two other species, *C. dentex* (Bloch and Schneider) and *C. lugubris* Poey, may occur there, but no authentic records exist. Unquestioned records of *C. lugubris* exist for Cuba, the Bahamas, and Bermuda, and of *C. dentex* for Bermuda. Two other species of Carangidae, *Hemicaranx fasciatus* (Cuvier) and *Uraspis heidi* Fowler, are briefly considered relative to their affinity to the genus *Caranx*.

Nichols has published a series of papers (see Literature Cited, p. 530) over the past several decades, giving descriptions, comparisons, and records of distribution for young *Caranx* in the Western Atlantic. Ginsburg (1952) gave accounts of late juveniles and adults of four of the species, primarily from the Gulf of Mexico. Other information on the young of *Caranx* is meager, particularly in the area considered (off the south Atlantic coast of the United States). The nomenclature of five of the seven species is still in question.

The specimens of young *Caranx* taken on eight of the nine cruises of the *Theodore N. Gill* during 1953–54 in the waters off the Atlantic coast of the southeastern United States by the U. S. Fish and Wildlife Service's South Atlantic Fishery Investigations represent the most complete series of young of three of the species ever collected in this area. This collection was supplemented by specimens from the U. S. National Museum (USNM), University of Florida Museum (UF), Bingham Oceanographic Collection (BOC), Academy of Natural Sciences of Philadelphia (ANSP), Chaplin Bahaman Shore Fish Program (CBSFP), Museum of Comparative Zoology (MCZ), American Museum of Natural History (AMNH), Charleston Museum (ChM), Bears Bluff Laboratories (BBL), and the U. S. Fish and Wildlife Service's Gulf Fisheries Exploration and Gear Research (GFEGR) at Pascagoula, Miss., Gulf Fisheries Investigations (GFI) at Galveston, Tex., and Menhaden Investigations (MI) at Beaufort, N. C., and personally acquired and local collections of the South Atlantic Fishery Investigations (SAFI) at Brunswick, Ga.

Although concerned primarily with the *Gill* collections and museum specimens from waters off the southeastern Atlantic coast of the United States, this discussion cannot be confined to that area. Because the larvae of the five common species of *Caranx* and the juveniles of three of them apparently are associated with the Gulf Stream in this area, it is quite likely that the developing young in this area represent only a portion of the population of each species, and that the populations, associated with current systems, extend from off the northern coast of South America into the Caribbean Sea and Gulf of Mexico, through the Florida Straits and along the

NOTE.—Approved for publication, May 7, 1958. Fishery Bulletin 152.

northern Bahamas, into the North Atlantic Current east of the Grand Banks. If such is the case, spawning might be expected to occur along all but the more northern portions of the route, and the young forms might be expected to follow or be moved by the drift of the Gulf Stream and the currents contributing to the Stream until a critical stage, at which time they would act against the effects of the stream.

The purposes of the present work are to expand the known definitions and variability of the morphological, morphometric, and meristic characters of *Caranx* species off the Atlantic coast of the United States, principally the five common species, to facilitate their identification and to furnish a basis for comparison with the poorly known relationships of closely related species or forms from other geographic areas; to provide a set of serial illustrations to depict the changes from the smallest larval forms available into the better-known juvenile stages; to depict growth relationships for selected body parts; and to discuss distribution and theories of time and place of reproduction in waters off the southeastern United States.

I am grateful to Isaac Ginsburg and Elbert H. Ahlstrom of the U. S. Fish and Wildlife Service for their critical review of the manuscript and to John C. Briggs and Arnold B. Grobman of the University of Florida for their propitious suggestions. The loan or procurement of specimens and information on specimens by the following were instrumental in the study: Leonard P. Schultz, U. S. National Museum; John C. Briggs, University of Florida Museum; James E. Böhlke, Academy of Natural Sciences of Philadelphia and Chaplin Bahaman Shore Fish Program; E. Milby Burton, Charleston Museum; James E. Morrow, Bingham Oceanographic Collection; Myvanwy M. Dick, Museum of Comparative Zoology; G. Robert Lunz, Bears Bluff Laboratories; John T. Nichols, American Museum of Natural History; Harvey R. Bullis, Jr., Edgar L. Arnold, Jr., Fred C. June, David K. Caldwell, Doyle Sutherland, and Melba Wilson, U. S. Fish and Wildlife Service; E. Lowe Pierce and Benjamin B. Leavitt, University of Florida; G. Palmer, British Museum (Natural History); David H. Gould, Robert H. Godley, J. A. Jones, and William F. Ricks, Georgia Game and Fish Commission; Edwin H. Chandler, Lewis Crab Co., Brunswick, Ga.; and J. B. Siebenaler and Winfield Brady, Gulfarium, Fort Walton Beach, Fla. The assistance and suggestions of members of the staff of the South Atlantic Fishery Investigations were most helpful in preparation of the manuscript.

METHODS

COUNTS

Meristic counts on fish of less than about 200 mm. standard length were made under magnification. Aberrant counts, such as occur on injured specimens, were either omitted or specifically described.

MEASUREMENTS

All measurements of fish of less than about 45 mm. standard length were made with a calibrated micrometer eyepiece and a stereoscopic microscope, as were smaller structures on fish above this size. Other measurements were made with a pair of fine-point dividers. Measurements of preopercular spines were recorded to the nearest one-one hundredth millimeter. All other measurements were recorded as follows: Up to 45 mm. standard length, to the nearest one-tenth millimeter; 45 to 100 mm. standard length, to the nearest one-half millimeter; over 100 mm. standard length, to the nearest millimeter—with the exception of the standard lengths of fish not included in the graphs, which were measured to the nearest one-half millimeter if smaller than 100 mm., and to the nearest millimeter if larger.

The figures and tables in this report do not include data on the relation of the lengths of the fourth dorsal spine, the second dorsal soft-ray, pelvic fin, and body depth at first anal spine to standard length; or measurements of the first and second anal soft-rays.

CONSTRUCTION AND INTERPRETATION OF GRAPHS

Graphs of the relation of the mean number of scutes, of the mean lateral-line ratio, and of the preopercular-angle spine length to standard length for the individual species have been fitted with visually estimated perimeters enclosing the dots or other described marks that represent coordinates of the individual specimens. The graphical area enclosed by each perimeter is intended to depict the range of variation for that relationship.

Although the perimeters were drawn liberally in an attempt to estimate population variations from the samples, some specimens may be expected to exceed the estimates. Still, it provides a useful treatment of these highly variable relationships. In the composite graphs of these relationships under Comparison of Species, page 426, the perimeter for each species is specifically symbolized.

On the graphs illustrating the relation of third dorsal spine length, first dorsal soft-ray length, pectoral length, body depth at pelvic, head length, eye diameter, and snout length to standard length, each dot or other described mark represents the coordinate of a single specimen. Arithmetical plots of individual variates indicated that in most instances the formula for a rectilinear regression, $Y=a+bX$, adequately described the relationships. The regression lines for the five common species were determined by the method of least squares over a designated size range of the specimens represented in each graph. A line so determined is referred to in the text as the "calculated regression line" and is illustrated in the graphs as a solid line. The trend of such a line is frequently extended on the graphs (as a line of dashes) to allow an estimate of the relation of specimens larger or smaller than those included in the calculated regression line. The composite graphs of these relations under Comparison of Species consist only of the calculated regression lines (specifically symbolized for each species). Because of the limitations of material and methods, only certain size ranges are suitable for comparison.

Use of the term "inflection," applied to the descriptions of the relations of body parts follows Martin (1949) and denotes a change in slope of the relative growth line.

FISH ILLUSTRATIONS

Fish less than 16 mm. standard length were drawn with a camera lucida. Fish above this size were photographed, and an enlargement of the negative was used to reproduce the outlines.

NOMENCLATURE AND SYNONYMY

The discussions of nomenclature point out, with the exception of *ruber* and *bartholomaei*, that the relationships of the Western Atlantic species of *Caranx* to certain closely related forms from other areas are uncertain; consequently, the nomenclature is tentative. Since authors have differed in opinion concerning the nomenclature and synonymy of forms ascribed to the genus *Caranx*, a comprehensive review of the literature was necessary to understand the problems involved. This is briefly outlined under the species concerned. The synonymies are mainly composed of only the earliest reference to each applicable binomial that I have found. The principal purpose is not to revise the nomenclature, but to point out discrepancies that exist and to stabilize the usage until adequate revisions are made.

THEODORE N. GILL COLLECTIONS

All methods employed on the *Gill* cruises—including plankton and dip-net collections, stomach contents of species caught by trolling and hand line, and network of collecting stations—are given by Anderson, Gehringer, and Cohen (1956). The following abbreviations apply to the *Gill* cruises and specimens: Reg. (regular station), Spc. (special station), Std. (standard station, east of Elbow Cay, Bahamas), and TO (Tongue of the Ocean station, Bahamas).

DEFINITIONS

The definitions of measurements and counts and descriptions of terms are arranged in the same sequence in which the characters are considered in this and the following sections. Frequently, descriptions of ontogenetic changes are included. Since earlier workers have used varied, and often inadequately described, methods, some explanations in this section have been expanded for clarification.

BODY LENGTHS

Standard length.—Measured from the tip of the snout to the end of the hypural bones (the caudal base). All body lengths referred to are in standard length unless otherwise noted.

Fork length.—Measured from the tip of the snout to the end of the shortest median caudal ray.

Total length.—Measured from the tip of the snout to a vertical at the tip of the longest lobe of the caudal fin.

Body length conversion factors.—The rectilinear regression formula, $Y=a+bX$, was used to determine the conversions of total length and fork length to standard length. Standard length was used as the independent variate so that fork length$=a+b$ (standard length); total length$=a+b$

(standard length). For conversion to standard length the following formulas apply:

$$\text{Standard length}=\frac{\text{fork length}-}{b}a;$$

$$\text{standard length}=\frac{\text{total length}-}{b}a.$$

The following a and b values were obtained:

crysos
Fork length: $a=0.947$, $b=1.077$
Total length (less than 85 mm. standard length and 104 mm. total length): $a=-0.228$, $b=1.224$
Total length (more than 85 mm. standard length and 104 mm. total length): $a=-4.879$, $b=1.280$
ruber
Fork length: $a=1.020$, $b=1.078$
Total length: $a=-0.896$, $b=1.251$
bartholomaei
Fork length: $a=1.260$, $b=1.073$
Total length (less than 50 mm. standard length and 61 mm. total length): $a=0.151$, $b=1.219$
Total length (more than 50 mm. standard length and 61 mm. total length): $a=-2.609$, $b=1.267$
latus
Fork length: $a=1.242$, $b=1.082$
Total length: $a=-2.671$, $b=1.275$
hippos
Fork length: $a=1.006$, $b=1.076$
Total length (less than 50 mm. standard length and 60 mm. total length): $a=0.326$, $b=1.198$
Total length (more than 50 mm. standard length and 60 mm. total length): $a=-2.936$, $b=1.272$

Body lengths given by workers in total length and fork length and converted to standard length are designated in the following manner: "about x mm. (converted)."

DORSAL AND ANAL SPINES

Counts and descriptions.—The usual number of dorsal spines is nine—eight comprise the first dorsal fin, and the ninth is the first element of the second dorsal fin. In the few specimens which had only 6 or 7 spines in the first dorsal fin, the base or position of the missing spine or spines could usually be determined. On specimens of *hippos* larger than 200 mm., the first dorsal spine is relatively small and partially overgrown by skin.

A procumbent or recumbent dorsal spine in advance of the first dorsal-fin spines has been mentioned or tabulated in the dorsal-spine count by many authors (Nichols, 1912: 185; Fowler, 1941a: 85; Roxas and Agco, 1941: 39; Weber and de Beaufort, 1931; and others). This is not an articulated dorsal spine, but is shown on cleared and stained specimens of the five common species to be a pointed, forward extension of the first pterygiophore (the third or fourth interneural spine). It is more pronounced on smaller specimens and is discernible in figures 69 to 71 and 81 to 83.

There are three anal spines—the first and second remain in close proximity and become appreciably separated from the third with an increase in body size. The third spine has a positional relation to the anal soft-rays identical to that of the last dorsal spine to the dorsal soft-rays. The last dorsal spine and the third anal spine have been ignored or incorporated in the soft-ray counts by many authors.

Lengths.—The spines were measured in an erected position (if possible, otherwise estimated) on a chord from the anterior points of emergence from the skin to the tips.

DORSAL AND ANAL SOFT-RAYS

Definition.—In the early larvae, those rays which from their position in the second dorsal or the anal fin were considered as potentially segmented were counted as soft-rays.

Counts.—The buds or the bases of the soft-rays are readily visible with magnification and transmitted light in specimens from 8 mm. to more than 100 mm. standard length. Occasionally, malformed dorsal and anal fin-ray elements and missing rays were encountered—these are discussed under Comparison of Species, page 428. Malformed rays were enumerated in the total soft-ray counts. Counts for fins with missing soft-rays, indicated by a ray base without a ray, or by an abnormally wide space between any two rays, were not included in establishing ranges.

Tabulations showing the relation of number of dorsal soft-rays to number of anal soft-rays are used because their numbers are apparently intraspecifically correlated.

Lengths.—Measurements were made as for the dorsal spines, except on larger specimens that had developed the fleshy, scale-covered sheath along the base of the fin—in which instance the proximal point of measurement was taken at the emergence of the erected ray from above this sheath.

INTERNEURAL AND INTERHEMAL SPINES

The interneural and interhemal spines (pterygiophores) of at least the five common Atlantic species of *Caranx* possess posterior lateral projections. These are discernible in illustrations by Hollister (1941) in a lateral view from stained and cleared specimens of *ruber* (p. 43, fig. 19) and *latus* (p. 44, fig. 20).

Within certain size ranges in two of the species (*latus* and *hippos*) these projections extend above the dorsal surface of the body along both sides of the soft-rays of the dorsal and anal fins. They are similar to fin spines in appearance, although not so pointed, and are covered by little, if any, epidermis. None of the other five species studied had these projections protruded or extended above the body surface.

CAUDAL FIN

Description.—The principal rays extend to the posterior margin of the fin—the most-dorsal principal ray and the most-ventral principal ray are the only two that remain unbranched. The secondary caudal rays also remain unbranched.

Counts.—The count is given as principal rays above the median line plus those below. The number of secondary rays was determined on only a portion of the specimens examined.

Urostyle.—Described as visible in normally preserved specimens.

PECTORAL AND PELVIC FINS

Counts.—Counts were made of the fins on one side only, usually the left. Each fin contained one spine plus a number of soft-rays. The spines of the paired fins were similar in construction to each other and to the spines of the dorsal and anal fins.

Lengths.—Measurement of the longer of each of the paired fins was recorded if the lengths varied. Each fin was measured from the insertion of its spine to the tip of the longest ray, with the fin against the body.

BODY DEPTH

Depth at pelvic.—Measured as the distance between the ventral midline of the body at the insertions of the pelvic fins and the origin of the first dorsal spine.

Depth at first anal spine.—Measured as the distance between origin of the first anal spine and origin of the spine of the second dorsal fin (the ninth dorsal spine.)

Description.—Both depths are near-vertical. The depth at pelvic is more subject to distortion by stomach contents, but is preferable to depth at the first anal spine, which has a more anterior location with respect to the spine of the second dorsal fin at lengths of more than 50 to 70 mm. standard length.

HEAD

Length.—Measured from the tip of the snout to the posterior edge of the fleshy portion of the operculum.

EYE

Diameter.—Measured as the maximum diameter from the anterior to the posterior inner margins of the circumorbitals.

SNOUT

Length.—Measured as the least distance from the tip of the snout to the anterior inner margin of the circumorbitals.

GILL RAKERS

Counts.—Gill-raker counts were made on the first arch, usually on the left side. A gill raker located at the junction of the upper and lower limbs was included with the count for the lower limb because the major portion of its base originates on the lower limb, and its inclusion facilitated the correlation of the numbers of upper- to lower-limb gill rakers. Rudimentary gill rakers (tubercles or very-shortened gill rakers) occurring at the origin of either limb were included in the total count for that limb. These rudimentary rakers are less definitive on larger specimens, but they could be accurately counted on the largest sizes of each species that were examined (up to 830 mm. standard length on *hippos*). Gill-raker counts on specimens less than 20 mm. were not included in the tables, although specimens between 14 mm. and 20 mm. apparently have formed the adult complement. Relation of the numbers of upper- to lower-limb gill rakers is used to show that they apparently are intraspecifically correlated.

SCUTES

Definition.—In *Caranx*, the term "completely developed scute" defines a modified scale situated

along the straight portion of the lateral line. It is vertically and usually horizontally expanded with respect to other body scales, usually is thicker and harder than other body scales, and the posterior margin either terminates in a posteriorly projecting, flattened or slightly elevated spine, or ends in an apex, with the angle of the scute formed by this margin being not greater than 110° to 120°. In the following accounts, a reference to scutes having completed their development implies that they have developed the structural characters that will fit this definition. The physical development of enlarging and hardening continues with growth of the fish.

Scales in the straight lateral line which have not developed the structural characters defined here, but whose positional relationship indicates that they would have become completely developed scutes, are termed "developing scutes."

Counts.—Scutes were counted on both sides of the fish from the most-anterior to the most-posterior completely developed scute.

Relationship.—The mean of the number of scutes of the right and left sides was used because approximately 80 percent of the specimens examined showed an individual bilateral variation in this character. This variation on individual specimens examined ranged from 1 to 5 scutes in *hippos*, 1 to 4 in *latus*, *crysos*, and *ruber*, and 1 to 3 in *bartholomaei*. There was little correlation of this feature with the length of the fish, except that more variation was found at the smallest sizes (less than 30 mm. standard length) when the first scutes to complete their formation do so rapidly.

Explanation.—Some scutes immediately following the most-anterior completely developed scutes may not end in a spine or an apex—on smaller fish they have not completed development and on larger fish they may represent scutes which will never develop spines or whose weak spines have worn off; in either case they are included in the scute count.

Nichols (1920b: 29) remarked, "The most anterior scutes near the angle of the lateral line are small and poorly developed and the most posterior ones minute, so that the personal equation enters into their count somewhat." This applies more to the smaller forms, for in most specimens of more than 100 mm. the scutes are completely developed to the point of junction with the curved part of the lateral line and the terminal scute at the caudal base has a strong spine. Because of the variation in scutes in smaller fish, and because the adult complement of scutes is not present until the fish has grown to a size greater than 100 mm., I have applied an exacting definition and count. This has resulted in my counts being lower for fish of less than 100 mm. than are those usually given in the literature; but the counts on larger fish should approximate previous counts within the limits of personal bias. Use of the mean number of scutes will result in ranges being less variable than is the case when scutes are counted on only one side of a fish.

Ontogeny.—The first scutes to complete their development are located near the posterior two-thirds of the straight part of the lateral line, and the extent of development of the other scutes is graduated from these toward both ends of the lateral line.

LATERAL LINE

Measurements.—The curved part of the lateral line was measured as a chord of the arch from its junction with the upper edge of the shoulder girdle to its junction with the straight part of the lateral line. The straight part of the lateral line was measured from its junction with the curved part of the lateral line to its termination on the caudal fin; on fish less than about 16 to 18 mm. standard length, the formation had not progressed posteriorly to the caudal base, but the measurement was taken to the caudal base. Measurements were taken on both sides of the fish.

The point of junction of the two parts of the lateral line on some fish was marked by an abrupt upturning of the curved part, and on others by a gradual upturning—which forced an estimation of this point. By definition, this point occurs where the curved part bends upward from the straight part. The straight part that continues forward with no scutes or pores marking the continuation is called the false lateral line and is difficult to see on most *Caranx*.

The extension of the lateral line onto the caudal fin in the species of *Caranx* examined is contrary to a statement by Gill (1883: 488) in his description of characteristics of the family: "Lateral line continuous to and ending at the base of the caudal fin."

Ratio.—The mean of the quotients, obtained by dividing the length of the straight part of the

lateral line by the length of the curved part of the lateral line from each side, was used as the mean lateral-line ratio. This is expressed by the following formula: [(straight right ÷ curved right) + (straight left ÷ curved left)] ÷ 2 = mean lateral-line ratio.

Use of three variates in determining the relationship of the lateral-line ratio to standard length illustrates the interspecific differences of the lateral line better than use of only two variates. Previous taxonomic emphasis was placed on the ratio by Nichols (1921b, 1937a, 1938b, 1939), Nichols and Breder (1927), Wakiya (1924), and others. The mean of the ratios from both sides was used because frequent and appreciable differences were found between the two sides of a fish. For example, on a 44-mm. specimen of *bartholomaei* the point of junction of the curved and straight parts of the lateral line on the left side was under the fifth dorsal ray and on the right side it was under the eleventh dorsal ray.

PREOPERCULAR SPINES

Description.—The five common species of *Caranx* possess a spine, the preopercular-angle spine, that protrudes from the posterior margin of the preoperculum in the smallest sizes examined and persists to 16 to 49 mm. standard length (the maximum size of retention is variable among the species). Fish within this range may also possess from 1 to 8 smaller spines, the preopercular upper- and lower-limb spines, arranged in graduated series on the margins of the upper and lower limbs of the preoperculum.

Ontogeny.—The preopercular spines increase in length only up to a certain size (possibly to 7 mm. in *crysos*). Above this size, the lengths diminish, due to a cessation or diminution of spine growth and ventral and posterior expansion of the preopercular margin, until the spines are completely absorbed by the preoperculum.

Counts.—Spines were counted only if they protruded from the margin of the preoperculum and were not covered by a thickened layer of skin.

Lengths.—The preopercular-angle spine (the longest preopercular spine and the last to be absorbed) was the only spine measured. The measurement taken is represented by line *a* in figure 24. The longer spine was measured for each fish that showed bilateral variation in this length; if damage was obvious, a spine was not measured.

PIGMENTATION

Descriptions of pigmentation represented in the illustrations were made from microscopic observations of preserved specimens. Most of the specimens were preserved in formalin—a few in ethyl or isopropyl alcohol. Consequently, the yellows, greens, and other shades present in living or freshly caught specimens are absent. Melanophores have apparently faded from some of the smaller specimens, and their pigment descriptions may be incomplete.

DEVELOPMENTAL STAGES

Larval.—Defined as the stage of development commencing with hatching and ending with the completion of formation of the adult complement of fin rays. A ray was considered to be completely formed when it became partially ossified, as indicated by its staining red when treated with alizarin. The secondary caudal-fin rays are the last rays to complete their formation, which progresses anteriorly. The size at termination of the larval stage was difficult to delimit because only a few larval specimens were available, larvae of all species were not identified, and intraspecific variation in the size at completion of fin-ray formation could not be determined. Study of a series of alizarin-stained specimens of *crysos* (the most complete series available) showed that the fin rays had not completed formation on fish 7.5 mm. standard length and smaller, and that the next largest specimen, 8.5 mm., and all larger specimens had adult complements of fin rays. The specimens identified as "*latus* and/or *hippos*" (see p. 487) and the two smallest specimens of *bartholomaei* apparently show a similar size on formation of the adult complement of fin rays. Of the "*latus* and/or *hippos*" series, the 8.3-mm. specimen had completed development of the fin rays and the 6.9-mm. specimen had not. The 6.0-mm. *bartholomaei* had only partially completed formation of the fin rays, the 8.1-mm. *bartholomaei* had completed the formation with the possible exception of one or two dorsal and ventral secondary caudal rays, and the 10.5-mm. *bartholomaei* had completed formation of all fin rays. By analogy, the size at transformation from larva to juvenile in *Caranx* is estimated to be about 8.0 mm. standard length.

Juvenile.—Defined as commencing with the end of the larval stage and terminating with the attainment of sexual maturity. Size at the juvenile–adult transition stage has not been determined for any species because of the scarcity of records and specimens of mature individuals (the smallest adult recorded is a 225-mm. *crysos*). The juvenile fish develop body bars (blotches in *bartholomaei*) at about 15 to 20 mm. that persist to about 100 to 200 mm.; the size at disappearance of the bars varies with the species. The loss of these bars may have some connection with the onset of sexual maturity. Spines on the preoperculum are present on larval forms and disappear during the juvenile stage (between 16 mm. and 45 mm., varying with the species). These spines are considered larval structures that persist into the juvenile stage rather than a character that delimits the larval stage.

Adult.—Defined as commencing with the onset of sexual maturity.

KEY TO WESTERN ATLANTIC SPECIES OF *CARANX*

A key that would identify the seven species at all sizes could not be constructed because a complete size series was not available for comparison. The following key is intended for use with specimens larger than approximately 14 mm. standard length, the minimum size at which counts of gill rakers can be considered adequately accurate for taxonomic separation (fig. 2). The adult complements of dorsal and anal soft-rays have completed formation by 8 mm. (fig. 1). Although *latus* and *hippos* were not separated in specimens less than 10 mm., a "*latus* and/or *hippos*" series can be distinguished as having a greater depth at pelvic than does *crysos* or *bartholomaei* (fig. 9). Below 10 mm., the second anal spine is shorter in *bartholomaei* than in *crysos* (fig. 4).

A. Lower-limb gill rakers 31 to 35 ..... *ruber*,
(D. 26 to 30; A. 23 to 26; G. R. 10 to 14 + 31 to 35)

AA. Lower-limb gill rakers, 23 to 28

B. Mean number of scutes more than 35 on specimens larger than 50 mm. Mean lateral-line ratio more than 1.0. Dorsal-fin third spine shorter than first soft-ray (on specimens larger than 70 mm.) ..... *crysos*,
(D. 22 to 25; A. 19 to 21; G. R. 10 to 14 + 23 to 28)

BB. Mean number of scutes less than 35 on specimens larger than 50 mm. Mean lateral-line ratio less than 1.0. Dorsal-fin third spine longer than first soft-ray on specimens larger than 70 mm ..... *dentex*,[1]
(D. 24 to 27; A. 20 to 23; G. R. 11 to 13 + 26 to 28)

AAA. Lower-limb gill rakers 16 to 21

C. Dorsal soft-rays 25 to 28 ..... *bartholomaei*,
(D. 25 to 28; A. 21 to 24; G. R. 6 to 9 + 18 to 21)

CC. Dorsal soft-rays 19 to 23

D. Color brown to sooty black ..... *lugubris*,[2]
(D. 21 to 23; A. 17 to 20; G. R. 6 or 7 + 19 to 21

DD. Color green, yellow, and silver in adults; dark body bars in juveniles to more than 100 mm.; never completely brown or black

E. Chest completely scaled on specimens larger than 20 to 25 mm. Pigment of first dorsal fin concentrated between first and fourth spines in specimens about 17 to 45 mm. Pigment of posterior three body bars terminates immediately below straight lateral line on most specimens between about 20 to 60 mm ..... *latus*,
(D. 19 to 22; A. 16 to 18; G. R. 6 or 7 + 16 to 18)

EE. Chest with only a small patch of scales before pelvics on specimens larger than 25 mm. (fig. 85). Pigment of first dorsal fin spread over entire fin on specimens about 17 to 45 mm. Pigment of posterior three body bars extends to base of anal fin on specimens between about 15 to 60 mm ..... *hippos*,[3]
(D. 19 to 21; A. 16 or 17; G. R. 6 to 9 + 16 to 19)

[1] Specimens of *dentex* of less than 87 mm. standard length apparently have not been described, and characters suggested for use below this size are speculative. A partial separation of *crysos* and *dentex* may be effected by the number of dorsal and anal soft-rays: *crysos* with D. 22 or 23, A. 19 and *dentex* with D. 26 or 27, A. 22 or 23.

[2] Specimens of *lugubris* below 240 mm. standard length apparently have not been described. Above this size *lugubris* can be separated from *latus* and *hippos* by its blunter profile, higher mean lateral-line ratio (see fig. 93), and longer second dorsal fin lobe or first soft-ray length. A partial separation may be effected by numbers of dorsal and anal soft-rays and lower-limb gill rakers: *lugubris* with D. 23, A. 19 or 20, G. R. 20 or 21, and *latus* and *hippos* with D. 19 or 20, A. 16, G. R. 16 to 18. A completely scaled chest separates *lugubris* from *hippos*.

[3] A partial separation of *latus* and *hippos* may be effected by mean number of scutes (fig. 13) and mean lateral-line ratio (fig. 14) on specimens larger than 16 mm. and by body depth at pelvic (fig. 8) for specimens smaller than 17 mm. It is suggested that coordinate points of a questionable specimen be plotted on these figures—a value that does not fall within the overlapping range of the estimated perimeters will indicate a specific identity.

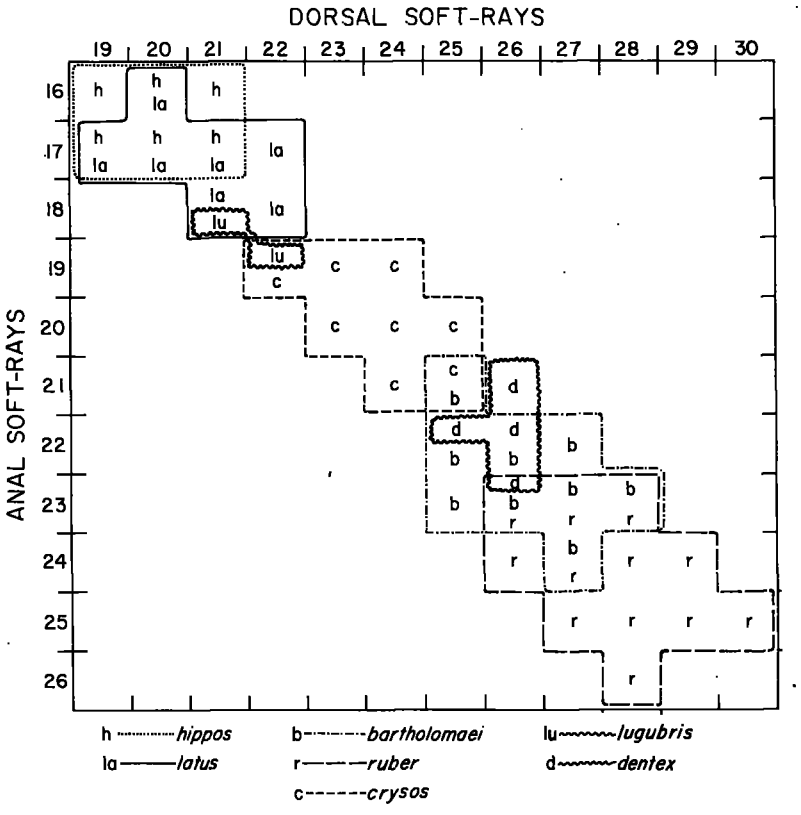

FIGURE 1.—Correlation of dorsal soft-rays and anal soft-rays for seven species of *Caranx*.

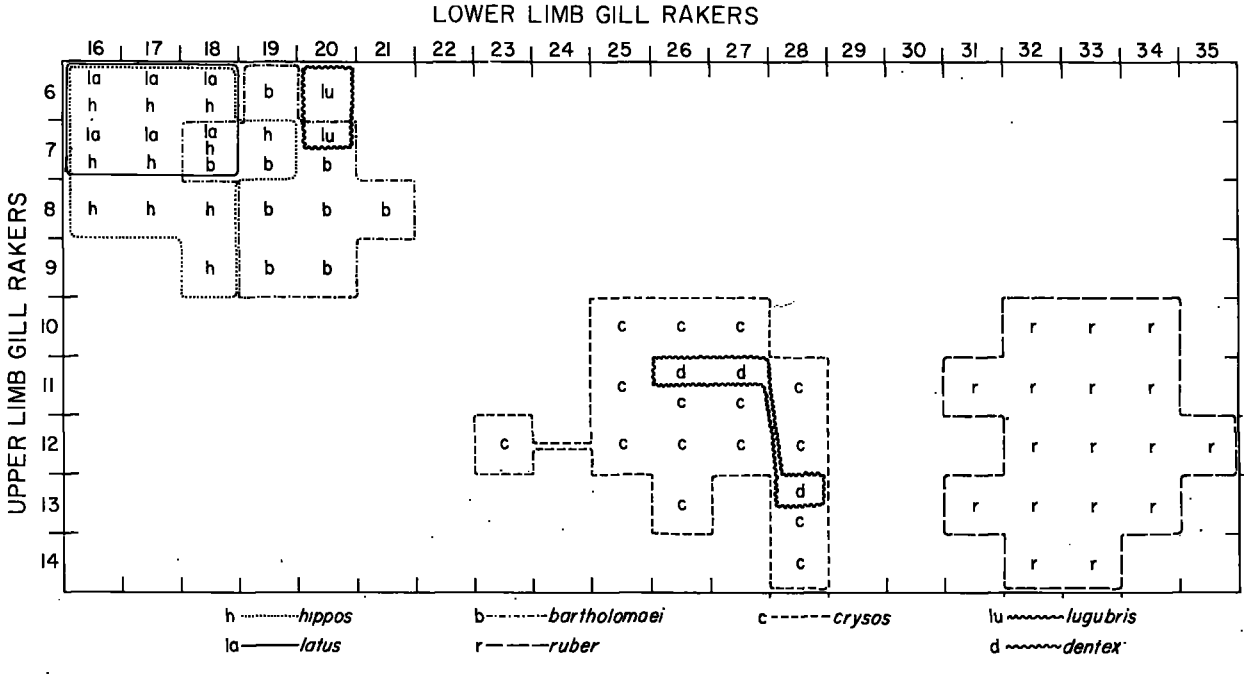

FIGURE 2.—Correlation of lower-limb gill rakers and upper-limb gill rakers for seven species of *Caranx*.

COMPARISON OF SPECIES

The five common species of *Caranx* in the Atlantic off the United States are compared with respect to selected characters—comparisons of *dentex* and *lugubris* with these are less complete. Regression lines for selected characters show trends of differences between the species, but in most instances they are not applicable to taxonomic separation because of the overlapping of individual measurements. Descriptions and comparisons apply to the size ranges given for each species.

Comparison of a series of morphometric characters of larval carangids morphologically similar to *Caranx* showed a converging of body proportions around 4 to 5 mm. standard length. Only species of *Decapterus* and *Selar* were compared, but gross study of other larger carangid larvae and juveniles indicated that species of *Trachurus*, *Chloroscombrus*, and *Hemicaranx* would follow the same trend. No suitable meristic characters were discovered to separate the genera at this size. A treatment of the larvae of most of the species in the family would be necessary to assure generic and specific separation below 5 mm. standard length, and the majority of these are undescribed. Consequently, the series of *crysos* and of the form referred to as *Caranx* sp. (*"latus* and/or *hippos"*) were begun with specimens of 5.4 mm.; but a 3.8-mm. specimen that is suspected to be *crysos* and a 4.9-mm. specimen that may belong to the *"latus* and/or *hippos"* group are illustrated. A 6.0-mm. form is the smallest one referred to *bartholomaei*, but an 8.1-mm. specimen is the smallest definitely identified *bartholomaei*. The smallest *ruber* is 12.4 mm. The smallest *latus* is 16.1 mm., but a specimen between 12.7 and 13.0 mm. is tentatively referred to this species. The smallest *hippos* is 15.3 mm., but a specimen of 12.7 mm. is tentatively referred to this species. The series of specimens between 5.4 and 8.3 mm. labeled *"latus* and/or *hippos"* represents either *latus* or *hippos*, or both species. The smallest *dentex* and only *lugubris* available for examination were 87 mm. and 242 mm., respectively.

The largest sizes examined were *crysos*, 267 mm.; *ruber*, 230 mm.; *bartholomaei*, 315 mm. (a damaged specimen) and 243 mm.; *latus*, 146 mm.; *hippos*, 830 mm.; *dentex*, 132 mm.; and *lugubris*, 242 mm.

CHARACTERS

Numbers preceding discussions of meristic characters are the counts or ranges found in the seven species combined. All body lengths are given in standard length unless otherwise noted.

Scales on chest.—All species have fully scaled chests except *hippos* which has a patch of scales anterior to the pelvics on an otherwise scaleless chest (fig. 85).

Dorsal spines.—VIII and I. Rarely 6 or 7 spines were counted in the first dorsal fin, and on such specimens the position of the missing spine or spines could usually be determined. The third spine averages the greatest length of the first dorsal-fin spines on specimens more than 30 to 40 mm. standard length; below this size it is exceeded in length only by the fourth spine. The interspinous membrane that connects the eighth and ninth spines persists to larger sizes in *crysos* and *bartholomaei* (to about 90 mm.) than in the other three species (about 75 to 80 mm.).

A composite graph of the regression lines for third dorsal spine length on standard length of the five common species is shown in figure 3. The species can be adequately compared between 20 mm. and 80 mm. *C. crysos* apparently has the fastest spine growth rate and *ruber* the slowest (0.13-mm. and 0.10-mm. increase in spine length, respectively, per 1.0 mm. increase in standard length). *C. latus* apparently averages the greatest spine length at comparable body lengths and *ruber* the least.

Anal spines.—II and I. The second spine is longer than the first in all species, except *hippos* below 20.4 mm., in which the first spine is the longer. For specimens less than 10 mm., a difference in lengths of the second anal spine is illustrated between *crysos* and *bartholomaei* in figure 4; specimens of the *"latus* and/or *hippos"* series overlap these two. The interspinous membrane connecting the second and third spines is lost at the smallest size in *hippos* (about 25 mm.) and at the largest size in *crysos* (about 45 mm.).

Dorsal soft-rays.—*C. latus*, *hippos*, and *lugubris* are separable from *bartholomaei*, *dentex*, and *ruber* by the smaller number of dorsal rays; *crysos* overlaps these two groups (fig. 1). The first soft-ray is generally the longest soft-ray of the dorsal fin on specimens above 30 to 40 mm. standard length; below this approximate size it is usually exceeded in length only by the second soft-ray.

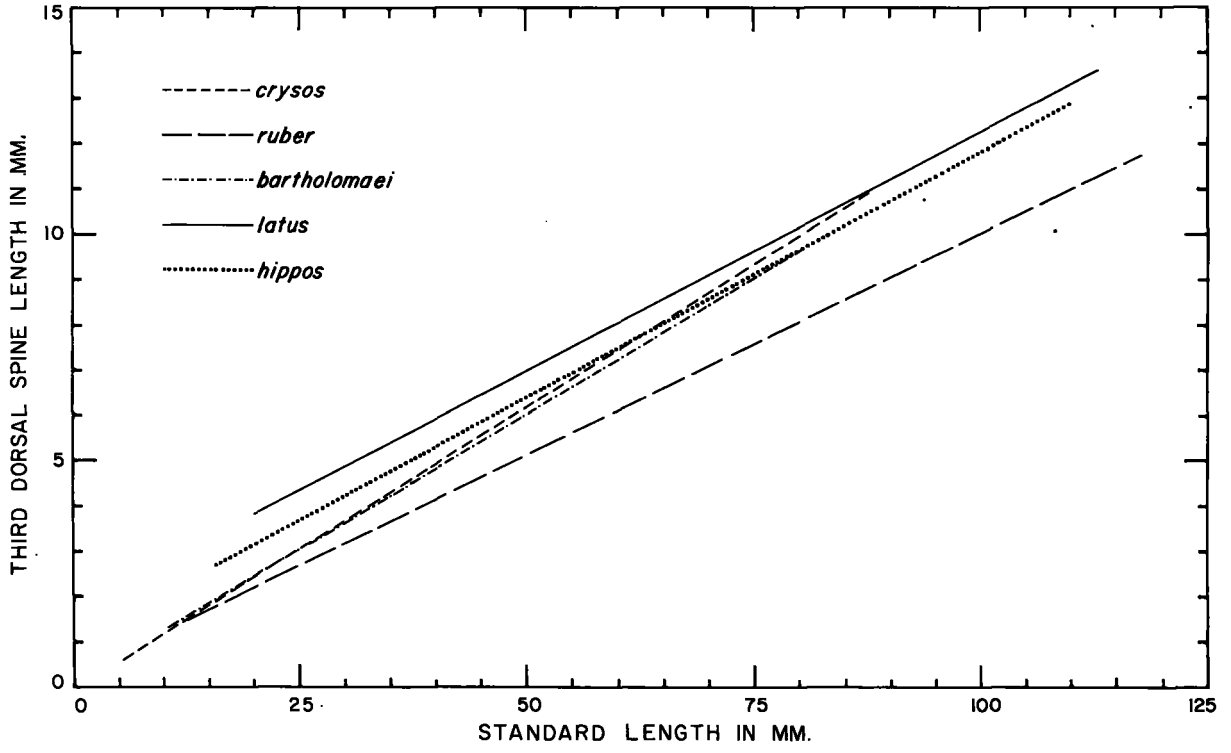

FIGURE 3.—Comparison of the regression lines for the relation of length of the third dorsal spine to standard length for five species of *Caranx*.

A composite graph of the regression lines for length of the first dorsal soft-ray on standard length of the five common species is shown in figure 5. The species can be adequately compared between about 32 mm. and 83 mm. standard length. *C. latus* apparently has the fastest soft-ray growth rate and *ruber* the slowest (0.21-and 0.12-mm. increase in soft-ray length, respectively, per 1.0-mm. increase in standard length). *C. hippos* apparently averages the greatest soft-ray length at comparable body lengths to about 80 mm. where it is equaled and at a larger size exceeded by *latus*. Above approximately 38 mm., *ruber* apparently averages the least soft-ray length at comparable body lengths.

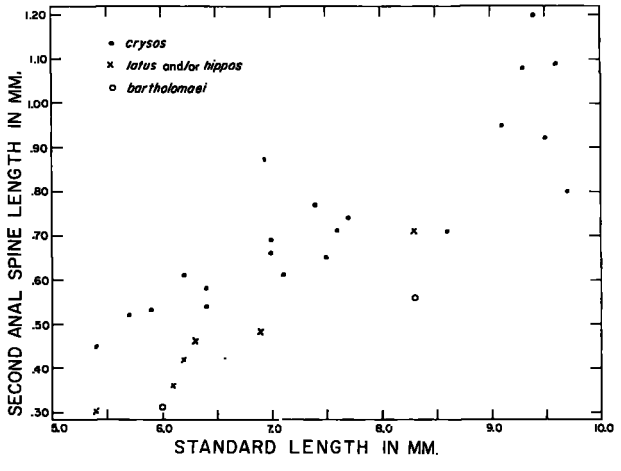

FIGURE 4.—*Caranx crysos*, *Caranx* sp. ("*latus* and/or *hippos*"), and *C. bartholomaei:* Relation of length of the second anal spine to standard length for specimens smaller than 10 mm. standard length.

The greater average length of the first soft-ray of *latus* and *hippos* above approximately 50 mm. standard length (fig. 5) expresses the more pronounced fin lobe of these two species as compared with that of *crysos*, *ruber*, and *bartholomaei*. The lobe of *lugubris* may be even more pronounced (fig. 98). *C. dentex* differs from the other six species in lacking a distinct lobe, and in having the third dorsal spine longer than the first dorsal soft-ray (figs. 25 and 97).

Anal soft-rays.—*C. latus*, *hippos*, and *lugubris* are separable from *bartholomaei*, *dentex*, and *ruber* by the lesser number of anal rays; *crysos* overlaps these two groups (fig. 1). A trend of direct relation between numbers of dorsal and anal soft-rays is shown for these members of the genus. The same intraspecific relationships of the lengths of the first and second soft-rays and interspecific

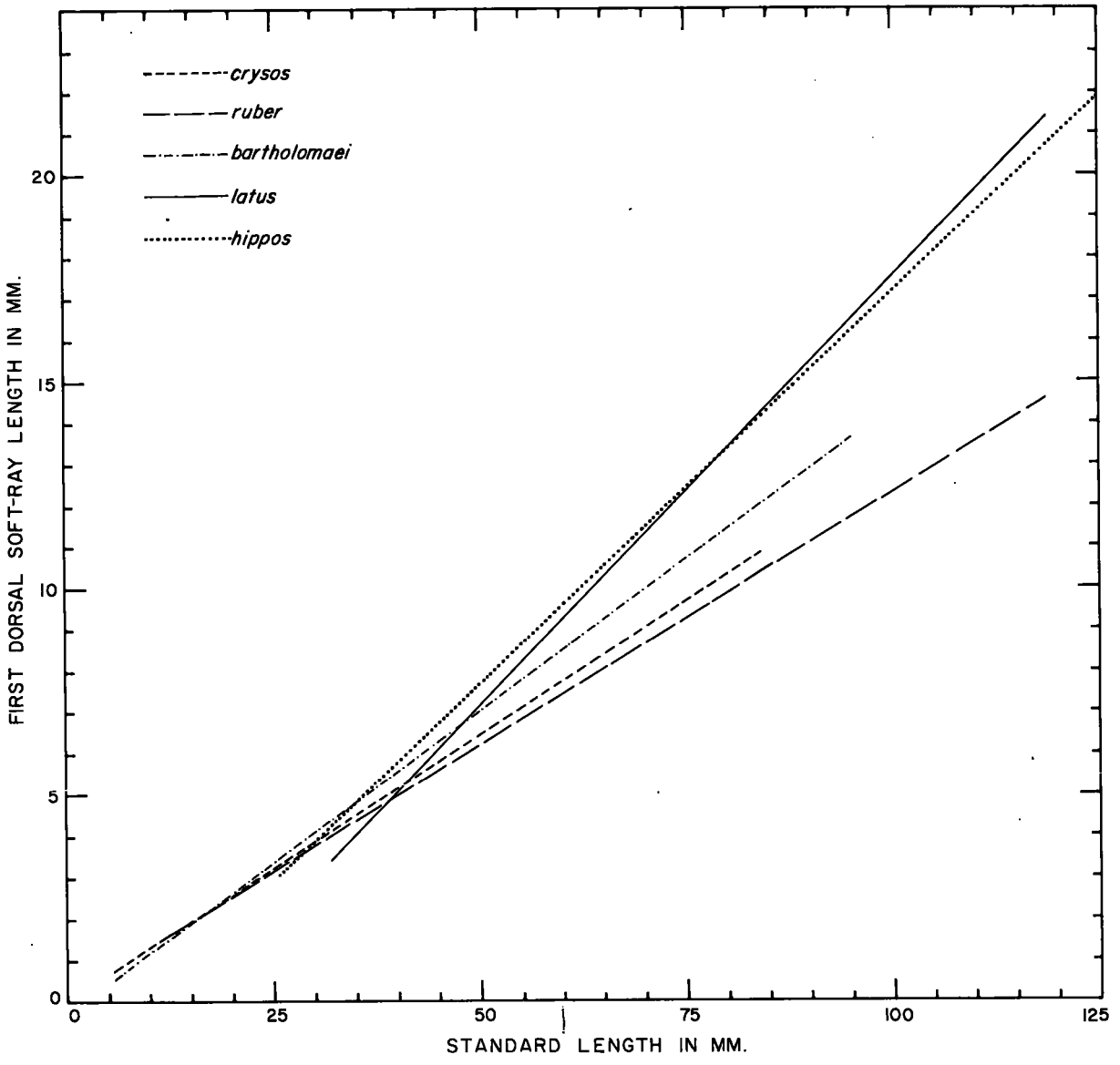

FIGURE 5.—Comparison of the regression lines for the relation of length of the first dorsal soft-ray to standard length for five species of *Caranx*.

relationships of the first soft-ray (fin lobe) lengths that apply to the dorsal soft-rays also apply to the anal soft-rays.

Distortion, loss, or absence of dorsal and anal soft-rays.—Distortion or absence of one or more soft-rays of the dorsal or anal fins were observed in all five of the common species. Some of the rays were of similar length to other rays in the fin, but were bent or thickened; others were rudimentary, their distal ends tapering to a point and of much shorter length than the normal rays. The dorsal and anal fins of fish possessing rudimentary or missing rays usually had distorted rays. Judging from the extent of distortion of these abnormal rays, they could not have regenerated to a normal size and structure. If these abnormal specimens had attained maturity, their soft-ray counts would have been confusing, because the overgrowth of the scaly sheath at the fin bases and the enlargement and near-coalescing of the rays would tend to obliterate evidence of the missing or rudimentary rays.

This abnormality was observed to the greatest degree in specimens of *ruber* from the *Gill* dip-net

collections. Of 231 specimens taken, 6.9 percent had rudimentary rays in the dorsal or anal fins, or in both. Six (13.3 percent) of the forty-five dip-net collections containing *ruber* had specimens with rudimentary rays. These collections were distributed in time and place from April through August and from the Bahamas to off North Carolina. Of the six collections containing specimens with rudimentary rays, 22.2 percent of the specimens had rudimentary rays. The most aberrant of these had 8 rudimentary dorsal soft-rays and 5 rudimentary anal soft-rays; the least aberrant, 1 and none, respectively.

No rudimentary rays were found in the caudal, pectoral, or pelvic fins, although specimens with extremely distorted or rudimentary dorsal and anal rays frequently also had misshapen caudal and pelvic rays. Other morphometric characters of these fish were within the range of predicted normality. The size range of specimens examined with aberrant rays was 23 to 77 mm.

Interneural and interhemal spines.—Posterior lateral projections of these spines protrude above the body surface along the bases of the dorsal and anal soft-rays in *latus* and *hippos*, at least within the following size ranges, 16.1 to 141 mm. and 15.3 to 164 mm. They were not present in this protruded manner in any specimens of the other species.

Caudal.—9+8 principal rays. A minimum of interspecific and intraspecific variation was found in the ray counts and development of the fin.

The generic character of paired caudal keels on each side of the body—one beginning above and

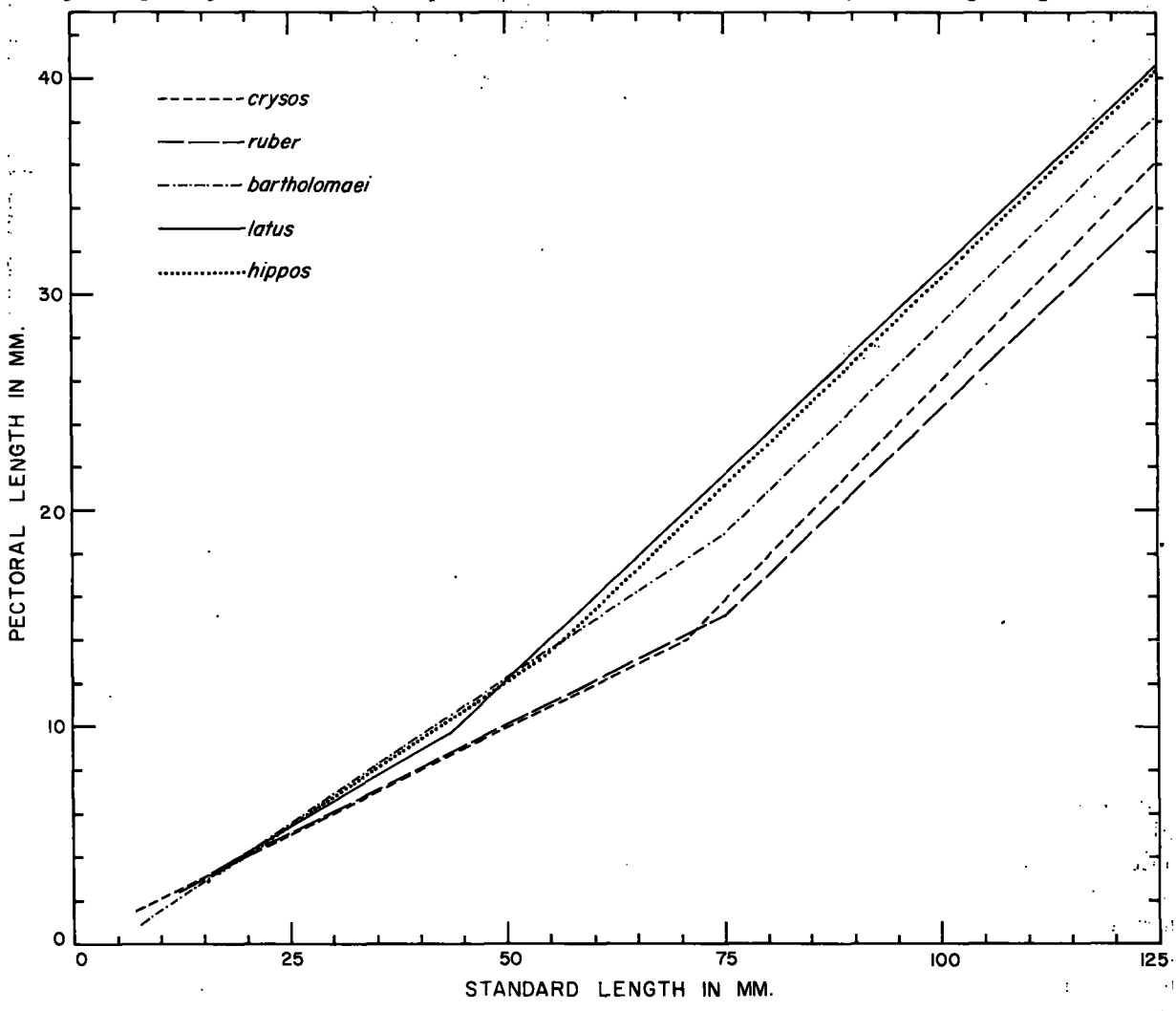

FIGURE 6.—Comparison of the regression lines for the relation of pectoral length to standard length for five species of *Caranx*.

489286 O—59——2

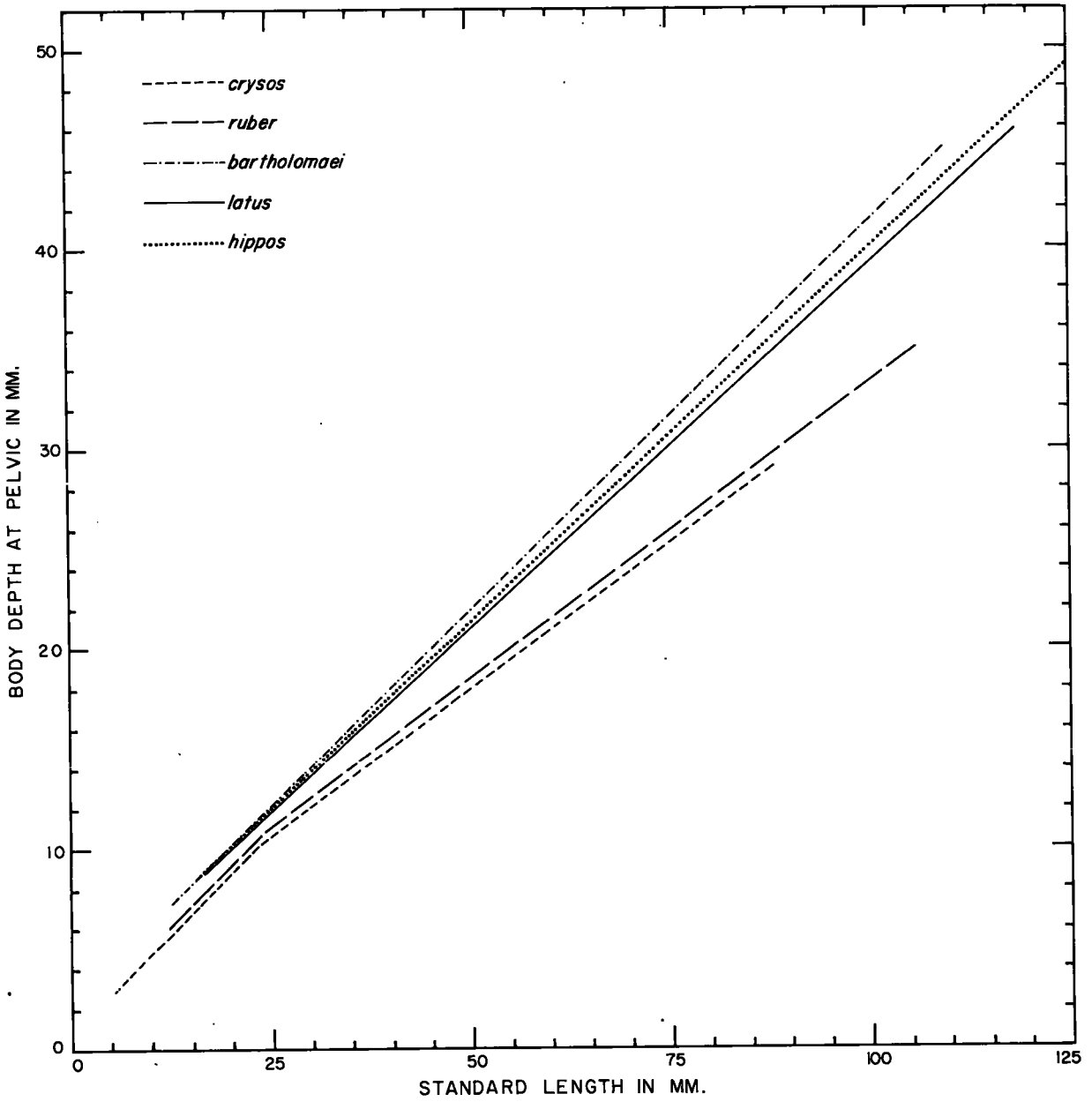

FIGURE 7.—Comparison of the regression lines for the relation of body depth at pelvic to standard length for five species of *Caranx*.

one below the lateral line on the posterior portion of the peduncle, converging toward the lateral line, and ending on the fleshy part of the caudal—is not produced until about 60 to 75 mm. standard length in the five common species examined (present on the smallest *dentex* of 78.5 mm.). This character is more pronounced at sizes larger than 100 mm. The paired caudal keels form at about 30 mm. on *crysos*, *ruber*, and *bartholomaei* (at slightly larger sizes in *latus* and *hippos*) on the fleshy part of the caudal fin posterior to the caudal base.

Pectoral.—I–18 to 23. *C. crysos* averages the greatest number of rays; *ruber*, the least.

A composite graph of the regression lines for pectoral length on standard length of the five common species is shown in figure 6. These species can be adequately compared between 16.1 mm. and 125 mm. standard length. Within this size range all species have an inflection followed

by an increased pectoral growth rate. This occurs at the smallest body sizes in *latus* and *hippos* (approximately 43 mm. and 54 mm.) and at the largest in *ruber*, *bartholomaei*, and *crysos* (approximately 75 mm., 75 mm., and 70 mm.). Preceding their inflections, *bartholomaei* and *hippos* apparently have the fastest pectoral growth rates and *crysos* the slowest (0.27-mm. and 0.195-mm. increase in pectoral length per 1.0-mm. increase in standard length). Subsequent to these inflections, *crysos* apparently has the fastest pectoral growth rate and *latus* the slowest (0.41-mm. and 0.37-mm. increase in pectoral length per 1.0-mm. increase in standard length). Above approximately 20 mm., *bartholomaei*, *latus*, and *hippos* apparently average greater pectoral lengths than *crysos* and *ruber*; and above approximately 65 mm., *latus* and *hippos* apparently average the greatest pectoral length and *ruber* the least at comparable body lengths.

Pelvic.—I–5. Generally, similar pelvic lengths occur at corresponding body sizes in all species. *C. dentex* may evidence a significantly greater pelvic length than the other species above 110 or 130 mm. standard length.

Body depth.—A composite graph of the regression lines for body depth at pelvic on standard length of the five common species is shown in figure 7. At approximately 23 or 24 mm. standard length, *crysos* and *ruber* have inflections followed by a decrease in body-depth growth rate; and similar inflections are suspected to occur at smaller sizes in the other three species. The species can be adequately compared between 24 mm. and 88 mm. *C. bartholomaei* apparently has the fastest body-depth growth rate and *crysos* and *ruber* the slowest (0.39-mm. and 0.29-mm. increase in body depth per 1.0-mm. increase in standard length). *C. bartholomaei* apparently averages the greatest body depth and *crysos* the least at comparable body lengths. *C. dentex* compares in depth with *ruber* and *crysos*. The one specimen of *lugubris* has a greater depth than *hippos* at a comparable size.

Figure 8 illustrates the relation of body depth at pelvic to standard length for specimens of *latus* and *hippos* of 30 mm. standard length and smaller. The smallest specimen plotted of each (about 12.7 mm.) is damaged and tentatively identified, but these coordinates represent fairly accurate measurements. At sizes smaller than approximately

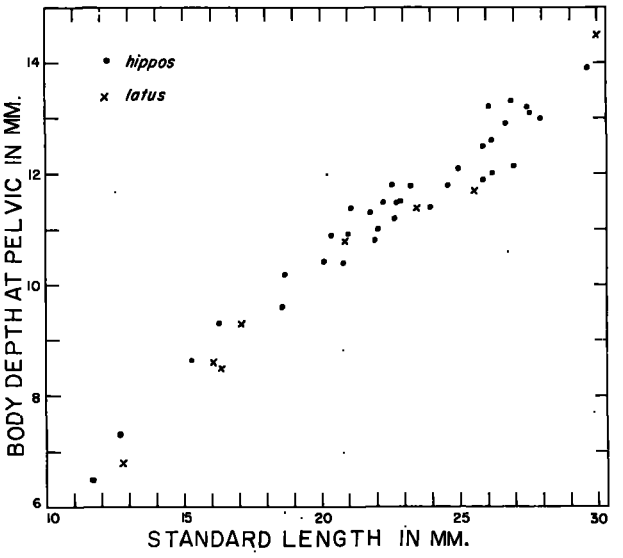

FIGURE 8.—*Caranx latus* and *C. hippos:* Relation of body depth at pelvic to standard length for specimens 30 mm. standard length and smaller.

25 mm., *latus* averages a lesser body depth than *hippos*.

Figure 9 illustrates differences in depth at pelvic of specimens below 10 mm.—the *"latus* and/or *hippos"* series averages a greater depth than *crysos* and *bartholomaei*.

Shapiro (1943: 94) graphically illustrated *hippos* (116 to 312 mm., measured from snout to least depth of peduncle) to be relatively heavier than *crysos* (96 to 203 mm., snout to least depth of peduncle) with a tendency for convergence of

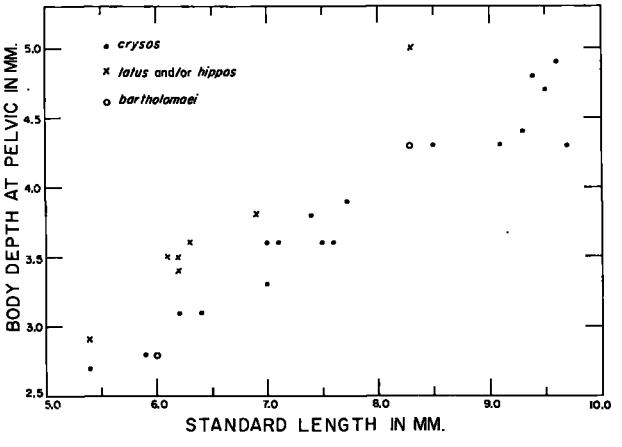

FIGURE 9.—*Caranx crysos*, *Caranx* sp. (*"latus* and/or *hippos"*), and *C. bartholomaei:* Relation of body depth at pelvic to standard length for specimens smaller than 10 mm. standard length.

relative growth rates at larger sizes. He stated that these two species can be separated by their constant differential length-weight growth ratio, as well as by differences in weight at the same length.

Recorded maximum sizes of the species have not received much attention. The following maximum total lengths and weights represent a partial abstract of the literature:

crysos—about 28 in. (750 mm., Fowler 1953: 57); about 4 lb. (Bigelow and Schroeder, 1953: 376).

ruber—12.1 in. (308 mm., UF 3538).

bartholomaei—about 39 in. (1,000 mm., Fowler 1953: 57).

latus—to 22 in. (Beebe and Tee-Van, 1928: 108).

hippos—40 in. (1,020 mm., SAFI collection); maximum recorded weight 36 lb. (Bigelow and Schroeder, 1953: 376). Several eyewitness accounts of large jack crevalles of more than 5 feet in length from the Gulf of Mexico may have been this species. Stewart Springer reported (personal communication) having preserved and mounted a 41-lb. *hippos* caught off the Mississippi coast.

dentex—24 in. (Jordan and Evermann, 1896: 927).

lugubris—about 39 in. (about 1,000 mm., Fowler 1953: 58); 15.5 lb. (Woods and Kanazawa, 1951: 631).

Head length.—A composite graph of the regression lines for head length on standard length of the five common species is shown in figure 10. At approximately 22 mm. standard length, *crysos*

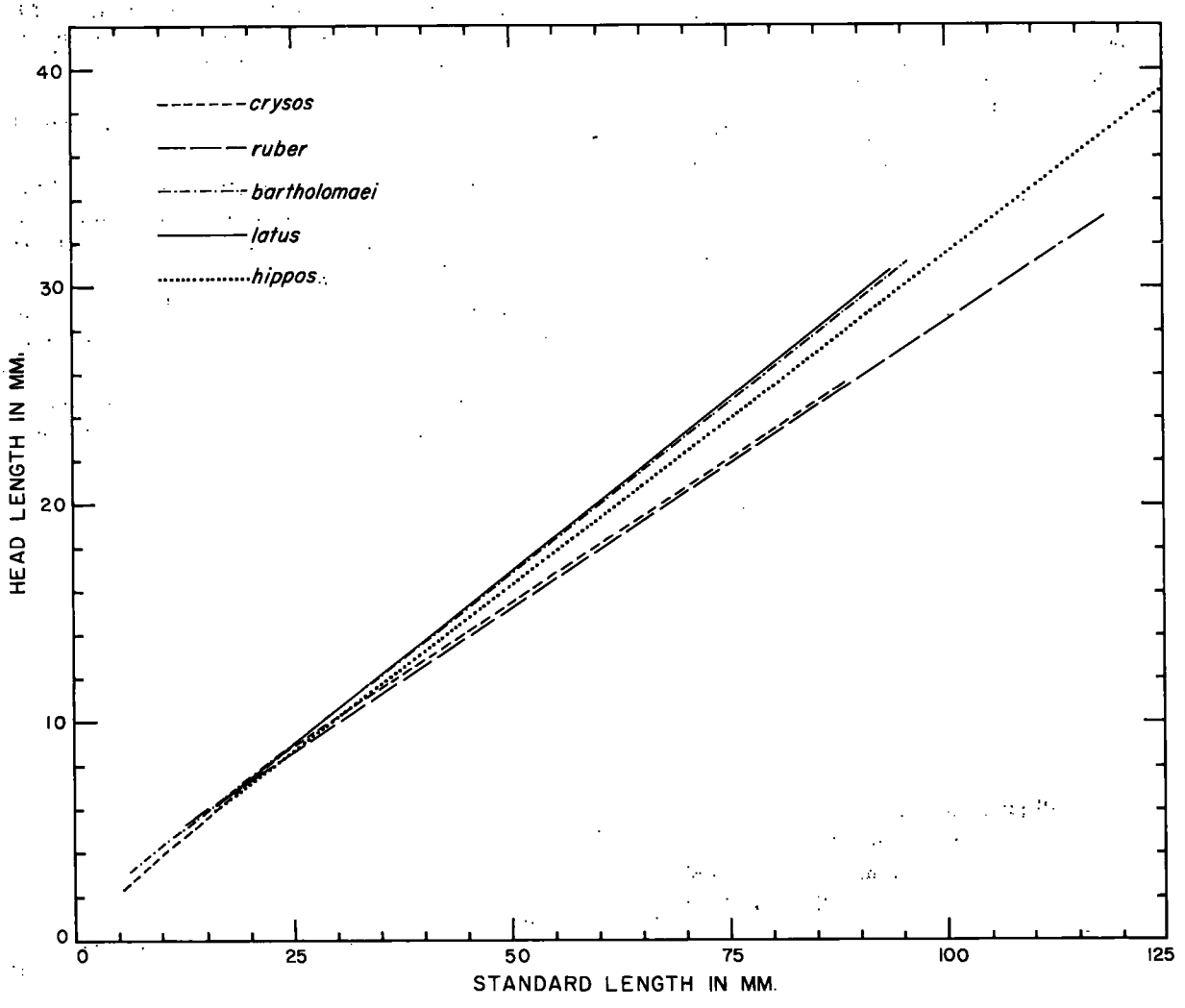

FIGURE 10.—Comparison of the regression lines for the relation of head length to standard length for five species of *Caranx*.

has an inflection followed by a decrease in head growth rate; and the other species evidenced a single regression line within the size ranges that were considered for each. The species can be adequately compared between about 25 mm. and 88 mm. standard length . *C. latus* apparently has the fastest head growth rate and *crysos* the slowest (0.32-and 0.26-mm. increase in head length per 1.0-mm. increase in standard length). *C. bartholomaei* and *larus* apparently average the greatest head lengths and *crysos* and *ruber* the least at comparable body lengths.

Eye diameter.—A composite graph of the regression lines for eye diameter on standard length for the five common species is shown in figure 11. Inflections occur in this relationship for *crysos*, *ruber*, and *hippos* at approximately 22 mm., 34 mm., and 55 mm. standard length; and *bartholomaei* and *latus* evidenced no inflections in the size range of each that was treated statistically. The species are adequately comparable between approximately 16 mm. and 83 mm. standard length. Above 22 mm., *bartholomaei* apparently has the fastest eye growth rate and above 34 mm., *ruber* apparently has the slowest (0.095-mm. and 0.058-mm. increase in eye diameter per 1.0-mm. increase in standard length). *C. bartholomaei* and *latus* apparently average the greatest eye diameter and *crysos* and *ruber* the least at comparable body lengths.

A decrease in the eye growth rate of *bartholomaei*, as suggested later, causes *latus to* average the greatest eye diameter above approximately 100 mm.; and the large eye size of *latus* has earned for it the common name of "horse-eye jack."

Snout length.—A composite graph of the regression lines for snout length on standard length of the five common species is shown in figure 12. The species can be adequately compared between 16 mm. and 89 mm. standard length. *C. bartholomaei* apparently has the fastest snout growth rate and *crysos* and *hippos* the slowest (0.11-mm. and 0.08-mm. increase in snout length per 1.0-mm. increase in standard length). Above approximately 20 mm. standard length, *bartholomaei* apparently averages the greatest snout length and *hippos* the least at comparable body lengths. *C. dentex* may average a snout length similar to that of *bartholomaei*.

Gill rakers.—The relation of the numbers of

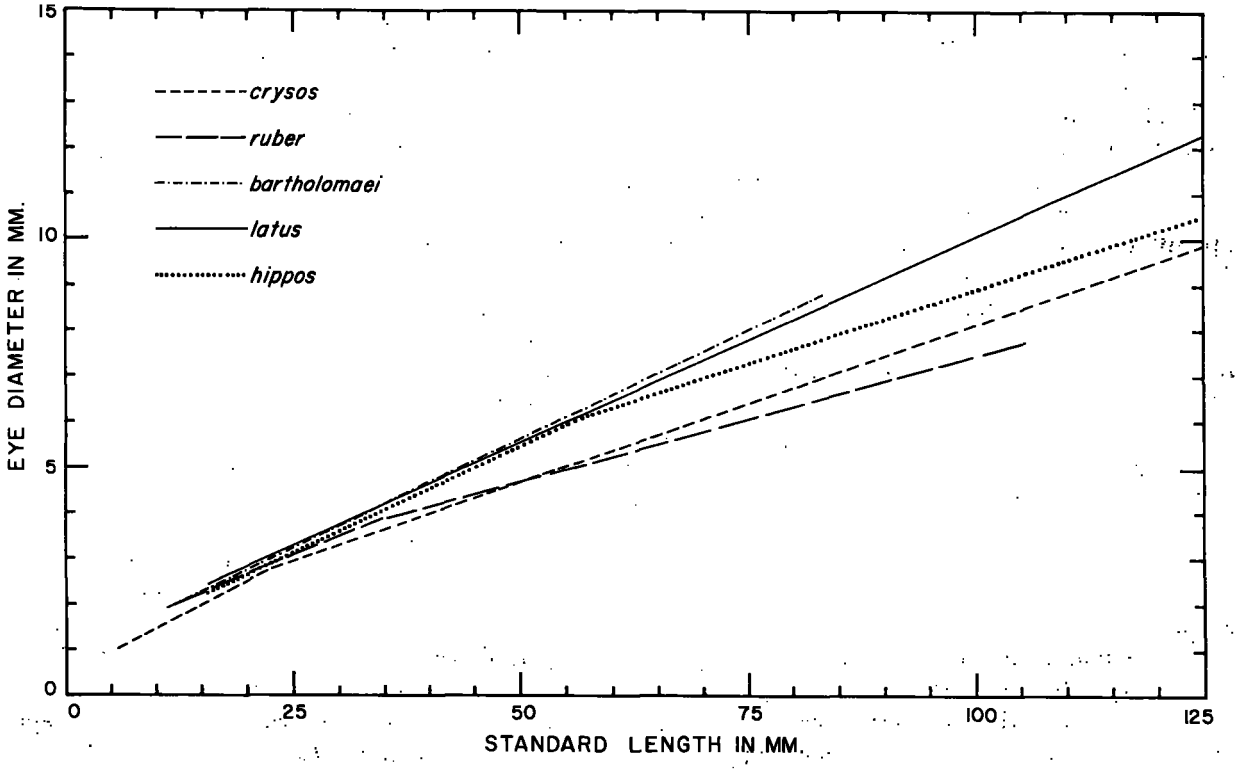

FIGURE 11.—Comparison of the regression lines for the relation of eye diameter to standard length for five species of *Caranx*.

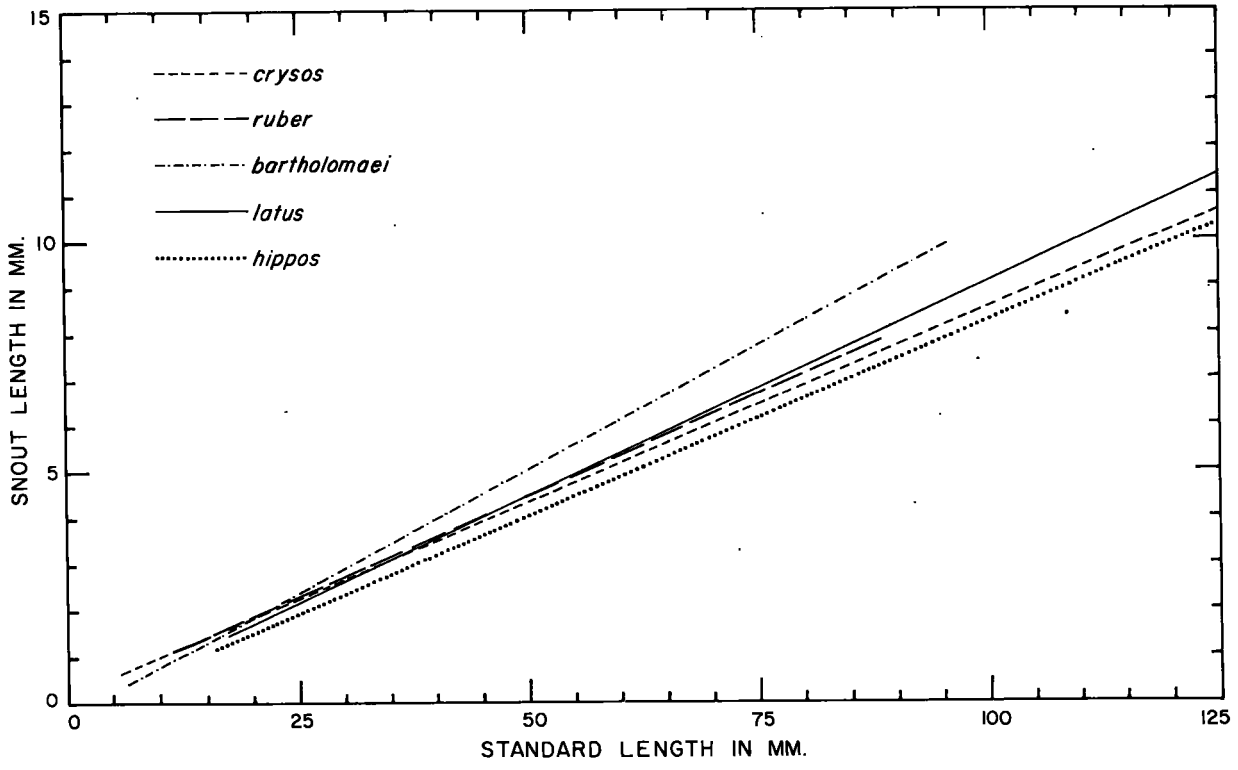

FIGURE 12.—Comparison of the regression lines for the relation of snout length to standard length for five species of *Caranx*.

lower-limb to upper-limb gill rakers (fig. 2) divides the seven species of *Caranx* into three distinct taxonomic groups: (1) *latus*, *hippos*, *bartholomaei*, and *lugubris;* (2) *crysos* and *dentex*; and (3) *ruber*. A general trend of a direct relation between upper-limb and lower-limb gill rakers is apparent, but this relation is not as sharply defined as is the dorsal ray–anal ray relation.

It is estimated from examination of many small specimens that the full complement of gill rakers for an individual fish will be formed by a size of 14 mm. Three of the species, *bartholomaei*, *latus*, and *hippos*, exhibit a tendency for gill rakers at the origins of both limbs to become smaller or rudimentary with growth, but *crysos* and *ruber* do not.

Branchiostegals.—Branchiostegal rays were counted on more than 300 specimens, representing all species examined. Seven rays were found on each side in all counts made—the number reported as generally characteristic of the family.

Scutes.—The estimated perimeters of the ranges of the mean number of scutes evidence appreciable overlapping in the individual species (fig. 13); but this character may be used for interspecific identification. A few scutes have completed their individual development on *hippos* and *latus* by 15.3 mm. and 16.1 mm., respectively. The smallest size at which completely developed scutes may be present on these two species is unknown; probably it is around 13.5 mm. The first scutes to complete their development on the other three common species do so between about 18 mm. and 24 mm. As predicted by the perimeters, the range of the mean number of scutes of *crysos* does not overlap that of *ruber* or *bartholomaei* above 25 mm., and does not overlap that of *hippos* above about 35 mm., and of *latus* above about 55 mm.; the range of *latus* does not overlap that of *ruber* or *bartholomaei* and averages a greater number of scutes, but it overlaps *hippos* at all sizes; the range of *hippos* does not overlap that of *ruber* or *bartholomaei* below about 25 mm., but does above this size; and the ranges of *ruber* and *bartholomaei* overlap at all sizes. The four specimens of *dentex* show an overlap in this character with *hippos*, *ruber*, and *bartholomaei*, but the true range for the species may be below that of *latus*. An estimated range of 26 to 33 scutes for *lugubris* (from the specimen examined and published accounts) is similar to that

of *hippos* and overlaps all but *crysos* in this character.

The relationship of the number of scutes and length of fish has been dealt with for another member of the family. Blegvad (1944) suggested that the number of scutes of *Selar kalla* (Cuvier) increased with the total length. Bapat and Prasad (1952: 114) combined their observations with Blegvad's and showed a scute increase from 21 to 22 at 35 mm. total length to about 40 at about 128 to 134 mm. total length.

Lateral line.—As shown by the estimated perimeters of the ranges of the mean lateral-line ratios (fig. 14), a slight overlap of *crysos* and *latus* with *hippos* occurs in this character. The interspecific relationships of the mean lateral-line ratios are similar to those of the mean number of scutes for the five common species of *Caranx*; i. e., the longer the length of the straight lateral line relative to the length of the curved lateral line, the greater the number of scutes. The specimens of *dentex* and *lugubris* do not conform to this—the range of the

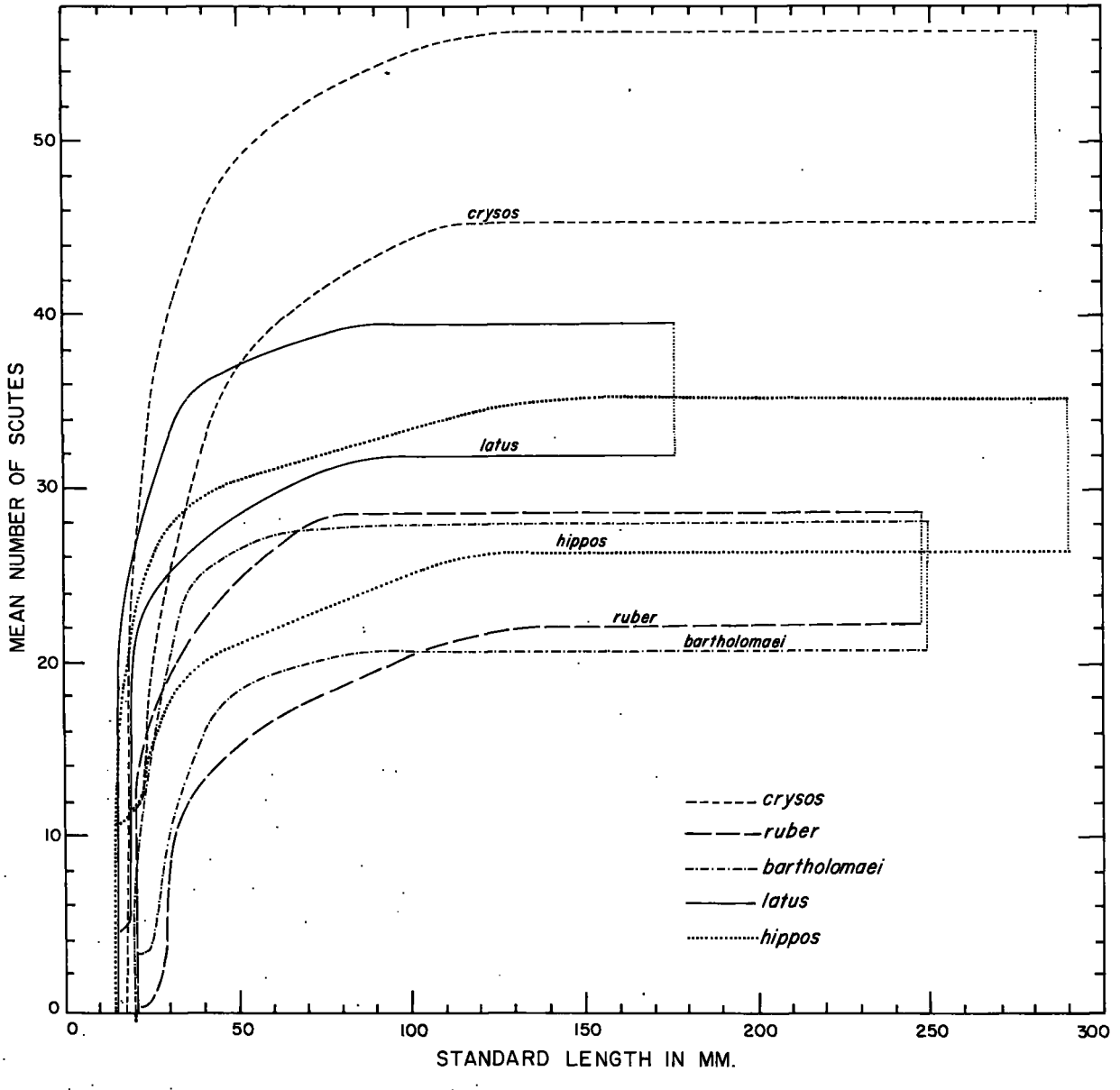

FIGURE 13.—Comparison of the variations of the mean number of scutes with respect to standard length for five species of *Caranx*.

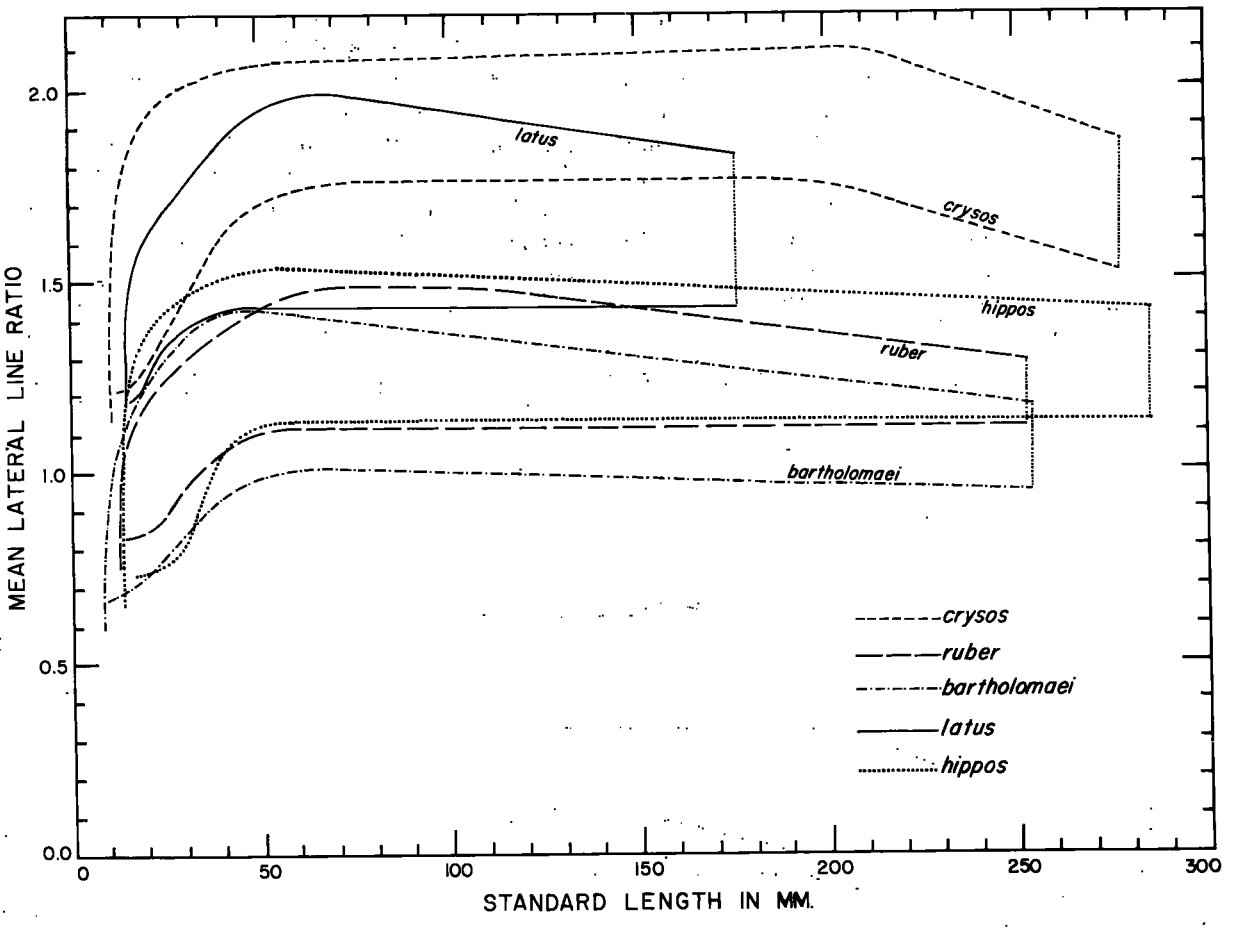

FIGURE 14.—Comparison of the variations of the mean lateral-line ratio with respect to standard length for five species of *Caranx*.

mean number of scutes in *dentex* overlaps the upper portion of this range in *bartholomaei*, while the range of the mean lateral-line ratio falls below that in *bartholomaei;* and the mean number of scutes of the one specimen of *lugubris* falls within the scute range of *hippos* while the lateral-line ratio of *lugubris* is well above the range of the lateral-line ratio of *hippos*. However, intraspecifically no obvious correlation between the mean number of scutes and the mean lateral-line ratio occurs in specimens larger than about 70 mm. standard length.

Preopercular spines.—There are indications that the preopercular-angle spines cease to grow between about 5.4 mm. and 7 mm. standard length in *crysos* and the "*latus* and/or *hippos*" series, and they begin to decrease in length between this size range and 10 mm. (fig. 15). The angle spines of *ruber* and *bartholomaei* apparently begin to decrease in length at sizes smaller than 18 mm. and 12 mm., respectively. The angle spines, the last remaining spines, have been absorbed or overgrown by the expanding margin of the preoperculum between 16 to 20 mm. in *latus*, 21 to 22.5 mm. in *hippos*, about 38 mm. in *bartholomaei*, and about 44 mm. in *crysos* and *ruber*. The number of preopercular upper-limb and lower-limb spines varies to such a great degree intraspecifically that only slight interspecific differences can be adjudged (table 1). *C. crysos* averages a higher number of spines on both limbs than do the other species. The lower limb of all species averages more spines than the upper. The number of spines on both limbs decreases above about 15 mm.—the spines on both limbs nearest the angle spine are the last to disappear.

Pigmentation.—Comparative reference to the illustrations will point out most of the interspecific differences in pigmentation of larval and juvenile forms. A few distinctions are listed here.

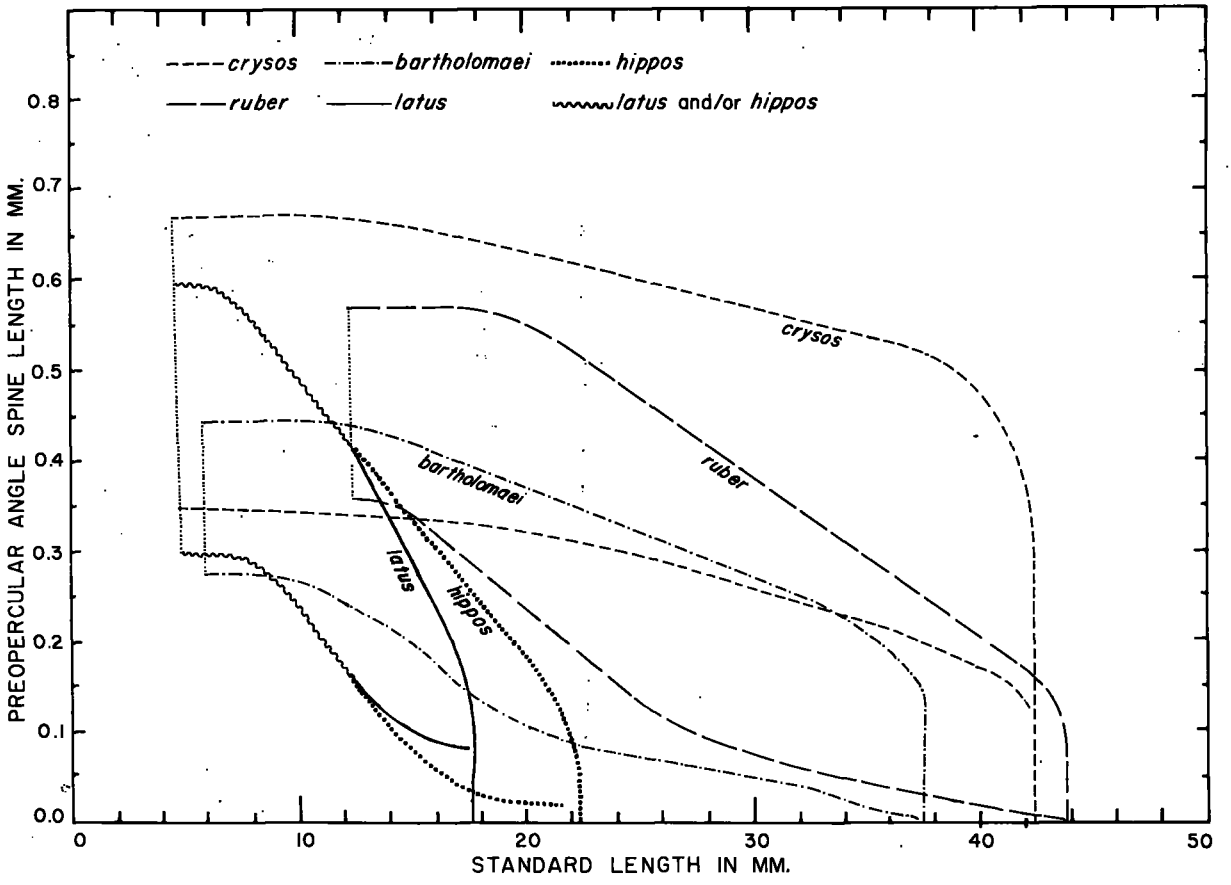

FIGURE 15.—Comparison of the variations of length of the preopercular-angle spine with respect to standard length for five species of *Caranx*.

TABLE 1.—*Ranges in numbers of spines on the upper and lower limbs of the preoperculum, by 5-mm. intervals, for five species of* Caranx

Standard length of fish	Number of preopercular spines on—									
	Lower limb					Upper limb				
	crysos	*ruber*	*bartholomaei*	*latus*	*hippos*	*crysos*	*ruber*	*bartholomaei*	*latus*	*hippos*
0.0–4.9 mm										
5.0–9.9 mm	4–6		5	4–6		2–5		3–4	3–4	
10.0–14.9 mm	5–7	4–6	4–6	5	?	4–5	4–5	3–5	1	?
15.0–19.9 mm	4–7	1–5	0–7	4–5	4–6	4–6	0–4	0–6	0	0
20.0–24.9 mm	2–8	1–3	3–6	0	3–5	2–7	0–4	0–3	0	0
25.0–29.9 mm	2–6	0–3	2–5	0	0	0–5	0–1	0–3	0	0
30.0–34.9 mm	0–3	0–1	3–5	0	0	0–2	0	1	0	0
35.0–39.9 mm	0–3	0	0–1	0	0	0–2	0	0	0	0
40.0–44.9 mm	2	0–3	0	0	0	0	0–1	0	0	0

(1) Specimens of *hippos* from about 20 to 45 mm. have intense pigmentation over most of the first dorsal fin; in comparable sizes of *latus* this is associated primarily with the second, third, and fourth spines.

(2) On *hippos* of 15.3 to 60 mm., the pigment of the posterior 3 bars extends nearly to the base of the anal fin; on most specimens of *latus* of more than 20 mm., these bars terminate ventrally on or slightly below the straight lateral line.

(3) The bars of juvenile *latus* larger than 26 mm. are wider than those of *hippos* of comparable size, but this character is most difficult to measure.

(4) Commonly, 5 body bars occur on *latus*, *hippos*, and *bartholomaei*, 6 on *ruber*, and 7 on *crysos*.

(5) The presence of body bars (and blotches on *bartholomaei*) is probably characteristic only of the juvenile stage. These bars persist to the largest sizes on *hippos*, disappearing at some size between 164 mm. and 248 mm. The bars of *latus* disappear at some size between 90.5 mm. and 116 mm., those of *ruber* at probably a little over 105 mm., and those of *crysos* at about 110 mm. The bars of *bartholomaei* begin to break up at about 28 mm.,

and its juvenile blotches persist to a little over 95 mm.

(6) The opercular spot of *hippos* is much more prominent and is definitive at a smaller body size than is that of *crysos*. The opercular spot of *latus* is less prominent than in both of the preceding species. *C. ruber* and *bartholomaei* lack an opercular spot.

(7) *C. dentex* may be distinguishable from other species by a dark-tipped upper caudal lobe at certain sizes.

(8) *C. lugubris* seems distinguishable from the other species, at least above 240 mm., by a sooty black or brownish body color.

DISTRIBUTION OF WESTERN ATLANTIC SPECIES OF *CARANX*

General Distribution

crysos: Western Atlantic—Cananeia, Sao Paulo, Brazil (Carvalho 1941: 53) to Herring Cove, Nova Scotia (Vladykov 1935: 4). ?Eastern Atlantic. ?Mediterranean.

ruber: Western Atlantic—Rio de Janeiro, Brazil (Fowler 1940: 766, as *Caranx crysos*, locality questioned), Union Island, British West Indies (Beebe and Hollister, 1935: 214), and Caledonia Bay, Panama (Breder 1925: 153) to Cape Hatteras, N. C. (text, p. 468; USNM 53109), and 39°13′ N., 71°13′ W. (Mather 1954: 293).

bartholomaei: Western Atlantic—Maceio, Brazil (Gilbert 1900: 167) to Woods Hole, Mass. (Smith 1898: 98).

latus: Western Atlantic—Rio de Janeiro, Brazil (Castelnau 1855) to Squan River (Manasquan River), N. J. (Fowler 1905b: 258).

hippos: Western Atlantic—35°30′ W. off Uruguay (Pozzi and Bordale, 1935: 164) to Musquodoboit Harbor, Nova Scotia (Vladykov 1935: 4). Eastern Atlantic. Eastern and Western Pacific. Indian Ocean.

dentex: Western Atlantic—Rio de Janeiro, Brazil (Cuvier, *in* Cuvier and Valenciennes, 1833: 87) to Bermuda (Bean 1906: 47); not on United States coast. Eastern Atlantic. Eastern and Western Pacific. Indian Ocean.

lugubris: Western Atlantic—Santos, Brazil (Miranda Ribeiro 1918: 52) to Bermuda (Woods and Kanazawa, 1951: 631); not on United States coast. Eastern Atlantic. Eastern and Western Pacific. Indian Ocean.

Distribution off Southeastern Atlantic Coast of the United States

Early juveniles of *crysos*, *ruber*, and *bartholomaei* have pelagic offshore habitats, probably directly associated with the Gulf Stream. As late juveniles, at least part of the populations of *crysos* and *bartholomaei* move into inshore waters—*crysos* is the most common *Caranx* in inshore waters along the Atlantic coast. Juveniles and adults of *ruber* maintain a pelagic offshore habitat, and the rare inshore records probably represent stray specimens. Larvae and early juveniles of *latus* and *hippos* apparently have an initial pelagic offshore habitat, but at least some of the early and older juveniles and the adults of these two species occur in inshore and even brackish-water habitats—*hippos* is the second most common *Caranx* in inshore waters along the Atlantic coast. There are no reliable records of *dentex* and *lugubris* from inshore waters along the Atlantic and Gulf coasts of the United States, but both might be expected as strays. Records of *dentex* and *lugubris* denote them to be offshore, or at least insular species.

The occurrence of young of the five common species in this area is seasonal, and the larvae of all species and the juveniles of at least *crysos*, *ruber*, and *bartholomaei* probably comprise populations which move northward in the Gulf Stream each year from about March to December. Some of the annual recruitment of these populations may result from spawning within this area, but the major recruitment to each probably comes from more southern waters that contribute to the Gulf Stream off the southeastern United States (around southern Florida, Cuba, and the Bahamas and from the eastern Gulf and the northern Caribbean). Larval and juvenile *crysos* and juvenile *ruber* are most abundant in this part of the Stream from June through August.

The factors that promote an association of larvae and juveniles of *Caranx* species with the offshore waters of the Gulf Stream are unknown. The relation of their food habits to organisms that might be associated with these waters and a tropism to the currents may be involved, and there are indications that temperature and salinity may be influencing factors. Larvae and juveniles were collected at *Gill* stations where surface temperatures ranged from 20.4° to 29.4° C. and surface salinity values ranged from 35.2 to 36.7 parts per thousand; however, at two-thirds of the stations where they were taken, the temperature range was only 27.4° to 29.4° C. and the salinity range 36.0 to 36.3 parts per thousand. Generally, the *Gill* stations closest to inshore waters at which *Caranx* specimens were taken had higher temperature and/or salinity values than successive stations closer to shore where *Caranx* were not taken. The minimum temperature and salinity values of these stations closest to inshore waters at which *Caranx* species were taken varied with each cruise, however.

Data from the dip-net collections of the *Gill* cruises are interpreted to indicate the relative distribution and abundance of the larval and juvenile stages of the five common species in this area by comparison of the number of occurrences in the collections and the total number of specimens of each species:

	Number of occurrences	*Number of specimens*
crysos	31	307
ruber	45	231
bartholomaei	20	35
latus	4	8
hippos	1	1

C. ruber is most widely distributed, but *crysos* is most abundant. *C. bartholomaei* is more restricted in both occurrence and numbers than *crysos* and *ruber*. The scarcity of *latus* and *hippos* is attributed to their apparent tendency to migrate to inshore waters at about 21 to 50 mm. standard length. The majority of these dip-net collections were made in association with floating sargassum. The collections were about evenly divided between day and night hours.

The juveniles of the five common species are frequently found in the same locality. Two or three species were taken together in 28 of the 67 dip-net collections of the *Gill* cruises that contained *Caranx* species. The following combinations occurred (number of occurrences in parentheses): *ruber-bartholomaei* (9), *crysos-ruber* (11), *crysos-ruber-bartholomaei* (5), *crysos-bartholomaei* (1), *crysos-latus* (1), *crysos-ruber-latus* (1). Records of a few stations of the M/V *Oregon* from the Gulf of Mexico, of a few collections of the U. S. National Museum, and collections of the *Combat* from the Western Atlantic added the following combinations: *bartholomaei-latus*, *bartholomaei-hippos*, *latus-hippos*, *crysos-hippos*, *crysos-latus-hippos*, *ruber-bartholomaei-hippos*, *crysos-ruber-bartholomaei-hippos*, and *crysos-ruber-latus-hippos*. In all of these collections the sizes or size ranges of concurrent species were nearly equal or overlapping.

The stomach contents of 26 fish taken by trolling on the *Gill* cruises collectively contained all five of the common species of *Caranx*. Data on these *Caranx* specimens are given in table 2. These specimens have not been included in the tables of individual species locations.

TABLE 2.—*Occurrence of* Caranx *species in the stomachs of 26 fish caught by trolling on* Gill *cruises, listed by predator species*

[An asterisk (*) indicates estimated size]

Caranx species	Standard length (mm.)	Location		Date
		N. latitude	W. longitude	
Sphyraena barracuda (Walbaum):				
ruber	*167	25°53′	77°51′	Oct. 11, 1953
hippos	21.2			
hippos (?)	12.7			
hippos (?)	*15	26°05′	78°12′	Nov. 11, 1953
hippos (?)	*18			
hippos (?)	*21			
hippos (?)	*22			
Scriola dumerili Risso: crysos(?).	*90	32°42′	78°52′	Aug. 15, 1953
Coryphaena hippurus Linnaeus:				
ruber	*76	23°40.5′	76°50′	June 19, 1954
bartholomaei	*38			
bartholomaei	*40	23°40.5′	76°50′	June 19, 1954
bartholomaei	*52			
bartholomaei	*56			
Caranx sp.	*55	23°40.5′	76°50′	June 19, 1954
bartholomaei	*55	23°44′	76°54′	June 18, 1954
bartholomaei	*58			
crysos	*98	27°02′	79°23′	July 25, 1953
crysos	*115	28°04′	79°09′	July 26, 1953
ruber	*85			
bartholomaei	*83			
crysos	*100	28°04′	79°09′	July 26, 1953
crysos	*110			
ruber	*23	29°01′	80°02′	Apr. 27, 1954
ruber	33			
crysos	*51	31°33′	79°00′	Aug. 5, 1953
crysos	*52			
latus or *hippos*	*62			
crysos	*45	31°34′	79°27′	Aug. 5, 1953
crysos	*50			
ruber	*65	34°15′	74°28′	May 12, 1953
bartholomaei	*140			
Lobotes surinamensis (Bloch):[1]				
ruber	*31	26°21.2′	76°46.5′	July 19, 1953
ruber	*32			
ruber	*32			
ruber	*32			
ruber	*44			
ruber	*45			
ruber	*45			
ruber	*50			
ruber	*55			
ruber	65			
Katsuwonus pelamis (Linnaeus):				
latus	*31	25°56.5′	77°54′	June 22, 1954
latus	32			
latus	*36	25°57′	77°55′	June 22, 1954
crysos	77	26°09.5′	78°13.5′	June 22, 1954
crysos				
Euthynnus alletteratus (Rafinesque):				
crysos	*25	29°07′	80°25′	Aug. 28, 1954
latus	*28	32°09′	79°28′	Oct. 25, 1953
Thunnus atlanticus (Lesson):				
hippos	28.5	26°06′	78°08′	June 22, 1954
crysos (?)	*12.3	30°20′	80°01′	June 26, 1954
Thunnus albacares (Bonnaterre):				
Caranx sp.	*28	25°57.5′	77°56′	June 22, 1954
crysos	*33	26°01.5′	78°01.5′	June 22, 1954
crysos	*39			
crysos	*48			
ruber	58			
ruber	61			
ruber	73			
ruber	74			
ruber	*87			
ruber	89			
bartholomaei (?)	*51			
Caranx sp.	*25			
Caranx sp.				
Caranx sp.	*90			
ruber	49	26°06′	78°08′	June 22, 1954
ruber	60			
latus	36	28°16′	77°01′	Nov. 5, 1954

[1] About 450 mm. standard length; taken at night by dip net.

Records of Eggs, Larvae, and Early Juveniles of *Caranx* Species that Occur in the Western North Atlantic

Apparently the only published record of eggs and larvae of species of *Caranx* that occur in the Western Atlantic is by Chacko (1950: 171) in his account of plankton around the Krusadi Island in the Gulf of Mannar, India. For *Caranx hippos* (Linnaeus) he gave the following information: Spawning season, August to September; diameter of egg, 0.7 to 0.9 mm.; chief characters of egg, segmented yolk and one yellowish oil globule of 0.18 mm. diameter with dark pigments; chief characters of larva, 1.6 to 1.8 mm. in length, brown pigments on dorsal side of body, and 12 preanal myotomes. In citing this reference in his bibliography of the development of Indian fishes, Jones (1950: 129) assigned it to the synonymy of *C. sexfasciatus* Quoy and Gaimard; but his reasons for doing this are not given, and the correct identity of Chacko's specimens is uncertain.

Schnakenbeck (1931: 17, fig. 12) illustrated a 20-mm. total length specimen taken south of Crete, which he questionably identified as *Caranx fusus* Geoffroy. The illustration and soft-ray counts are very similar to the closely related, if not identical, Atlantic *crysos*. According to this observation and Tortonese's (1952) review of the Mediterranean Carangidae, the specimen is *fusus*.

Schnakenbeck (1931: 18, figs. 13 to 16) illustrated a 6-mm. total length specimen questionably identified as *C. dentex* taken between Crete and North Africa, and recorded the same identity to a 5-mm. total length specimen from around Corsica. He stated that the identification was based upon supposition. Although the specimen illustrated may belong to the genus *Caranx*, it would be better unassociated with any species designation pending the acquisition and study of identifiable series of the Mediterranean species.

Nichols (1938b: 1) illustrated and gave proportions of a 22-mm. juvenile *crysos* taken in the Gulf Stream off Bimini, Bahamas; and illustrated a 30-mm. juvenile *ruber*.

Nichols (1939) gave proportions and pigment descriptions for juveniles of five species of *Caranx* from the West Indies: *crysos*, 12 to 72 mm.; *ruber*, 13 to 62 mm.; *bartholomaei*, 16 to 51 mm.; *latus* (=*sexfasciatus*), 12 to 25 mm.; and *hippos*, 13 mm. His key to young *Caranx* of the West Indian region does not allow for changes in ratios with changes in relationships of body parts or the intraspecific variation and interspecific overlap that is characteristic of these species.

Fowler (1945: 292) misidentified a juvenile from Boca Chica, Key West, Fla., as *dentex* (under the name of *guara*)—the specimen is a 24.4-mm. *bartholomaei*.

Fowler (1950: 70) misidentified a juvenile *bartholomaei*, 17.4 mm., from northwest of Cay Sal Bank, as *latus*.

Fowler (1950: 70, fig. 3) misidentified 2 juvenile specimens of *bartholomaei*, 15.8 and 17.2 mm., from northwest of Cay Sal Bank, as *dentex* (under the name of *guara*).

Padoa, *in* Padoa et al. (1956: 54–5) reproduced the illustrations of *Caranx* which Schnakenbeck (1931) had identified as *dentex* and *fusus*, and expressed doubt on the identity of the former and concurred with the identity of the latter.

Lütken (1880: 535) briefly described differences in comparative measurements (body depth, head and pectoral lengths) between small and large sizes of three species of *Caranx: C. ruber*, under the name of *C. blochii* Cuvier; *C. hippos;* and *C. crysos*, under the name of *C. pisquetus* Cuvier. He mentioned minimum lengths of 13 mm. for *ruber* and 34 mm. for *crysos*. He (*op. cit.:* 538) said that the body bars of young *C. latus* (under the name of *C. fallax* Cuvier) disappeared comparatively early.

SPAWNING

Published data relating to the spawning of *hippos* and *crysos* are very meager, and apparently are nonexistent for the other species of *Caranx*. Spawning may occur in waters off the southeastern Atlantic coast of the United States for *latus* and *hippos* (whether this applies to one or both species is dependent in part on the specific identity of the "*latus* and/or *hippos*" series of specimens), for *crysos* and *ruber*, and possibly for *bartholomaei*. The major areas of spawning are probably to the south of this area. Since the larvae and early juveniles are associated with the Gulf Stream, spawning must occur in offshore waters of the Gulf Stream or in currents contributing to it.

The spawning season that contributes *Caranx* to this area is estimated to extend from February into September.

DESCRIPTION OF SPECIES

Numbers preceeding discussion of each meristic character are the counts or ranges found in adult fish, unless otherwise indicated. Body lengths are given in standard length unless otherwise noted. The development of all characters is described as a continuous series as far as is practical, following the "dynamic approach" used by Ahlstrom and Ball (1954: 215).

Caranx crysos (Mitchill)

(Figures 17–24)

Scomber crysos Mitchill, 1815, p. 424, pl. IV, fig. 2 (New York Bay).
Scomber chrysos, Cuvier, *in* Cuvier and Valenciennes, 1833, p. 98 (listed as synonymous with *Scomber hippos* Linnaeus; New York).
Caranx pisquetus Cuvier, *in* Cuvier and Valenciennes, 1833, p. 97 (Saint-Domingue; Cuba; Brazil).
Caranx crysos, DeKay, 1842, p. 121, pl. XVII, fig. 85 (New York).
Trachurus squamosus Gronow, *in* Gray, 1854, p. 125 (Carolina).
Caranx chrysos, Gill, 1857, p. 262 (New York market).
Caranx hippos (*non* Linnaeus), Holbrook, 1860, p. 90, pl. XII, fig. 2 (Massachusetts to Florida).
Paratractus pisquetus, Gill, 1863, p. 432 (eastern coast of United States).
Carangus chrysos, Gill, 1873, p. 803 (Cape Cod to Florida).
Paratractus pisquetos, Gill, 1873, p. 803 (Cape Cod to Florida).
Paratractus chrysos, Poey, 1875, p. 76 (Cuba).
Carangus chrysus, Jordan and Gilbert, 1879, p. 376 (Beaufort Harbor, N. C.).
Carangus pisquetos, Jordan and Gilbert, 1879, p. 376 (Beaufort, N. C.).
Carangus pisquetus, Goode and Bean, 1880, p. 339 (West Florida).
Caranx caballus (*non* Günther), Günther, 1880, p. 10 (Bermuda).
Caranx pisquetus, Goode and Bean, 1882, p. 237 (Gulf of Mexico).
Caranx chrysus, Jordan and Gilbert, 1882b, p. 970 (in key).
Carangus crysos, Kendall, 1908, p. 81 (Massachusetts, Rhode Island).
Paratractus crysos, Jordan, Evermann, and Clark, 1930, p. 272 (Cape Cod to Brazil).
Paratractos chrysos, Gunter, 1935, p. 40 (off Louisiana).

Nomenclature

Caranx crysos (Mitchill 1815) of the Western Atlantic should be recorded as distinct from the closely related, if not identical, *C. caballus* Günther (1869) of the Eastern Pacific and *C. fusus* Geoffroy-Saint-Hilaire (1809) of the Mediterranean until the true relationships of the three forms become known. This will distinguish the three populations and conform to more common usage until adequate comparisons of the three have been made.

Conflicting opinions on the relationship of *C. caballus* and *C. crysos* have been given by Nichols (1920a: 29; 1921b: 45) and Nichols and Breder (1927: 113), who considered the two forms conspecific; by Evermann and Jenkins (1891: 138) and Nichols and Murphy (1944: 243) who considered them to be subspecies; and by Jordan and Evermann (1896) and Meek and Hildebrand (1925: 348) who considered them to be distinct species.

Caranx fusus has been regarded as a distinct species endemic to the Mediterranean. Recently, Enrico Tortonese suggested (personal communication) that *C. fusus* and *C. crysos* might be the same. Ben-Tuvia (1953: 19), whose specimens from the Mediterranean off Israel were identified by Dr. J. T. Nichols, placed *C. fusus* in the synonymy of *C. crysos*. If they are the same, *C. crysos* will become a synonym of *C. fusus*. *C. crysos*, abundant in the Western Atlantic, has also been recorded from the Eastern Atlantic and West Africa (Steindachner 1894: 20; Metzelaar 1919: 265; Fowler 1936: 698; Nichols 1939: 4). If these latter records are valid, the currently enforced concept that *C. fusus* is distinct from *C. crysos* and is endemic to the Mediterranean is improbable.

Material

Measurements and counts were taken on a series of 120 specimens from 5.4 to 267 mm. standard length and meristic values were recorded for an additional 122 specimens within this size range. The 683 specimens identified are listed in table 6.

A specimen, measuring 3.8 mm. from snout to a vertical from the tip of the urostyle, tentatively identified as *Caranx* sp., and illustrated in figure 16 may be this species. The specimen has a depth at pelvic of 1.6 mm. and a preopercular-angle spine length of 0.35 mm. It was taken with several other specimens of *crysos* (USNM 164486) ranging from 5.7 to 7.7 mm. standard length, 33 miles south of Lookout Lightship in the Gulf Stream.

Four specimens of *dentex* are included and distinguished on the graphs with *crysos*.

FIGURE 16.—*Caranx* sp. larva, 3.8 mm. standard length, measured from tip of snout to vertical from tip of urostyle (USNM 164486). It is suspected to be *C. crysos*.

Characters

Dorsal spines.—VIII and I. All spines are well formed at 5.4 mm. standard length (fig. 17). The fourth spine averages the greatest length to about 37 mm.; above 37 mm., the third spine is longest. An interspinous membrane connects the first and second dorsal fins (eighth and ninth spines) to about 90 mm.

The regression of length of third dorsal spine on standard length is shown in figure 25 and table 3. A line fitted to this regression for specimens from 5.4 to 88.0 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.13-mm. increase in spine length per 1.0-mm. increase in standard length). The majority of the coordinates of specimens larger than 88 mm. fall above the extension of the calculated regression line, indicating an increase in the spine growth rate above this size.

Anal spines.—II and I. All spines are well

FIGURE 17.—*Caranx crysos* larva, 5.4 mm. standard length (*Gill* 3, Reg. 38).

TABLE 3.—Caranx crysos: *Statistics describing regressions of body parts on standard length*

$\bar{x}$=mean of independent variable x
$\bar{y}$=mean of dependent variable y
N=number of specimens
b=rate of increase of y
a=y-intercept of regression line
$Sy{\cdot}x$=standard deviation from regression (standard error of estimate)

Independent variable x	Dependent variable y	Size range of specimens (mm.)	$\bar{x}$	$\bar{y}$	N	b	a	$Sy{\cdot}x$
Standard length	Dorsal-fin spine length (3d)	5.4–88.0	30.56	3.73	97	0.126	−0.124	0.358
Do	Dorsal soft-ray length (1st)	5.6–83.5	30.65	3.98	93	.129	.038	.261
Do	Pectoral length	7.0–58.5	20.94	4.25	74	.195	.160	.244
Do	do	58.5–266	124.51	35.88	37	.406	−14.664	2.321
Do	Body depth	5.4–22.9	12.95	6.03	55	.413	.683	.289
Do	do	22.9–88.0	50.27	18.03	46	.293	3.292	.565
Do	Head length	5.4–22.9	12.95	4.93	55	.354	.349	.238
Do	do	22.9–88.0	50.27	15.56	46	.263	2.362	.332
Do	Eye diameter	5.4–30.3	15.51	2.04	67	.108	.359	.123
Do	do	30.3–145	74.23	6.34	43	.069	1.188	.414
Do	Snout length	5.4–145	38.54	3.40	109	.084	.170	.247

formed at 5.4 mm. standard length (fig. 17). The second spine is longer than the first. An interspinous membrane connects the second and third spines to about 45 mm. The relation of second anal spine length to standard length for specimens smaller than 10 mm. is shown in figure 4.

Dorsal soft-rays.—22 to 25 (table 4). The full complement is formed between about 7.5 and 8.5 mm. standard length. Segment marks are present above 6.5 mm. (fig. 18). Branching of the last ray occurs at about 8.5 mm. and of the other rays at about 17 to 20 mm. (fig. 22). The extension of the anterior 5 or 6 rays to produce the lobe begins at about 14 mm. (fig. 21). The second ray averages the greatest length to about 35 mm.; above 35 mm., the first ray is longest. The longest ray averages a greater length than the longest spine.

The regression of first dorsal soft-ray length on standard length is shown in figure 25 and table 3. A line fitted to this regression for specimens from 5.6 to 83.5 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.13-mm. increase in soft-ray length per 1.0-mm. increase in standard length). The coordinates larger than 83.5 mm. fall above the extension of the calculated regression line,

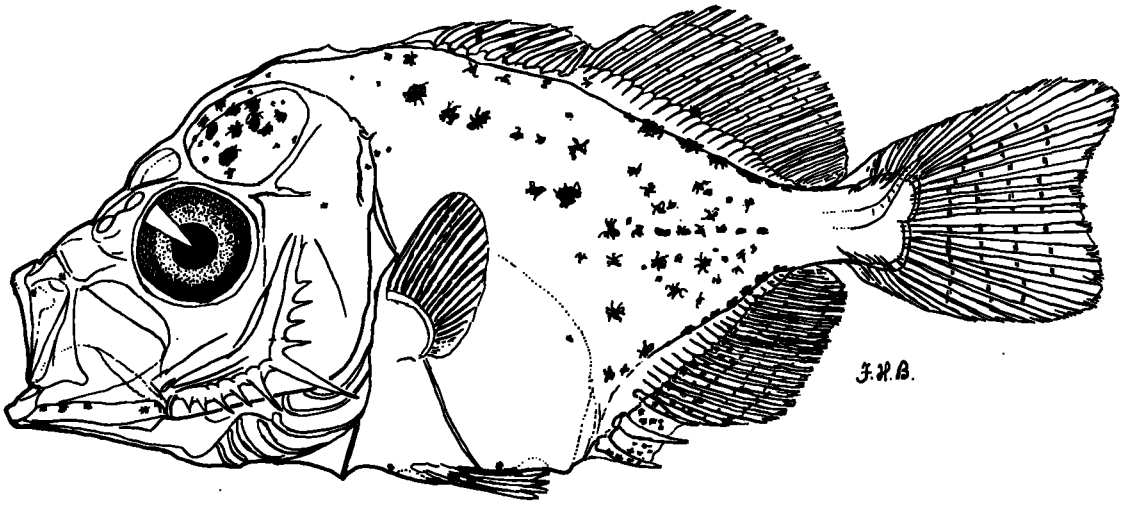

FIGURE 18.—*Caranx crysos* larva, 7.0 mm. standard length (*Gill* 3, Reg. 60).

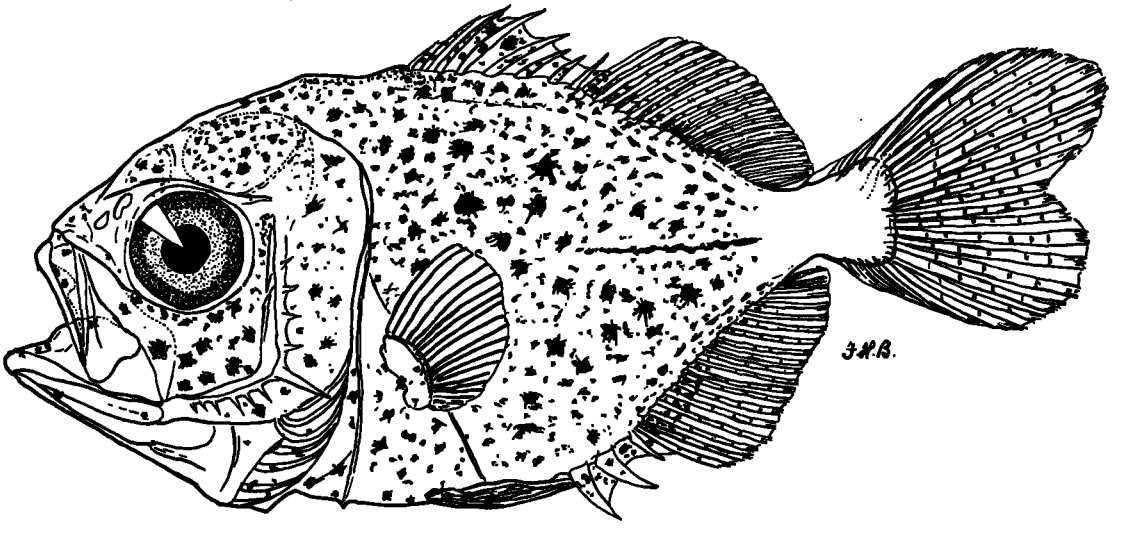

FIGURE 19.—*Caranx crysos* juvenile, 8.5 mm. standard length (*Gill* 3, Reg. 52).

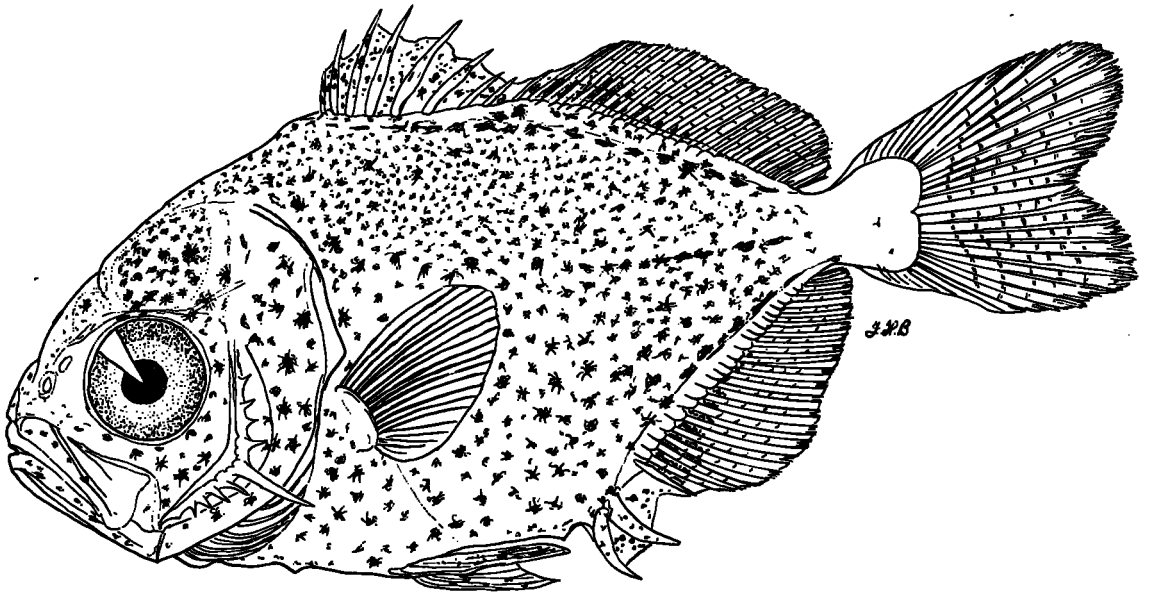

FIGURE 20.—*Caranx crysos* juvenile, 10.6 mm. standard length (*Gill* 3, Reg. 61).

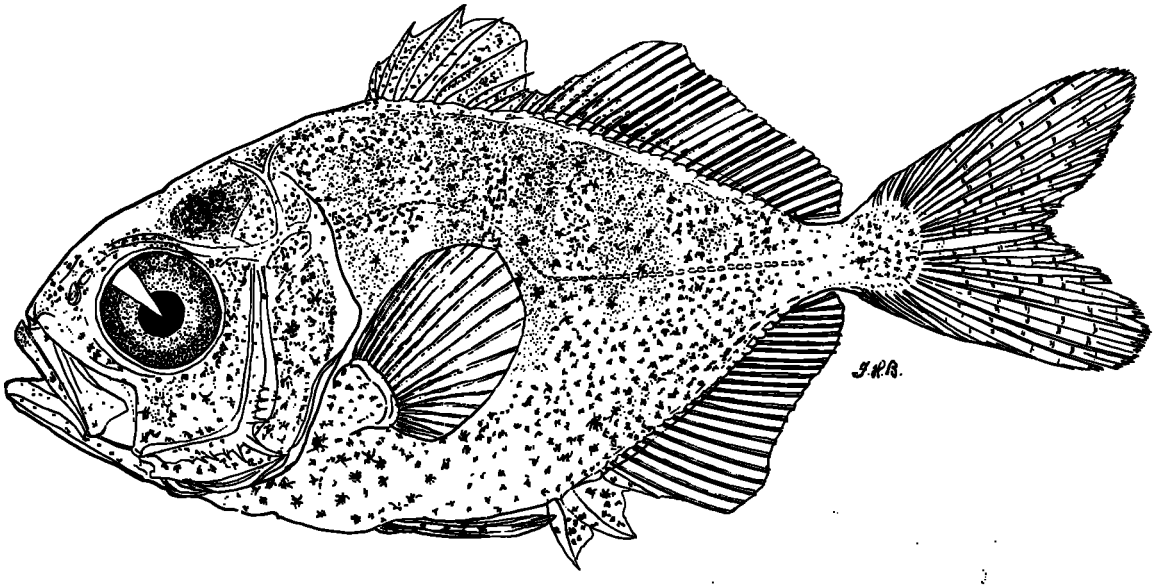

FIGURE 21.—*Caranx crysos* juvenile, 15.6 mm. standard length (*Gill* 8, Reg. 29 to 30).

indicating an increase in soft-ray growth rate at about this size.

Anal soft-rays.—19 to 21 (table 4). Formation, segmentation, branching, and lobation occur about as in the dorsal rays The second ray averages the greatest length to about 22 mm. standard length; above 22 mm., the first ray is longest. The longest dorsal and anal rays are of approximately equal length to about 31 mm.; above this size the dorsal averages slightly longer. The second anal spine is slightly shorter than the longest anal ray on specimens below 8 mm., is only one-half as long from 40 to 70 mm., and one-third as long at 219 mm.

Interneural and interhemal spines.—The posterior lateral projections of these spines are not extended above the body surface (as occurs in *latus* and *hippos*).

TABLE 4.—Caranx crysos: *Correlation of the numbers of dorsal and anal soft-rays of 231 specimens*

[The upper number in each block is the count obtained for that combination and the number in parentheses below is the approximate percentage of that count in the total sample]

ANAL SOFT-RAYS	DORSAL SOFT-RAYS 22	23	24	25
19	2 (.9)	51 (22.1)	12 (5.2)	
20		69 (30.0)	91 (39.4)	1 (.4)
21			3 (1.3)	2 (.9)

Caudal.—9+8 principal rays; 9 or 8+8 or 9 secondary rays. The principal rays are all present and segmentation has begun at 5.4 mm. standard length (fig. 17). The secondary rays are all present at 8.5 mm., but not at 7.5 mm. Branching begins at about 10 mm. (fig. 20), and is pronounced at about 15 mm. (fig. 21). Forking of the tail is represented by a slight indentation at 5.4 mm. (fig. 17) and is pronounced by about 8 mm. (fig. 19).

The urostyle is visible in preserved specimens to about 9 mm. (figs. 17 to 19).

Pectoral.—I–19 to 23. The full complement of rays is present at 8.5 mm. standard length (fig. 19). Branching has begun by 25 mm. The distal end of the fin is rounded from 5.4 to about 35 mm., above which it becomes pointed and falcation begins (figs. 17 to 23). Falcation is pronounced by 100 mm.

The regression of pectoral length on standard

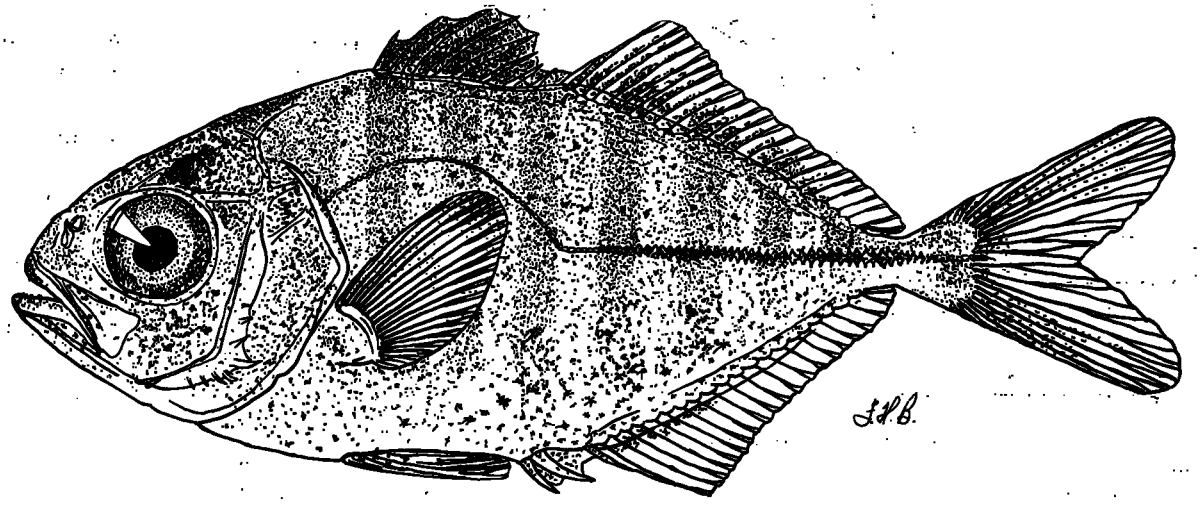

FIGURE 22.—*Caranx crysos* juvenile. 29.1 mm. standard length (*Gill* 4, Reg. 61).

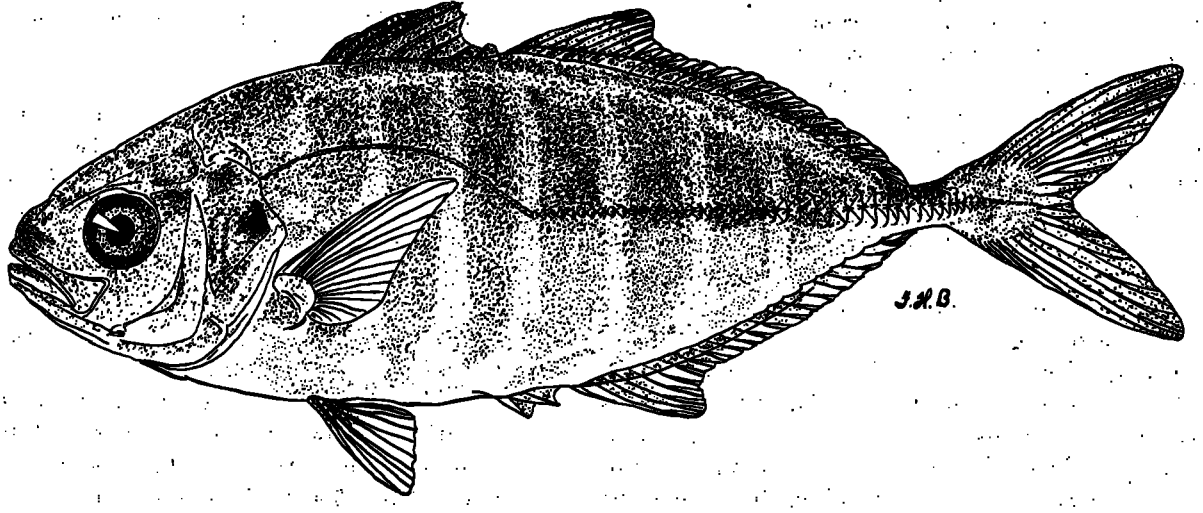

FIGURE 23.—*Caranx crysos* juvenile, 82 mm. standard length (*Gill* 3, Reg. 62).

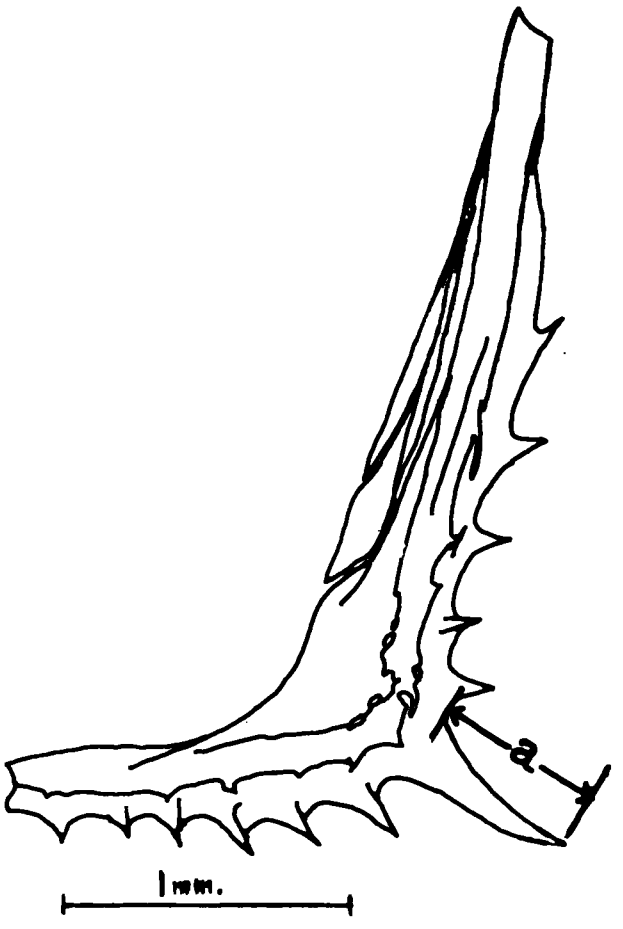

FIGURE 24.—*Caranx crysos*: Preopercular spines of a 14-mm. specimen, showing measurement (a) of the length of the preopercular-angle spine.

length is shown in figure 26 and table 3. Two lines were fitted to this regression: for specimens from 7.0 to 58.5 mm. and from 58.5 to 266 mm. standard length. An extension of the lower line intersects the upper line at approximately 70 mm., indicating that an inflection occurs at about that size and that a faster pectoral growth rate prevails above that size. The proportional rates of increase for the two variates are 0.195-mm. (below 70 mm.) and 0.41-mm. (above 70 mm.) increase in pectoral length per 1.0-mm. increase in standard length.

Pelvic.—I–5. The pelvic fin has formed by 5.4 mm. standard length (fig. 17), but the 6 rays are not distinguishable below about 6.2 mm. (fig. 18). Branching has begun by about 15 mm.

Body depth.—At corresponding body lengths the depth at first anal spine averages less than the depth at pelvic from 16.1 to about 40 mm. standard length, approximately equals the latter to about 75 mm., and averages greater above 75 mm. The body depth at pelvic for specimens smaller than 10 mm. is illustrated in figure 9.

The regression of body depth at pelvic on standard length is shown in figure 27 and table 3. Two lines were fitted to this regression: for specimens from 5.4 to 22.9 mm. and from 22.9 to 88.0 mm. standard length. The lines intersect at 23 mm., indicating that an inflection occurs at about that size and that a slower body-depth growth rate prevails above that size. The proportional rates of increase for the two variates are 0.41-mm. (below 23 mm.) and 0.29-mm. (above 23 mm.) increase in body depth per 1.0-mm. increase in standard length. The majority of the coordinates larger than 150 mm. fall below the extension of the calculated regression line, indicating a possible further decrease in body-depth growth rate somewhere above that size.

Head.—The nostril becomes divided at about 8 mm. standard length (figs. 17 to 19). The serrations on the supraoccipital crest persist to about 7 mm. (figs. 17 and 18). Three posterolaterally projecting spines are located on the cleithrum just below its junction with the operculum at 5.4 mm. (fig. 17); 1 to 2 similar spines occur on specimens 5.6 to 7.5 mm.; and none is present at 8.5 mm. or above.

The regression of head length on standard length is shown in figure 27 and table 3. Two lines were fitted to this regression: for specimens from 5.4 to 22.9 mm. and from 22.9 to 88.0 mm. standard length. The lines intersect at approximately 22 mm., indicating that an inflection occurs at about that size and that a slower head growth rate prevails above that size. The proportional rates of increase for the two variates are 0.35-mm. (below 22 mm.) and 0.26-mm. (above 22 mm.) increase in head length per 1.0-mm. increase in standard length. The coordinates of specimens larger than 88 mm. fall above the extension of the calculated regression line, indicating an increase in the head growth rate at around that size.

Eye.—The regression of eye diameter on standard length is shown in figure 28 and table 3. Two lines were fitted to this regression: for specimens from 5.4 to 30.3 mm. and from 30.3 to 145 mm. standard length. An extension of

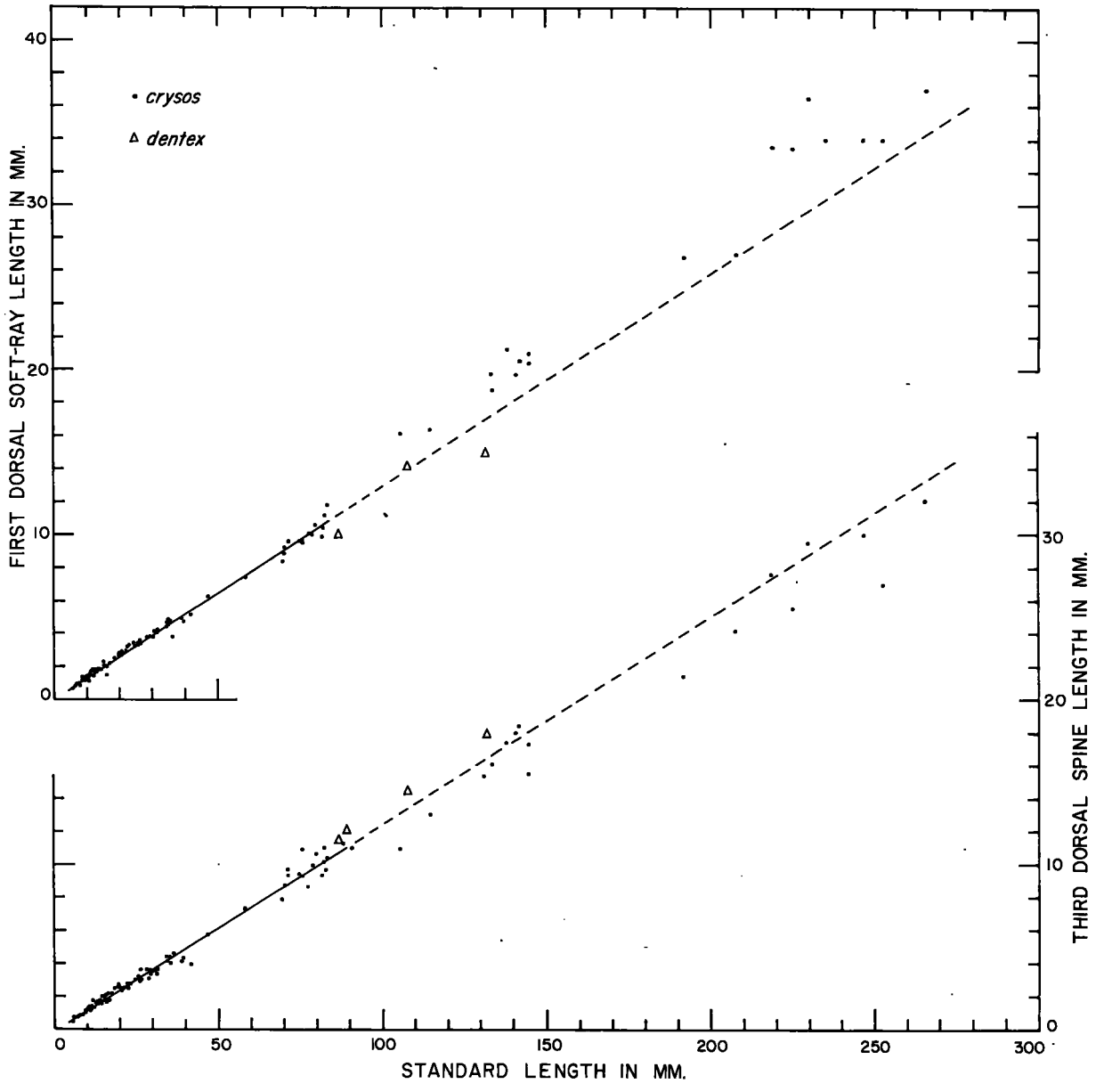

FIGURE 25.—*Caranx crysos* and *C. dentex:* Relation of length of first dorsal soft-ray and of third dorsal spine to standard length.

the upper line intersects the lower line at approximately 22 mm., indicating that an inflection occurs at about that size and that a slower eye growth rate prevails above that size. The proportional rates of increase for the two variates are 0.11-mm. (below 22 mm.) and 0.07-mm. (above 22 mm.) increase in eye diameter per 1.0-mm. increase in standard length. The spread of the coordinates of specimens larger than 145 mm. around the extension of the calculated regression line is variable, but suggests that eye diameter growth may continue at the same proportional rate.

Snout.—The regression of snout length on standard length is shown in figure 28 and table 3. A line fitted to this regression for specimens from 5.4 to 145 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.08-mm. increase in snout length per 1.0-mm. increase in standard length). The

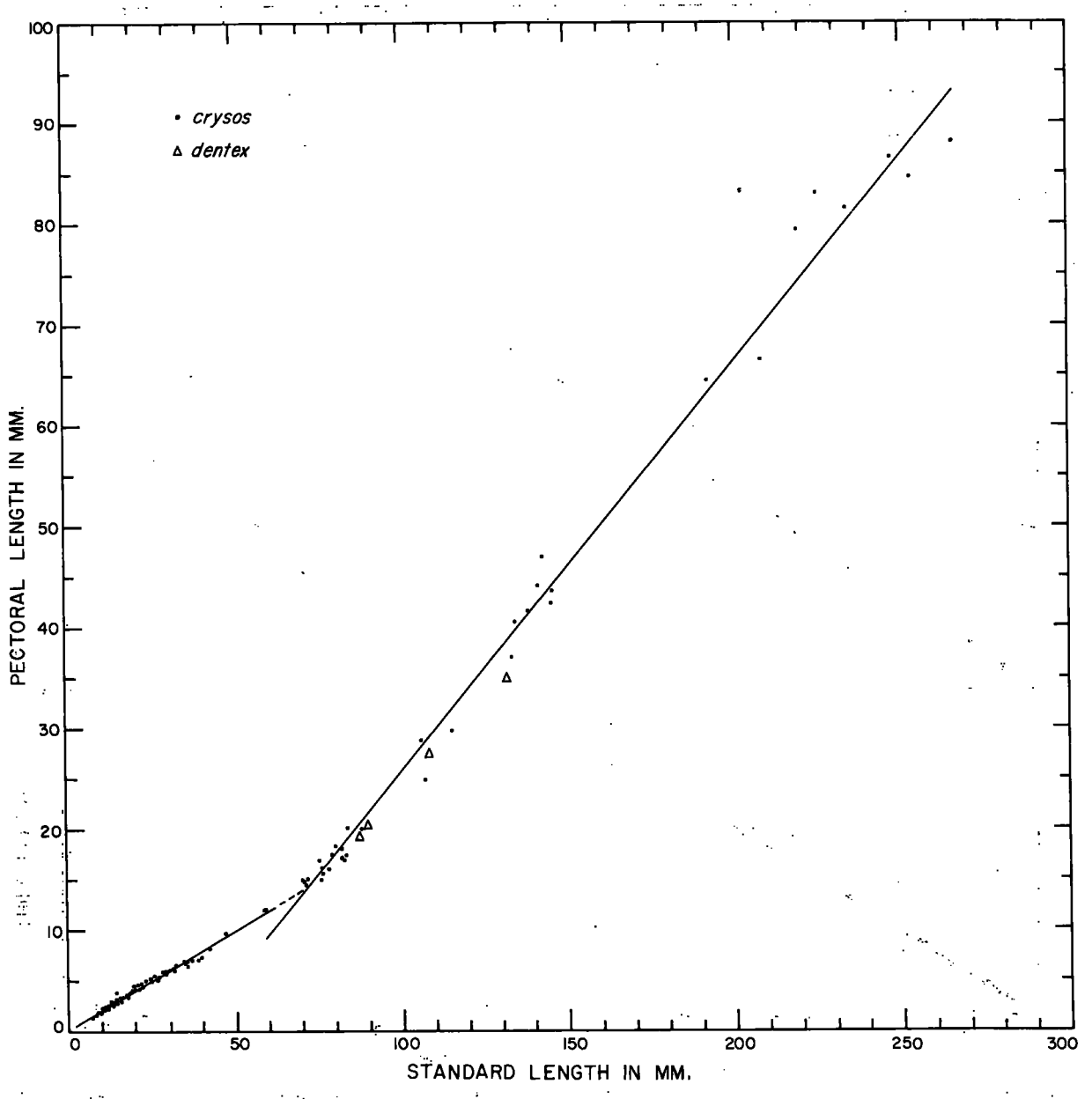

FIGURE 26.—*Caranx crysos* and *C. dentex:* Relation of pectoral length to standard length.

coordinates of specimens larger than 145 mm. fall along the extension of the calculated regression line, indicating that snout growth may continue at the same proportional rate.

Gill rakers:—Lower limb, 23 to 28; upper limb, 10 to 14; total, 35 to 42 (table 5). Nichols (1938b: 2) listed a range on the lower limb of 25 to 33 (his average, 27.9) for 28 specimens. In view of the maximum number on the lower limb (28) obtained by Ginsburg (1952: 97) and myself, abnormal specimens might account for the high number reported by Nichols.

About 20 percent of the specimens above 20 mm. had 1 or 2 rudimentary gill rakers at the origin of the lower limb; none on the upper limb. The presence or absence of these rudiments is apparently independent of body size relationship, as the specimens possessing rudiments were interspersed throughout the range of sizes examined.

Scutes.—Range of the mean number of scutes above 100 mm. standard length: about 46 to 56 (fig. 29). Ginsburg (1952: 97), working with specimens up to about 426 mm. (converted), gave an upper limit of 54 scutes. Nichols (1938b: 2), examining 28 specimens ranging from 103 to 311 mm. standard length, found scutes to vary from 40 to 50. The developing scutes appear between 12 and 13 mm. (figs. 20 and 21). The first scutes to complete their individual development do so at about 19 mm. All scutes of fish above 100 mm. have completed, or nearly completed, their individual development (fig. 29).

Lateral line.—Range of mean lateral-line ratio

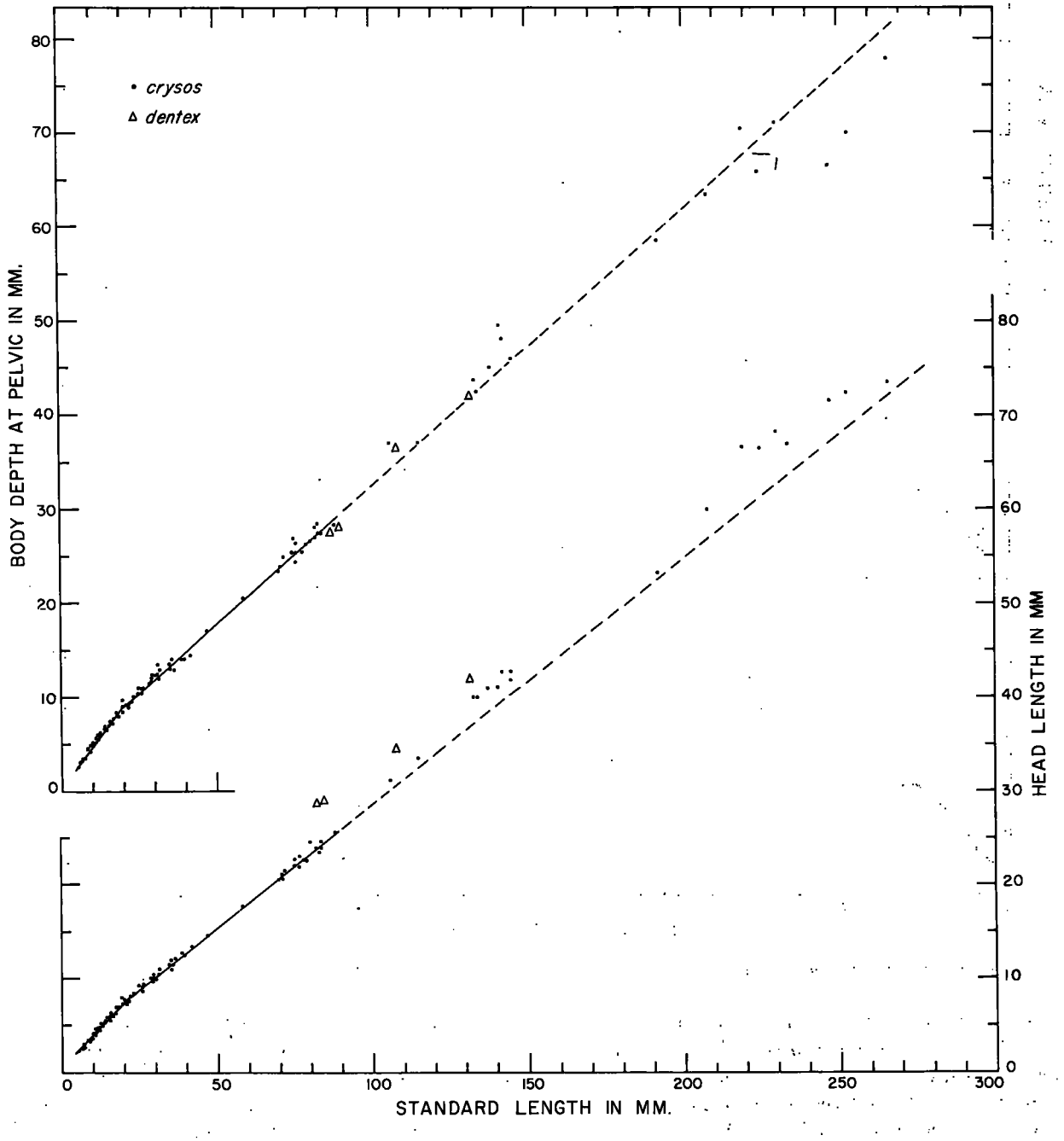

FIGURE 27.—*Caranx crysos* and *C. dentex:* Relation of body depth at pelvic and of head length to standard length.

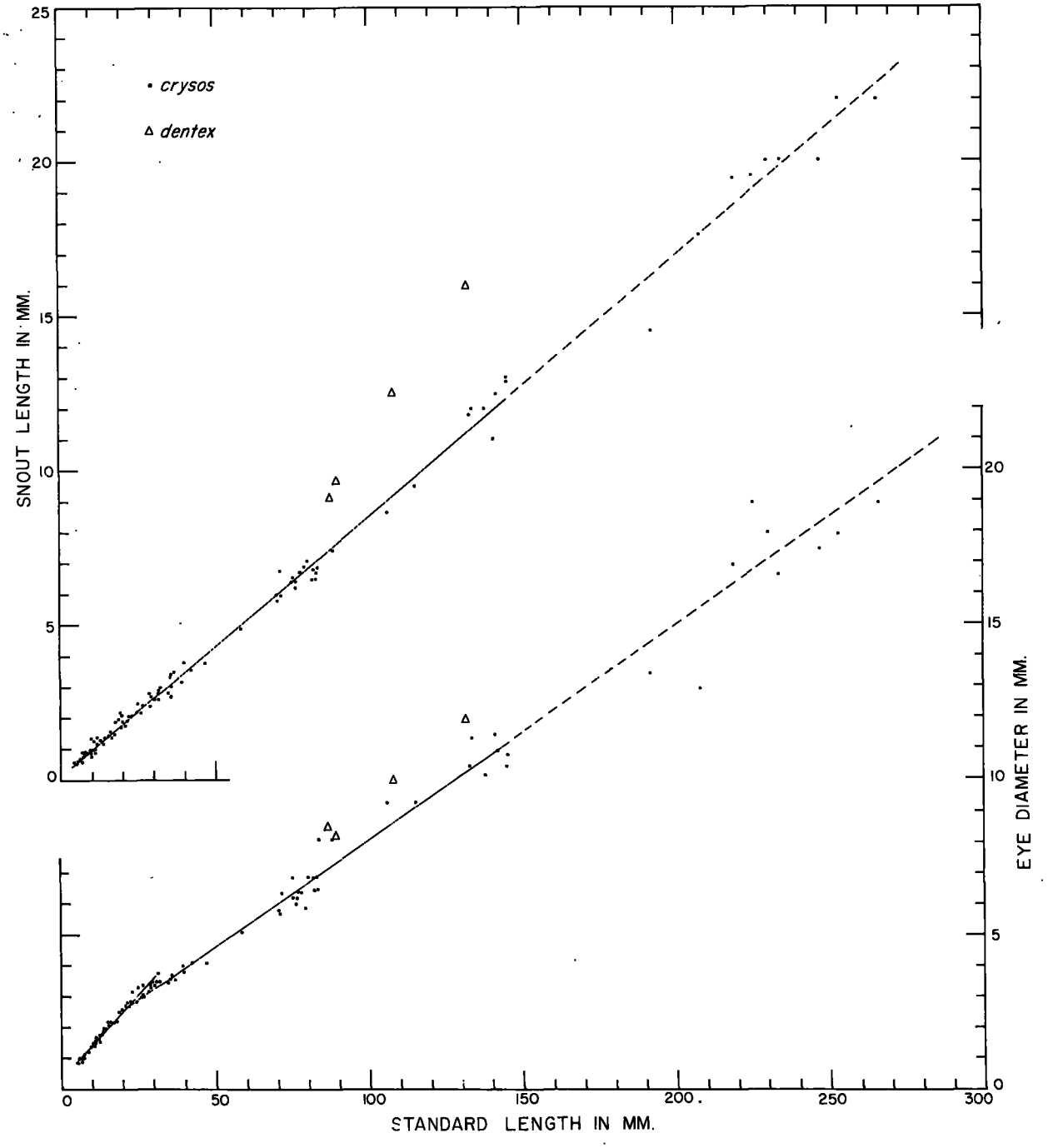

FIGURE 28.—*Caranx crysos* and *C. denlex:* Relation of snout length and of eye diameter to standard length.

from 70 to 200 mm. standard length: 1.75 to 2.1 (fig. 30). The relationship is highly variable, but the ratio shows a trend of increase up to about 50 or 60 mm. and a decrease above 200 mm. The ratio of 1.7 given by Nichols (1938b: 1) for a 22-mm. standard length specimen is within the range I have established. However, the majority of the ratios he gives for 103- to 311-mm. specimens are too low to fall within the perimeters established by my specimens. This may be due to variations in our methods. The values of 1.5 to 1.8 given by Nichols (1939: 5, 6) for specimens 12 mm. and

72 mm. fall within my predicted range, but in the lower portion and with less variation that I encountered.

Preopercular spines.—Because of the appreciable individual variation in this character, it is not possible from the specimens examined to predict accurately at what size the preopercular-angle spine ceases to increase in length—this probably occurs at some size around 7 mm. standard length. Above approximately 10 mm. the length of this spine decreases due to expansion of the posterior margin of the preoperculum (fig. 31). This spine is completely absorbed within the preopercular margin between 42 and 47 mm. The numbers of preopercular upper- and lower-limb spines are variable but tend to decrease with an increase in standard length (table 1). The preoperculum and the preopercular spines of an alizarin-stained 14-mm. specimen are illustrated in figure 24.

Pigmentation.—There are three rows of elongated melanophores on the body of the 5.4-mm. specimen—below the base of the dorsal fin, above

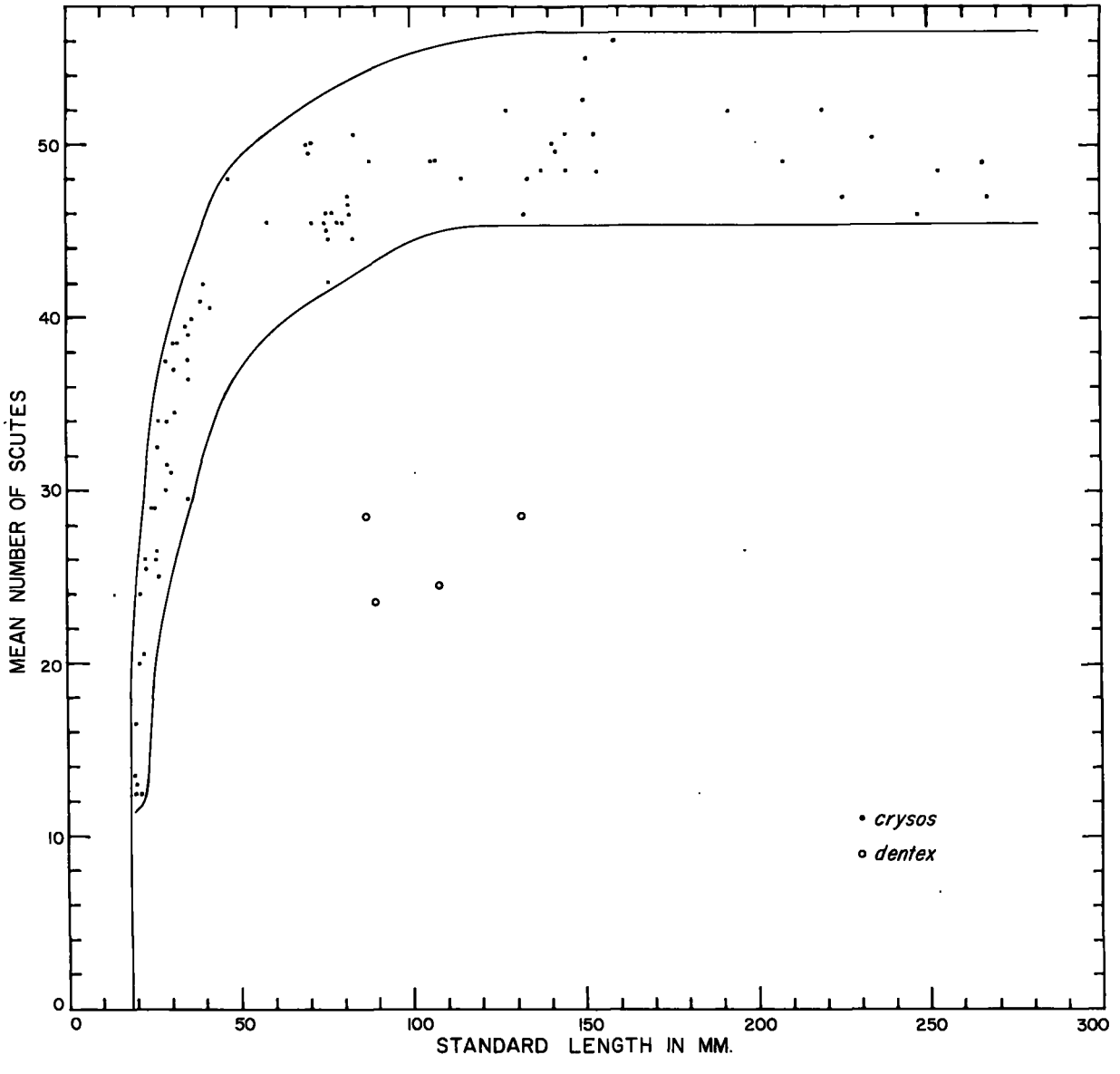

FIGURE 29.—*Caranx crysos* and *C. dentex:* Relation of the mean number of scutes to standard length.

TABLE 5.—Caranx crysos: *Correlation of the numbers of lower-limb to upper-limb gill rakers of 73 specimens*

[The upper number in each block is the count obtained for that combination, and the number in parentheses below is the approximate percentage of that count in the total sample]

UPPER-LIMB GILL RAKERS	LOWER-LIMB GILL RAKERS 23	24	25	26	27	28
10			4 (5.5)	11 (15.1)	2 (2.7)	
11			6 (8.2)	14 (19.2)	11 (15.1)	1 (1.4)
12	1 (1.4)		2 (2.7)	7 (9.7)	6 (8.2)	4 (5.5)
13				2 (2.7)		1 (1.4)
14						1 (1.4)

the base of the anal fin, and on the midline posteriorly. A few melanophores are scattered over the body, upper and lower jaws, and operculum. A group of larger melanophores occurs over the eye on the transparent portion of the head. A few pigment spots are on the interspinous membranes of the dorsal and anal fins, and a row of melanophores occurs along the base of the anal soft-rays (fig. 17).

By about 12 mm. standard length the 3 rows of elongated melanophores begin to intergrade with the other body pigmentation (figs. 18 to 21). The body bars begin to form between 15 mm. and 19 mm.—the rudiments of 5 bars are present in the 15.6-mm. specimen (fig. 21). The number of bars increases to the normal complement of 7 by about 23 mm. (fig. 22). Rarely 6 or 8 bars may be counted on one or both sides of fish above 23 mm. The bars are not distinct on some specimens above 60 mm., but on six freshly preserved specimens from Brunswick, Ga., bars were present on specimens of 105 mm., 105 mm., 111 mm., and 134 mm., but not on specimens of 110 mm. and 124 mm. The caudal peduncle is unpigmented to about 13 mm. (figs. 17 to 20). A dense mass of pigment begins to develop on the upper portion of the peduncle at about 28 mm. (figs. 22 and 23).

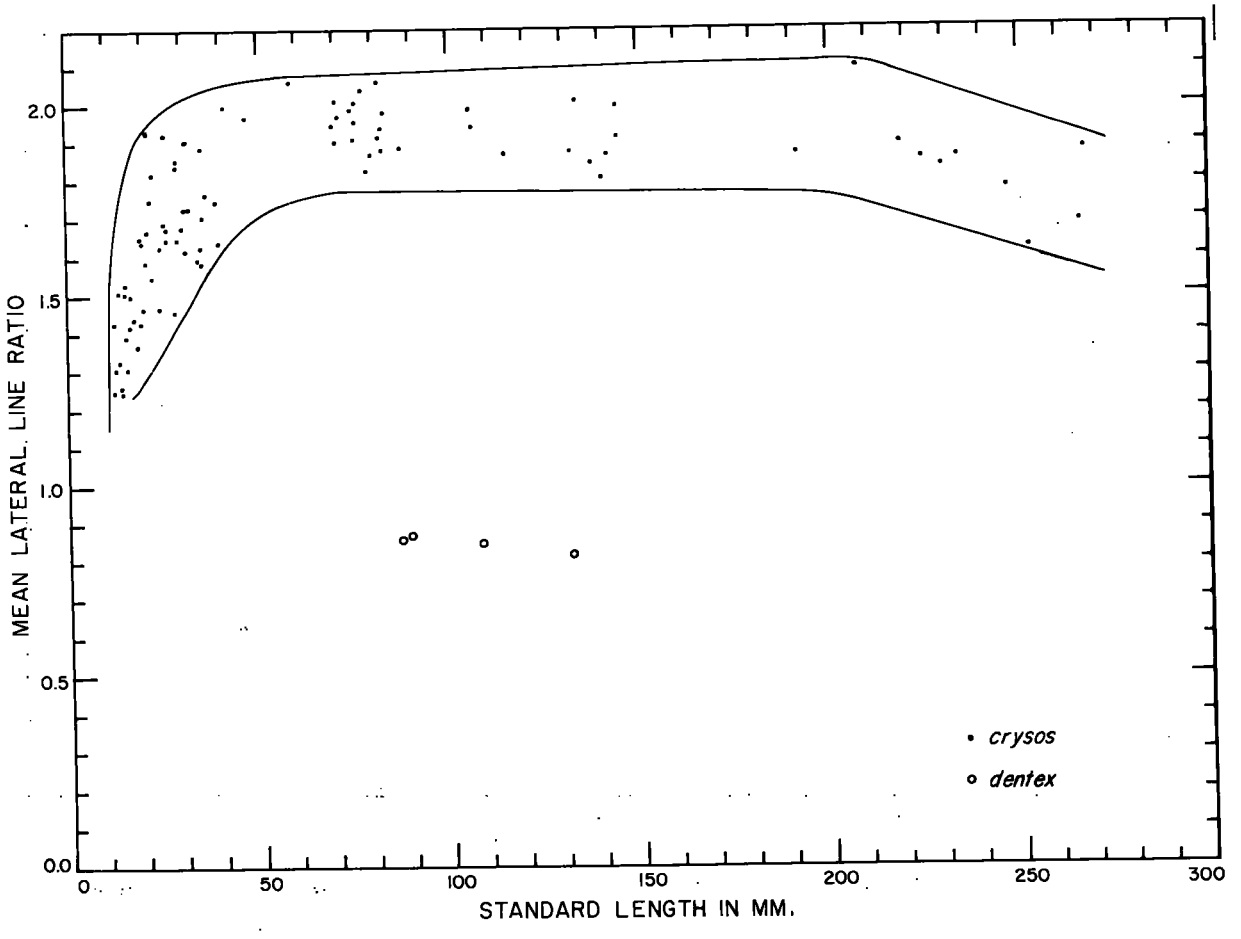

FIGURE 30.—*Caranx crysos* and *C. dentex:* Relation of the mean lateral-line ratio to standard length.

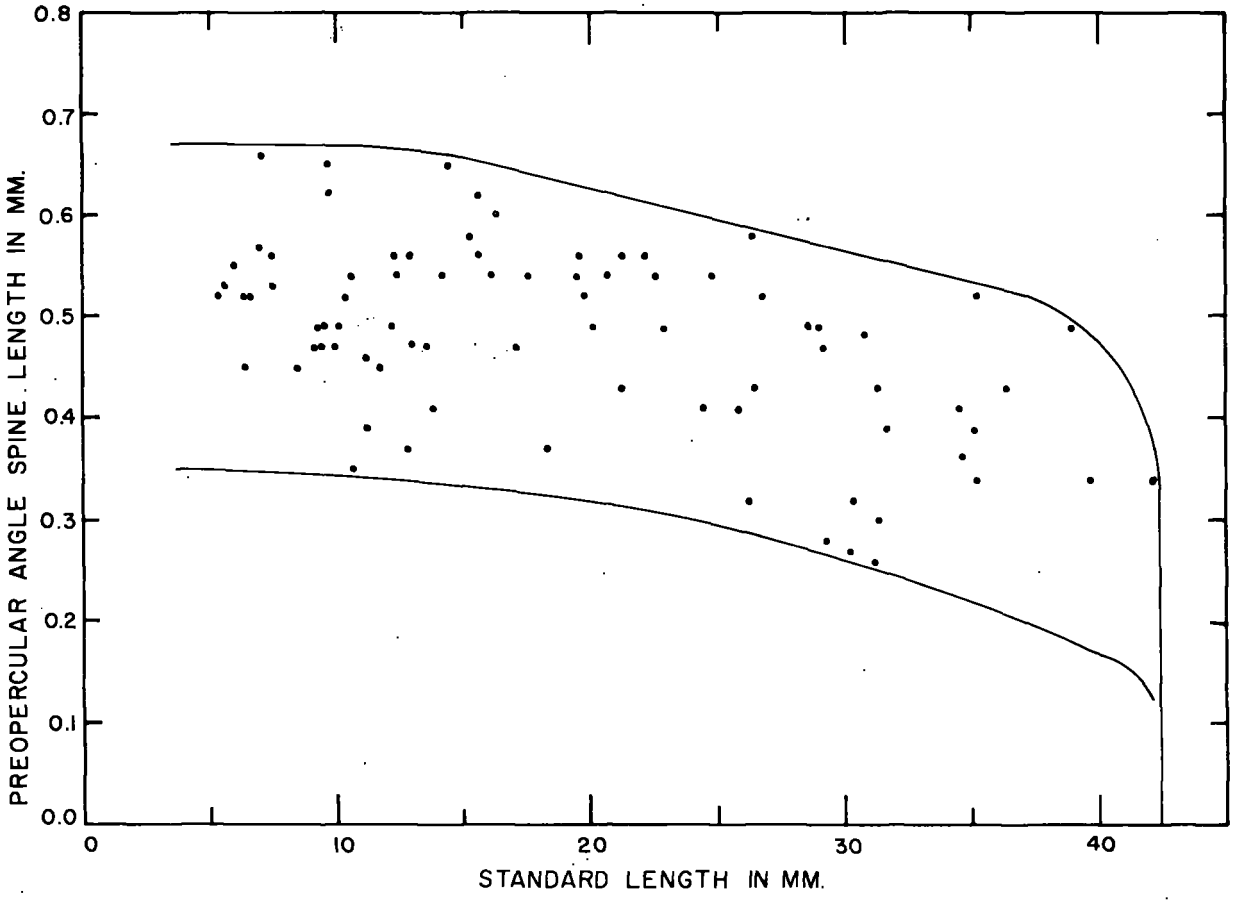

FIGURE 31.—*Caranx crysos:* Relation of length of the preopercular-angle spine to standard length.

This may have been referred to as an additional body bar by Nichols (1939: 6), Beebe and Tee-Van (1928: 110), Fowler (1936: 699), and possibly others.

The pigmentation on the brain case changes from a few large melanophores on the transparent portion to a pigment mass which is projected posterodorsally and which forms the nuchal band by about 29 mm. (figs. 17 to 21). The brain case becomes opaque between 10 mm. and 15 mm. (figs. 20 and 21). Concentrations of pigment below the eye and on the eye above and below the pupil give the impression that the nuchal band bends downward and continues through the eye. A vertically elongated spot forms on the operculum from about 30 to 40 mm., becomes prominent at about 60 mm., and is reduced in size and located on the upper and outer margin of the operculum by about 100 mm.

Pigment on the first dorsal fin intensifies to about 82 mm. standard length and diminishes at larger sizes; that of the anal interspinous membranes is similar but never as concentrated as on the first dorsal (figs. 17 to 23). Pigmentation on the second dorsal and anal fins is pronounced at 8.5 mm. (fig. 19) and intensifies to above 82 mm. (figs. 20 to 23). Pigment spots are present on the pelvics by 7.0 mm. (fig. 18) and on the caudal and pectorals by 29 mm. (fig. 22), but these fins are never heavily pigmented.

Five specimens with enlarged gonads, which were approaching spawning condition, were darker than other specimens examined. Described from preservation in isopropyl alcohol: the 4 females (247 to 267 mm.) were dark above and light below the lateral line, with clear pelvics and slightly dusky anal fins; the 225-mm. male was black above and leaden below the lateral line, and all the fins were dark with the pelvics very black.

Distribution off Southeastern Atlantic Coast of the United States

Caranx crysos has been reported from the following specific localities within this area: Nassau, Bahamas, by Lee (1889: 670), Bean (1905: 302), Parr (1930: 45), and Ginsburg (1952: 96); the Gulf Stream off Bimini, Bahamas, by Nichols (1938b: 1); Biscayne Bay, Fla., by McCormick, *in* Smith (1896: 174); Boca Raton, Fla., by Fowler (1945: 292); St. Johns River, Fla., by Goode (1879: 112; 1882: 35); Fort Macon, N. C., by Goode (1882: 32); Cape Romain and Charleston, S. C., by Fowler (1945: 191); and Beaufort, N. C., by Goode (1882: 35), Jordan (1886a: 27), Yarrow (1877: 208), Jordan and Gilbert (1879: 376), Smith (1907: 84), and Nichols (1938a: 1).

Figure 32 shows the locations of specimens taken on the *Gill* cruises, specimens taken by the *Combat* off Florida, other specimens in the SAFI collection (Brunswick, Ga.), USNM specimens examined (33 miles south of the Lookout Light Ship in Gulf Stream), and ChM specimens examined (Charleston and Cape Romain, S. C.) (tables 2 and 6); and specimens reported by Nichols (1938a: 1; in the Gulf Stream off Bimini, Bahamas, 22 mm.) and Fowler (1945: 292; Boca Raton, Fla., about 63 mm., converted). The specimens recorded on this chart are larvae and juveniles with the exception of the inshore records of larger specimens from South Carolina which may have been adult. The locations of capture of the larvae and juveniles were generally near or beyond the 100-fathom line and indicate an association with the Gulf Stream, as depicted by the approximate axis of the Stream in figure 32. Because of the relatively less-concentrated collecting by the *Gill* east of the axis of the Gulf Stream, it is not possible to estimate accurately the relative abundance of these forms for that area. This occurrence of young in the Gulf Stream extends from about May into November, but in heaviest concentration from mid-June to mid-August (fig. 33).

Specimens of *crysos* above 100 mm. standard length have commonly been taken inshore along the Atlantic coast of the United States. Specimens below this size occasionally occur inshore on the Atlantic coast of southern Florida and at Cape Lookout and Cape Hatteras, N. C. (where the Gulf Stream moves in relatively close to the shore). I have found few published inshore records of *crysos* less than 100 mm. other than from these two localities: Smith (1898: 98) reported specimens of about 36 mm. and 51 mm. (converted) from Woods Hole, Mass., in summer. Breder's (1926: 124) record of "a small example of about 30 mm." identified as *crysos* from Sandy Hook Bay, N. Y., is not convincing because he describes the body as banded with five intense black vertical bars, which description normally applies to *hippos* or possibly *latus*. The larvae and juveniles evidently have an affinity for the Gulf Stream and offshore waters to a size of 80 to 100 mm., above which size at least a part of the Stream population moves inshore. Records of *crysos* taken inshore north of North Carolina support this: Bean (1891: 87) reported specimens of about 105 to 145 mm. (converted) from Cape Charles City, Va., September 16 to October 3; Murphy and Harper (1915: 41), specimens of about 135 mm. (converted) from Long Island, N. Y., in September; Latham (1918: 55), specimens about 115 mm. (converted) on October 23 and about 141 mm. (converted) on November 4 from Long Island, N. Y.; Latham (1920: 92), specimens about 95.5 mm. (converted) from Long Island, N. Y., July 26; Bigelow and Schroeder (1953: 377), specimens about 115 to 155 mm. (converted) from Cape Cod Bay, Mass., in September; Leim (1930: xlvi, *fide* Bigelow and Schroeder, 1953: 377), specimens about 95 mm. (converted) from Halifax, Nova Scotia; and Vladykov (1935: 4), a specimen about 141 mm. (converted) from Pubnico, Nova Scotia, September 1.

I believe that the larvae and young juveniles in the Gulf Stream are carried northward by the Stream currents—a northward movement of young is also probably effected by the Antilles Current. At a juvenile size of 80 to 100 mm. a portion of this developing population migrates to Atlantic coast inshore waters, but another portion may, at least temporarily, continue its movement eastward with the Stream. A continuation in movement with the Stream to Africa is also possible. Nichols (1939: 5) hypothesized, "a regular interchange between the continents of America and Africa, eastward in the north and westward in the south." Records of *crysos* from the Azores and West Africa sponsored this theory, but the inadequately known relations of this species with *C. fusus* of the Mediterranean limit its acceptability. If young *crysos* taken in the Gulf Stream off the southeastern United States

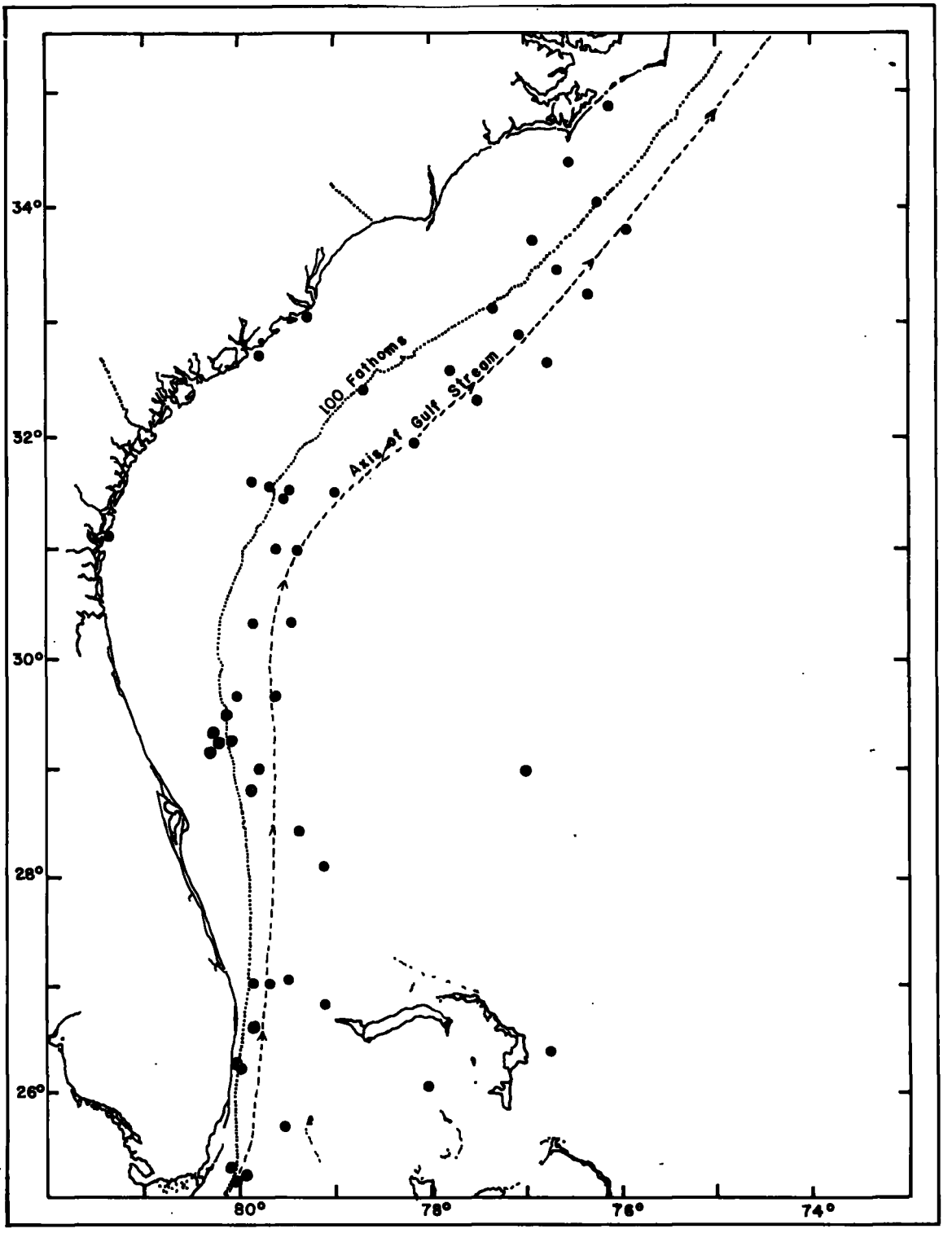

FIGURE 32.—*Caranx crysos:* Locations of capture off the southeastern Atlantic coast of the United States.

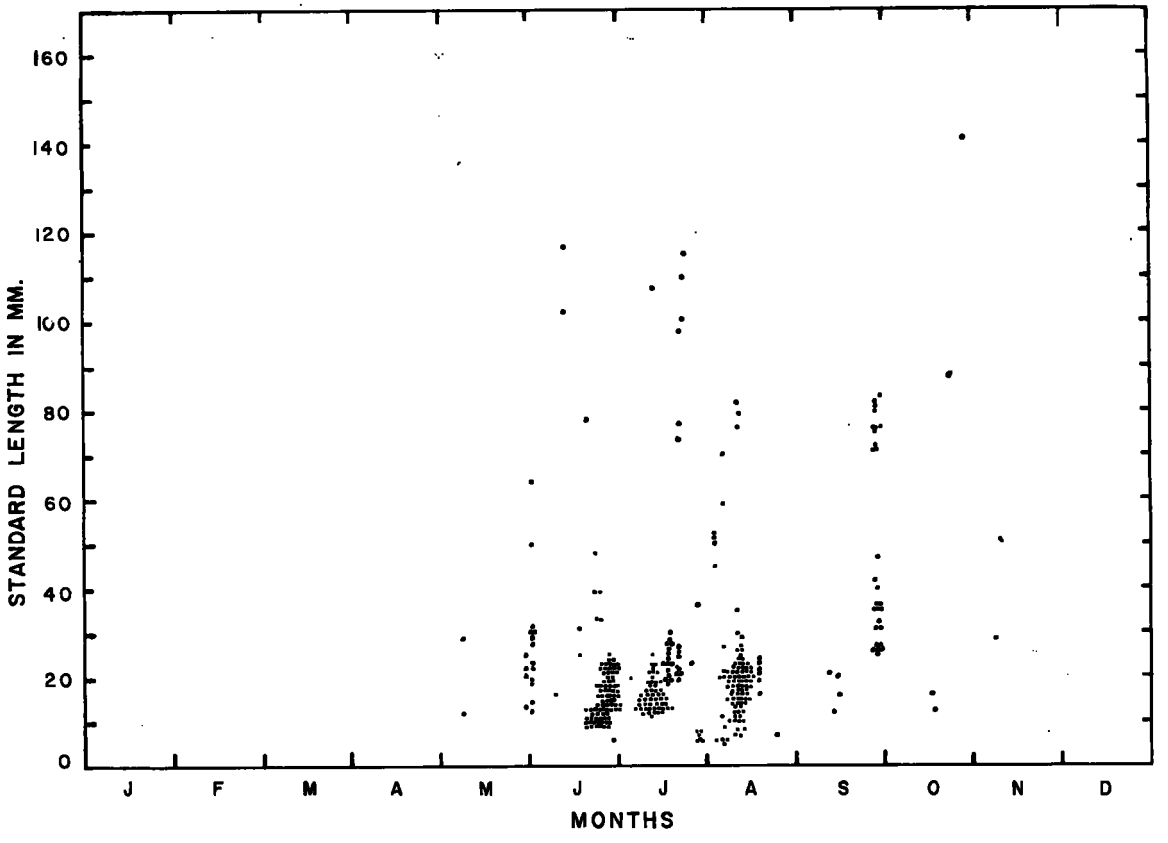

FIGURE 33.—*Caranx crysos:* Size distribution, by months, of specimens taken off the southeastern Atlantic coast of the United States.

represent a population that occurs each year from summer to fall and moves northward in the Stream and the Antilles Current, then much of this population must be recruited from areas that contribute to this portion of the Stream, although some part of the population may be the result of reproduction within the area.

On the basis of two collections of *crysos* from 12 to 72 mm., Nichols (1939: 5 and 8) predicted a "nursery ground" for the species in the Gulf Stream off Maryland (37°12′ N., 67°39′ W. to 38°59′ N., 69°46′ W.) in late August. These fish probably represented a northward continuation of the population which occurs yearly off the coast of the Southeastern States.

The absence of records of *crysos* from inshore waters along the Atlantic coast from December through June indicates that the larger fish which have been reported from the coast during July through November either migrate to the south or move offshore to the warmer waters of the Stream during the colder months.

Spawning

The spawning season that contributes young *crysos* to this area may be estimated, from the smallest specimens taken in May (12.4 mm.) and in October (13.2 mm.), to extend from early April to early September (fig. 33).

The only specimens of *Caranx* with developed gonads that were examined during this study were five *crysos* taken by the *Oregon* from about 50 to 60 miles east-southeast of South Pass, La., July 20–26, 1956. None of these fish were running-ripe; but the four females (247 mm., 253 mm., 266 mm., and 267 mm. standard length) had enlarged ovaries about 50 mm. long containing macroscopically visible eggs, and the one male (225 mm.) had enlarged testes about 50 mm. long. The pigmentation of these specimens was unusual, and is described under the section on Pigmentation, page 453.

Erdman (1956: 230) noted *crysos* in spawning condition in May at Puerto Rico. Holbrook (1860: 93) described the testes of *crysos* from

South Carolina—possibly indicating the presence of ripening males from that locality, but he gave no season or definite locality.

Referring to *crysos* that appeared at Pensacola, Fla., in April and May, Stearns, *in* Goode (1882: 32), stated—

> On their arrival the larger fish contain spawn, which in July and August becomes quite full, after which none are seen but the young fish of about 10 inches in length, until there is a general movement towards the sea. It is believed that the adult fish spawn in the bays, but the only evidence to support that belief is that they come inside with spawn, go away without it, and that very young fish are found there.

This reasoning is analogous to that which for many years was applied to the Atlantic coast species of *Mugil*. Anderson (1957), however, has shown that spawning of *M. curema* occurs in offshore waters, and that the young do not come into the coast and bays until after attaining a certain size. Since larvae of *crysos* were abundant offshore and smaller larvae have never been recorded inshore, it is probable that *crysos* also spawns offshore.

If, as suggested, there is a motile, northward-moving population of developing young, the majority of the specimens taken by the *Gill* would have been the result of spawning that occurred to the south of this area. Some of the smaller specimens (5.4 to 7.5 mm.) taken by the *Gill* off Georgia to North Carolina and the 5.7 to 7.7-mm. specimens taken by the *Fish Hawk* from near the Lookout Light Ship (table 6) may have been spawned within this area.

TABLE 6.—Caranx crysos: *Location and date of capture, number and size range (in mm.) of 683 specimens examined*

[See pp. 417 and 419 for explanation of abbreviations used; measurements in standard length]

Location	Date captured	Collection	Number of specimens	Size (mm.)
ATLANTIC OCEAN:				
24°04′ N., 79°15′ W.	July 24, 1957	SAFI, *Combat* 448	28	18.5–35
24°13′ N., 81°42′ W.	July 21, 1957	SAFI, *Combat* 436	4	26–64
25°10′ N., 80°02′ W.	July 22, 1957	SAFI, *Combat* 438	17	18.5–30
25°11′ N., 79°56′ W.	do	SAFI, *Combat* 443	10	19.5–77
25°16′ N., 80°07′ W.	July 26, 1956	SAFI, *Combat* 457	1	23
26°21.2′ N., 76°46.5′ W.	July 19, 1953	SAFI, *Gill* 3, Std.	1	77.5
Do.	(July 23, 1953) (July 24, 1953)	do.	1	17.6
26°37′ N., 79°51′ W.	July 28, 1957	SAFI, *Combat* 458	1	36.5
26°54′ N., 79°07′ W.	Aug. 29, 1954	SAFI, *Gill* 8, Settlement Point, Bahamas	18	24.5–70.5
27°01′ N., 79°45′ W.	June 23, 1954	SAFI, *Gill* 7, leaving Reg. 2	30	9.1–14.4
27°11′ N., 79°55′ W.	July 23, 1953	SAFI, *Gill* 3, Reg. 2 to Reg. 3	1	6.6
28°17.5′ N., 79°28′ W.	Sept. 12, 1954	SAFI, *Gill* 8, Reg. 8	1	20.7
28°18.5′ N., 79°26′ W.	July 26, 1953	SAFI, *Gill* 3, Reg. 8	9	17–25
28°48′ N., 79°53′ W.	June 13, 1956	SAFI, *Pelican* 67	2	102–117
28°56.3′ N., 79°45.6′ W.	July 27, 1953	SAFI, *Gill* 3, Reg. 15	1	20.1
29°00′ N., 77°00′ W.	July 17, 1953	SAFI, *Gill* 3, Spc. 6	2	24.8–31.3
29°10′ N., 80°19′ W.	June 1, 1957	SAFI, *Combat* 336	2	28.5–31.5
29°10′ N., 80°19′ W. to 29°19′ N., 80°15′ W.	do	SAFI, *Combat* 336 to 337	4	22.5–31.5
29°16′ N., 80°04′ W.	May 30, 1957	SAFI, *Combat* 328	1	25
29°19′ N., 80°18′ W.	June 1, 1957	SAFI, *Combat* 339	4	12.5–19.5
Do.	do.	SAFI, *Combat* 343	2	50–64
29°28′ N., 80°09′ W.	May 30, 1957	SAFI, *Combat* 326	3	13.4–22
29°29′ N., 80°09′ W.	Aug. 18, 1957	SAFI, *Combat* 485	7	16.5–24
29°36.2′ N., 79°59.8′ W.	July 28, 1953	SAFI, *Gill* 3, Reg. 18	1	6.4
29°38′ N., 79°36.5′ W.	June 25, 1954	SAFI, *Gill* 7, Reg. 17	1	33
29°40′ N., 80°00′ W.	do	SAFI, *Gill* 7, Reg. 18	1	39
Do.	Sept. 13, 1954	SAFI, *Gill* 8, Reg. 18	1	12.2
30°20′ N., 79°50′ W.	June 26, 1954	SAFI, *Gill* 7, Reg. 27	1	22.9
30°20.5′ N., 79°27′ W.	Sept. 14, 1954	SAFI, *Gill* 8, Reg. 28	1	19.6
30°56.8′ N., 79°37.4′ W.	July 29, 1953	SAFI, *Gill* 3, Reg. 30	1	22.6
30°58′ N., 79°37.5′ W.	June 27, 1954	SAFI, *Gill* 7, Reg. 30	62	12–24
30°59′ N., 79°14′ W. to 30°59.5′ N., 79°36.5′ W.	Sept. 15, 1954	SAFI, *Gill* 8, Reg. 29 to Reg. 30	1	15.6
Commercial trawling area, Brunswick, Ga.	Sept. 14, 1956	SAFI	4	105–124
Do.	Sept. 16, 1956	do.	1	111
Do.	Oct. 9–10, 1956	do.	1	135
Do.	Nov. 9, 1956	SAFI	4	151–158
Do.	Nov. 13, 1956	do.	10	128–154
31°32′ N., 79°28′ W.	Aug. 5, 1953	SAFI, *Gill* 3, Reg. 39	1	10.7
31°33′ N., 79°39.5′ W.	do.	SAFI, *Gill* 3, Reg. 38 to Reg. 39	1	6.0
31°35′ N., 79°51′ W.	do.	SAFI, *Gill* 3, Reg. 38	3	5.4–6.4
31°56′ N., 75°08.5′ W.	July 4, 1954	SAFI, *Gill* 7, Reg. 50	1	20.0
31°57′ N., 78°09′ W.	Aug. 6, 1953	SAFI, *Gill* 3, Reg. 50	2	19.5–26.7
32°19′ N., 77°34′ W.	Aug. 7, 1953	SAFI, *Gill* 3, Reg. 51	3	21.2–70
32°24′ N., 78°44′ W.	Aug. 6, 1953	SAFI, *Gill* 3, Reg. 48	1	19.8
32°35′ N., 77°46′ W.	Aug. 7, 1953	SAFI, *Gill* 3, Reg. 52	1	8.5
32°39′ N., 76°46′ W.	Aug. 10, 1953	SAFI, *Gill* 3, Reg. 62	7	22.2–82
Charleston Harbor, S. C.	Aug. 11, 1937	ChM 35.181	1	234
Off Charleston, S. C.	July 3, 1934	ChM 34.174	1	208
Do.	Oct. 28, 1940	ChM 40.200	1	141
Off Blackfish Bank, Charleston, S. C.	May 19, 1939	ChM 39.93.1	1	192
32°53′ N., 77°03.5′ W.	Nov. 8, 1953	SAFI, *Gill* 4, Reg. 61	1	29.1
32°54′ N., 77°04′ W.	Aug. 10, 1953	SAFI, *Gill* 3, Reg. 61	2	7.1–7.5
Do.	do.	do.	8	9.5–12.3

TABLE 6.—Caranx crysos: *Location and date of capture, number and size range (in mm.) of 683 specimens examined*—Con.

Location	Date captured	Collection	Number of specimens	Size (mm.)
ATLANTIC OCEAN—Continued				
Cape Romain, S. C.	July 11, 1933	ChM 33.176.3	1	107
33°07′ N., 77°20′ W.	Aug. 10, 1953	SAFI, *Gill* 3, Reg. 60	1	7.0
33°14.7′ N., 76°23′ W.	May 8, 1953	SAFI, *Gill* 2, Reg. 63	2	12.4–29.3
33°24′ N., 76°25′ W.	Aug. 11, 1953	do	1	79
33°29′ N., 76°40′ W.	do	SAFI, *Gill* 3, Reg. 64	68	12–29
33°43.5′ N., 76°56′ W.	Sept. 28, 1954	SAFI, *Gill* 8, Reg. 65	7	71–82
33°44′ N., 77°00′ W.	Aug. 11, 1953	SAFI, *Gill* 3, Reg. 65	1	13.8
33°50′ N., 75°58′ W.	Aug. 12, 1953	SAFI, *Gill* 3, Reg. 72	1	7.5
33°50′ N., 75°59′ W.	July 10, 1954	SAFI, *Gill* 7, Reg. 72	14	17–24.5
34°02.5′ N., 76°15.5′ W.	Sept. 28, 1954	SAFI, *Gill* 8, Reg. 71	1	82.5
34°03.7′ N., 76°14.5′ W.	July 10, 1954	SAFI, *Gill* 7, Reg. 71	53	11–19
Gulf Stream, 33 mi. south Lookout Lightship	July 28, 1915	USNM 164486, *Fish Hawk*	6	5.7–7.7
35°01′ N., 75°45′ W.	Sept. 29, 1954	SAFI, *Gill* 8, Reg. 77	2	76–83
35°08′30″ N., 75°10′ W.	Oct. 17, 1885	USNM 164536, *Albatross* Sta. 2596	2	13.2–16.5
Edge of Gulf Stream, off Cape Hatteras	June 6, 1903	USNM 53106	1	16.6
Mouth of York River, Va.	July 8, 1953	UF 884	2	106–115
37°48′30″ N., 69°43′30″ W.	Sept. 7, 1884	USNM 131600, *Albatross* Sta. 2223	2	21.0–24.2
38°49.3′ N., 71°37′ W.	Aug. 3, 1952	SAFI, *Caryn*	9	90–105
39°26′ N., 68°03′30″ W.	Aug. 31, 1885	USNM 92618, *Albatross* Sta. 2569	1	25.5
39°58′30″ N., 70°16′ W.	Sept. 1, 1899	USNM 73248, *Fish Hawk* Sta. 7070	1	52.5
GULF OF MEXICO:				
Dry Tortugas, Fla.		USNM 38597	1	88
Bonefish Bank, Fla.	Nov. 27, 1906	USNM 57312, *Orian*	1	83.5
28°17′ N., 88°27′ W.	July 22, 1956	UF 3914, *Oregon* 1587	3	80–145
28°17′ N., 88°35′ W.	do	UF 3911, *Oregon* 1586	3	225–266
28°17′ N., 88°37′ W.	Aug. 22, 1955	GFEGR, *Oregon* 1380	5	19–23
28°20′ N., 88°37′ W.	July 21, 1956	UF 3917, *Oregon* 1585	9	34.5–49.5
150 mi. South of Mobile Bay	Aug. 1955	GFEGR, *Oregon*	7	54.5–72
Bayport, Fla.	Sept. 25, 1954	UF 3744	6	133–219
28°45′ N., 88°03′ W.	July 24, 1956	UF 3920, *Oregon* 1590	2	37.5–41.5
28°47′ N., 87°56′ W.	July 23, 1956	UF 3915, *Oregon* 1589	5	12–37.5
28°47′ N., 87°57′ W.	Aug. 15, 1955	GFEGR, *Oregon* 1367	4	20.5–44
28°48′ N., 87°50′ W.	Aug. 14, 1955	GFEGR, *Oregon* 1365	3	23.5–44
28°50′ N., 87°58′ W.	July 24, 1956	UF 3918, *Oregon* 1591	29	17–59
Do.	July 26, 1956	UF 3912, *Oregon* 1593	2	247–267
Do.	do	UF 3919, *Oregon* 1593	57	14.5–37.5
28°50′ N., 87°50′ W.	Aug. 13, 1955	GFI, *Oregon* 1363	1	14
28°55′ N., 87°50′ W.	Aug. 10, 1955	GFEGR, *Oregon* 1356	15	22.5–86
28°55′ N., 87°30′ W.	June 21, 1957	SAFI, *Oregon* 1835	1	15.5
28°55′ N., 87°57′ W.	Aug. 21, 1955	GFEGR, *Oregon* 1372	25	15–72
28°55′ N., 88°00′ W.	Aug. 20, 1955	GFEGR, *Oregon* 1370	15	20–49
28°58′ N., 87°55′ W.	July 20, 1956	UF 3916, *Oregon* 1582	2	27.5–33
29°01′ N., 87°48′ W.	Aug. 22, 1955	GFEGR, *Oregon* 1374	29	17.5–53
Do.	do	GFI, *Oregon* 1374	2	27.5–41
Do.		do	1	17
Yankeetown, Fla.	Oct. 26, 1930	UF 1420	1	142
Cedar Key, Fla.	Sept. 1956	SAFI	1	191
Do.	Oct. 28, 1956	do	1	193
CARIBBEAN SEA:				
Rocky Point, Jamaica	June 23, 1957	UF (uncataloged)	1	230

Caranx ruber (Bloch)

(Figures 34–38)

Scomber ruber Bloch, 1793, p. 75, pl. CCCXLII (St. Croix, West Indies).

Caranx ruber, Bloch and Schneider, 1801, p. 29.

Caranx blochii Cuvier, *in* Cuvier and Valenciennes, 1833, p. 69 (St. Croix, West Indies; Gulf of Mexico).

?*Caranx dentex* (*non* Bloch and Schneider), Günther, 1860, p. 441 (New Orleans).

Caranx iridinus Poey, 1860, p. 266 (Cuba).

Carangoides iridinus, Poey, 1868, p. 366.

Caranx (*Elaphrotoxon*) *ruber*, Fowler, 1905a, p. 76 (new subgenus).

Elaphotoxon ruber, Jordan, Evermann, and Clark, 1930, p. 271 (altered orthography; West Indies and coast of the Carolinas).

Caranx crysos (*non* Mitchill), Fowler, 1940, p. 766 (Rio de Janeiro, Brazil, but locality questioned).

Nomenclature

The nomenclature of *Caranx ruber* (Bloch) has been decisive since Jordan and Gilbert (1884: 32) amended their earlier synonymization (1883: 198) of this species with *C. bartholomaei* Cuvier.

Material

Measurements and counts were taken on a series of 76 fish from 12.4 to 246 mm. standard length, and meristic values were recorded for an additional 78 specimens within this size range. The 426 specimens identified are listed in table 10.

Three young specimens from New Orleans (presumably Louisiana) that are in the British Museum (Natural History) and were recorded by Günther (1860: 441) as *dentex* are not that species, but apparently are *ruber*. G. Palmer of the Museum has kindly furnished information on these specimens: 41 mm., 51 mm., and 59 mm. standard length; dorsal soft-rays 27 (2), and 28 (1); anal soft-rays 24 (3); lower-limb gill rakers 33 (3); lateral-line ratio 1.31 (1), and 1.37 (2); no pig-

mentation is apparent; and paired caudal keels above and below the lateral line are present. In the family Carangidae, this combination of characters is attributable only to *ruber*.

Characters

Dorsal spines.—VIII and I. All spines are well formed at 12.4 mm. standard length (fig. 34). The fourth spine averages the greatest length to about 33 mm.; above 33 mm., the third spine is longest. An interspinous membrane connects the first and second dorsal fins (eighth and ninth spines) to about 75 mm. On specimens 230 mm. and 246 mm., the membrane connecting the seventh and eighth spines has disappeared.

The regression of length of the third dorsal spine on standard length is shown in figure 39 and table 7. A line fitted to this regression for specimens from 12.4 to 118 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.10-mm. increase in spine length per 1.0-mm. increase in standard length). The coordinates of the four specimens larger than 118 mm. fall along the extension of the calculated regression line, indicating that the spine growth may continue at the same proportional rate.

Anal spines.—II and I. All spines are well formed at 12.4 mm. standard length (fig. 34). The second spine is longer than the first at all sizes. An interspinous membrane connects the second and third spines to about 42 mm.

Dorsal soft-rays.—26 to 30 (table 8). Counts of 2 specimens with only 24 soft-rays given by Nichols and Roemhild (1946, fig. 1) could repre-

TABLE 7.—Caranx ruber: *Statistics describing regressions of body parts on standard length*

$\bar{x}$=mean of independent variable x
$\bar{y}$=mean of dependent variable y
N=number of specimens
b=rate of increase of y
a=y-intercept of regression line
$Sy{\cdot}x$=standard deviation from regression (standard error of estimate)

Independent variable x	Dependent variable y	Size range of specimens (mm.)	$\bar{x}$	$\bar{y}$	N	b	a	$Sy{\cdot}x$
Standard length	Dorsal-fin spine length (3d)	12.4–118	44.70	4.61	68	0.098	1.708	0.435
Do	Dorsal soft-ray length (1st)	12.4–118	45.72	5.72	66	.121	.174	.376
Do	Pectoral length	12.4–74.5	34.44	7.01	57	.201	.094	.336
Do	do	74.5–230	106.27	26.90	15	.381	−13.588	1.961
Do	Body depth	12.4–23.1	18.61	8.67	23	.406	1.107	.302
Do	do	23.1–106	52.82	19.30	47	.294	3.776	.638
Do	Head length	12.4–118	43.91	13.65	71	.265	2.014	.523
Do	Eye diameter	12.4–34.1	22.84	2.90	39	.080	1.080	.143
Do	do	34.1–106	65.50	5.55	31	.058	1.736	.165
Do	Snout length	12.4–88.5	38.31	3.45	65	.088	.087	.219

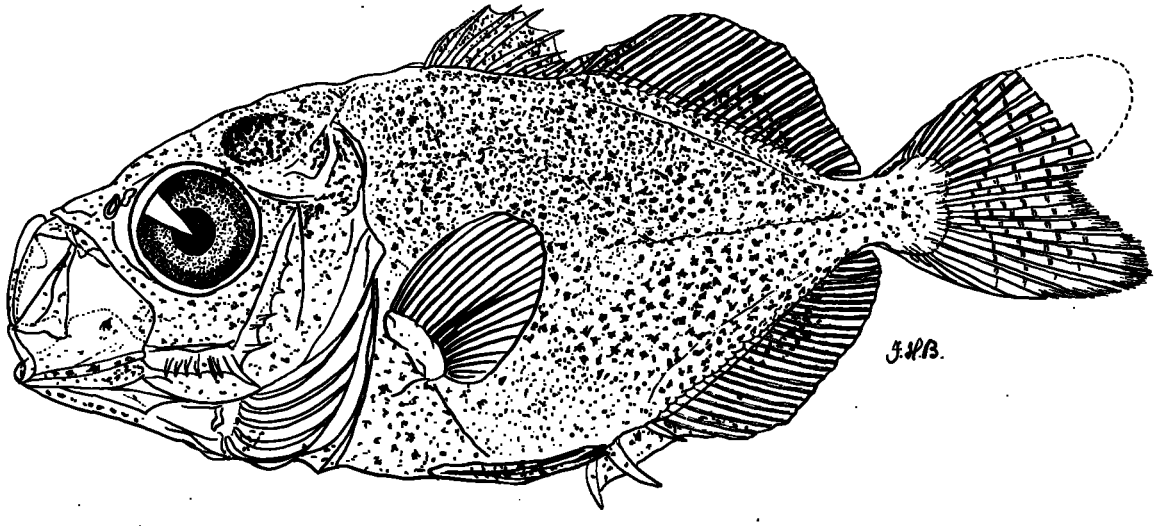

FIGURE 34.—*Caranx ruber* juvenile, 12.4 mm. standard length (*Gill* 7, Reg. 71).

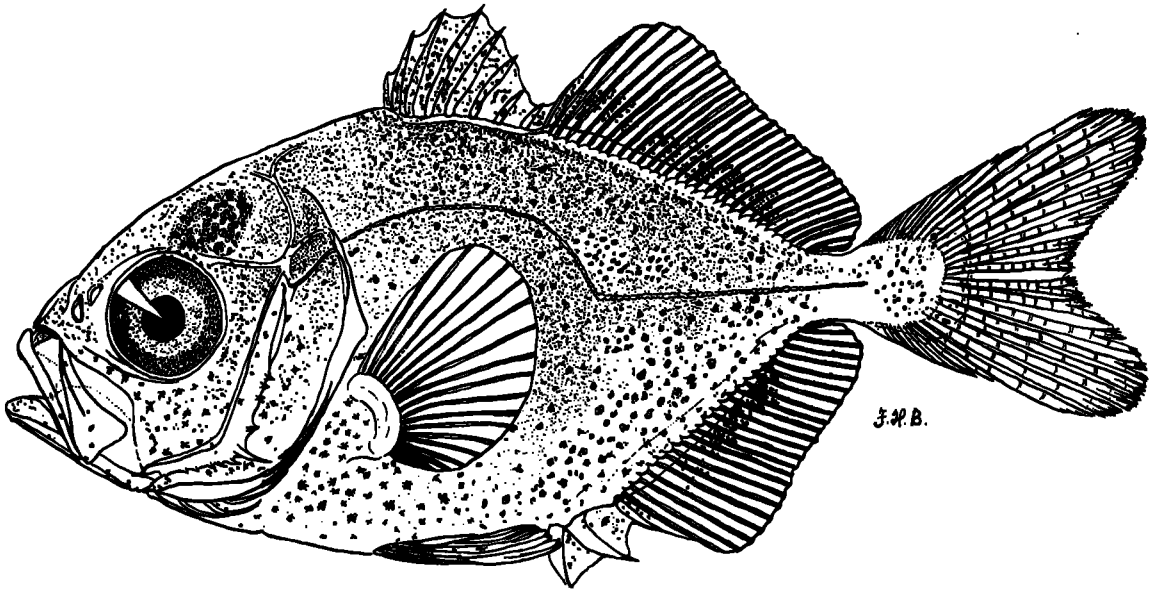

FIGURE 35.—*Caranx ruber* juvenile, 14.9 mm. standard length (*Gill* 7, Reg. 71).

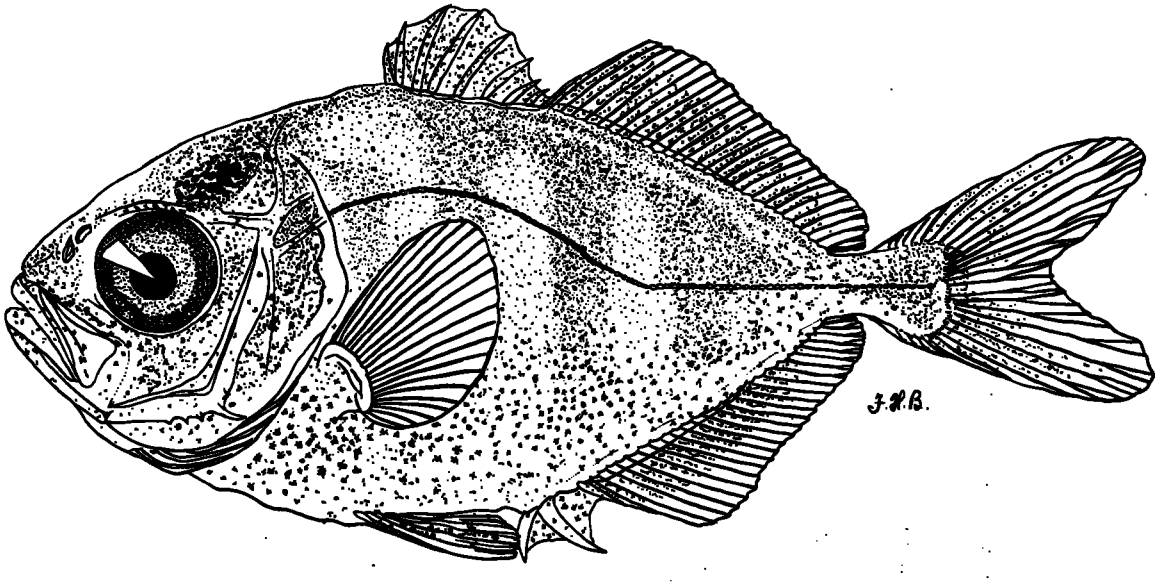

FIGURE 36.—*Caranx ruber* juvenile, 18.0 mm. standard length (*Gill* 4, Reg. 2).

sent specimens with missing rays (see Comparison of Species, p. 428). They gave a modal value (comprising 40 percent of their specimens) of 26 dorsal soft-rays, while 62 percent of my specimens had a bimodality of 27 and 28 soft-rays. All soft-rays are well formed, segmentation has begun, and the terminal ray is branched to its base at 12.4 mm. (fig. 34). Several other posterior rays are branched at 18 mm. (fig. 36), and all soft-rays are branched at 31.9 mm. (fig. 37). Extension of the anterior 5 or 6 rays to produce the fin lobe begins at about 20 mm. (fig. 37). The second ray averages the greatest length to about 28 mm.; above 28 mm., the first ray is longest. The longest ray averages a greater length than the longest spine (fig. 39).

The regression of length of the dorsal soft-ray on standard length is shown in figure 39 and table 7. A line fitted to this regression for specimens from 12.4 to 118 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.12-mm. increase

TABLE 8.—Caranx ruber: *Correlation of the numbers of dorsal and anal soft-rays of 152 specimens*

[The upper number in each block is the count obtained for that combination, and the number in parentheses below is the approximate percentage of that count in the total sample]

ANAL SOFT-RAYS	DORSAL SOFT-RAYS 26	27	28	29	30
23	1 (.7)	11 (7.2)	3 (2.0)		
24	1 (.7)	48 (31.6)	48 (31.6)	1 (.7)	
25		3 (2.0)	25 (16.4)	9 (5.9)	1 (.7)
26			1 (.7)		

in soft-ray length per 1.0-mm. increase in standard length). The coordinates of the four specimens larger than 118 mm. fall along the extension of the calculated regression line, suggesting that soft-ray growth may continue at the same proportional rate.

Anal soft-rays.—23 to 26 (table 8). Formation, segmentation, branching, and lobation occur about as with the dorsal soft-rays. The second soft-ray averages the greatest length to about 22 mm. standard length; above 22 mm., the first ray is longest. The longest anal ray approximates the length of the longest dorsal ray to about 25 mm.

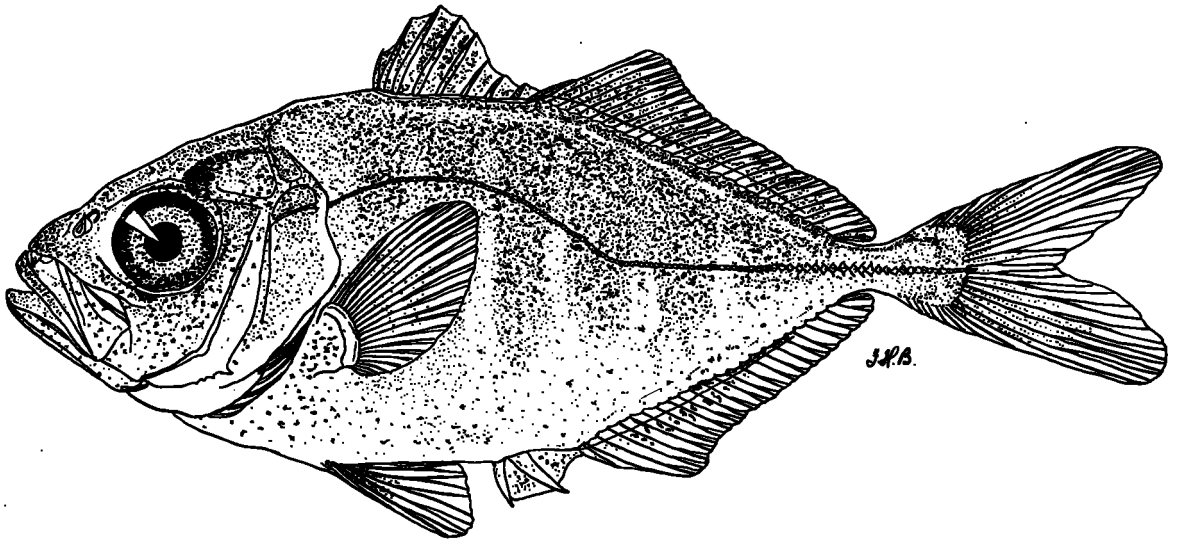

FIGURE 37.—*Caranx ruber* juvenile, 31.9 mm. standard length (*Gill* 6, Reg 14.).

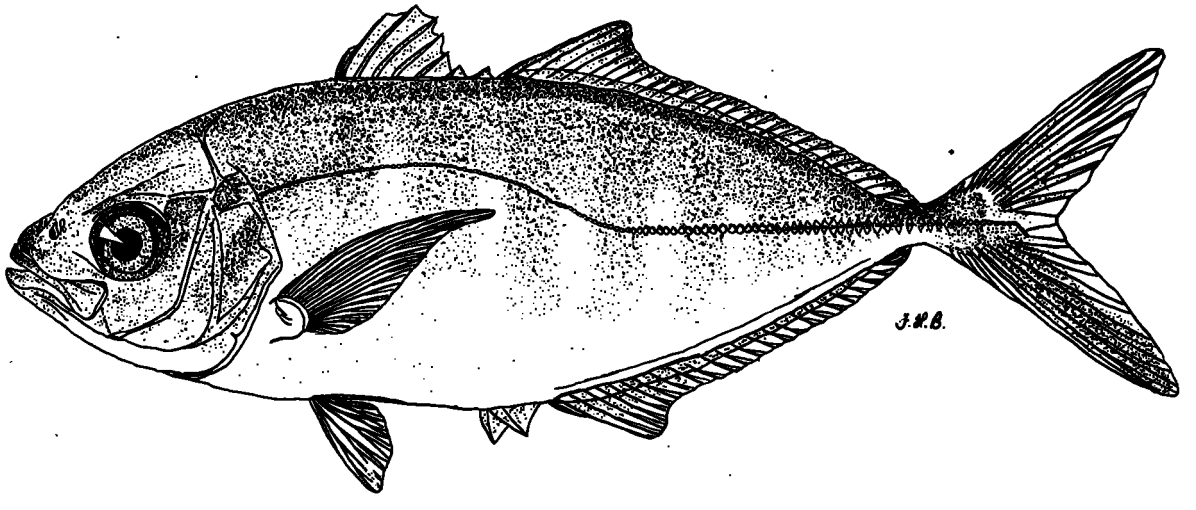

FIGURE 38.—*Caranx ruber* juvenile, 83.5 mm. standard length (*Gill* 3, Std., July 19, 1953; 0000–0400).

489286 O—59——4

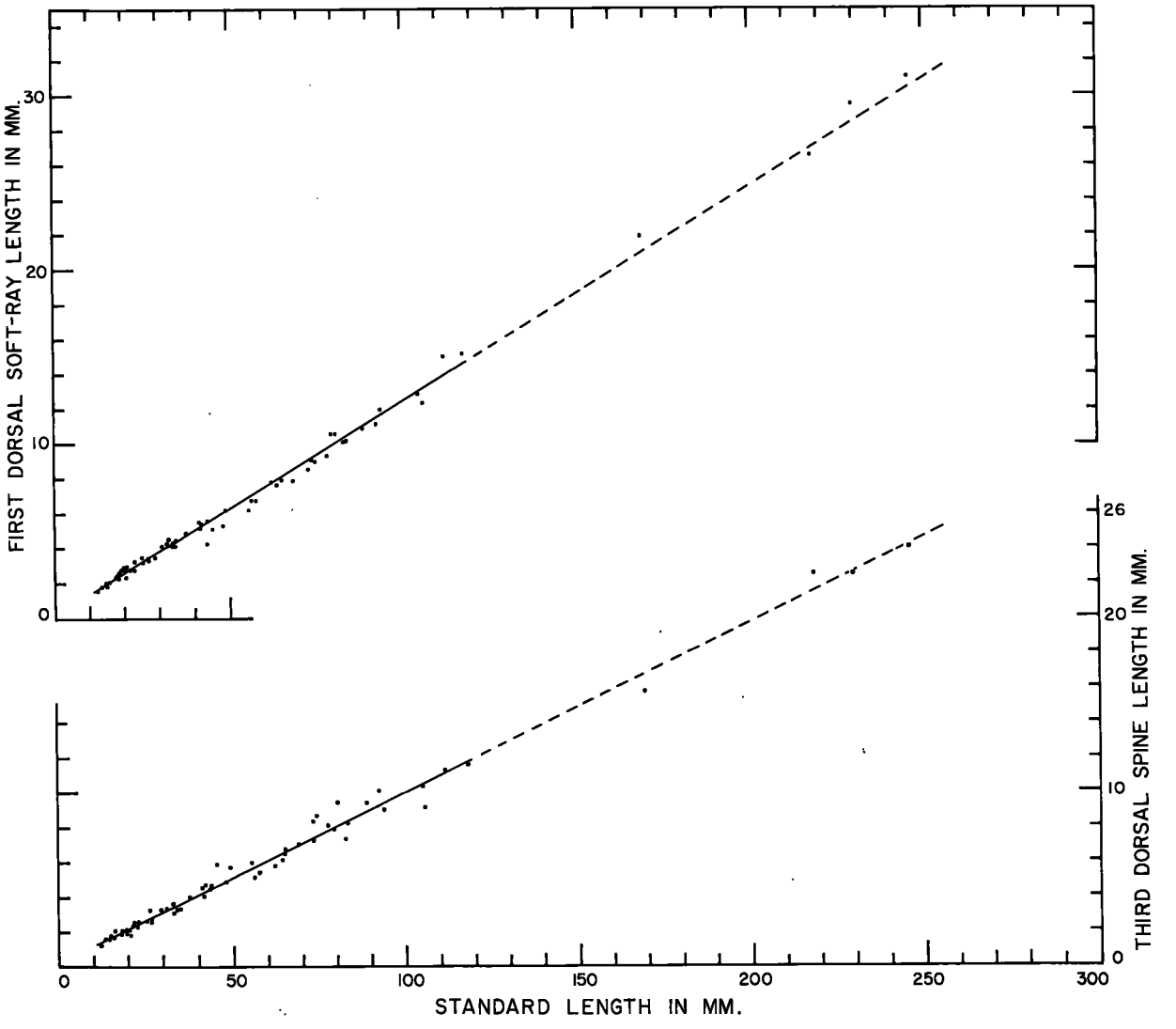

FIGURE 39.—*Caranx ruber:* Relation of length of the first dorsal soft-ray and of the third dorsal spine to standard length.

standard length; above 25 mm., the dorsal ray averages the greater length. The second anal spine averages slightly more than one-half the length of the longest anal ray to about 75 mm., and only about one-third at 169 mm. and 246 mm.

Interneural and interhemal spines.—Posterior lateral projections of these spines are not extended above the body surface (as occurs in *latus* and *hippos*).

Caudal.—9+8 principal rays; about 7 to 9+7 or 8 secondary rays. The principal rays are all segmented, branching has occurred, and forking of the tail is pronounced at 12.4 mm. (fig. 34). Branching is pronounced at about 15 mm. (figs. 35 and 36).

Pectoral.—I–18 to 21. The full complement of rays is formed at 12.4 mm. standard length (fig. 34). Branching has begun by 25 mm. The distal end of the fin is rounded from 12.4 mm. to about 35 mm., above which it becomes pointed and falcation begins (figs. 34 to 37). Falcation is pronounced by 83 mm.

The regression of pectoral length on standard length is shown in figure 40 and table 7. Two lines were fitted to this regression: for specimens from 12.4 to 74.5 mm. and from 74.5 to 230 mm. standard length.. The lines intersect at approximately 75 mm., indicating that an inflection occurs at about that size and that a faster pectoral growth rate prevails above that size. The propor-

tional rates of increase for the two variates are 0.20-mm. (below 75 mm.) and 0.38-mm. (above 75 mm.) increase in pectoral length per 1.0-mm. increase in standard length.

Pelvic.—I–5. The rays are well formed at 12.4 mm. standard length (fig. 34), and branching has begun by 15 mm. (fig. 35).

Body depth.—At corresponding body lengths the depth at first anal spine averages less than the depth at pelvic to about 35 mm. standard length, approximately equals the latter from 35 mm. to about 55 mm., and averages greater above 55 mm.

The regression of body depth at pelvic on standard length is shown in figure 41 and table 7. Two lines were fitted to this regression: for specimens from 12.4 to 23.1 mm. and from 23.1 to 106 mm. standard length. The lines intersect at approximately 24 mm., indicating that an inflection occurs at about that size and that a slower body-depth growth rate prevails above that size. The proportional rates of increase for the two variates are 0.41-mm. (below 24 mm.) and 0.29-mm. (above 24 mm.) increase in body depth per 1.0-mm. increase in standard length. The coordinates of the four specimens larger than 106 mm. fall slightly below the extension of the calculated regression line, but these data are insufficient to indicate a possible decrease in body-depth growth rate.

Head.—The regression of head length on standard length is shown in figure 41 and table 7. A line fitted to this regression for specimens from 12.4 to 118 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.27-mm. increase in head length per 1.0-mm. increase in standard length). The

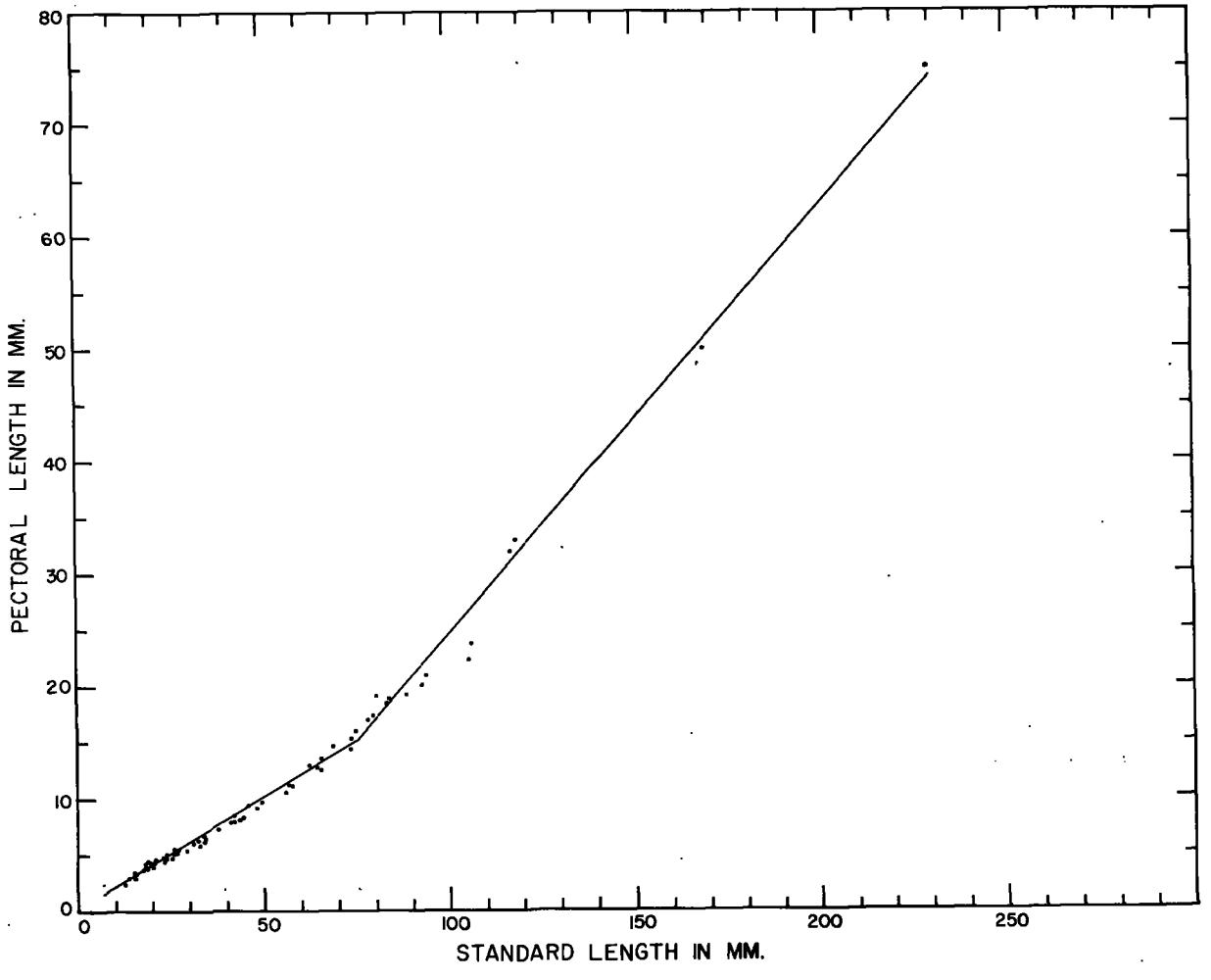

FIGURE 40.—*Caranx ruber:* Relation of pectoral length to standard length.

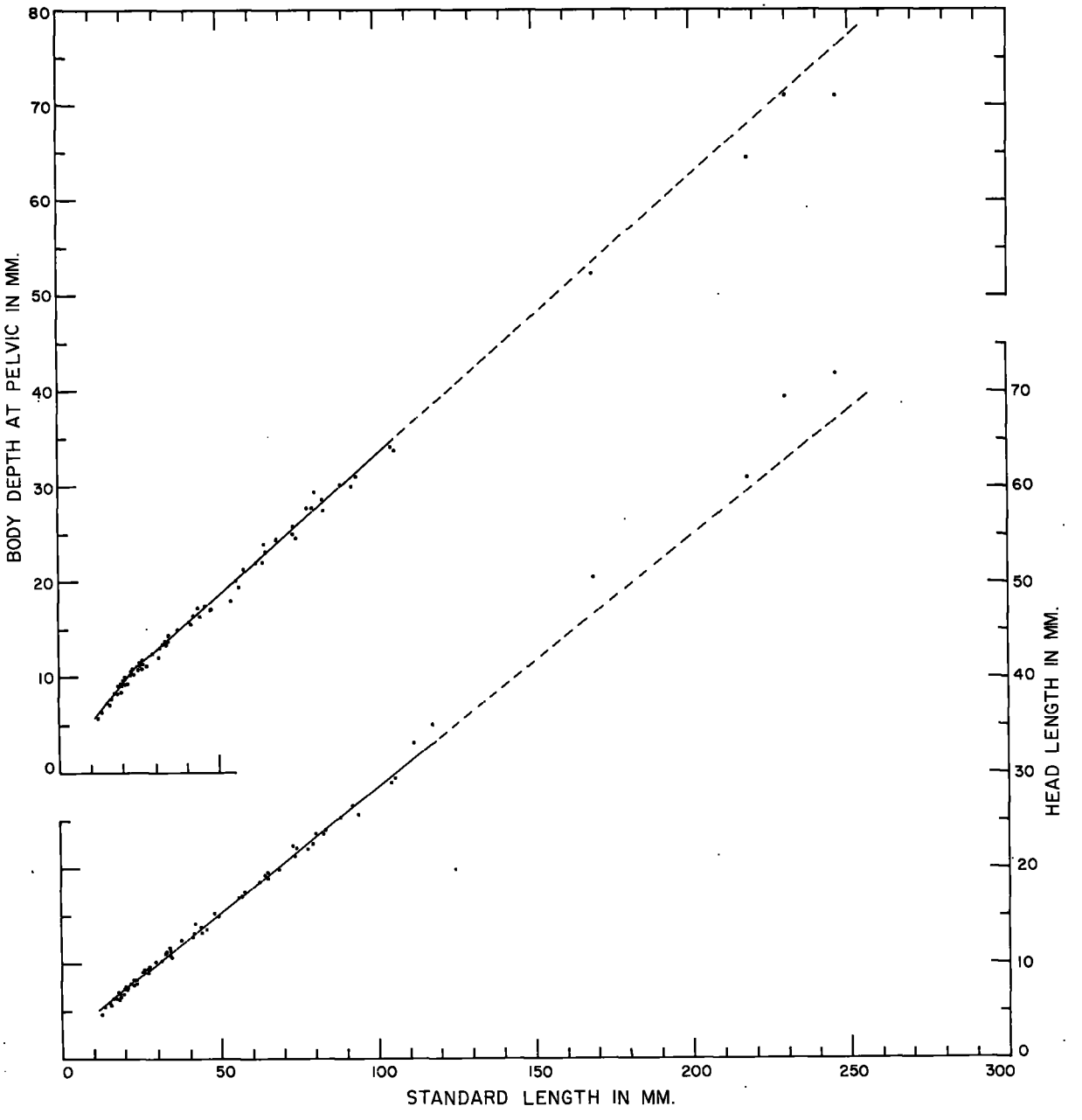

FIGURE 41.—*Caranx ruber:* Relation of body depth at pelvic and of head length to standard length.

alinement of the coordinates of the four largest specimens above the extension of the calculated regression line suggests an increase in head growth rate at some size around 118 mm.

Eye.—The regression of eye diameter on standard length is shown in figure 42 and table 7. Two lines were fitted to this regression: for specimens from 12.4 to 34.1 mm. and from 34.1 to 106 mm. standard length. The lines intersect at approximately 34 mm., indicating that an inflection occurs at about that size and that a slower growth rate prevails above that size. The proportional rates of increase for the two variates are 0.08-mm. (below 34 mm.) and 0.058-mm. (above 34 mm.) increase in eye diameter per 1.0-mm. increase in standard length. The coordinates of the six specimens larger than 106 mm. fall well above the extension of the calculated regression line, indicating an increase in eye growth rate around 106 mm.

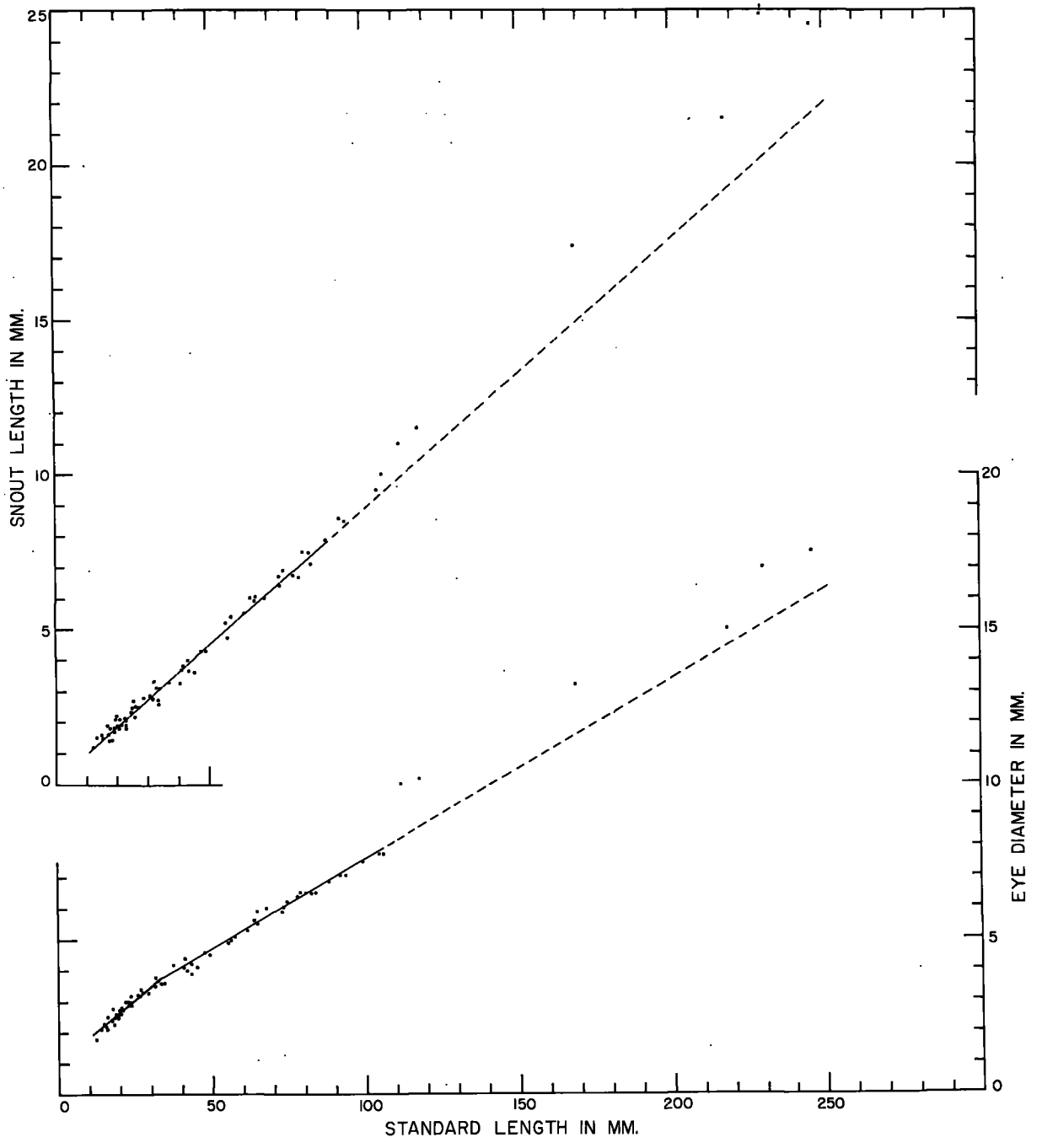

FIGURE 42.—*Caranx ruber:* Relation of snout length and of eye diameter to standard length.

Snout.—The regression of snout length on standard length is shown in figure 42 and table 7. A line fitted to this regression for specimens from 12.4 to 88.5 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.09-mm. increase in snout length per 1.0-mm. increase in standard length). The alinement of coordinates of specimens larger than 88.5 mm. above the extension of the calculated regression line indicates that an increase occurs in snout growth rate at about that size.

Gill rakers.—Lower limb, 31 to 35; upper limb, 10 to 14; total, 42 to 47 (table 9). About 15 percent of the specimens had one shortened or

rudimentary gill raker at the origin of the lower limb; the 169-mm. specimen had two; and there was none on a 230-mm. specimen. Only one of the specimens had a shortened gill raker at the origin of the upper limb. There is no apparent correlation between body size and number of rudimentary gill rakers, at least up to 230 mm.

Scutes.—Range of the mean number of scutes at more than 100 mm. standard length: about 23 to 29 (fig. 43). The developing scutes appear below 15 mm. (fig. 35). The first scutes to complete their individual development do so at 22 to 24 mm. Development of all scutes of fish above 100 mm. is completed, or nearly completed (fig. 43).

TABLE 9.—Caranx ruber: *Correlation of the numbers of lower-limb to upper-limb gill rakers of 73 specimens*

[The upper number in each block is the count obtained for that combination, and the number in parentheses below is the approximate percentage of that count in the total sample]

UPPER-LIMB GILL RAKERS	LOWER-LIMB GILL RAKERS 31	32	33	34	35
10		11 (15.1)	4 (5.5)	4 (5.5)	
11	4 (5.5)	5 (6.8)	7 (10.0)	4 (5.5)	
12		13 (17.8)	5 (6.8)	1 (1.4)	2 (2.7)
13	1 (1.4)	1 (1.4)	2 (2.7)	7 (10.0)	
14		1 (1.4)	1 (1.4)		

Lateral line.—Range of mean lateral-line ratio at more than 55 mm.: about 1.1 to 1.5 (fig. 44). Nichols (1939: 9) gave a ratio range for small specimens of 1.0 to 1.3. The mean ratio increases up to about 65 mm.

Preopercular spines.—The preopercular angle spine has apparently ceased to grow by 12.4 mm. standard length and to decrease in length at some size smaller than 18 mm. It is completely absorbed within the preopercular margin between 41 mm. and 44 mm. (fig. 45). The number of preopercular upper-limb and lower-limb spines is variable, but tends to decrease with an increase in body size (table 1).

Pigmentation.—The body, head, and mouth parts of the 12.4-mm. specimen are covered with pigment spots. A group of larger melanophores occurs on the transparent portion of the brain case. The pelvic fins and the dorsal and anal interspinous membranes are well pigmented, and

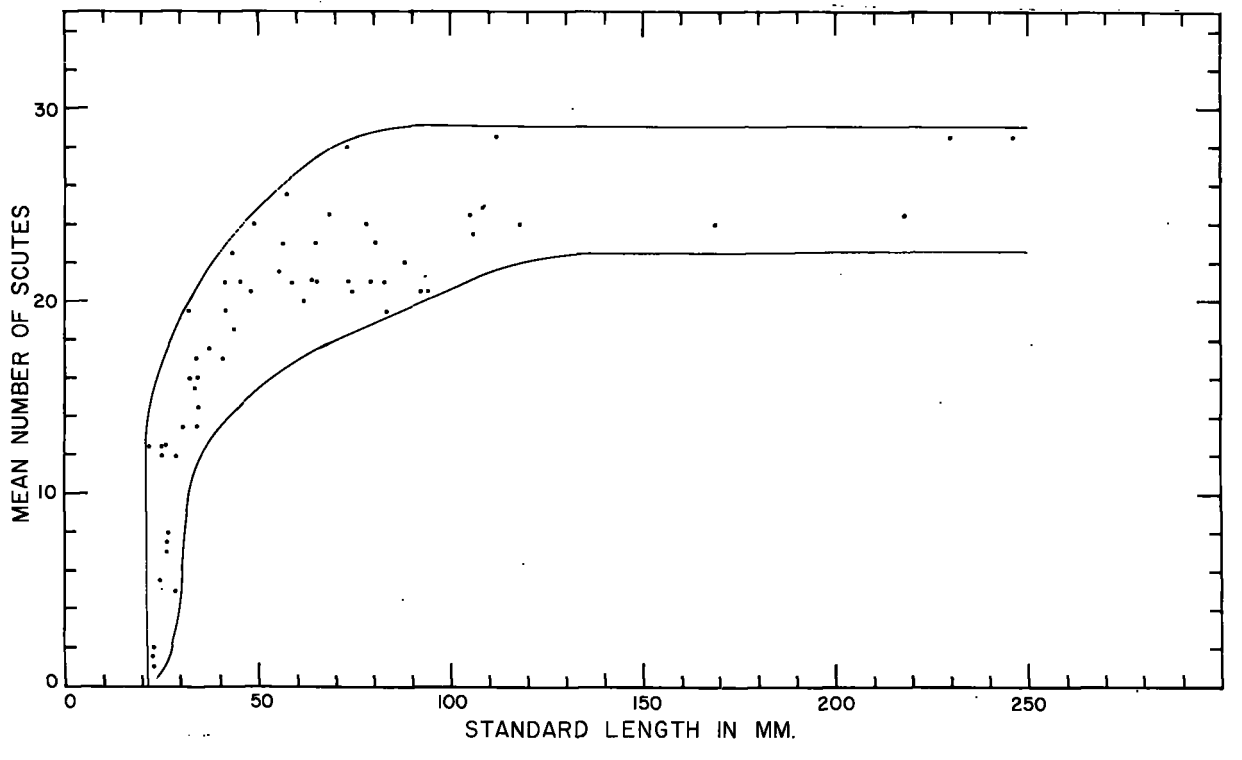

FIGURE 43.—*Caranx ruber:* Relation of the mean number of scutes to standard length.

a few pigment spots are present distal to the bases of the dorsal and anal soft-rays (fig. 34).

Pigmentation on the sides of the body intensifies and becomes blotched between about 15 mm. and 17 mm. standard length (fig. 35). Between about 17 mm. and 19 mm., from 3 to 5 indistinct bars are present on the sides (fig. 36). At sizes slightly over 19 mm., the full complement of 6 bars (infrequently, 5 or 7) is present (figs. 37 and 38). At about 40 mm. the lower parts of the bars below the straight part of the lateral line begin to fade, and the upper portions merge into a uniform pigmentation along the back. Indistinct traces of the bars remain on some specimens to over 105 mm., although they may have faded out or may be indistinct on some specimens as small as 30 mm. By 40 mm. a dense mass of pigment has developed on the upper portion of the caudal peduncle and the fleshy portion of the caudal fin. Above 60 mm. this pigmentation extends as a dark stripe to the tip of the lower caudal lobe (fig. 38).

The indistinct nuchal band is formed by about 30 mm. by the development of a posterodorsally projected pigment mass above and behind the eye (figs. 34 to 38). A slight concentration of pigment occurs directly below the eye on some specimens from about 18 to 40 mm. A vague vertically elongated spot is present on the operculum of some specimens between 40 mm. and 80 mm.

Pigment spots are present on the caudal and pectoral fins on some specimens by 16 mm. (fig. 35). The slight pigmentation found in the dorsal, anal, pectoral, and pelvic fins is illustrated in figures 34 to 38. The caudal pigmentation has been previously described.

Distribution off Southeastern Atlantic Coast of the United States

Caranx ruber has been reported from the following localities within this area: the northern Bahamas by Fowler (1919b: 150; 1944: 443), Bean (1905: 302), Lee (1889: 670), Meek and Hildebrand (1925: 357), and Ginsburg (1952: 91); the Gulf Stream off Bimini, Bahamas, by Nichols (1937b: 236; 1938b: 1); Cape Lookout and Beaufort, N. C., by Nichols (1912: 185; 1935: 268) and Smith (1907: 204); and from Charleston, S. C., by Nichols (1939: 1) and Fowler (1945: 189).

Figure 46 shows the location of specimens taken on the *Gill* cruises, by the *Combat* in the Gulf Stream off Florida and South Carolina, USNM specimens examined (Cape Hatteras and Cape Lookout, N. C.; on the 1,000-fathom line off Cape

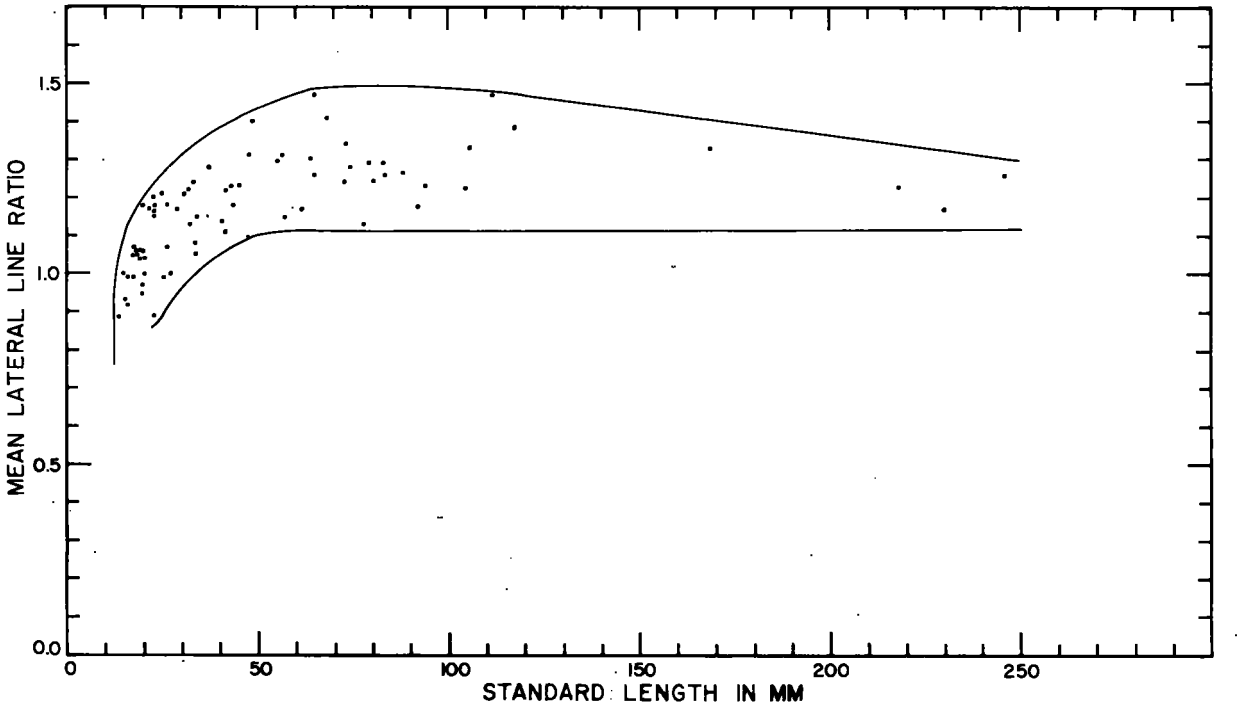

FIGURE 44.—*Caranx ruber:* Relation of the mean lateral-line ratio to standard length.

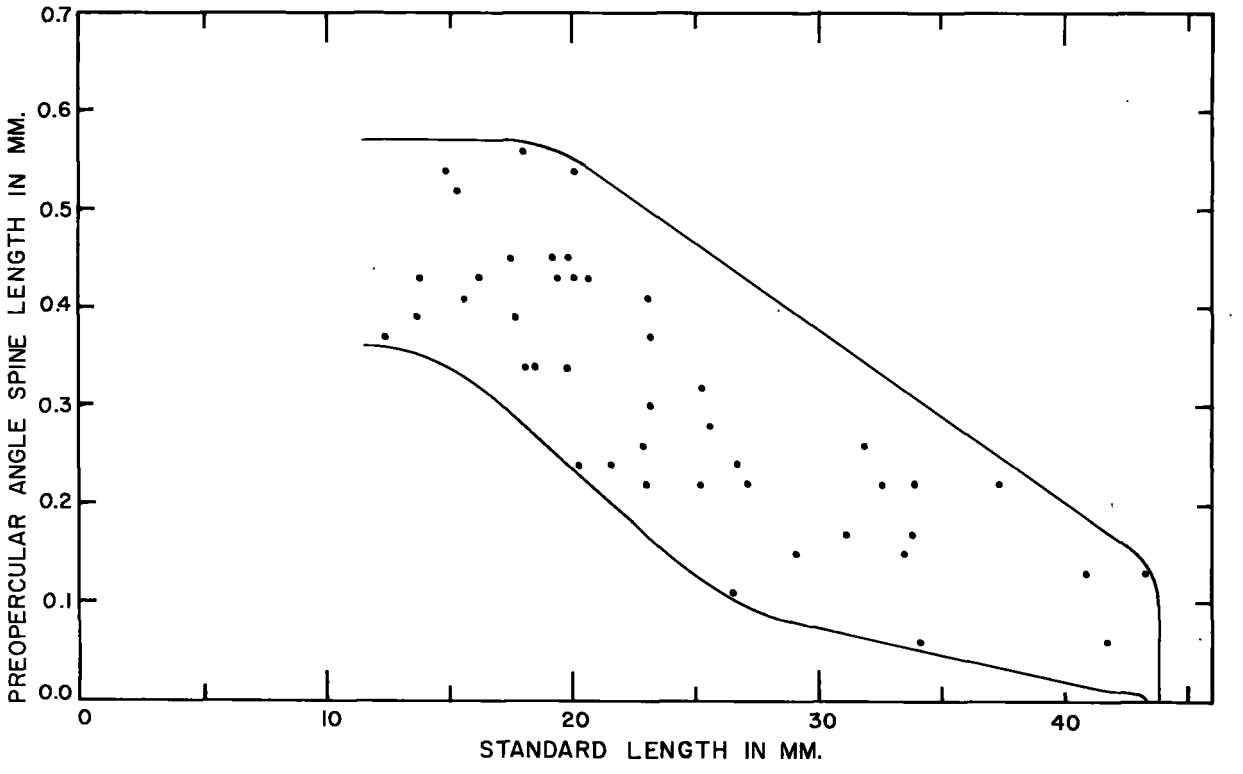

FIGURE 45.—*Caranx ruber:* Relation of the length of the preopercular-angle spine to standard length.

Lookout, N. C.; on the 100-fathom line off Cape Hatteras, N. C.; and east of the axis of the Gulf Stream off Cape Canaveral, Fla.), and a ChM specimen examined (Charleston, S. C.) (tables 2 and 10). The locations of capture recorded on this chart are for juvenile specimens. These juveniles were generally captured beyond the 100-fathom line and an association with the Gulf Stream (as depicted by the approximate axis of the Stream in figure 46) is indicated. Collections by the *Gill* were relatively less concentrated to the east of the Stream axis, and the occurrence of *ruber* is not as well depicted for this area, but the several deeper-water records indicate that the species is common there. Young *ruber* occur in the Gulf Stream from late April to November and are in greatest concentration from May through August (fig. 47).

The only published records of *ruber* that I have found from inshore waters of the United States are for Texas (Baughman 1947: 280); Tortugas, Fla. (Gudger 1929: 169; Longley and Hildebrand, 1941: 77; and Ginsburg 1952: 91); Charleston, S. C. (Fowler 1945: 189; Nichols 1939: 1); and Beaufort and Cape Lookout, N. C. (Smith 1907: 204; Nichols 1912: 185, 1935: 268). I have examined the Charleston, S. C., specimen reported by Fowler, and USNM specimens from Tortugas, Fla., and near Cape Hatteras, N. C. The USNM specimen, taken near Cape Hatteras, is the most northern inshore record for the species. The most-northern record is from 39°13′ N., 71°13′ W., in the Gulf Stream south of Georges Bank (Mather 1954: 293). This compilation indicates that *ruber* is rare in inshore waters. The North Carolina and South Carolina records are of specimens below 70 mm., which could have been drifted inshore by temporary currents.

The *Gill* collections indicate that juvenile forms of *ruber* are both widespread and abundant in the offshore waters of this area, primarily in association with the Gulf Stream and the merging Antilles Current. I believe that these developing young are carried northward by the currents. Absence of inshore records of the species north of North Carolina indicates that the Stream-grown juveniles and adults do not migrate in this direction, and absence of records from the Azores and waters farther east suggests that they discontinue their movement with the Stream to the east. It is possible

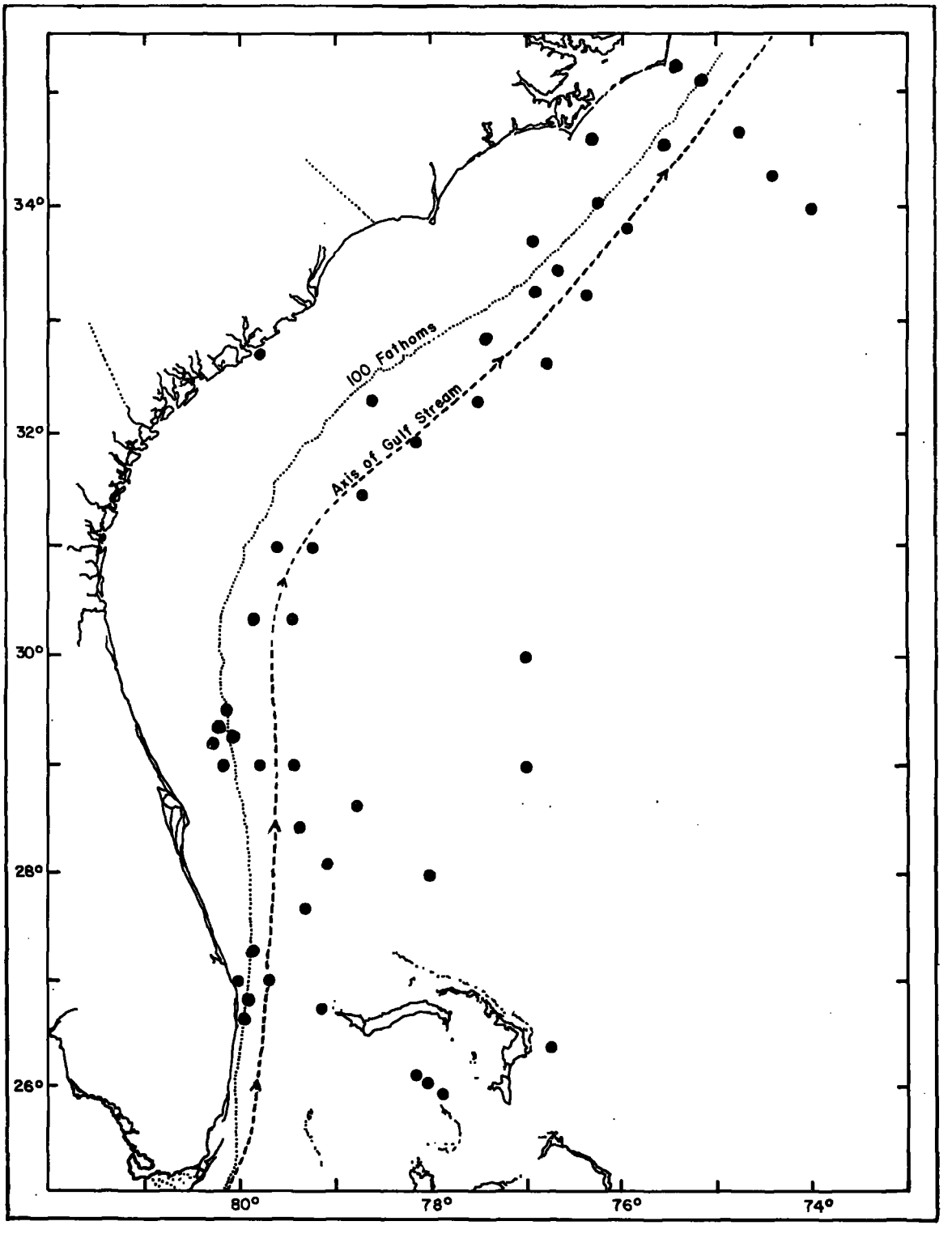

FIGURE 46.—*Caranx ruber:* Locations of capture off the southeastern Atlantic coast of the United States.

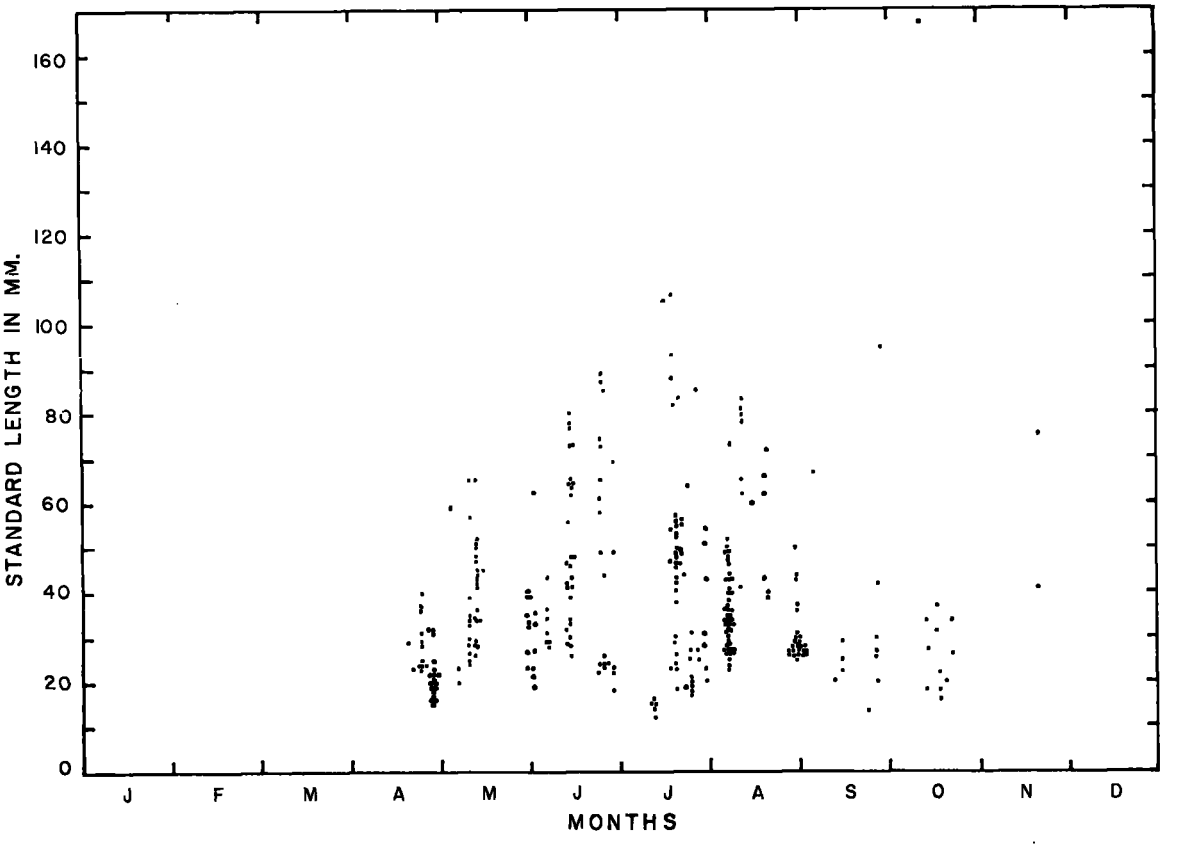

FIGURE 47.—*Caranx ruber:* Size distribution, by months, of specimens taken off the southeastern Atlantic coast of the United States.

that the major portion of this population returns southward, either against the currents of the Gulf Stream or through the Sargasso Sea, to supplement the adult population of the West Indies.

Although apparently very abundant off the Atlantic coast of the United States, *ruber* appears to be relatively rare in the northern Gulf of Mexico. It was reported from the Port Isabel area of Texas by Baughman (1947: 280). Ginsburg (1952: 91) found no specimens from the northern Gulf coast. The specimens reported by Günther (1860:441) as *dentex*, which probably were *ruber*, were listed ambiguously from New Orleans. I have examined two specimens of *ruber* taken by the *Silver Bay* about 11 miles southwest of Cedar Key, Fla., and specimens taken by the *Oregon* about 55 miles southeast and about 60 miles east of South Pass, La., and 150 miles south of Mobile Bay (table 10). Other than from around Havana and Torgugas, the only other records I have found for this species in the Gulf of Mexico are from five *Oregon* stations reported by Springer and Bullis (1956: 74).

On the basis of two collections of *ruber* from the Gulf Stream (off Bimini, Bahamas, and about 350 miles east of Virginia), Nichols (1939:2) postulated, "The Gulf Stream is obviously their Atlantic nursery ground." He suggested that the young might enter the Gulf Stream mainly from its easterly edge, "or perhaps they frequent the current rather than slack waters at the edges until large enough to migrate independently, when they must of necessity strike southward or be lost."

Spawning

The spawning season may be estimated, from the smallest specimens taken in April (15 mm.) and in October (18 mm.), to extend from mid-February to mid-August (fig. 47).

If, as suggested, there is a mobile, northward-moving population of developing young in the Gulf Stream, the majority of the specimens taken by the *Gill* would have developed from spawning that occurred to the south of this area. The small sizes of several specimens listed in table 10 suggest

TABLE 10.—Caranx ruber: *Location and date of capture, number and size range (in mm.) of 426 specimens examined*

[See pp. 417 and 419 for explanation of abbreviations used; measurements in standard length]

Location	Date captured	Collection	Number of specimens	Size (mm.)
ATLANTIC OCEAN:				
22°42′33″ N., 74°23′ W	Mar. 29, 1927	BOC 1343, *Pawnee* Sta. 39	1	14.5
24°04′ N., 79°15′ W	July 24, 1957	SAFI, *Combat* 448	50	15–56.5
24°13′ N., 81°42′ W	July 21, 1957	SAFI, *Combat* 436	1	20
Nassau fish market, Bahamas	Aug. 17–20, 1956	UF 3538	2	230–246
25°10′ N., 80°02′ W	July 22, 1957	SAFI, *Combat* 438	1	19.5
26°21.2′ N., 76°46.5′ W	July 18–19, 1953	SAFI, *Gill* 3, Std	26	18.5–106
Do	July 19, 1953	do	4	44–83.5
Do	July 23, 1953	do	1	64
26°27′ N., 76°44′ W	June 12–13, 1954	SAFI, *Gill* 7, Std	16	27.5–79.5
Do	June 13–14, 1954	do	2	45.5–73
Do	June 14, 1954	do	4	25.6–27.5
26°37′ N., 79°51′ W	July 28, 1957	SAFI, *Combat* 458	1	28.5
26°47′ N., 79°53′ W	do	SAFI, *Combat* 459	1	31
26°54′ N., 79°07′ W	Aug. 29, 1954	SAFI, *Gill* 8, Settlement Point, Bahamas	25	25–49.5
26°58.5′ N., 79°40′ W	Oct. 12, 1953	SAFI, *Gill* 4, Reg. 2	1	18
27°01′ N., 80°04′ W	Apr. 23, 1953	SAFI, *Gill* 2, Reg. 3	1	22.5
27°14′ N., 79°50′ W	July 29, 1957	SAFI, *Combat* 462	3	43–54.5
27°40′ N., 79°18.5′ W	Apr. 23, 1953	SAFI, *Gill* 2, Reg. 7	2	23.2–23.2
Do	Oct. 13, 1953	SAFI, *Gill* 4, Reg. 7	2	26.7–33.5
Do	June 23, 1954	SAFI, *Gill* 7, Reg. 7	1	21
28°00′ N., 78°00′ W	July 16, 1953	SAFI, *Gill* 3, Spc. 8	1	92.5
28°17.5′ N., 79°28′ W	Sept. 12, 1954	SAFI, *Gill* 8, Reg. 8	1	19.8
28°18.5′ N., 79°26′ W	July 26, 1953	SAFI, *Gill* 3, Reg. 8	8	17.5–31.1
28°19′ N., 79°26′ W	Apr. 24, 1953	SAFI, *Gill* 2, Reg. 8	7	25–40
28°40′ N., 78°46′ W	May 3, 1886	USNM 148334, *Albatross* Sta. 2660	1	59
28°56.3′ N., 79°45.6′ W	July 27, 1953	SAFI, *Gill* 3, Reg. 15	2	25–27
28°59.5′ N., 79°26.5′ W	June 25, 1954	SAFI, *Gill* 7, Reg. 16	7	23–84.5
29°00′ N., 77°00′ W	July 17, 1953	SAFI, *Gill* 3, Spc. 6	3	23–54
29°10′ N., 80°19′ W	June 1, 1957	SAFI, *Combat* 336	3	27.5–35.5
29°10′ N., 80°19′ W to 29°19′ N., 80°15′ W	do	SAFI, *Combat* 336 to *Combat* 337	3	19.4–23.5
29°16′ N., 80°04′ W	May 30, 1957	SAFI, *Combat* 328	5	27–40.5
29°19′ N., 80°18′ W	June 1, 1957	SAFI, *Combat* 343	1	63
29°20′ N., 80°04′ W	Apr. 27, 1957	SAFI, *Combat* 316	1	25
29°26′ N., 80°08′ W	do	SAFI, *Combat* 315	10	17.5–32
Do	do	do	10	15–22
29°28′ N., 80°09′ W	May 30, 1957	SAFI, *Combat* 326	2	23.5–35
29°29′ N., 80°09′ W	Aug. 18, 1957	SAFI, *Combat* 485	3	43.5–66
29°29′ N., 80°10′ W	Aug. 19, 1957	SAFI, *Combat* 490	3	39–72
29°38′ N., 80°12′ W	Aug. 14, 1957	SAFI, *Combat* 474	1	60
29°47′ N., 80°05′45″ W	May 4, 1886	USNM 134076, *Albatross* Sta. 2665	5	28.3–36
30°00′ N., 77°00′ W	July 16, 1953	SAFI, *Gill* 3, Spc. 5	1	105
Do	June 10, 1954	SAFI, *Gill* 7, Spc. 5	5	31.5–56
30°19.5′ N., 79°50′ W	Sept. 14, 1954	SAFI, *Gill* 8, Reg. 27	3	23–29
30°19.8′ N., 79°25.5′ W	Oct. 16, 1953	SAFI, *Gill* 4, Reg. 28	1	31
30°20′ N., 79°50′ W	June 26, 1954	SAFI, *Gill* 7, Reg. 27	4	21.6–68.5
30°56.8′ N., 79°37.4′ W	July 29, 1953	SAFI, *Gill* 3, Reg. 30	2	20–23
30°57′ N., 79°14.5′ W	Nov. 19, 1954	SAFI, *Gill* 9, Reg. 29	2	41–74.5
30°58′ N., 79°37.5′ W	Oct. 16, 1953	SAFI, *Gill* 4, Reg. 30	1	37.3
Do	June 27, 1954	SAFI, *Gill* 7, Reg. 30	1	18.1
31°29.1′ N., 78°41′ W	May 5, 1953	SAFI, *Gill* 2, Reg. 40	2	20.1–23
31°57′ N., 78°09′ W	Aug. 6, 1953	SAFI, *Gill* 3, Reg. 50	44	23–49.5
32°15′ N., 78°32′ W	Sept. 25, 1954	SAFI, *Gill* 8, Reg. 48 to Reg. 49	1	13.8
32°19′ N., 77°34′ W	Aug. 7, 1953	SAFI, *Gill* 3, Reg. 51	1	73
32°39′ N., 76°46′ W	Aug. 10, 1953	SAFI, *Gill* 3, Reg. 62	1	41
32°43′ N., 76°47.5′ W	May 8, 1953	SAFI, *Gill* 2, Reg. 62	3	24–33
Off Charleston, S. C	Sept. 4, 1938	ChM 38.207.9	1	67
32°50′ N., 77°27′ W	Apr. 21, 1957	SAFI, *Combat* 295	1	23.5
33°13′ N., 76°55′W	Apr. 20, 1957	SAFI, *Combat* 290	1	29
33°14′ N., 76°25′ W	Sept. 27, 1954	SAFI, *Gill* 8, Reg. 63	1	19.9
33°14.7′ N., 76°23′ W	May 8, 1953	SAFI, *Gill* 2, Reg. 63	8	25.2–57
33°24′ N., 76°25′ W	Aug. 11, 1953	SAFI, *Gill* 3, Reg. 63	5	62–83
33°29′ N., 76°37.5′ W	Sept. 28, 1954	SAFI, *Gill* 8, Reg. 64	1	94
33°29′ N., 76°40′ W	Aug. 11, 1953	SAFI, *Gill* 3, Reg. 64	1	65
33°43.5′ N., 76°56′ W	Sept. 28, 1954	SAFI, *Gill* 8, Reg. 65	1	41.5
33°49′ N., 75°59′ W	May 10, 1953	SAFI, *Gill* 2, Reg. 72	1	65
34°00′ N., 74°14.5′ W	May 14, 1953	SAFI, *Gill* 2, Spc. 1	1	45
34°03.7′ N., 76°14.5′ W	July 10, 1954	SAFI, *Gill* 7, Reg. 71	5	12.4–15.7
34°33.5′ N., 74°55′ W	Sept. 29, 1954	SAFI, *Gill* 8, Reg. 80	3	26–30
34°37.7′ N., 74°45.5′ W	May 12, 1953	SAFI, *Gill* 2, Reg. 80	17	26–52
34°39′ N., 76°12′ W	Oct. 19, 1885	USNM 92619, *Albatross* Sta. 2607	2	26.4–34.5
34°39′30″ N., 75°35′30″ W	Oct. 18, 1885	USNM 111788, *Albatross* Sta. 2600	1	20.3
35°08′30″ N., 75°10′ W	Oct. 17, 1885	USNM 101523, *Albatross* Sta. 2596	3	16.2–22.1
Near Cape Hatteras, N. C	June 5, 1903	UNSM 53109	1	43
35°24′ N., 67°33′ W to 36°48′ N., 68°55′ W	Aug. 26–27	BOC 1358, *Atlantis* Sta. 1934	2	14–17
38°07′ N., 68°45′ W to 37°12′ N., 67°39′ W	Aug. 21–22	BOC, *Atlantis* Sta. 1954	14	14.5–49
Havanna, Cuba, to New York	May 10–15, 1932	BOC 3457, *Mable Taylor*	33	15–34
GULF OF MEXICO:				
Havana market, Batabano, Cuba	Nov. 17, 1954	UF 5349	1	169
Tortugas, Fla	Nov. 25, 1919	USNM 144018, *Albatross*	18	93.5–119
150 mi. south of Mobile Bay	Aug. 1955	GFEGR, *Oregon*	1	53.5
28°17′ N., 88°37′ W	Aug. 25, 1955	GFEGR, *Oregon* 1380	5	18.5–31.5
28°58′ N., 87°55′ W	July 20, 1956	UF 3921, *Oregon* 1582	1	24.5
29°01′ N., 83°21′ W	Aug. 21, 1957	SAFI, *Silver Bay* 152	2	129–137
CARIBBEAN SEA:				
Rocky Point, Jamaica	June 23, 1957	UF (uncataloged)	1	218

that they may have been spawned within this area (12.4 to 15.7 mm. and 14 to 17 mm. specimens off North Carolina, and 14.5 to 49 mm. specimens about 350 miles off Virginia). Spawning in this area probably occurs in association with the Gulf Stream since the small juveniles are found there. Spawning to the south of this area that contributes young *ruber* to the area probably occurs in waters contributing to the Gulf Stream.

Caranx bartholomaei Cuvier

(Figures 48–54)

Caranx bartholomaei Cuvier, *in* Cuvier and Valenciennes, 1833, p. 100 (Saint-Barthelemi, West Indies).
Caranx cibi Poey, 1860, p. 224 (Cuba).
Carangus bartholomaei, Poey, 1866, p. 14 (Cuba).
Carangoides cibi, Poey, 1866, p. 15 (Cuba).
Caranx beani Jordan, 1881, p. 486 (Beaufort, N. C.).
Carangus cibi, Jordan and Gilbert, 1882b, p. 436 (West Indies to Florida).
Carangus beani, Jordan and Gilbert, 1882b, p. 436 (Beaufort, N. C.).
Caranx ruber (*non* Bloch), Jordan and Gilbert, 1883, p. 198 (in part; West Indies to North Carolina).
Caranx pisquetus (*non* Cuvier), McCormick, *in* Smith, 1896, p. 175 (Biscayne Bay, Fla.).
Caranx latus (*non* Agassiz), Jordan and Evermann, 1900, pl. CXLII, fig. 389 (figure only). Fowler, 1950, p. 70 (northwest of Cay Sal Bank).
Elaphotoxon bartholomaei, Jordan, Evermann, and Clark, 1930, p. 272 (West Indies, north to North Carolina).
Caranx guara (*non* Bonnaterre, *fide* Jordan and Evermann), Fowler, 1945, p. 292, fig. 307 (Boca Chica, Key West, Fla.). Fowler, 1950, p. 70, fig. 3 (northwest of Cay Sal Bank).

Nomenclature

The nomenclature of *Caranx bartholomaei* Cuvier has been decisive since Jordan and Gilbert (1884: 32) amended their earlier consolidation (1883: 198) of this species with *C. ruber*. As pointed out by Bailey (1951: 251), Cuvier should be recognized as the sole author. However, Fowler (1944: 443; 1952a: 127; 1952b: 99; and elsewhere) has regarded Valenciennes as the only author.

Material

Measurements and counts were taken on a series of 78 fish from 6.0 to 243 mm. standard length, and meristic values were recorded for an additional 8 specimens within this size range. The 6.0-mm. specimen is tentatively identified as this species. A damaged specimen of 315 mm. was the largest examined. The 125 specimens identified are listed in table 14.

A 17.4-mm. specimen of *bartholomaei*, ANSP 72689, northwest of Cay Sal Bank, 23°50′N., 80°40′W., March 26, 1948, identified as a 22-mm. total length *latus* by Fowler (1950: 70) has 26 dorsal and 22 anal soft-rays, 20 lower-limb gill rakers, 4 upper-limb and 7 lower-limb preopercular spines, and traces of 4 vague bars above the lateral line. This combination of characters distinguishes *bartholomaei* of this size from the other species of Western Atlantic *Caranx*.

Two specimens of *bartholomaei*, ANSP 70973–74, 24.4 mm. and 45 mm. standard length, from Boca Chica, Key West, Fla., that were labeled *guara*,

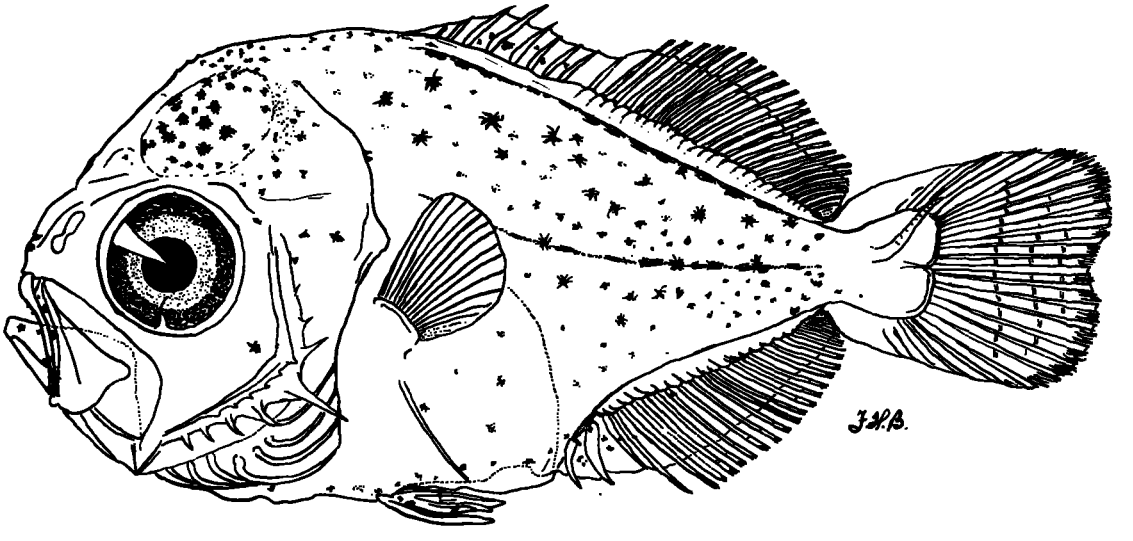

FIGURE 48.—*Caranx bartholomaei* (?) larva, 6.0 mm. standard length (*Gill* 2, Reg. 2).

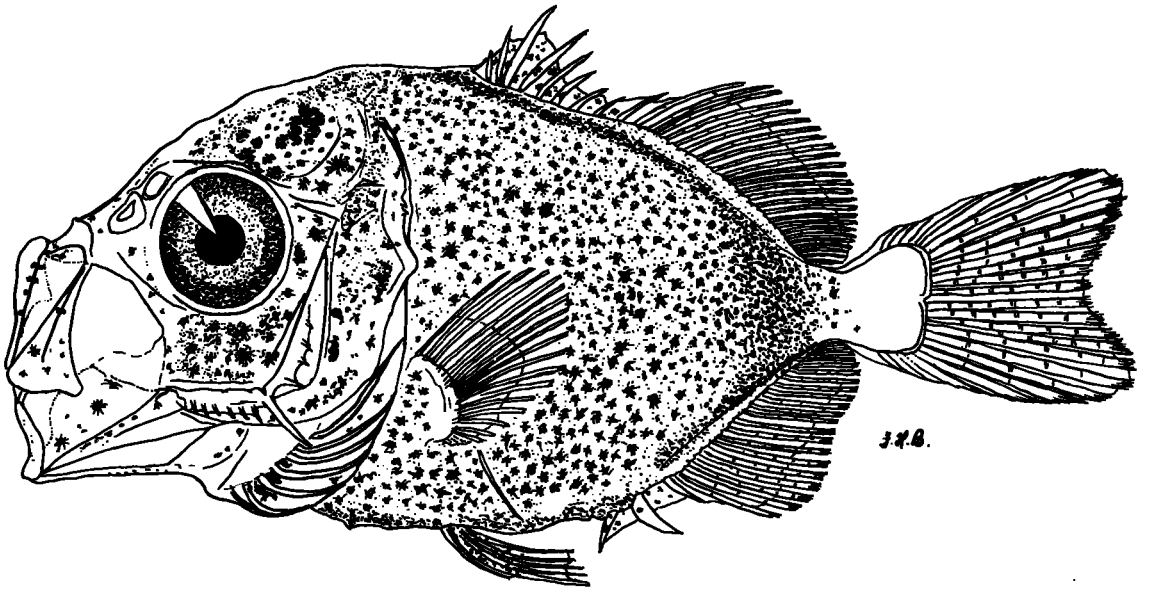

FIGURE 49.—*Caranx bartholomaei* larva, 8.1 mm. standard length (*Gill* 4, Reg. 50).

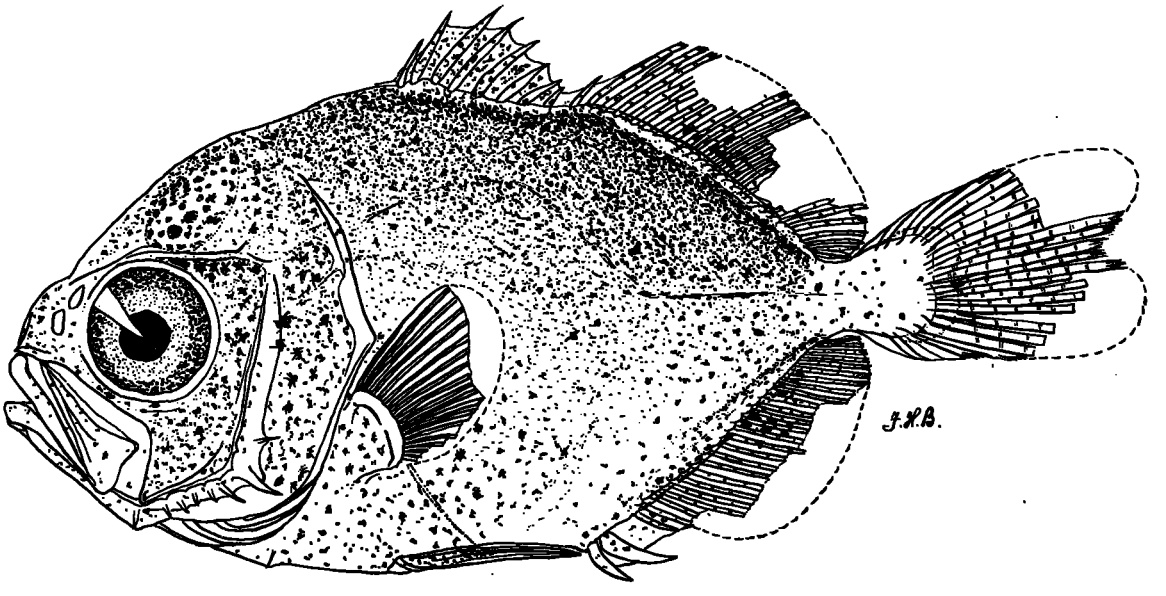

FIGURE 50.—*Caranx bartholomaei* juvenile, 10.5 mm. standard length (USNM 164537).

apparently furnished the basis for the identification of a 28-mm. total length specimen of *guara* (=*dentex*) by Fowler (1945: 292, fig. 307). Fowler's identification records the same locality, date, collector's name, and *Physalia* association contained on the label with the two specimens from Boca Chica. The 24.4-mm. specimen, presumably the one referred to as *guara* (=*dentex*) by Fowler, has D. VIII–I–26, A. II–I–23, and 4 to 5 completely developed scutes. It has a slightly greater depth than two other *bartholomaei* of about the same length, but this excess is well within the range of observed individual variation. Both of the ANSP specimens have 20 lower-limb gill rakers. The posterior body bars of the 24.4-mm. specimen are more angular than depicted in

Fowler's figure 307. Fowler (1950: 70) recognized this misidentification, but his statements concerning his recognition are not clear.

Two specimens of *bartholomaei*, ANSP 72693, 15.8 mm. and 17.2 mm. standard length taken at 23°50′ N., 80°40′ W. (northwest of Cay Sal Bank), March 26, 1948, on the Catherwood-Chaplin West Indies Expedition were labeled *guara* (=*dentex*) and referred to as such by Fowler (1950: 70, fig. 3). Both specimens have 5 slightly bent body bars and 7 upper-limb and 19 lower-limb gill rakers. The 17.2-mm. specimen has 26 dorsal and 23 anal soft-rays. The 28 dorsal and 25 anal soft-rays of the 15.8-mm. specimen are slightly wavy

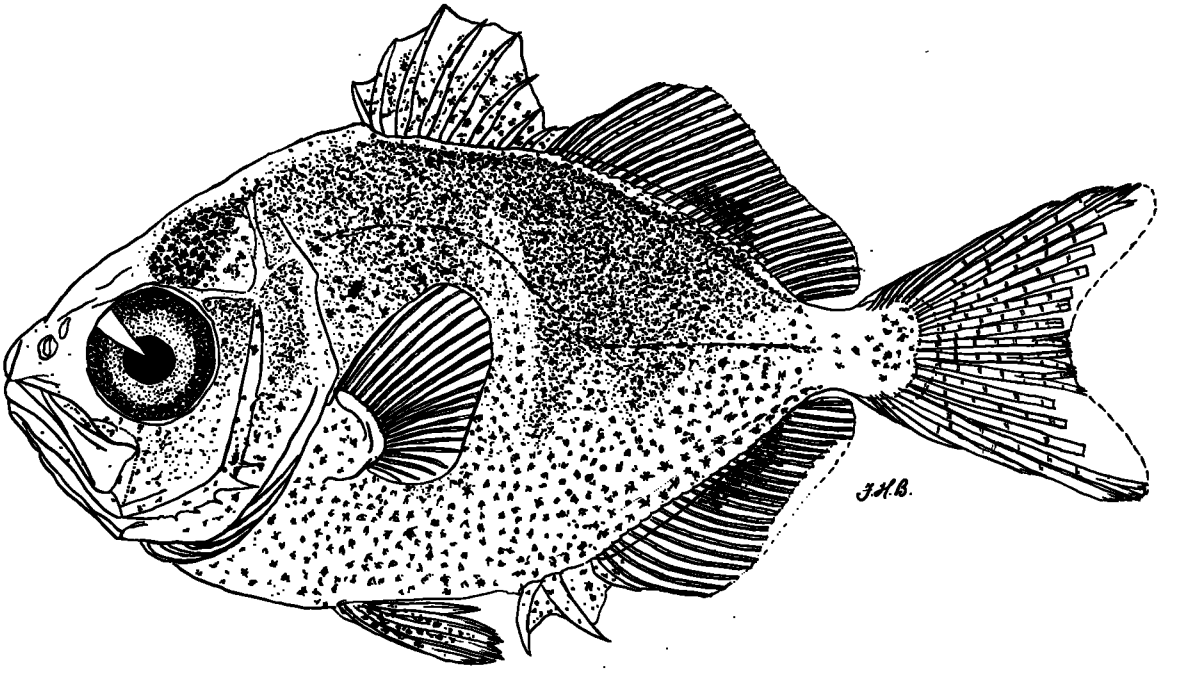

FIGURE 51.—*Caranx bartholomaei* juvenile, 14.3 mm. standard length (*Gill* 8, Reg. 6).

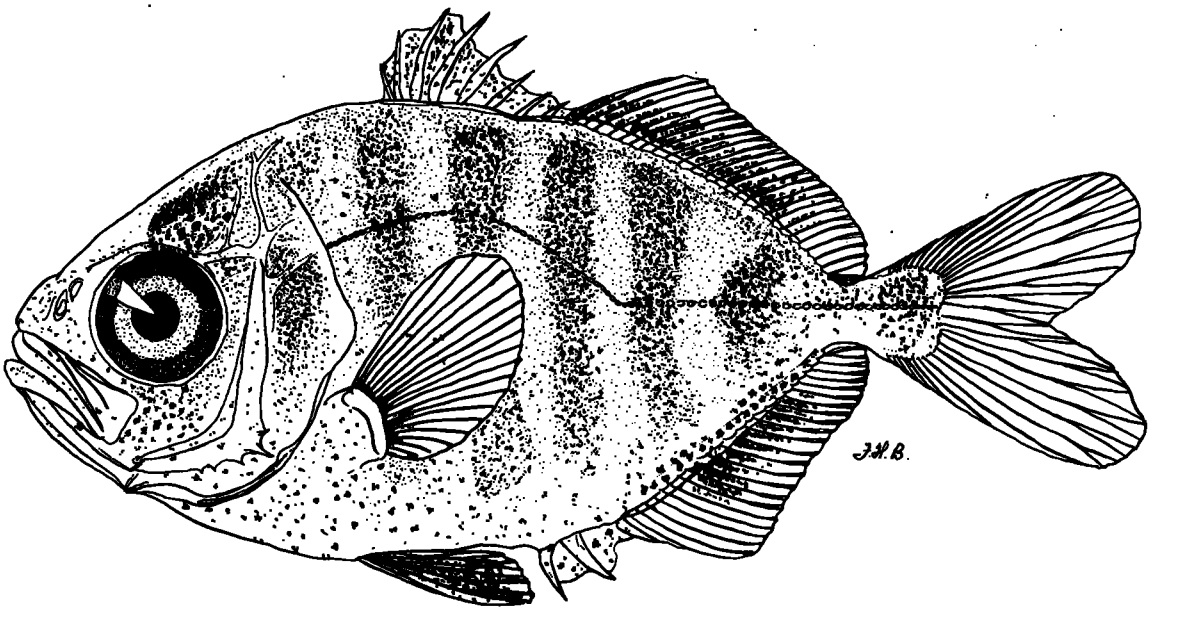

FIGURE 52.—*Caranx bartholomaei* juvenile, 17.4 mm. standard length (*Gill* 4, Reg. 16).

or distorted; and the first element of the second dorsal fin (normally the ninth dorsal spine), although having the thickened, shortened, and pointed appearance of a spine, has three segment marks.

Characters

Dorsal spines.—VIII and I. All spines are well formed at 6.0 mm. (fig. 48). The fourth spine averages the greatest length to about 33 mm. standard length; above 33 mm., the third spine is longest. An interspinous membrane connects the eighth and ninth spines to about 90 mm. On specimens 176 to 315 mm. the membrane connecting the seventh and eighth spines has disappeared.

The regression of third dorsal-spine length on standard length is shown in figure 55 and table 12. A line fitted to this regression for specimens from 10.5 to 79.5 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.12-mm. increase in spine length per 1.0-mm. increase in standard length). The coordinates of the seven specimens larger than 79.5 mm. fall below the extension of the calculated regression line, indicating a decrease in spine growth rate above this size.

Anal spines.—II and I. The spines are well formed at 6.0 mm. (fig. 48). The second spine is longer than the first at all sizes. An interspinous membrane connects the second and third spines to about 35 mm. standard length (figs. 48 and 53). The second anal spine length for the two specimens smaller than 10 mm. is illustrated in figure 4.

Dorsal soft-rays.—25 to 28 (table 12). The 6.0-mm. specimen has 25 soft-rays—one or more are probably unformed (fig. 48). The 25 soft-rays of the 8.1-mm specimen (fig. 49) may represent the full complement of this fish. Segmentation has begun at 6.0 mm. standard length (fig. 48). The terminal ray is branched to its base by 10.5 mm. (fig. 50), and the other rays become branched between about 17 mm. and 20 mm. (fig. 53). The extension of the anterior 5 or 6 rays to produce the lobe begins at about 15 mm. (fig. 52) and is pronounced by 30 mm. (fig. 53). The second ray averages the greatest length to about 23 mm.; above 23 mm., the first ray is longest. The longest soft-ray averages a greater length than the longest dorsal spine (fig. 55).

The regression of length of the first dorsal soft-ray on standard length is shown in figure 55 and table 11. A line fitted to this regression for specimens from 6.0 to 95.0 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.15-mm. increase in soft-ray length per 1.0-mm. increase in standard length). The spread of the coordinates of specimens larger than 95.0 mm. on both sides of the extension of the calculated regression line is

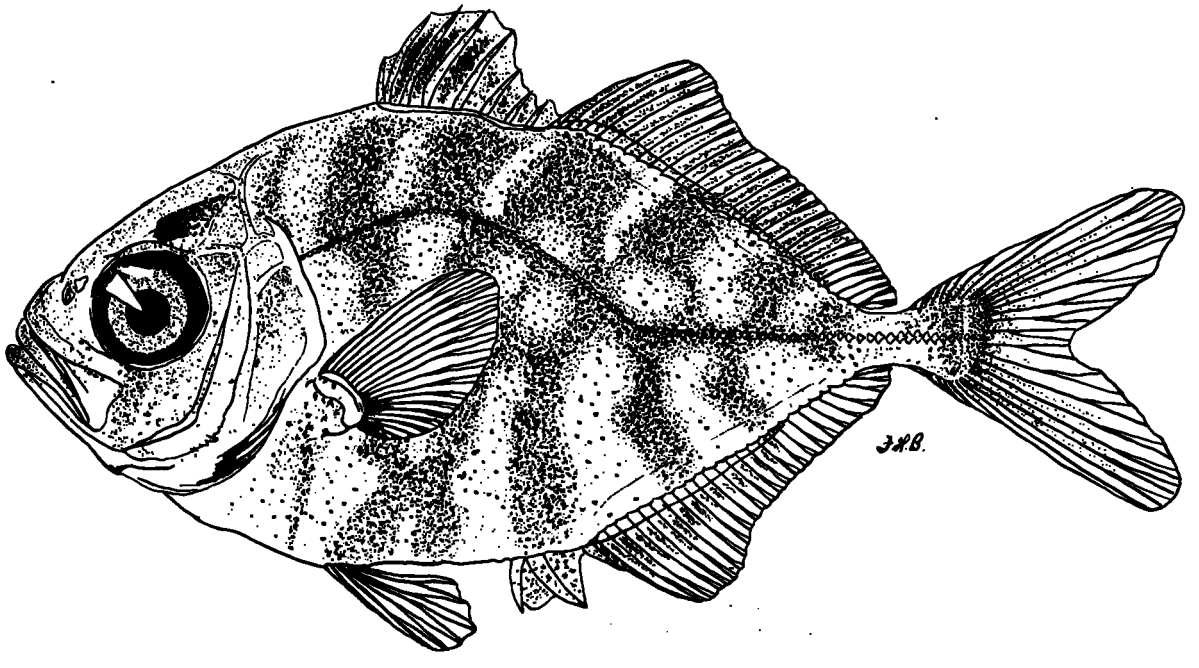

FIGURE 53.—*Caranx bartholomaei* juvenile, 30.7 mm. standard length (*Gill* 7, Reg. 27).

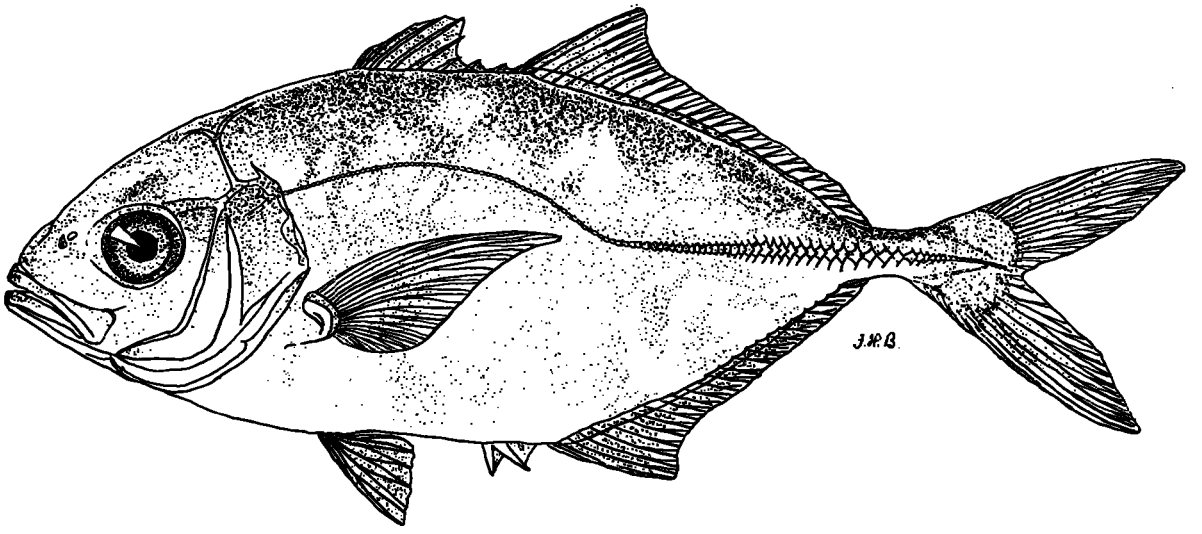

FIGURE 54.—*Caranx bartholomaei* juvenile, 95 mm. standard length (*Gill* 3, Reg. 62).

TABLE 11.—Caranx bartholomaei: *Statistics describing regressions of body parts on standard length*

$\bar{x}$=mean of independent variable x
$\bar{y}$=mean of dependent variable y
N=number of specimens
b=rate of increase of y
a=y-intercept of regression line
$Sy{\cdot}x$=standard deviation from regression (standard error of estimate)

Independent variable x	Dependent variable y	Size range of specimens (mm.)	$\bar{x}$	$\bar{y}$	N	b	a	$Sy{\cdot}x$
Standard length	Dorsal-fin spine length (3d)	10. 5–79. 5	35. 29	4. 24	56	0. 121	−0. 017	0. 378
Do	Dorsal soft-ray length (1st)	6. 0–95. 0	33. 97	4. 69	48	. 146	−. 279	. 502
Do	Pectoral length	8. 1–66. 5	34. 54	8. 16	59	. 265	−1. 001	. 551
Do	do	66. 5–243	124. 75	38. 09	12	. 388	−10. 261	1. 521
Do	Body depth	12. 7–108	43. 46	19. 35	69	. 388	2. 508	. 952
Do	Head length	6. 0–95. 0	38. 51	13. 27	69	. 314	1. 197	. 647
Do	Eye diameter	6. 0–83. 5	37. 68	4. 47	68	. 095	. 875	. 277
Do	Snout length	6. 0–95. 0	38. 48	3. 67	69	. 106	−. 209	. 373

insufficient to suggest a possible change in growth rate, and the same rate may prevail at these larger sizes.

Anal soft-rays.—21 to 24 (table 12). Formation, segmentation, branching, and lobation occur about as with the second dorsal fin. The second ray averages the longest to about 23 mm. standard length; above 23 mm., the first ray is longest. The longest anal and dorsal rays are nearly equal to about 40 mm.; above 40 mm., the dorsal is the longer. The second anal spine is two-thirds as long as the longest anal ray at 6.0 mm. standard length, one-half as long at 60 mm., less than one-third as long at 151 mm., and almost one-fourth as long at 243 mm.

Interneural and interhemal spines.—Posterior lateral projections of these spines are not extended above the body surface (as occurs in *latus* and *hippos*).

TABLE 12.—Caranx bartholomaei: *Correlation of the numbers of dorsal and anal soft-rays of 115 specimens*

[The upper number in each block is the count obtained for that combination, and the number in parentheses below is the approximate percentage of that count in the total sample]

ANAL SOFT-RAYS	DORSAL SOFT-RAYS 25	26	27	28
21	3 (2.6)			
22	5 (4.3)	27 (23.5)	1 (.9)	
23	1 (.9)	47 (40.9)	28 (24.3)	2 (1.7)
24			1 (.9)	

Caudal.—9+8 principal rays; about 8 or 9+7 to 9 secondary rays. The principal rays are all present and segmentation has begun at 6.0 mm. standard length (fig. 48). One or two dorsal and ventral secondary rays are probably unformed at 8.1 mm., but the full complement is present at

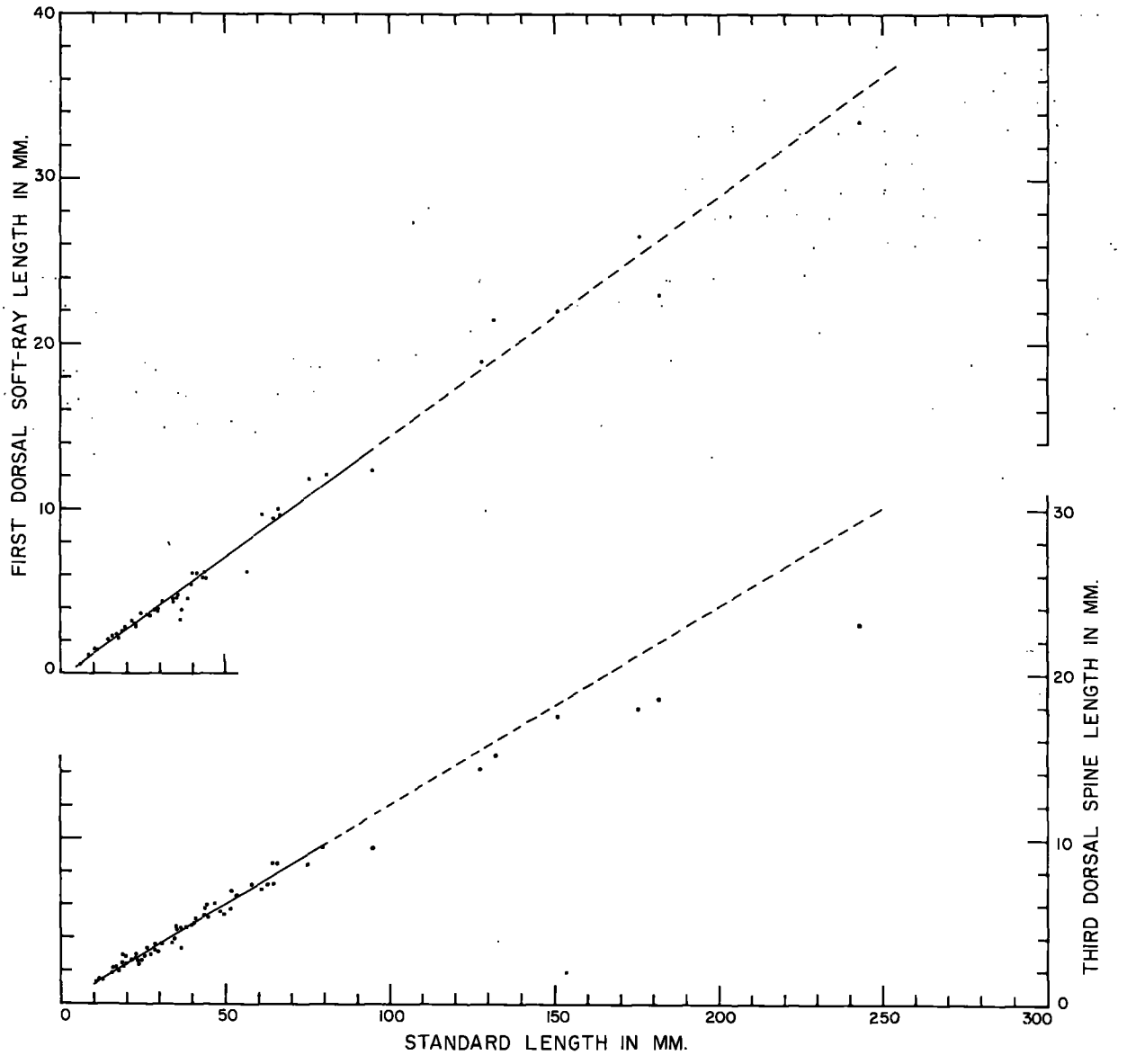

FIGURE 55.—*Caranx bartholomaei:* Relation of length of first dorsal soft-ray and of third dorsal spine to standard length.

10.5 mm. Branching begins at about 10 mm. (fig. 50) and is pronounced at about 16 mm. (fig. 52). Forking of the tail is represented by a slight indentation at 6.0 mm. (fig. 48) and is pronounced at 8.0 mm. (fig. 49). The urostyle is visible at 6.0 mm. (fig. 48) but not at 8.1 mm. (fig. 49).

Pectoral.—I–19 to 21. About 14 rays are developed at 6.0 mm. standard length (fig. 48), and the full complement apparently is formed at 8.1 mm. Branching of the rays has begun by 25 mm. The distal end of the fin is rounded from 6.0 mm. to about 35 mm., above which it becomes pointed and falcation begins (figs. 48 to 53). Falcation is pronounced by 95 mm. (fig. 54).

The regression of pectoral length on standard length is shown in figure 56 and table 11. Two lines were fitted to this regression: for specimens from 8.1 to 66.5 mm. and for specimens from 66.5 to 243 mm. standard length. An extension of the lower line intersects the upper line at approximately 75 mm., indicating that an inflection occurs at about that size and that a faster pectoral growth rate prevails above that size. The proportional rates of increase for the two variates are 0.27-mm.

489286 O—59——5

(below 75 mm.) and 0.39-mm. (above 75 mm.) increase in pectoral length per 1.0-mm. increase in standard length.

Pelvic.—I–5. All the rays are discernible at 6.0 mm. (fig. 48). Branching has begun by 15 mm. standard length.

Body depth.—The depth at first anal spine averages less than depth at pelvic to about 45 mm., is nearly equal from about 45 to 55 mm., and averages greater above 55 mm. standard length. The body depth at pelvic for the two specimens smaller than 10 mm. is illustrated in figure 9.

The regression of body depth at pelvic on standard length is shown in figure 57 and table 11. A line fitted to this regression for specimens from 12.7 to 108 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.36-mm. increase in body depth per 1.0-mm. increase in standard length). The alinement of the coordinates of the four smallest specimens below the extension of the calculated regression line indicates that a faster body-depth growth rate prevails below approximately 13 mm. The alinement of the coordinates of the five largest specimens below the extension of the calculated regression line indicates that a decrease in body-depth growth rate occurs between approximately 110 mm. and 150 mm. standard length.

Head.—The nostril is undivided at 6.0 mm. (fig. 48) and divided at 8.1 mm. (fig. 49). Serrations occur on the supraoccipital crest at 6.0 mm. (fig. 48); none at 8.1 mm. (fig. 49). Two posterolaterally projecting spines are located on

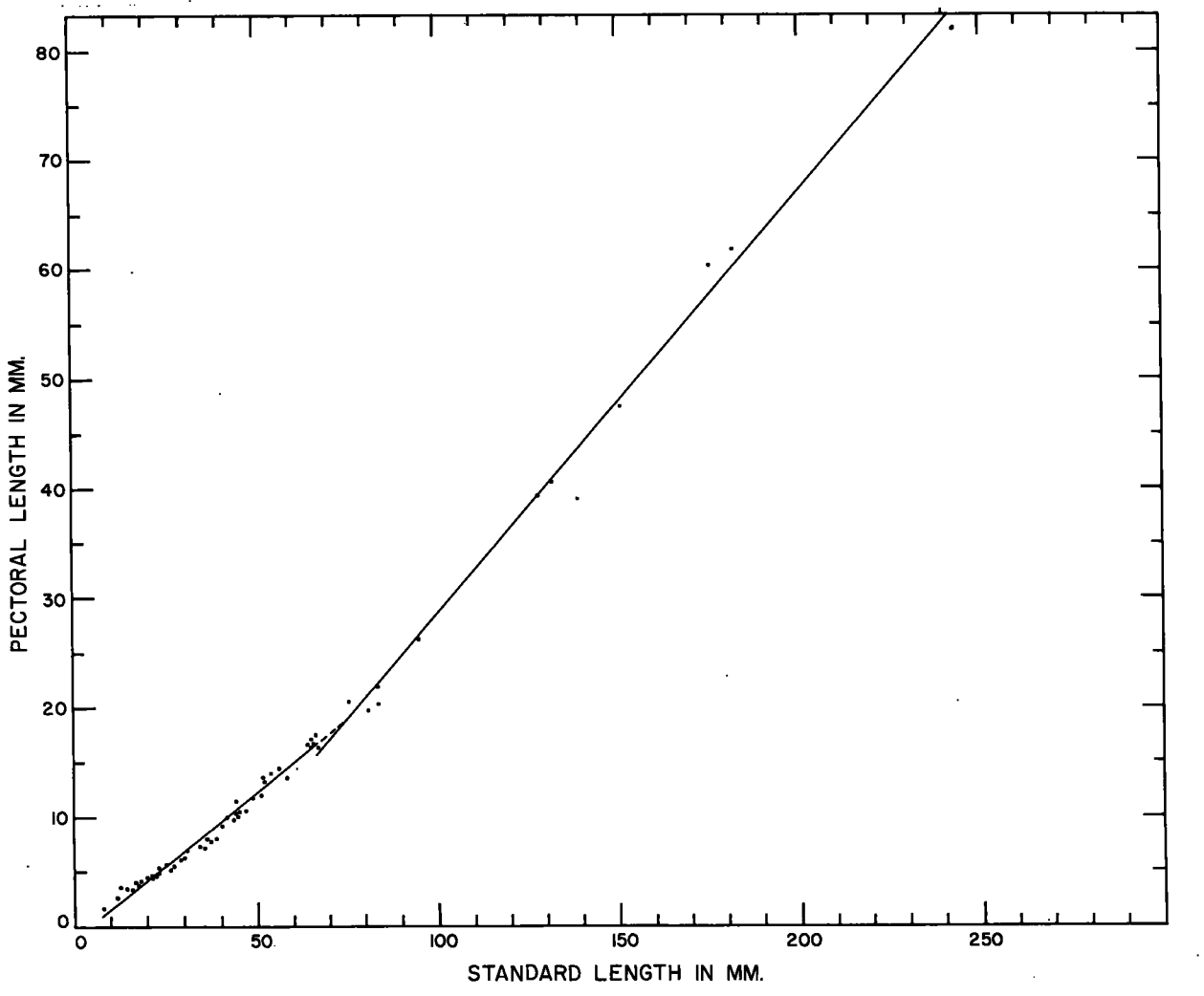

FIGURE 56.—*Caranx bartholomaei:* Relation of pectoral length to standard length.

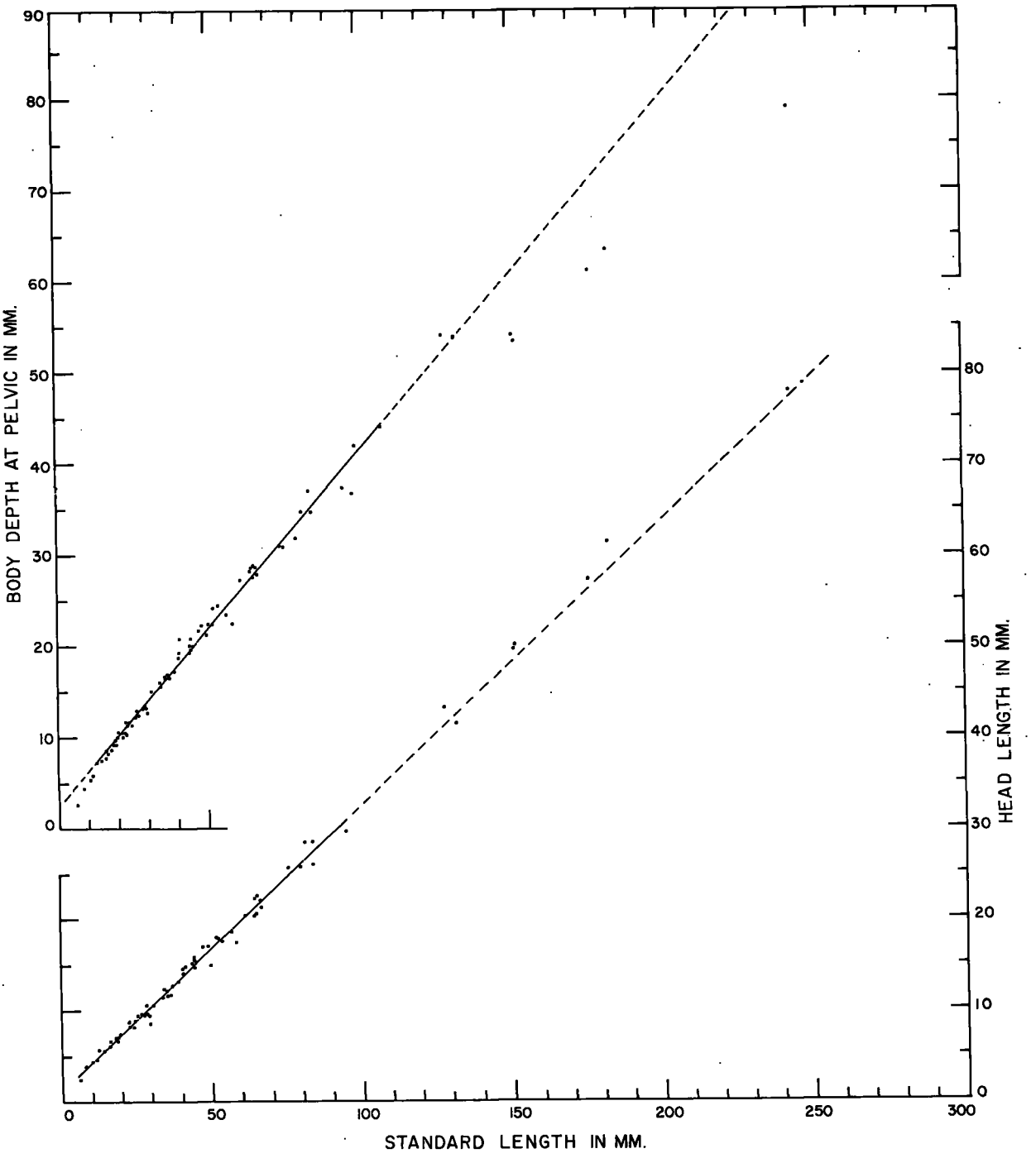

FIGURE 57.—*Caranx bartholomaei:* Relation of body depth at pelvic and of head length to standard length.

the cleithrum just below its junction with the operculum on the 6.0-mm. specimen. These spines are not present at 8.1 mm. or above.

The regression of head length on standard length is shown in figure 57 and table 11. A line fitted to this regression for specimens from 6.0 to 95.0 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.31-mm. increase in head length per 1.0-mm. increase in standard length). The

coordinates of the specimens larger than 95 mm. fall along the extension of the calculated regression line, indicating that the head growth may continue at the same proportional rate.

Eye.—The regression of eye diameter on standard length is shown in figure 58 and table 11. A line fitted to this regression for specimens from 6.0 to 83.5 mm. standard length shows a proportional rate of increase for the two variates from about 12 to 83.5 mm. (0.095-mm. increase in eye diameter per 1.0-mm. increase in standard length). The alinement of the two smallest specimens suggests that a faster eye growth rate may prevail for specimens below approximately 12 mm. The coordinates of the specimens larger than 83.5 mm. fall below the extension of the calculated regression line, indicating a decrease in eye growth rate above this size.

Snout.—The regression of snout length on standard length is shown in figure 58 and table 11. A line fitted to this regression for specimens from 6.0 to 95.0 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.11-mm. increase in snout length per 1.0-mm. increase in standard length). The alinement of coordinates of specimens larger than 95 mm. above the extension of the calculated regression line suggests that an increase occurs in snout growth rate at about that size.

Gill rakers.—Lower limb, 18 to 21; upper limb, 6 to 9; total, 25 to 29 (table 13). About 80 percent of the specimens examined above 20 mm. had one or more rudimentary gill rakers at the origin of the lower limb; one was present on specimens up to 131 mm., 2 at 151 mm. and 176 mm., 4 at 182 mm., and 5 at 243 mm. and 315 mm. About 75 percent of the specimens above 20 mm. had one or more shorter or rudimentary rakers at the origin of the upper limb; one was present on specimens up to 151 mm., 2 at 176 mm. and 182 mm., 3 at 243 mm., and 6 at 315 mm. Ginsburg (1952: 96) reported 3 to 4 upper-limb and 1 to 2 lower-limb rudiments in large specimens (up to about 278 mm., converted). Apparently, there is an association between increase in body size and increase in number of gill rakers which become smaller or rudimentary.

TABLE 13.—Caranx bartholomaei: *Correlation of numbers of lower-limb to upper-limb gill rakers of 84 specimens*

[The upper number in each block is the count obtained for that combination, and the number in parentheses below is the approximate percentage of that count in the total sample]

UPPER-LIMB GILL RAKERS	LOWER-LIMB GILL RAKERS 18	19	20	21
6		1 (1.2)		
7	2 (2.4)	14 (16.7)	13 (15.5)	
8		10 (11.9)	31 (36.9)	1 (1.2)
9		4 (4.8)	8 (9.5)	

Scutes.—Range of the mean number of scutes above 100 mm. standard length: about 22 to 28 (fig. 59). Ginsburg (1952: 96), working with specimens about 26.5 to 278 mm. (converted), gave a scute range of 20 to 31. Meek and Hildebrand (1925: 352), with specimens up to about 120 mm. (converted), gave a range of "about 22 to 35." The developing scutes appear between 12.7 mm. and 14.3 mm. (figs. 50 and 51). The first scutes to complete their development are present between 22 and 23 mm. All scutes of fish above 80 to 100 mm. have completed, or nearly completed, their individual development (fig. 59).

Lateral line.—Range of mean lateral-line ratio above 60 mm. standard length: about 1.0 to 1.4 (fig. 60). The lateral-line ratio–standard length relation is variable, but the value of the ratio tends to increase with respect to standard length up to about 50 mm., and it may decrease gradually above this size. Nichols (1939: 9), with specimens 16 to 51 mm. standard length, declared the curved lateral line to be about equal to the straight lateral line. This generalization is accommodated by the perimeter of figure 60, but the variation and change of this ratio with growth are much greater than Nichols' statement indicates.

Preopercular spines.—There were too few small specimens to evidence the early growth of the preopercular angle spine. This spine apparently begins to decrease in length at some size smaller than 12 mm., and is completely covered by the preopercular margin between about 32.5 and 39 mm. (fig. 61). The number of preopercular upper- and lower-limb spines varies considerably with size, but a trend of decrease in number of spines with increase in body size is apparent (table 1).

Pigmentation.—There are two rows of elongated

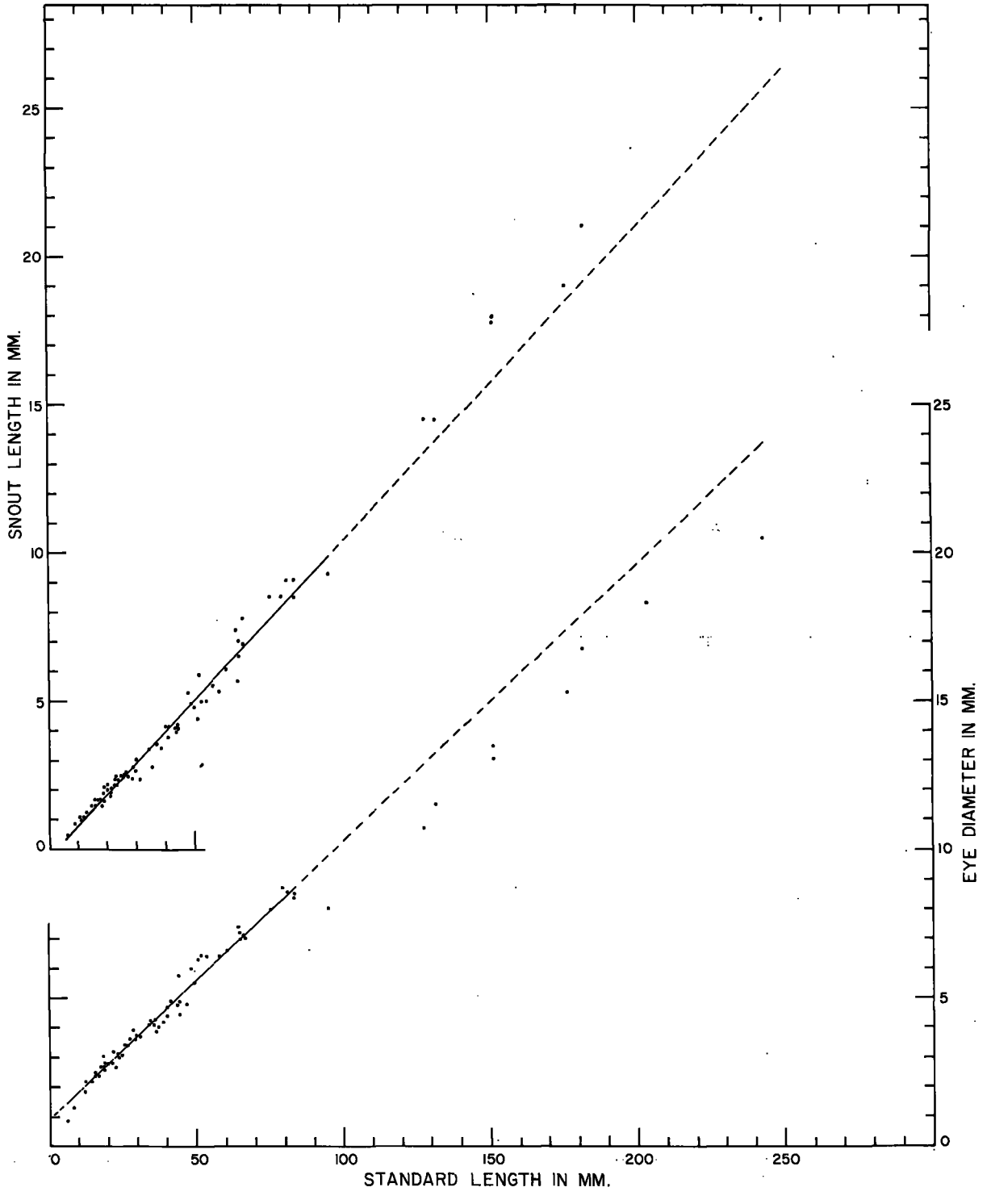

FIGURE 58.—*Caranx bartholomaei:* Relation of snout length and of eye diameter to standard length

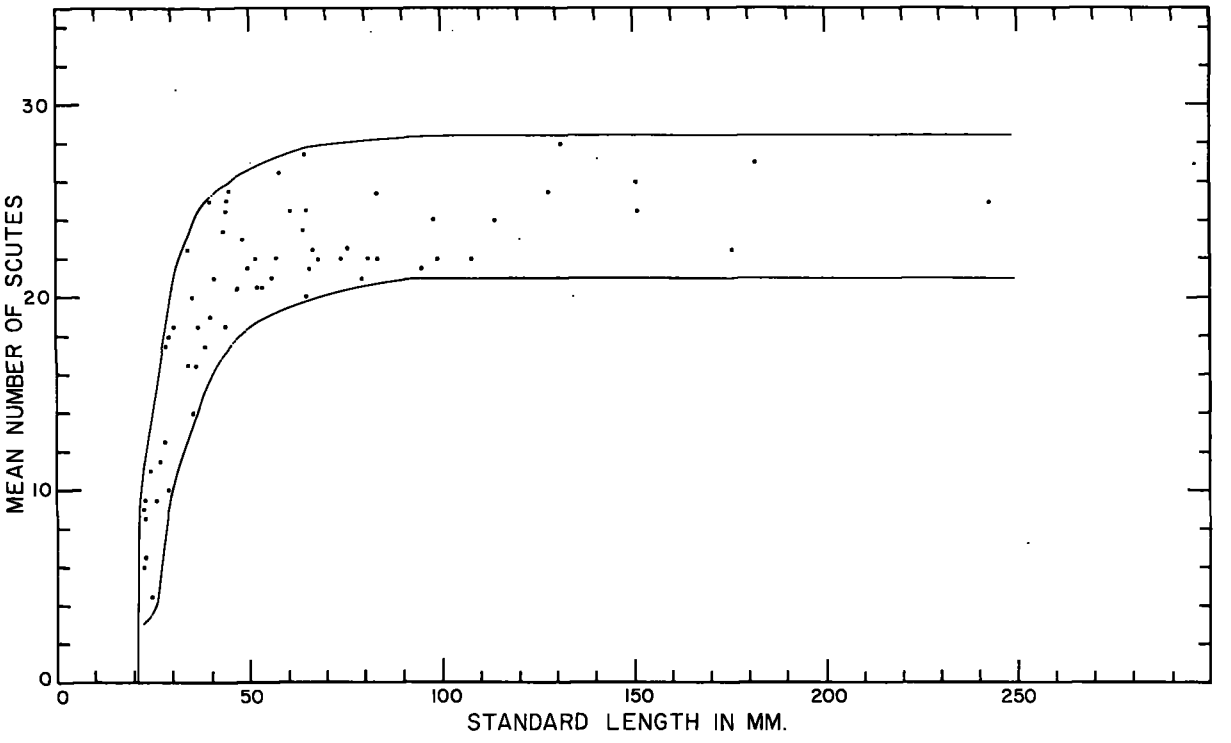

FIGURE 59.—*Caranx bartholomaei:* Relation of the mean number of scutes to standard length.

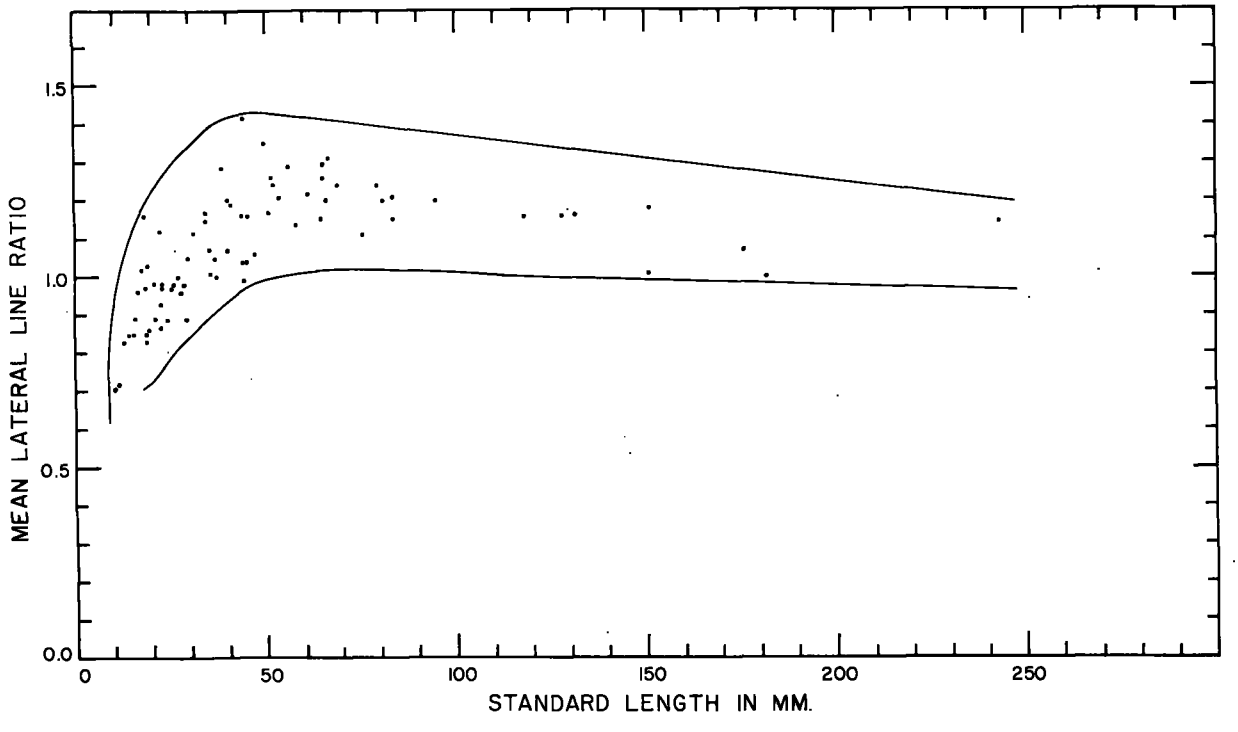

FIGURE 60.—*Caranx bartholomaei:* Relation of the mean lateral-line ratio to standard length.

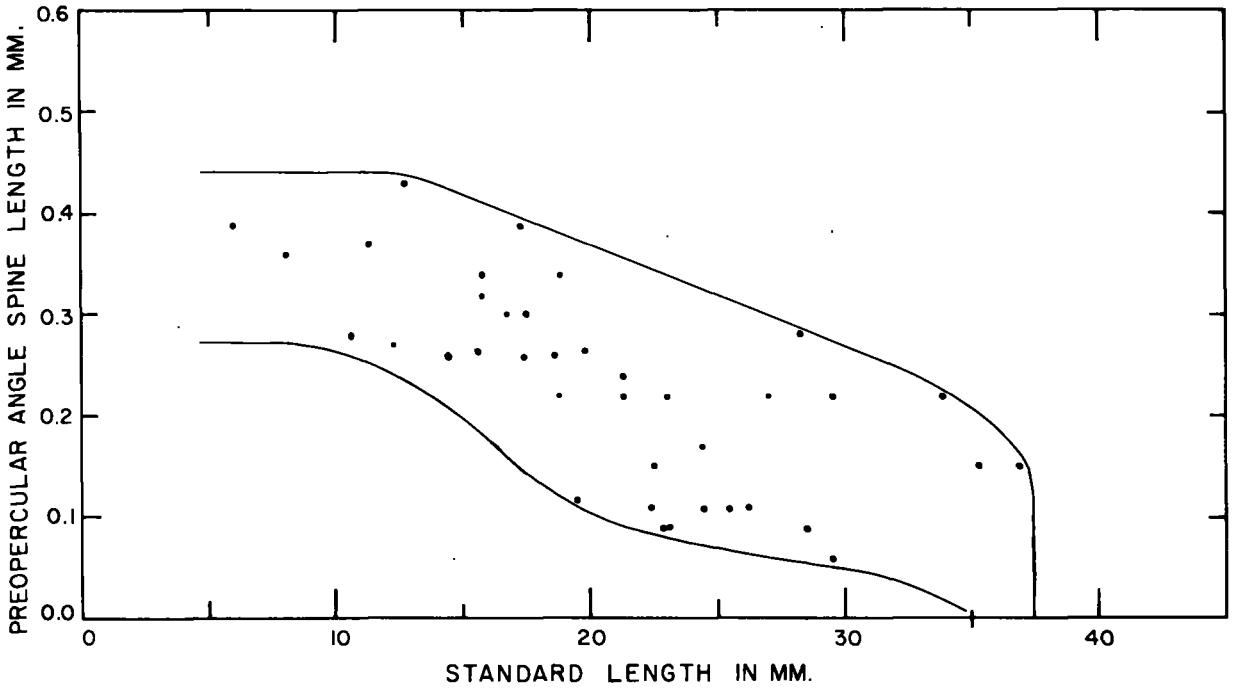

FIGURE 61.—*Caranx bartholomaei:* Relation of the length of the preopercular-angle spine to standard length.

melanophores on the body of the 6.0-mm. specimen—one below the base of the dorsal fin and one on the midline posteriorly. A few melanophores are scattered over the body, the snout, mouth parts, and operculum. A group of denser melanophores occurs over the eye on the transparent portion of the head. A few pigment spots occur on the interspinous membranes of the dorsal and anal fins, on the pelvic fins, and along the base of the anal soft-rays (fig. 48).

The 8.1-mm. specimen has an appreciable increase in the number of pigment spots on the body, head, and first dorsal and pelvic fins. Contrasting with the 6.0-mm. specimen, the two elongated rows of dorsal and lateral melanophores are not apparent, and there is only one pigment spot at the base of the anal soft-rays. A dense concentration of pigment occurs on the anterior portion of the caudal peduncle, and the fleshy portion of the caudal fin is conspicuously unpigmented (fig. 49).

Pigmentation of the body has intensified and appears dark between 10.5 and about 14 mm. standard length (fig. 50). Between 14 mm. and 17 mm., 3 to 5 vague bars have formed—the anterior ones are more distinct (fig. 51). Above 17 mm. (fig. 52) the full complement of 5 bars (rarely 4 or 6 on one or both sides of the body) is present. Above about 19 mm. the posterior 2 or 3 bars tend to become angular with their dorsal and ventral parts directed posteriorly and the lateral line extending through their apex; above about 22 mm. all of the bars become irregularly distorted or wavy. By about 28 mm., the bars begin to break into the mottled or spotted pattern that lasts to over 95 mm. (figs. 53 and 54), although this is not distinct in some specimens over 60 mm. Traces of the posterior 2 or 3 bars persist along the bases of the dorsal and anal fins of some specimens to about 48 mm.

The transparent part of the brain case has become opaque by 14 mm., and the melanophores on this area increase and are extended posterodorsally to form the nuchal band by about 17 mm. (fig. 52). A small accumulation of pigment below the eye gives the impression that the nuchal band passes vertically through the eye (figs. 52 to 54).

Pigment spots occur basally between the soft-rays of the dorsal and anal fins at 10.5 mm. (fig. 50). Pigmentation of the caudal fin is pronounced by 25 mm. (fig. 53). Pigmentation of all the fins intensifies to over 95 mm. (figs. 50 to 54).

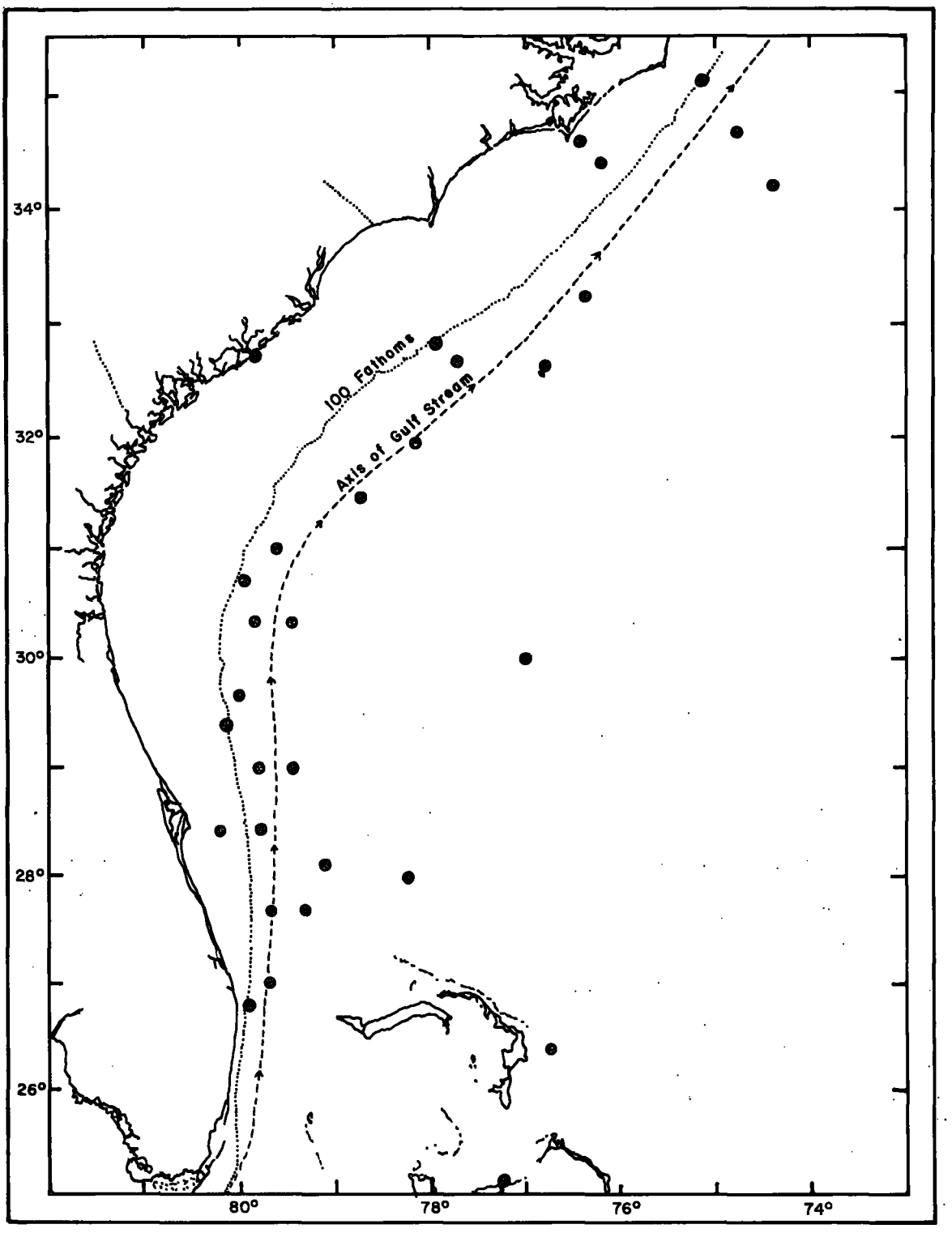

FIGURE 62.—*Caranx bartholomaei:* Locations of capture off the southeastern Atlantic coast of the United States.

Distribution off Southeastern Atlantic Coast of the United States

Specimens have previously been reported from the following specific localities within this area: Cape Lookout, N. C., by Nichols (1937c: 4); Beaufort, N. C., by Jordan (1881: 486), Smith (1907: 204), and Ginsburg (1952: 95); from North Carolina by Nichols (1912: 185; 1920a: 28); from Magnolia Beach, S. C., by Fowler (1945: 190); in the Gulf Stream off Bimini, Bahamas, by Nichols (1937b: 237); Bimini, Bahamas, by Fowler (1944: 443); Nassau, Bahamas, by Lee (1889: 670) and Bean (1905: 302); and Nassau and Green Turtle Cay, Bahamas, by Rosen (1911: 61).

Figure 62 shows the locations of specimens taken on the *Gill* cruises, by the *Combat* off Florida, Georgia, and South Carolina, USNM specimens examined (Cape Lookout and Beaufort, N. C.; 35°08′ N., 75°10′ W.; 34°39′ N., 76°12′ W.; and 27°57′ N., 78°15′ W.), CBSFP specimens examined (Nassau, Bahamas), and a ChM specimen examined (Magnolia Beach, S. C.) (tables 2 and 14).

Of these specimens, the two smallest, 6.0 mm. and 8.1 mm., are larvae taken off southern Florida and South Carolina on the axis of the Gulf Stream; the two largest, 176 mm. and 182 mm., from Nassau, are probably not large enough to be adult; and the others are juveniles. The locations of capture were generally beyond the 100-fathom line and indicate an association with the Gulf Stream (as depicted by the approximate axis of the Stream in figure 62). Specimens taken north of the Bahamas probably represent the effect of the northern dispersal of this species by the Antilles Current. Because of the relatively less-concentrated collecting by the *Gill* east of the axis of the Gulf Stream, it is not practical to estimate the relative abundance or distribution of young *bartholomaei* in that area. This occurrence of young in the Gulf Stream extends from about May into November (fig. 63).

The 38-mm. specimen recorded by Nichols (1937c: 4) from Cape Lookout, N. C., is the smallest *bartholomaei* that has been reported from

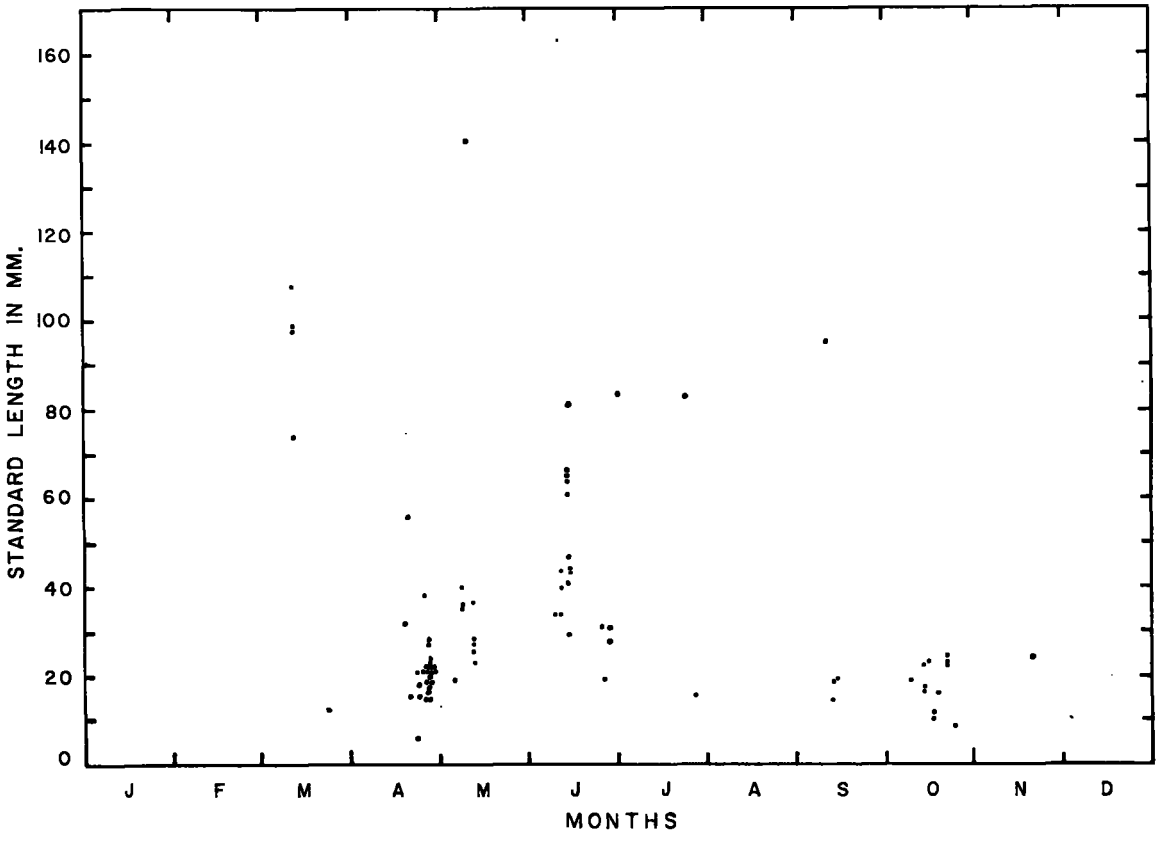

FIGURE 63.—*Caranx bartholomaei*: Size distribution, by months, of specimens taken off the southeastern Atlantic coast of the United States.

inshore waters of this Continent. A specimen of about 52 mm. (converted) reported by Smith (1898: 98) from Woods Hole, Mass., August 10, is the smallest specimen from northern inshore waters that has been recorded. A 32.5-mm. specimen, ANSP account No. 156 and 157, from Guana Island, Virgin Islands, March 22, and a 34.8-mm. specimen, CBSFP account No. 171, from Hog Island, Bahamas, March 28, are the two smallest specimens to be recorded from inshore collections. This is the approximate size by which the preopercular spines have been absorbed. The absence of inshore records of larvae and smaller juveniles indicates that these periods are spent in offshore currents.

I believe the young in this area represent a summer-to-fall population of larvae and juveniles that drifts northward in the Gulf Stream, with juveniles occasionally migrating or drifting inshore. This population appears to be largely the result of recruitment from waters to the south of this area, although some part may result from reproduction within the area. Absence of records of *bartholomaei* from inshore waters along the Atlantic coast of the United States during the colder months of the year indicates that during this period the species either returns to the south or moves to warmer offshore waters. It is doubtful that this species continues its movement with the Stream to the east since it has never been recorded east of the longitude of Bermuda along the route of the Gulf Stream or from the Eastern Atlantic.

Spawning

The spawning season that contributes larval and juvenile *bartholomaei* to this area may be estimated, from the smallest specimens taken in March (12.7 mm.) and October (8.1 mm.), to extend from mid-February to mid-September (fig. 63).

If, as suggested, there is a northward-drifting population of developing young, the majority of specimens taken by the *Gill* would probably have been spawned to the south of this area. The 8.1-mm. specimen taken in the Gulf Stream off South Carolina (table 14) may have been spawned in the southern portion of the area.

TABLE 14.—Caranx bartholomaei: *Location and date of capture, number and size range of 125 specimens examined*

[See pp. 412 and 419 for explanation of abbreviations used; measurements in standard length]

Location	Date captured	Collection	Number of specimens	Size (mm.)
ATLANTIC OCEAN:				
Guana Island, Virgin Is.	Mar. 22, 1953	ANSP Acct. No. 156-157	1	32. 5
Spanish Wells, Bahamas	July 4, 1903	USNM 164532	4	44-65
23°50′ N., 80°40′ W	Mar. 26, 1948	ANSP 72693	2	15. 8-17. 2
Do	do	ANSP 72689	1	17. 4
24°12′ N., 80°01′ W	July 25, 1957	SAFI, *Combat* 451	2	26-31. 5
24°28.5′ N., 77°28.5′ W	Oct. 8, 1953	SAFI, *Gill* 4, TO-2	1	18. 8
Nassau fish market, Bahamas	Aug. 17-20, 1955	UF 3539	1	243
Hog Island, Bahamas	Mar. 26, 1954	CBSFP Acct. No. 209	2	176-182
Do	Mar. 28, 1954	CBSFP Acct. No. 171	1	34. 8
Do	Mar. 12, 1954	CBSFP Acct. No. 186	4	74-108
Do	Aug. 19, 1955	CBSFP Acct. No. 251	1	51. 5
26°27′ N., 76°44′ W	June 12-13, 1954	SAFI, *Gill* 7, Std.	3	34-44
Do	June 13-14, 1954	do	2	40. 5-47
Do	June 14, 1954	do	3	29. 5-44. 5
26°47′ N., 79°53′ W	July 28, 1957	SAFI, *Combat* 459	2	28-31
26°56′ N., 79°41′ W	Apr. 23, 1953	SAFI, *Gill* 2, Reg. 2	1	6. 0
27°40′ N., 79°18.5′ W	do	SAFI, *Gill* 2, Reg. 7	1	21. 2
27°41′ N., 79°40.5′ W	Sept. 11, 1954	SAFI, *Gill* 8, Reg. 6	1	14. 3
27°57′ N., 78°15′ W	Mar. 22, 1914	USNM 148910, *Grampus* 10209	1	12. 7
28°19.5′ N., 80°10′ W	Apr. 27, 1954	SAFI, *Gill* 6, Reg. 10	1	38. 5
28°21′ N., 79°48′ W	Apr. 26, 1954	SAFI, *Gill* 6, Reg. 9	1	21. 2
28°56.3′ N., 79°45.6′ W	July 27, 1953	SAFI, *Gill* 3, Reg. 15	1	15. 5
29°00′ N., 79°26′ W	Oct. 14, 1953	SAFI, *Gill* 4, Reg. 16	3	16. 7-22. 4
29°26′ N., 80°08′ W	Apr. 27, 1957	SAFI, *Combat* 315	19	15-28
29°40′ N., 80°00′ W	Sept. 13, 1954	SAFI, *Gill* 8, Reg. 18	1	18. 5
30°00′ N., 77°00′ W	June 10, 1954	SAFI, *Gill* 7, Spc. 5	1	33. 9
30°19.5′ N., 79°50′ W	Sept. 14, 1954	SAFI, *Gill* 8, Reg. 27	1	19
30°19.8′ N., 79°25.5′ W	Oct. 16, 1953	SAFI, *Gill* 4, Reg. 28	1	23
30°20′ N., 79°50′ W	June 26, 1954	SAFI, *Gill* 7, Reg. 27	1	30. 7
30°40′ N., 79°57′ W	Apr. 24, 1957	SAFI, *Combat* 310	2	15. 5-18. 5
30°58′ N., 79°37.5′ W	June 27, 1954	SAFI, *Gill* 7, Reg. 30	1	19. 8
31°28′ N., 78°42′ W	Oct. 25, 1953	SAFI, *Gill* 4, Reg. 40	3	22. 5-24. 4
31°29′ N., 78°41′ W	May 5, 1953	SAFI, *Gill* 2, Reg. 40	1	19. 5
31°57′ N., 78°09′ W	Oct. 26, 1953	SAFI, *Gill* 4, Reg. 50	1	8. 1
32°39′ N., 76°46′ W	Aug. 10, 1953	SAFI, *Gill* 3, Reg. 62	1	95
32°40′ N., 77°40′ W	Apr. 21, 1957	SAFI, *Combat* 296	2	15. 5-57
Magnolia Beach, S. C.	Aug. 1933	ChM 34.55.5	1	68
32°49′ N., 77°56′ W	Apr. 19, 1957	SAFI, *Combat* 284	1	32
33°14.7′ N., 76°23′ W	May 8, 1953	SAFI, *Gill* 2, Reg. 63	3	35. 3-40

TABLE 14.—Caranx bartholomaei: *Location and date of capture, number and size range of 125 specimens examined—Con.*

Location	Date captured	Collection	Number of specimens	Size (mm.)
ATLANTIC OCEAN—Continued				
34°37.7′ N., 74°45.5′ W	May 12, 1953	SAFI, *Gill* 2, Reg. 80	5	23.1–36.9
34°39′ N., 76°12′ W	Oct. 19, 1885	USNM 164534, *Albatross*	1	15.8
35°08′30″ N., 75°10′ W	Oct. 17, 1885	USNM 164537, *Albatross* 2596	2	10.5–11.3
Cape Lookout, N. C	July 1912	USNM 74295	2	75.5–131
Beaufort, N. C	July–Aug., 1904	USNM 51929	1	128
Do	July–Aug., 1904	USNM 164533	1	48
Do	June 14, 1932	USNM 111786	5	61–81
Pivers Island, Beaufort, N. C	July 1, 1932	USNM 111785	1	83.5
41°28′30″ N., 65°35′30″ W	Aug. 27, 1886	USNM 39448, *Albatross* 2706	1	18
Woods Hole, Mass	1876	USNM 134291	2	64–83.5
Do	Sept. 15, 1877	USNM 144008	1	53
Do	Aug. 10, 1886	USNM 73483	1	50.5
GULF OF MEXICO:				
Cuba	1885	USNM 37521	1	56
Havana fish market, Cuba	Jan. 7, 1956	SAFI	1	315
Havana market, Batabano, Cuba	Nov. 7, 1954	UF 5348	1	151
Key West, Fla	1886	USNM 38731	1	52
Do	May 10, 1929	USNM 89787	1	35.3
Boca Chica, Key West, Fla	Feb. 18, 1942	ANSP 70873–74	2	24.4–45
Tortugas, Fla	No date.	USNM 116860	3	25.4–79.5
Do	June–Aug. 1926	USNM 88091	2	28.2–29.3
Tortugas, Fla	June 17, 1956	GFEGR, *Bowers*	5	54–80
Pensacola, Fla	No date.	USNM 30167	1	66.5
CARIBBEAN SEA:				
Galeta Point, Fort Randolph, Panama	Oct. 31, 1948	USNM 148667	1	44
20°50′ N., 86°10′ W	Apr. 28, 1955	GFI, *Oregon* 1297	1	22
Palisadoes, Kingston, Jamaica	June 15, 1957	UF (uncataloged)	1	114
Kingston Harbor, Jamaica	June 25, 1957	UF (uncataloged)	1	151

Caranx sp. ("*latus* and/or *hippos*")

(Figures 65–68)

Material

Nine specimens measuring from 5.4 to 8.3 mm. standard length (table 15) are included in this series (abbreviated in the text and figures to "*latus* and/or *hippos*") because no specimens of *latus* smaller than 16.1 mm. or of *hippos* smaller than 15.3 mm. standard length that were suitable for comparison were available. However, morphometric trends, meristic values, and pigmentation delimit the series to these two species. The term "*latus* and/or *hippos*" is utilized for convenience in briefly denoting relationship without implying a specific nomenclatorial identity. This series is not homogenous in all of the characters examined, but it is impossible to determine if one or both species are represented. I believe that the largest specimen (fig. 68) is *latus*, because of the nature of the pigmentation of the first dorsal fin (compare with figs. 69 and 81), and because the number of its anal rays (18) was found in 8 out of 82 specimens of *latus* that were counted while the maximum number counted in 132 specimens of *hippos* was 17. The 4.9-mm. specimen illustrated in figure 64 and identified as *Caranx* sp. may belong to this series. Several characters of the specimen suggest this: body depth (2.6 mm.), second anal spine length (0.23 mm.), and preopercular angle spine length (0.53 mm.). This specimen was taken at *Gill* 3, Reg. 60, 33°07′ N., 77°20′ W., August 10, 1953.

Morphometric values of the "*latus* and/or *hippos*" series have been plotted on the graphs of *latus* and *hippos*. Their description is treated separately here and not under the accounts of *latus* or *hippos*.

Characters

Dorsal spines.—VIII and I. The spines are well-formed at 5.4 mm. standard length (fig. 65). The third and fourth spines are the longest and are nearly equal in length at 5.4 mm. and 6.1

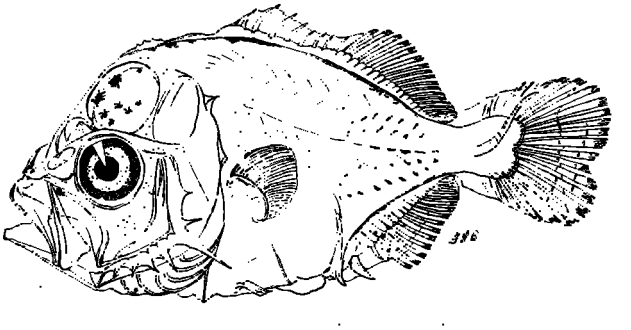

FIGURE 64.—*Caranx* sp. (*latus* or *hippos*?) larva, 4.9 mm. standard length (*Gill* 3, Reg. 60).

mm.; from 6.2 to 8.3 mm., the third spine is the longest. The coordinates of third dorsal spine length on standard length are plotted on figures 73 and 86.

Anal spines.—II and I. The spines are well formed at 5.4 mm. standard length (fig. 65). There is some variation in comparative lengths, but the second spine appears to be the longest from 5.4 to 6.3 mm., and the first is longest at 6.9 mm. and 8.3 mm. The length of the second anal spine of these specimens is illustrated in figure 4.

Dorsal soft-rays.—21 at 8.3 mm. standard length, 20 at 6.9 mm. On the specimens of 6.3 mm. and smaller the posterior soft-rays have not formed. The second ray is longer than the first on all specimens with unbroken dorsal fins. The third spine of the dorsal averages a greater length than the first soft-ray from 5.4 to 6.2 mm. standard length; at 8.3 mm. the first soft-ray is longer. The coordinates of first dorsal soft-ray length on standard length are plotted in figures 73 and 86.

Anal soft-rays.—18 at 8.3 mm. standard length, 16 at 6.9 mm. On the specimens of 6.3 mm. and smaller the posterior soft-rays have not formed. The second soft-ray is longer than the first on all specimens and has a slightly greater length than the longest dorsal ray on most specimens.

Interneural and interhemal spines.—The posterior lateral projections that extend above the body surface along both sides of the dorsal and anal soft-ray bases on larger *latus* and *hippos* have not protruded above the body surface by 8.3 mm.

Caudal.—9+8 principal rays; 8+8 secondary rays (at 8.3 mm. standard length). Only 6 dorsal and 6 ventral secondary rays are present at 6.9 mm.—less than the adult complement of *latus* or *hippos*. The number of secondary caudal rays of the 8.3-mm. specimen is within the range of the adult complement of *latus* and *hippos*. Segmentation has begun by 5.4 mm. (fig. 65), but branching has not begun by 8.3 mm. (fig. 68). Forking of the tail is represented by a slight indentation at 5.4 mm. and is pronounced at 8.3 mm. The urostyle remains visible at 8.3 mm.

Pectoral.—The full complement of rays is present at 8.3 mm. but not at 6.9 mm. The distal end of the fin is rounded at all sizes (figs. 65 to 68). The coordinate of pectoral length on standard length of the 8.3-mm. specimen is plotted in figures 74 and 87.

Pelvic.—The fin is very small and incompletely formed at 5.4 mm. standard length (fig. 65). The full count of rays is present at 6.9 mm. (fig. 67), and segmentation is present on the unbranched rays at 8.3 mm. (fig. 68).

Body depth.—At corresponding body lengths, the depth at first anal spine is less than the depth at pelvic. The coordinates of body depth at pelvic on standard length are plotted in figures 9, 75, and 88.

Head.—The nostril is not completely divided

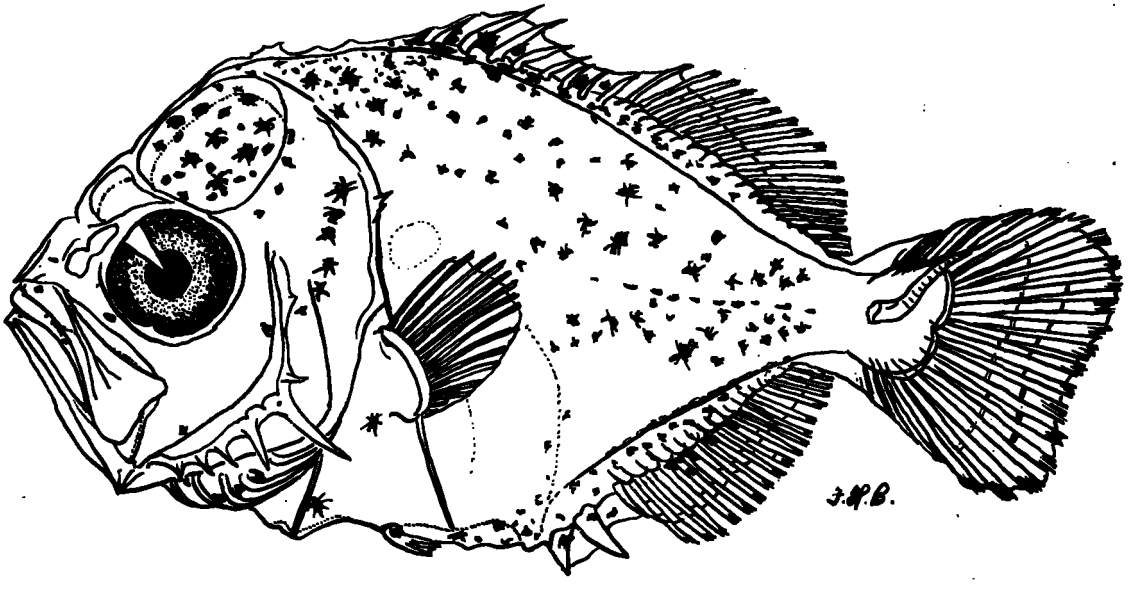

FIGURE 65.—*Caranx* sp. (*latus* or *hippos*) larva, 5.4 mm. standard length (*Gill* 7, Reg. 79).

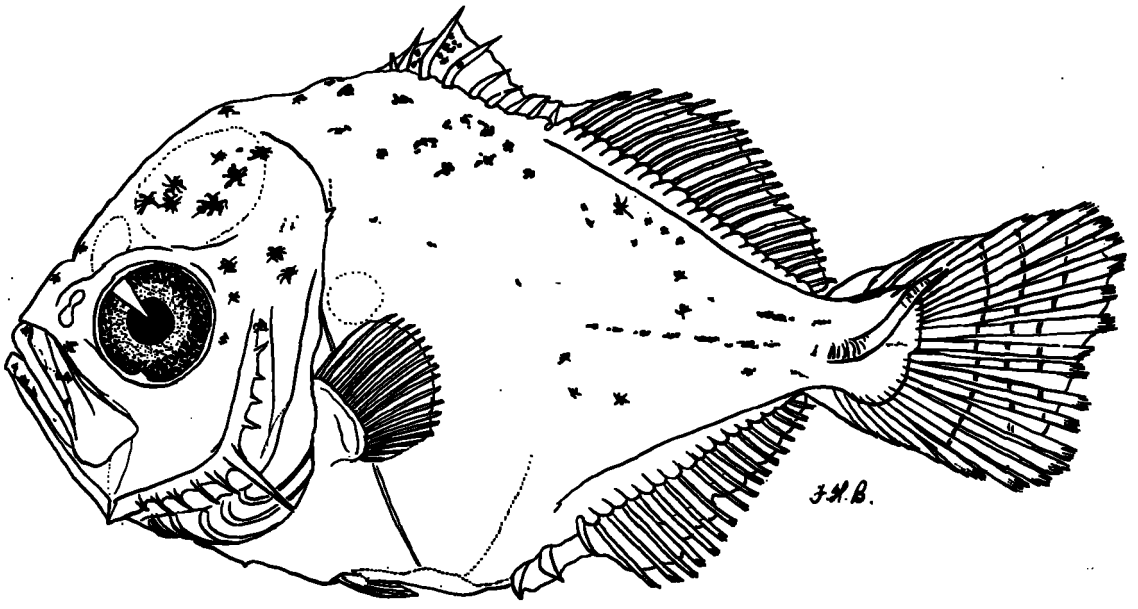

FIGURE 66.—*Caranx* sp. (*latus* or *hippos*) larva, 6.2 mm. standard length (*Gill* 2, Reg. 6).

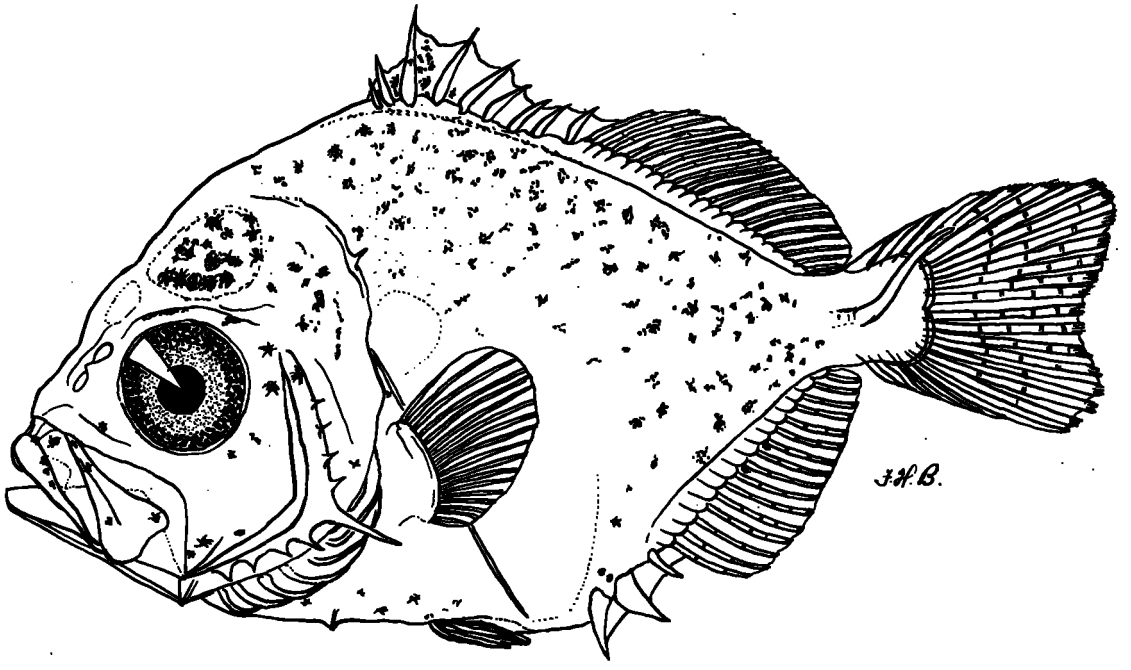

FIGURE 67.—*Caranx* sp. (*latus* or *hippos*) larva, 6.9 mm. standard length (*Gill* 2, Reg. 6).

at 6.9 mm. or below (figs. 65 to 67), but is divided at 8.3 mm. (fig. 68). The supraorbital crest has a serrated edge at 5.4 and 5.7 mm. (fig. 65), but not at 6.2 mm. or above (figs. 66 to 68). A single posterolaterally projecting spine is located on the cleithrum just below its junction with the operculum on all except the 8.3-mm. specimen (figs. 65 to 67). The coordinates of head length on standard length are plotted in figures 75 and 88.

Eye.—The coordinates of eye diameter on standard length are plotted in figures 76 and 89.

Snout.—The coordinates of snout length on standard length are plotted in figures 76 and 89.

Scutes.—Not developed by 8.3 mm. standard length.

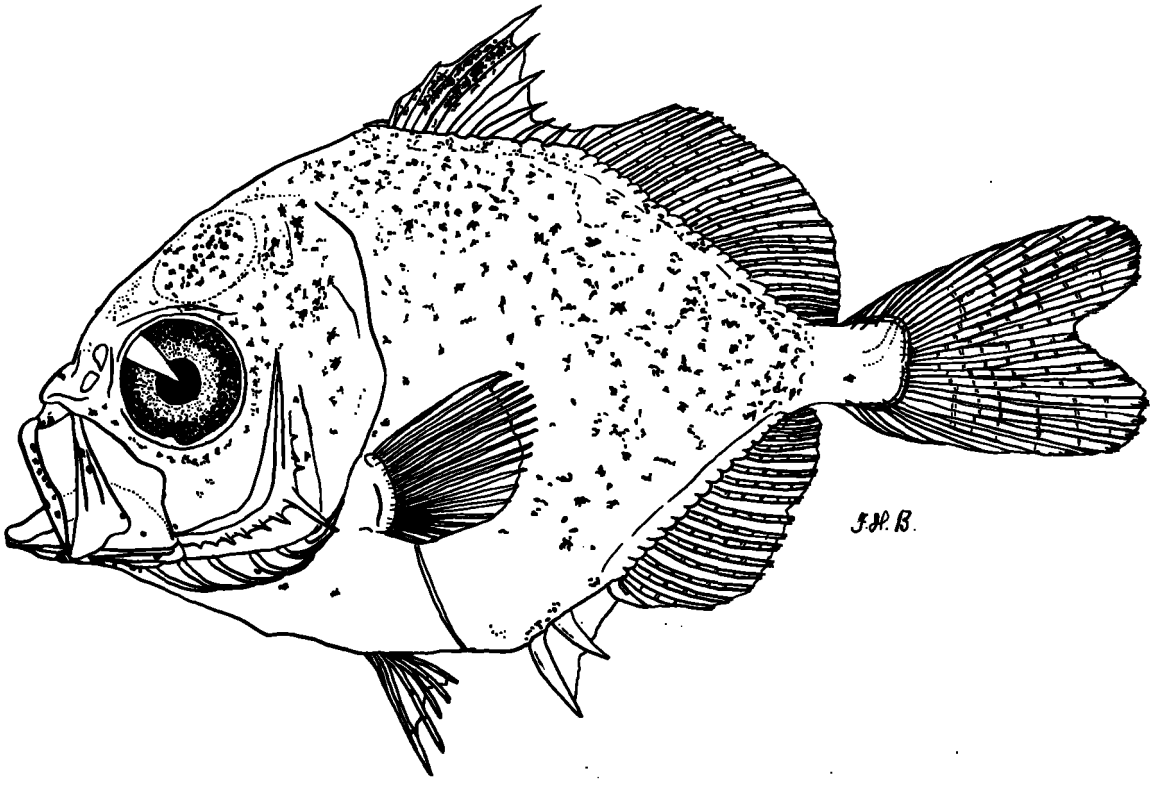

FIGURE 68.—*Caranx* sp. (*latus* or *hippos*) juvenile, 8.3 mm. standard length (*Gill* 3, Spc. 8).

Lateral line.—Not developed by 8.3 mm. standard length.

Preopercular spines.—Apparently the preopercular-angle spine begins to decrease in length at some size between 5.4 to 8.3 mm. (figs. 79 and 94). The preopercular upper-limb spines number 3 or 4, and the lower-limb spines range from 4 to 6 (table 1).

Pigmentation.—A row of elongated melanophores is present on the midline posteriorly of specimens 5.4 to 6.3 mm. (figs. 65 and 66), but this is absent at 6.9 and 8.3 mm. (figs. 67 and 68). The scattered body-pigment spots and larger melanophores on the transparent part of the brain case increase in number from 5.4 to 8.3 mm. (figs. 65 to 68).

A few pigment spots occur on the anal fin at its base on some specimens (figs. 65 and 67), not on others (figs. 66 and 68). Three pigment spots occur on the membranes of the anal spines at 5.4 mm. (fig. 65), but not at other lengths. The interspinous membrane of the first dorsal fin has a few melanophores at 5.4 mm. (fig. 65); these increase in number to 8.3 mm., and tend to become associated with the first 4 spines by 8.3 mm. (figs. 66 to 68).

Distribution off Southeastern Atlantic Coast of the United States

All specimens (table 15) were taken to the east of the 100-fathom line. One location of capture was directly north of the Bahamas; the other six were in association with the Gulf Stream (as depicted by the approximate axis of the Stream in figure 95).

Spawning

The spawning season, estimated from the size ranges of the few larvae taken within this area, extends at least from early February to early July (figs. 80 and 96). By comparison, the spawning of *latus* may terminate in July (fig. 80), but that of *hippos* apparently extends into September (fig. 96). Specimens of the two most northern locations of capture, 5.7 mm. and 6.3 mm., from off South Carolina, may have been spawned within this area (table 15).

TABLE 15.—Caranx *sp.* ("latus *and/or* hippos"): *Location and date of capture, number and size range of 9 specimens examined*

[See pp. 417 and 419 for explanation of abbreviations used; measurements in standard length]

Location	Date captured	Collection	Number of specimens	Size (mm.)
ATLANTIC OCEAN:				
34°53′ N., 75°04′ W	July 11, 1954	SAFI, *Gill* 7, Reg. 79	1	5.4
27°40′ N., 79°41′ W	Apr. 23, 1953	SAFI, *Gill* 2, Reg. 6	2	6.2–6.9
28°00′ N., 78°00′ W	July 18, 1953	SAFI, *Gill* 3, Spc. 8	2	5.7–8.3
28°20′ N., 79°48′ W	Apr. 24, 1953	SAFI, *Gill* 2, Reg. 9	1	6.2
31°00.2′ N., 79°38.3′ W	Apr. 27, 1953	SAFI, *Gill* 2, Reg. 30	1	6.1
32°35′ N., 77°46′ W	Aug. 7, 1953	SAFI, *Gill* 3, Reg. 52	1	6.3
33°08′ N., 77°20′ W	Mar. 3, 1953	SAFI, *Gill* 1, Reg. 60	1	5.7

Caranx latus Agassiz

(Figures 69–72)

Caranx latus Agassiz, *in* Spix and Agassiz, 1831, p. 105, pl. LVI b, fig. 1 (Brazil).

Caranx lepturus Agassiz, *in* Spix and Agassiz, 1831, p. 106, pl. LVI b, fig. 2 (Brazil).

Caranx fallax Cuvier, *in* Cuvier and Valenciennes, 1833, p. 95 (West Indies and Brazil).

Caranx richardi Holbrook, 1860, p. 96, pl. XIII, fig. 1 (near Charleston, S. C.).

Caranx hippos (*non* Linnaeus), Günther, 1860, p. 449 (in part; St. Vincent; Jamaica; Puerto Cabello; South America; West Indies; excluding records other than Atlantic).

Carangus fallax, Gill, 1863, p. 433 (Charleston, S. C.).

Carangus aureus Poey, 1875, p. 76 (Cuba).

Caranx sexfasciatus (*non* Quoy and Gaimard), Jordan, 1886b, p. 36 (Havana, Cuba).

Xurel lata, Jordan, Evermann, and Clark, 1930, p. 272 (tropical Atlantic to Virginia).

Caranx sexfasciatus latus Agassiz (*non* Quoy and Gaimard), Nichols, 1936, p. 119 ("more or less replaces *C. hippos* on off-shore islands of the Atlantic").

Caranx sexfasciatus fallax Cuvier (*non* Quoy and Gaimard), Nichols, 1938a, p. 2 (Bermuda; West Indies; Florida and northward;? Atlantic coast of Panama).

Nomenclature

A geographic distinction based on usage should be applied to *Caranx latus* of the Western Atlantic and the closely related, if not identical, *C. sexfasciatus* Quoy and Gaimard of the Indo-Pacific until significant comparisons of the two populations have been made.

Earlier authors (Jordan and Gilbert, 1883: 200; Jordan 1887: 531; Jordan and Evermann, 1896: 923; and others) considered the name *C. sexfasciatus* to be unidentifiable and referred to both populations as *C. latus*. Jordan and Evermann (1903: 337) and Jordan and Seale (1906: 231) later used *C. sexfasciatus* to refer to the Pacific forms. The practice then evolved to use the geographic distinction stated here. Nichols (1938a) incorporated these two forms into a circumtropical species divisible into five subspecies of *C. sexfasciatus*; but, because he used a relatively small number of specimens and his criteria of separation were not too convincing, his treatment has not been generally accepted.

Material

Measurements and counts were taken on a series of 57 specimens from 16.1 to 172 mm. standard length, and meristic values were recorded for an additional 31 specimens within this size range. The 106 specimens identified are shown in table 19.

Nichols (1939: 6) described two specimens of *latus* (under the name *C. sexfasciatus fallax* Cuvier) of 12 and 15 mm., from *Atlantis* station 1934, 36°48′ N., 68°55′ W. to 38°59′ N., 69°46′ W., August 27 to 28. I examined two specimens from the Bingham Collection which are similarly cataloged and may be the ones examined by Nichols, but they are so badly damaged that identification of them as *latus* is tentative. The smaller specimen measures between 12.7 and 13.0 mm., the larger about 16.4 mm. Measurements of body parts of these specimens that were not too distorted are included on the graphs.

Three specimens of *latus* from Bermuda were apparently misidentified as *hippos* by Barbour (1905: 119). This negates one of the two records of *hippos* from Bermuda that I have found. Barbour described as *hippos* a specimen taken on hook-and-line and two specimens of MCZ 28989. The collection number given for the last two seems to be incorrect—the jar of specimens, 37 mm. and 57.5 mm. in length, is numbered MCZ 28979. A third fish, MCZ 32076, 77 mm. long, is labeled *hippos* from Bermuda of the Barbour Collection, and may be the specimen described as taken on hook-and-line. These three specimens are *latus*. They have completely scaled chests. The mean numbers of scutes for the fish measuring 37 mm., 57.5 mm., and 77 mm. respectively are 32.5, 35.5, 32.5; the mean lateral-

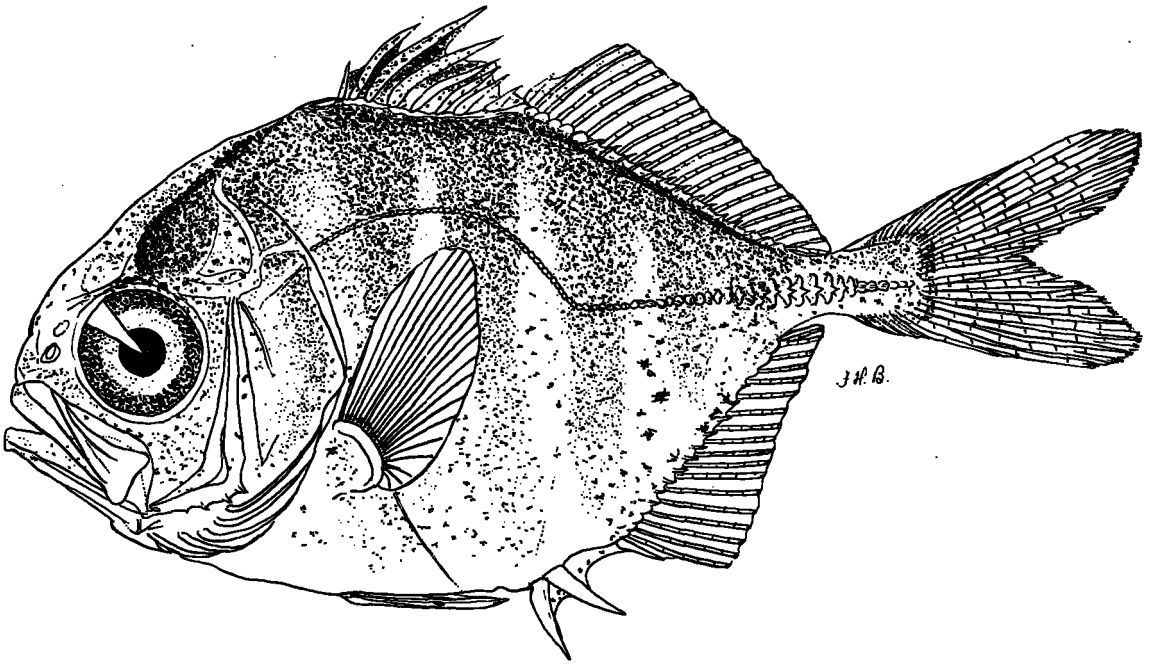

FIGURE 69.—*Caranx latus* juvenile, 16.1 mm. standard length (UF 4291).

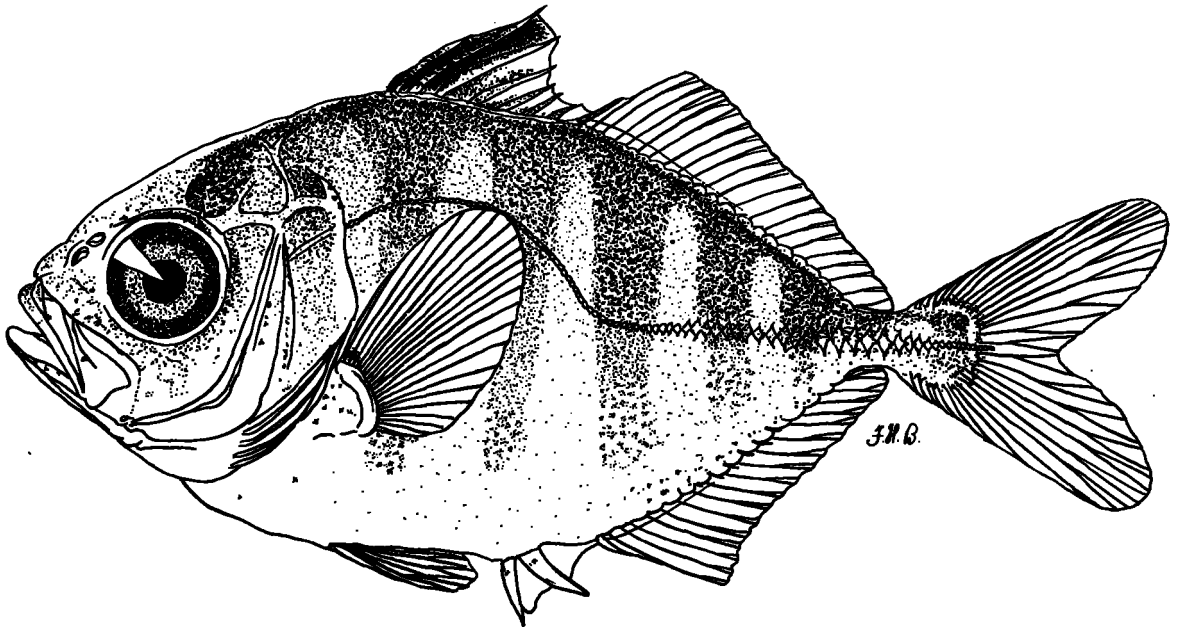

FIGURE 70.—*Caranx latus* juvenile, 21.8 mm. standard length (*Gill* 8, Reg. 29 to 30).

line ratios are 1.75, 1.80, 1.68. Of these two characters, the only value that overlaps the predicted range of *hippos* is the mean number of scutes on the 77-mm. specimen.

A 17.4-mm. specimen of *bartholomaei*, ANSP 72689, from northwest of Cay Sal Bank, which Fowler (1950: 90) identified as *latus*, is discussed under *bartholomaei*, page 472.

Characters

Dorsal spines.—VIII and I. The third spine is the longest at all sizes. An interspinous membrane connects the first and second dorsal fins

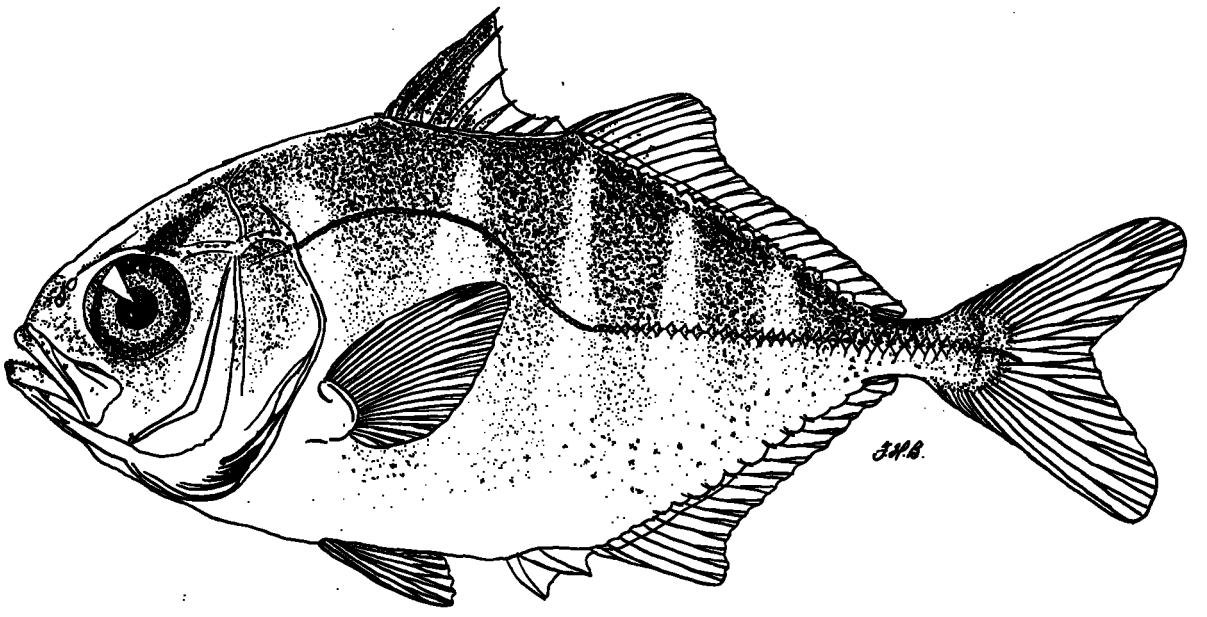

FIGURE 71.—*Caranx latus* juvenile, 31.9 mm. standard length (*Gill* 8, Settlement Point, Bahamas).

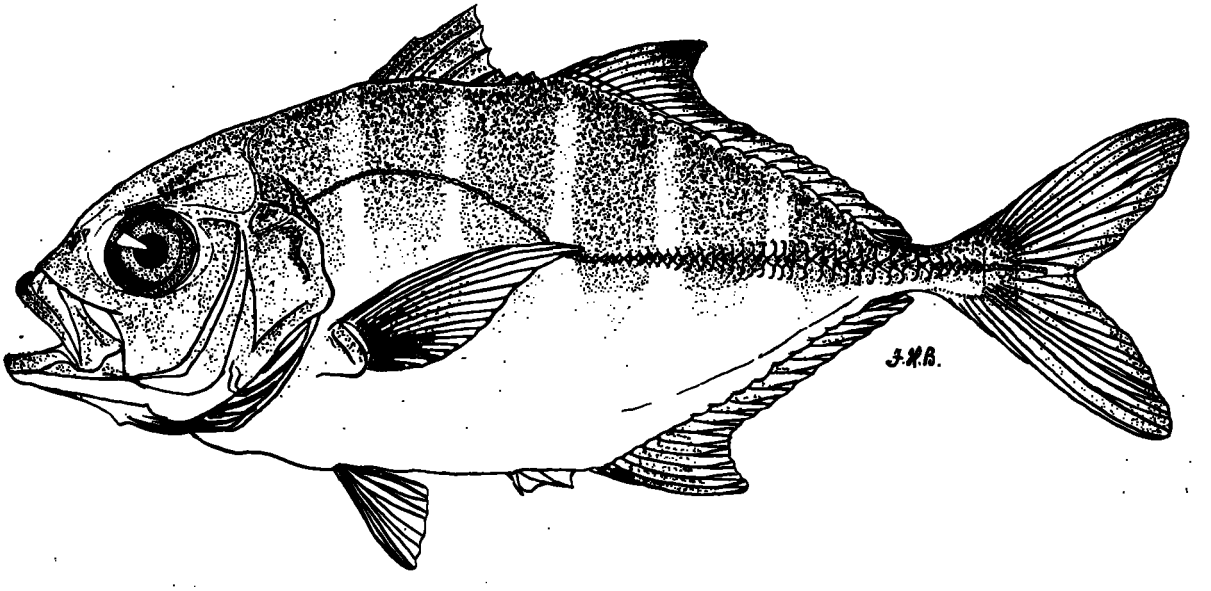

FIGURE 72.—*Caranx latus* juvenile, 83.5 mm. standard length (UF 3021).

(eighth and ninth spines) to about 75 mm. standard length.

The regression of length of the third dorsal spine on standard length is shown in figure 73 and table 16. A line fitted to this regression for specimens from 16.1 to 113 mm. standard length indicates that a proportional rate of increase of the two variates is maintained from about 22 to 113 mm. (0.105-mm. increase in spine length per 1.0-mm. increase in standard length). The alinement of the coordinates for the four specimens of *latus* smaller than 20 mm. and for specimens in the "*latus* and/or *hippos*" series suggests that a faster spine growth rate prevails below approximately 20 mm. The coordinates of the two specimens larger than 113 mm. fall above the extension of the calculated regression line, indicating an increase in spine growth rate at some size around 113 mm. standard length.

Anal spines.—II and I. The second spine is

TABLE 16.—Caranx latus: *Statistics describing regressions of body parts on standard length*

$\bar{x}$=mean of independent variable x
$\bar{y}$=mean of dependent variable y
N=number of specimens
b=rate of increase of y
a=y-intercept of regression line
$Sy{\cdot}x$=standard deviation from regression (standard error of estimate)

Independent variable x	Dependent variable y	Size range of specimens (mm.)	$\bar{x}$	$\bar{y}$	N	b	a	$Sy{\cdot}x$
Standard length	Dorsal-fin spine length (3d)	16.1–113	54.13	7.42	39	0.105	1.718	0.595
Do	Dorsal soft-ray length (1st)	31.9–119	63.76	10.02	35	.207	−3.172	1.210
Do	Pectoral length	16.1–42.5	33.34	7.40	17	.235	−.429	.475
Do	do	42.5–172	90.75	27.46	28	.377	−6.792	1.060
Do	Body depth	16.1–119	55.10	22.82	42	.364	2.793	.891
Do	Head length	16.1–94	50.53	17.04	39	.319	.937	.571
Do	Eye diameter	16.1–172	69.14	7.27	52	.091	1.012	.491
Do	Snout length	16.1–172	70.47	6.38	50	.092	−.106	.531

longer than the first at all sizes. An interspinous membrane connects the second and third spines to about 35 mm.

Dorsal soft-rays.—19 to 22 (table 17). At 16.1 mm. the posterior rays are beginning to branch (fig. 69). Extension of the anterior 5 or 6 soft-rays to produce the lobe has occurred by 31.9 mm. (fig. 71). The second ray averages the greatest length to about 34 mm. standard length; above 34 mm., the first ray is longest. The third dorsal spine averages longer than the first soft-ray to about 50 mm.; above 50 mm., the soft-ray is longer (fig. 73).

The regression of length of the first dorsal soft-ray on standard length is shown in figure 73 and table 16. A line fitted to this regression for specimens from 31.9 to 119 mm. standard length illustrates appreciable variation of coordinate values around the line, but indicates a proportional rate of increase for the two variates within this size range (0.21-mm. increase in soft-ray length per 1.0-mm. increase in standard length). Alinement of the coordinates of the three smallest specimens of *latus* and of the *"latus* and/or *hippos"* specimens suggests that a slower soft-ray growth rate prevails below approximately 30 mm. The coordinates of the specimens larger than 119 mm. fall above the extension of the calculated regression line, indicating an increase in soft-ray growth rate above that size.

TABLE 17.—Caranx latus: *Correlation of the numbers of dorsal and anal soft-rays of 88 specimens*

[The upper number in each block is the count obtained for that combination, and the number in parentheses below is the approximate percentage of that count in the total sample]

ANAL SOFT-RAYS	DORSAL SOFT-RAYS 19	20	21	22
16		7 (8.0)		
17	1 (1.1)	12 (13.6)	58 (65.9)	1 (1.1)
18			5 (5.7)	4 (4.6)

Anal soft-rays.—16 to 18 (table 17). Only the terminal ray is branched at 16.1 mm. standard length (fig. 69). Lobation occurs as with the dorsal fin. The second soft-ray is longest to 21.8 mm. standard length; the first and second rays are equal and the longest at 34.4 mm.; and the first ray is longest at 36.5 mm. and above. The longest anal ray is shorter than the longest dorsal ray at 16.1 mm. and above 34 mm.; and they are nearly equal in length from 21.8 to 34.1 mm. The second anal spine is about two-thirds as long as the longest anal soft-ray at 16.1 mm., only about one-half as long at 40 mm., and about one-fourth as long at 141 mm.

Interneural and interhemal spines.—The posterior lateral projections of these spines are well developed and extend above the body surface along the bases of the second dorsal and the anal fins at 16.1 mm. standard length (fig. 69). They remain externally discernible to 156 mm., but are much less prominent than at smaller sizes. At 172 mm., these projections along the dorsal fin base are covered by the fleshy sheath that covers the bases of the soft-rays, but approximately 6 of the projections of the interhemal spines along the anal fin base remain externally exposed.

Caudal.—9 + 8 principal rays; about 8 or 9 + 8 secondary rays. Branching has occurred at 16.1 mm. (fig. 69).

Pectoral.—I–18 to 20. The full complement of rays is formed by 16.1 mm. standard length (fig. 69). The distal end of the fin is rounded to about 32 mm. standard length, after which it becomes pointed and falcation begins (figs. 69 to 71). Fal-

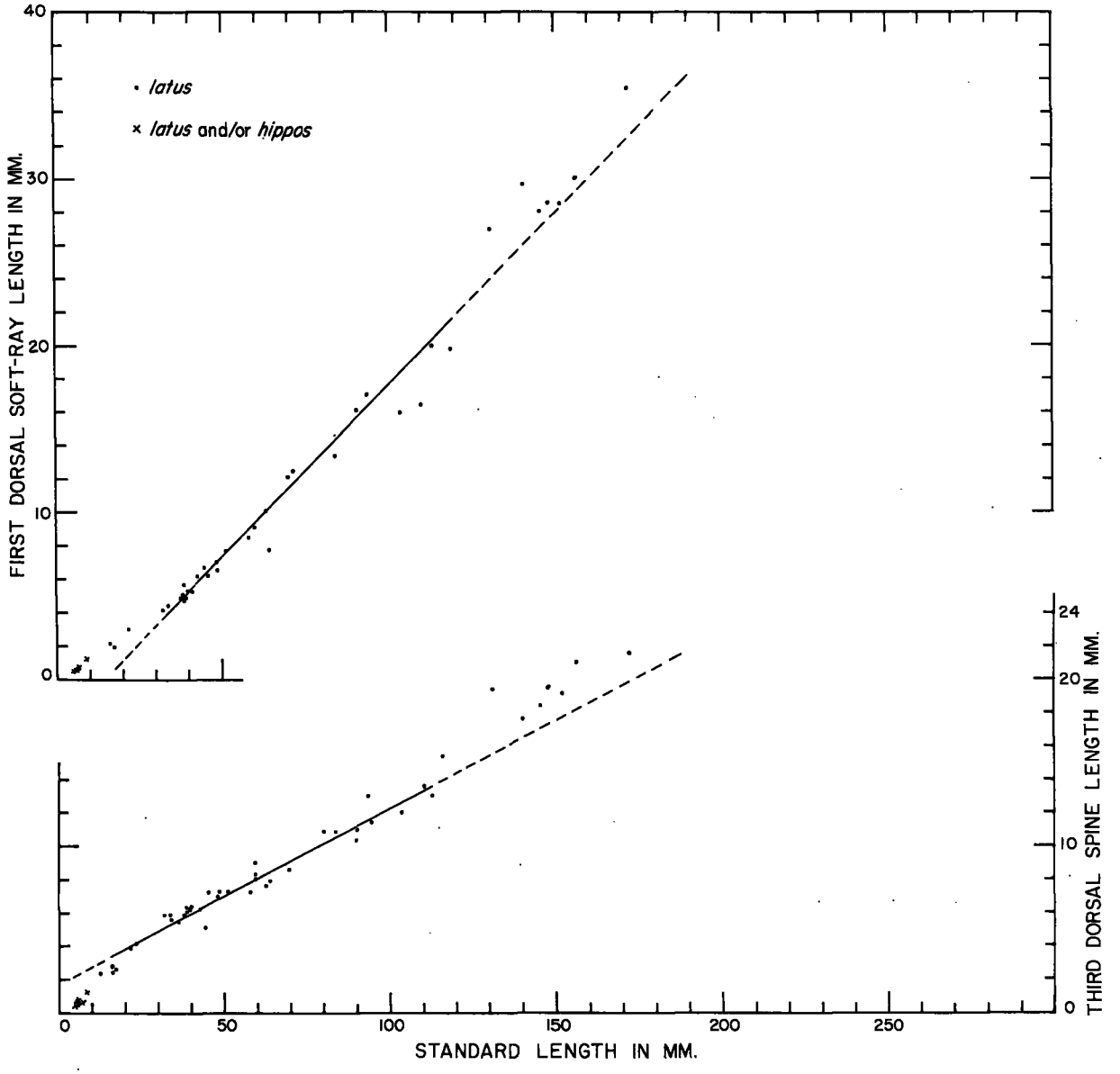

FIGURE 73.—*Caranx latus* and *Caranx* sp. (*"latus* and/or *hippos"*): Relation of length of first dorsal soft-ray and of third dorsal spine to standard length.

cation is pronounced at about 65 mm. and larger (fig. 72).

The regression of pectoral length on standard length is shown in figure 74 and table 16. Two lines were fitted to this regression: for specimens from 16.1 to 42.5 mm. and from 42.5 to 172 mm. standard length. The lines intersect at approximately 43 mm., indicating that an inflection occurs at about that size and that a faster pectoral growth rate prevails above that size. The proportional rates of increase for the two variates are 0.24-mm. (less than 43 mm.) and 0.38-mm. (more than 43 mm.) increase in pectoral length per 1.0-mm. increase in standard length.

Pelvic.—I–5. The rays are branched and segmented at 16.1 mm. standard length.

Body depth.—The depth at first anal spine averages less than the depth at pelvic from 16.1 to about 30 mm., is nearly equal from about 30 to 50 mm., and averages greater above 50 mm. The coordinates for depth at pelvic on standard length of specimens 30 mm. and smaller are plotted in figure 8.

The regression of body depth at pelvic on

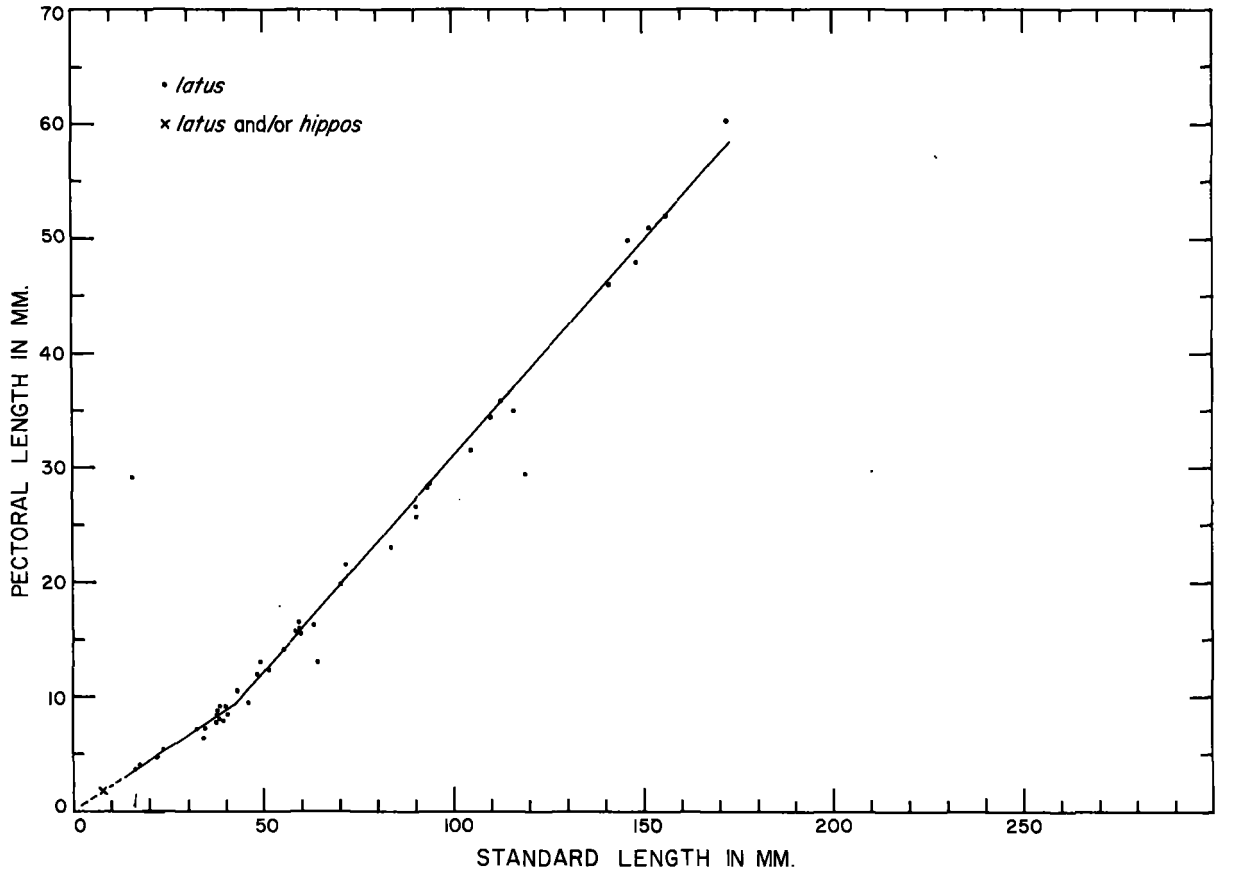

FIGURE 74.—*Caranx latus* and *Caranx* sp. (*"latus* and/or *hippos"*): Relation of pectoral length to standard length.

standard length is shown in figure 75 and table 16. A line fitted to this regression for specimens from 16.1 to 119 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.36-mm. increase in body depth per 1.0-mm. increase in standard length). The alinement of the coordinate at about 12.7 mm. with the coordinates of the *"latus* and/or *hippos"* specimens indicates that a faster body-depth growth rate occurs below approximately 16 mm. The position of the coordinates of the specimens larger than 119 mm. with respect to the extension of the calculated regression line, suggests that the body-depth growth may continue at the same proportional rate.

Head.—The regression of head length on standard length is shown in figure 75 and table 16. A line fitted to this regression for specimens from 16.1 to 94.0 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.32-mm. increase in head length per 1.0-mm. increase in standard length). The coordinates of specimens larger than 94 mm. fall along the extension of the calculated regression line, indicating that head growth may continue at the same proportional rate.

Eye.—The regression of eye diameter on standard length is shown in figure 76 and table 16. A line fitted to this regression for specimens from 16.1 to 172 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.09-mm. increase in eye diameter per 1.0-mm. increase in standard length). The position of the coordinates of the *"latus* and/or *hippos"* specimens suggests that a faster eye growth prevails below 15 or 20 mm.

Snout.—The regression of snout length on standard length is shown in figure 76 and table 16. A line fitted to this regression for specimens from 16.1 to 172 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.09-mm. increase in snout length per 1.0-mm. increase in standard length).

Gill rakers.—Lower limb, 16 to 18; upper limb, 6 or 7; total, 22 to 25 (table 18). Of the specimens examined above 20 mm., about 90 percent had from 1 to 3 rudimentary gill rakers at the origin of the lower limb (modally, 1 below 80 mm. and 2 above 80 mm.). All specimens of more than 60 mm. had these lower-limb rudiments. About 80 percent had from 2 to 5 rudimentary gill rakers at the origin of the upper limb (modally, 3 below 80 mm. and 3 to 5 above 80 mm.). All specimens above 45 mm. had these rudiments. Ginsburg (1952: 92) reported the upper 3 or 4 gill rakers on the upper limb to be short or tuberclelike in larger specimens (to about 366 mm., converted), and 1 or 2 tubercles in front on the lower limb. This indicates that gill rakers at the origins of both limbs become shorter or rudimentary with growth of the fish.

Scutes.—Range of the mean number of scutes above 100 mm. standard length: about 32 to 39 (fig. 77). Ginsburg (1952: 92), working with specimens from about 53 to 366 mm. (converted), found a scute range of 30 to 42. Nichols (1939: 4) gave an average number of scutes for his

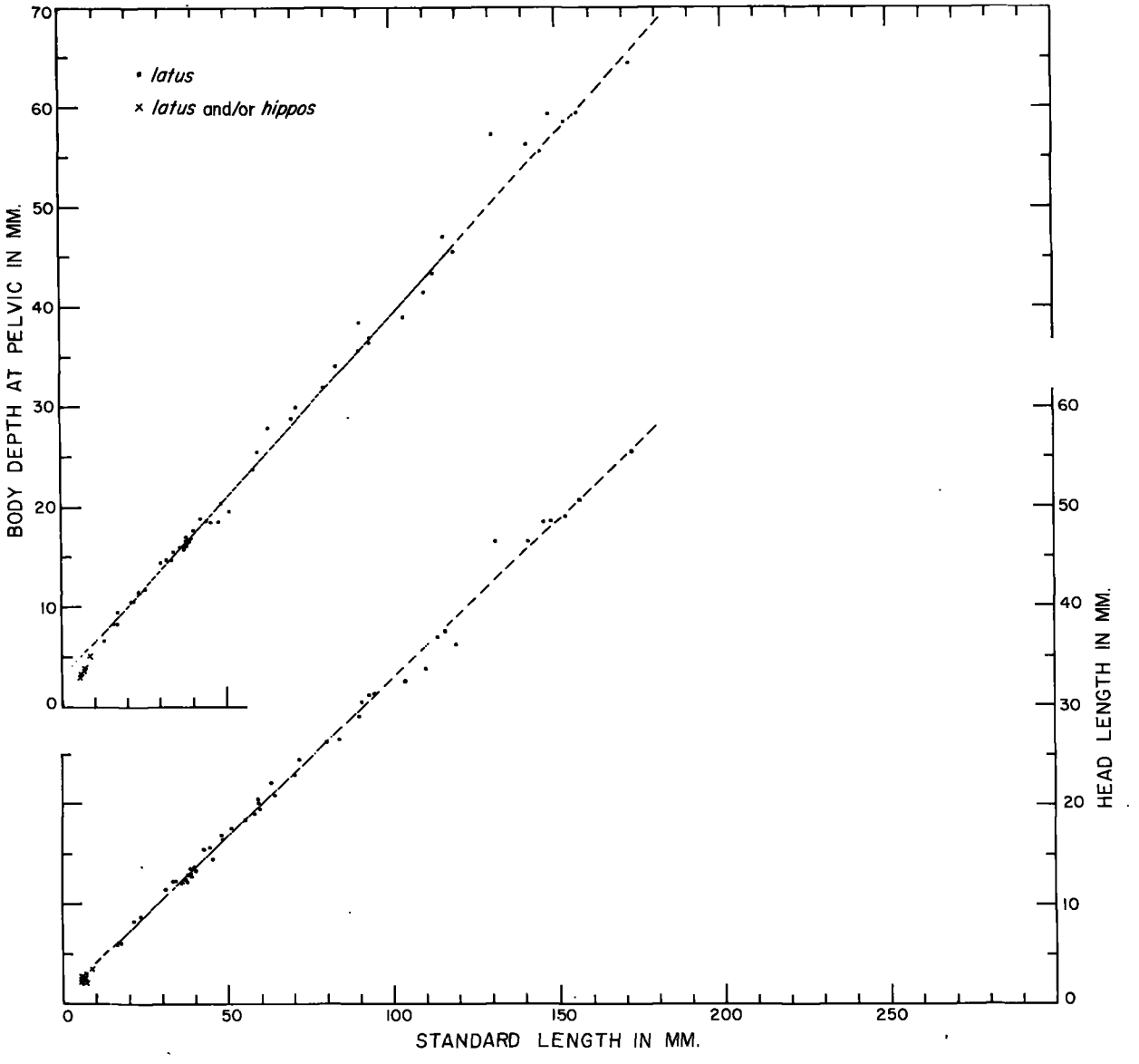

FIGURE 75.—*Caranx latus* and *Caranx* sp. ("*latus* and/or *hippos*"): Relation of body depth at pelvic and of head length to standard length.

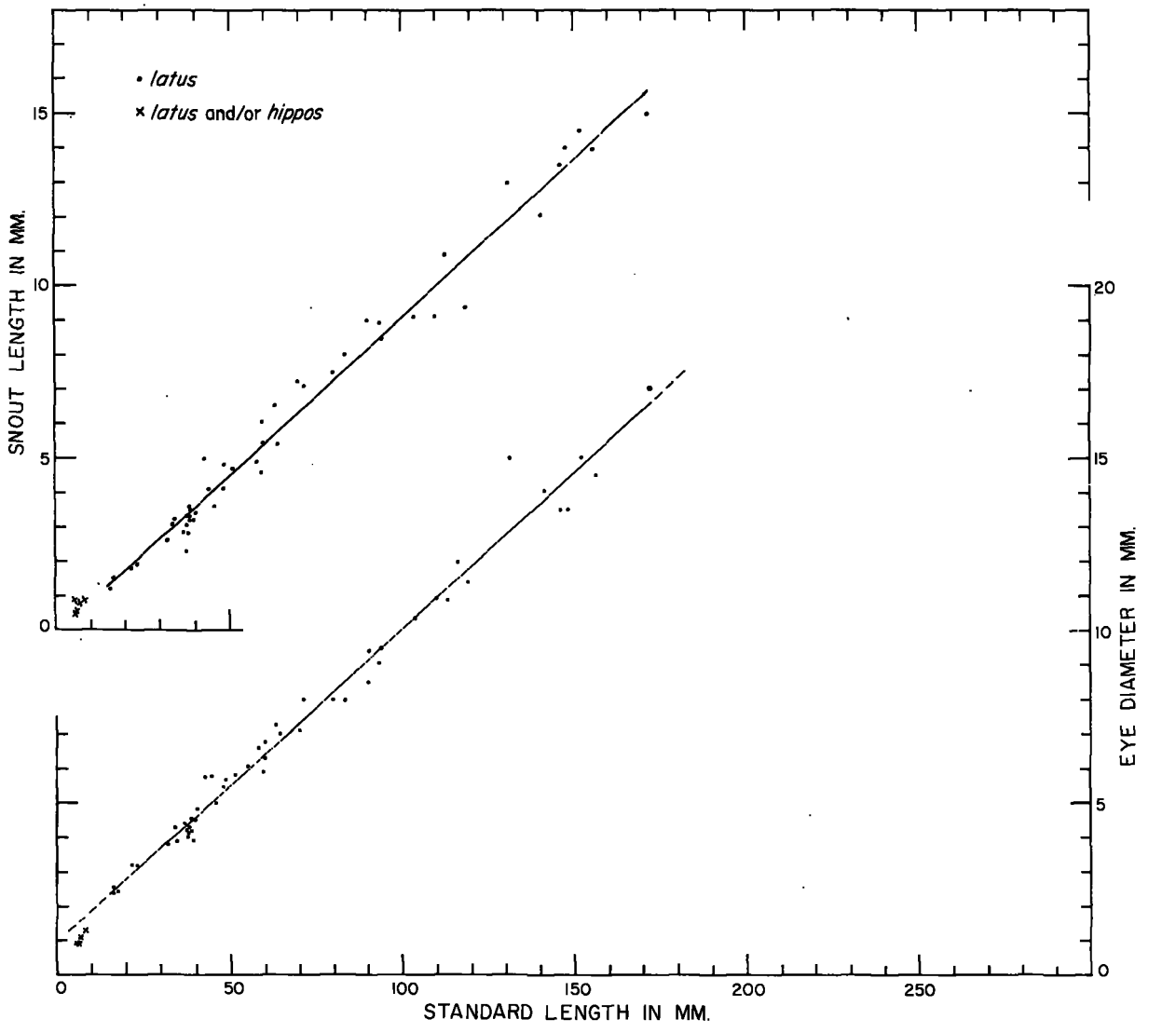

FIGURE 76.—*Caranx latus* and *Caranx* sp. (*"latus* and/or *hippos"*): Relation of snout length and of eye diameter to standard length.

TABLE 18.—Caranx latus: *Correlation of the numbers of lower-limb to upper-limb gill rakers of 78 specimens*

[The upper number of each block is the count obtained for that combination, and the number in parentheses below is the approximate percentage of that count in the total sample]

UPPER-LIMB GILL RAKERS	LOWER-LIMB GILL RAKERS 16	17	18
6	3 (3.8)	17 (21.8)	6 (7.7)
7	5 (6.4)	39 (50.0)	8 (10.3)

synonymous *C. s. fallax* as 32.6, which is within my established perimeter, but is much lower than would be expected for an average. Some of the scutes along the central part of the straight lateral line have completed their development by 16.1 mm.

Lateral line.—Range of mean lateral-line ratio above 60 mm. standard length: about 1.45 to 2.0 (fig. 78). Nichols (1939: 7) gave ratios of 1.35 and 1.4 for his specimens of 12 mm. and 15 mm., which conform to my estimated perimeter.

Preopercular spines.—Preopercular spines were present on the specimen of about 13 mm. standard length, and at 16.1 mm. and 17.1 mm. They were

absent on the specimen of about 16.4 mm. and at 20 mm. and above. Apparently, these spines are absorbed by the preopercular expansion between about 16 mm. and 20 mm. The lengths of the angle spine associate with the probable trend of decrease in spine length of the "*latus* and/or *hippos*" group (fig. 79). One preopercular upper-limb spine was present on the specimen of about 13 mm.; none at 16.1 or 17.1. Five lower-limb spines were present at 13 mm. and 17.1 mm. and 4 at 16.1 mm. (table 1).

Pigmentation.—The juvenile complement of five body bars is present at 16.1 mm. The pigmentation of the posterior three bars extends to the base of the anal fin. There is a heavily pigmented area on the brain case above the eye, and less-deeply pigmented areas on the upper portion of the operculum and the fleshy part of the tail. The first dorsal fin, the pelvic fins, and the interspinous membranes of the anal fin have pigment spots. The other fins are unpigmented (fig. 69).

The two damaged BOC specimens have vague and physically distorted bars. Other specimens from 16.1 to 90.5 mm. standard length have five bars, with the exception of a few whose pigment had faded out. Pigment of four specimens of 104 to 118 mm. had obviously faded after preservation. Specimens of 116 mm. and 131 mm. and larger appear to lack bars from growth changes rather than from fading. Apparently, the bars disappear between 90 and 116 mm. The pigmentation of the posterior three bars is not pronounced below the lateral line on the 16.1-mm. specimen, and on most specimens 20 mm. and larger the pigmentation of the last three bars terminates a short distance below the lateral line. At 26 mm. and above the body bars are wider than the interspaces (figs. 71 and 72). On a 34.1-mm. specimen, apparently normal in other

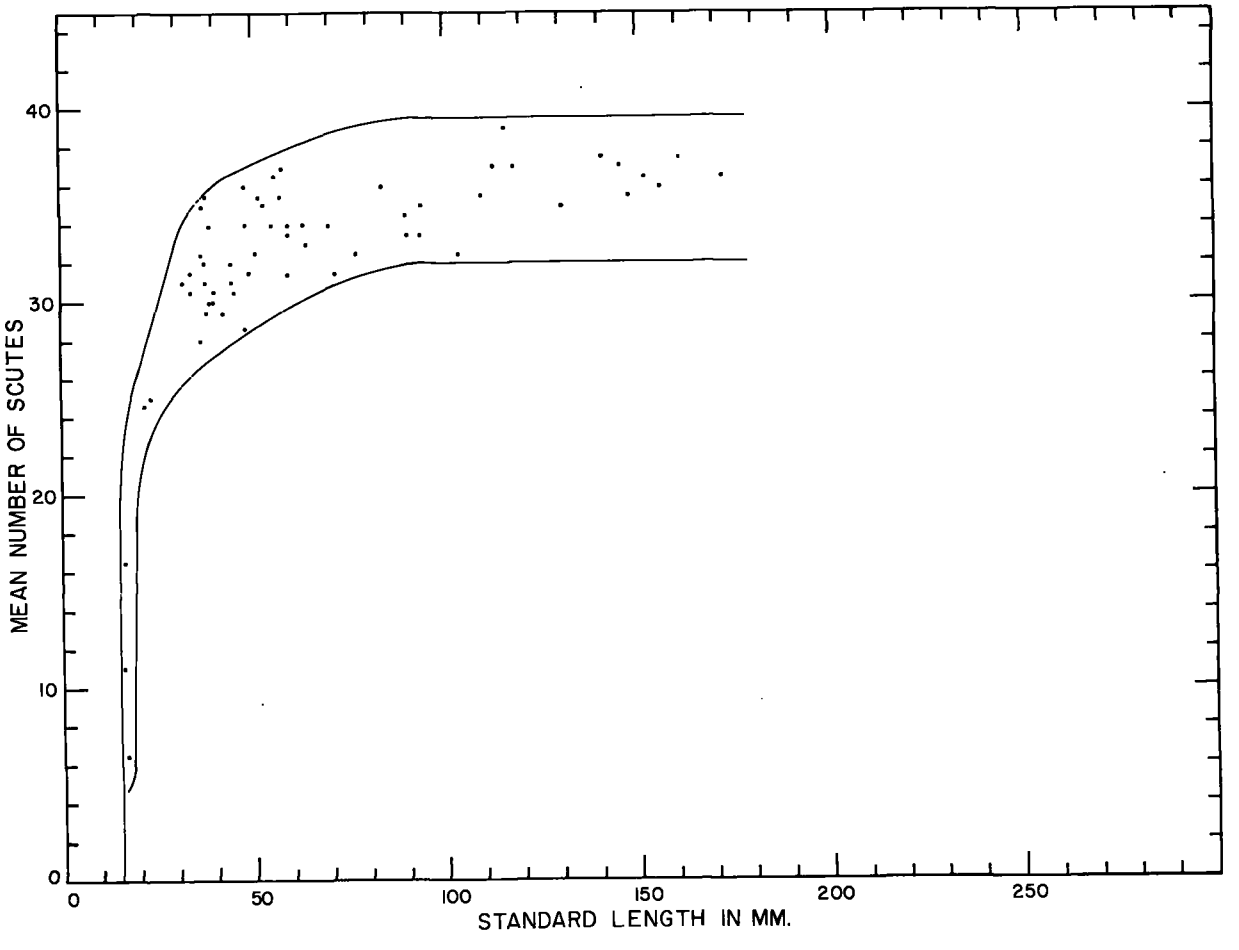

FIGURE 77.—*Caranx latus:* Relation of the mean number of scutes to standard length.

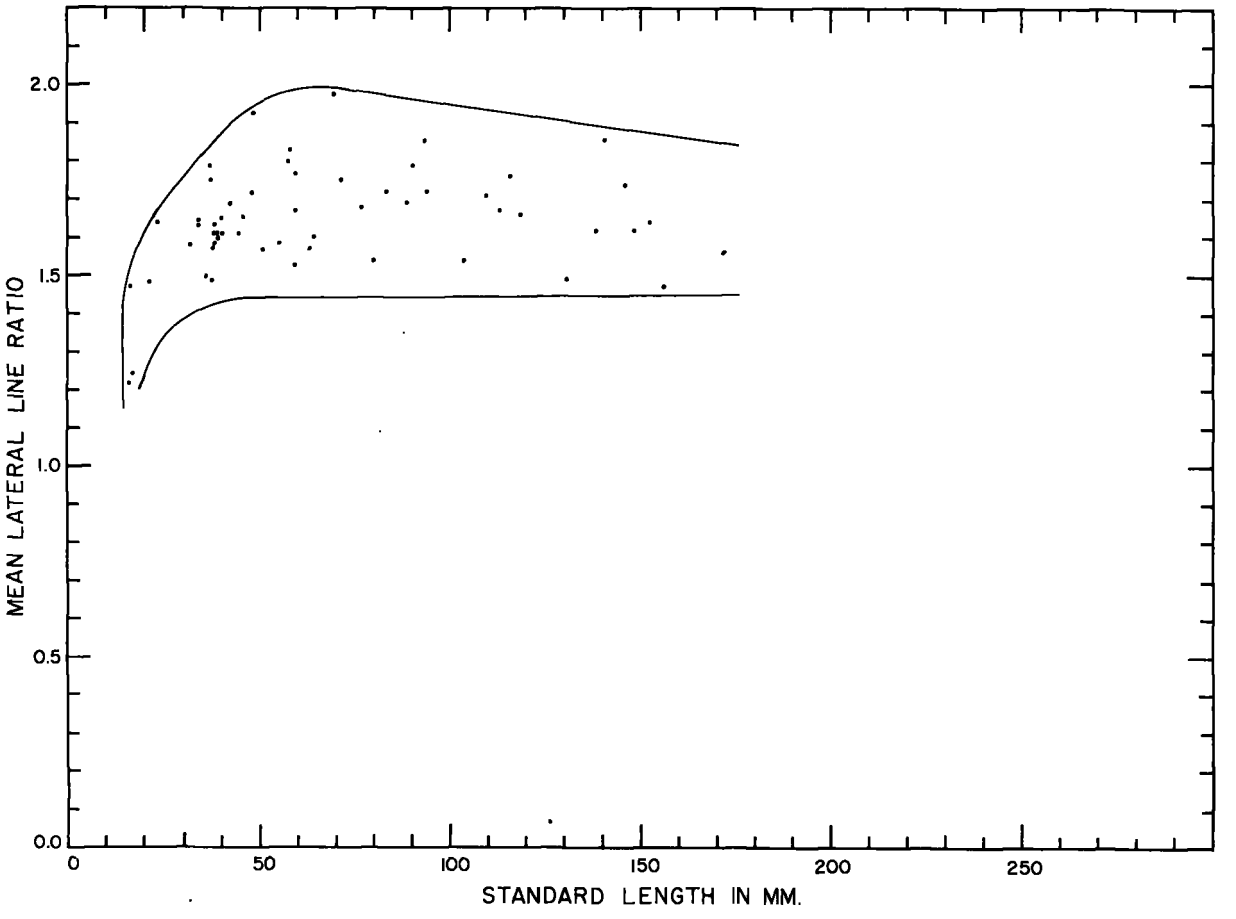

FIGURE 78.—*Caranx latus:* Relation of the mean lateral-line ratio to standard length.

respects, the fourth and fifth bars on the left side converged ventrally to unite at the lateral line and continue as a single bar for a short distance below the lateral line.

At 21.8 mm., pigmentation on the first dorsal fin is more intense than at 16.1 mm. and is largely restricted to the membranes connecting the second, third, and fourth spines (fig. 70). By 80 mm. it has spread over the fin (fig. 72). The anal spines and their membranes and the pelvic fins are unpigmented at 31.9 mm. and above. The second dorsal and the caudal fins have pigmentation at their bases at 31.9 mm. and the anal at a slightly larger size, although it is not as prominent on the anal or caudal fins as on the dorsal. Pigmentation intensifies and migrates to the edge of the dorsal fin by 40 to 60 mm. (fig. 72), and becomes concentrated on the distal half of the dorsal lobe.

Distribution off Southeastern Atlantic Coast of the United States

Specimens have been reported from the following specific localities within this area: The northern Bahamas by Lee (1889: 670), Bean (1905: 302), Breder (1934: 70; 1951: 170), Nichols (1937c: 3; 1938a: 2), Fowler (1944: 443), and Ginsburg (1952: 92); Palm Beach, Fla., by Fowler (1915: 248); Charleston, S. C., by Gill (1863: 433); Folly Island, S. C., by Nichols (1937c: 3) and Fowler (1945: 191); Perry Island, Bird Shoal, and Beaufort, N. C., by Smith (1907: 206); Beaufort, N. C., by Ginsburg (1952: 92); and near Cape Hatteras by Bean (1905: 302).

Figure 95 shows the locations for specimens taken on the *Gill* cruises, a USNM specimen examined (Cape Lookout, N. C.), the ChM specimen examined (Folly Island, S. C.), a specimen examined from Bears Bluff Laboratory

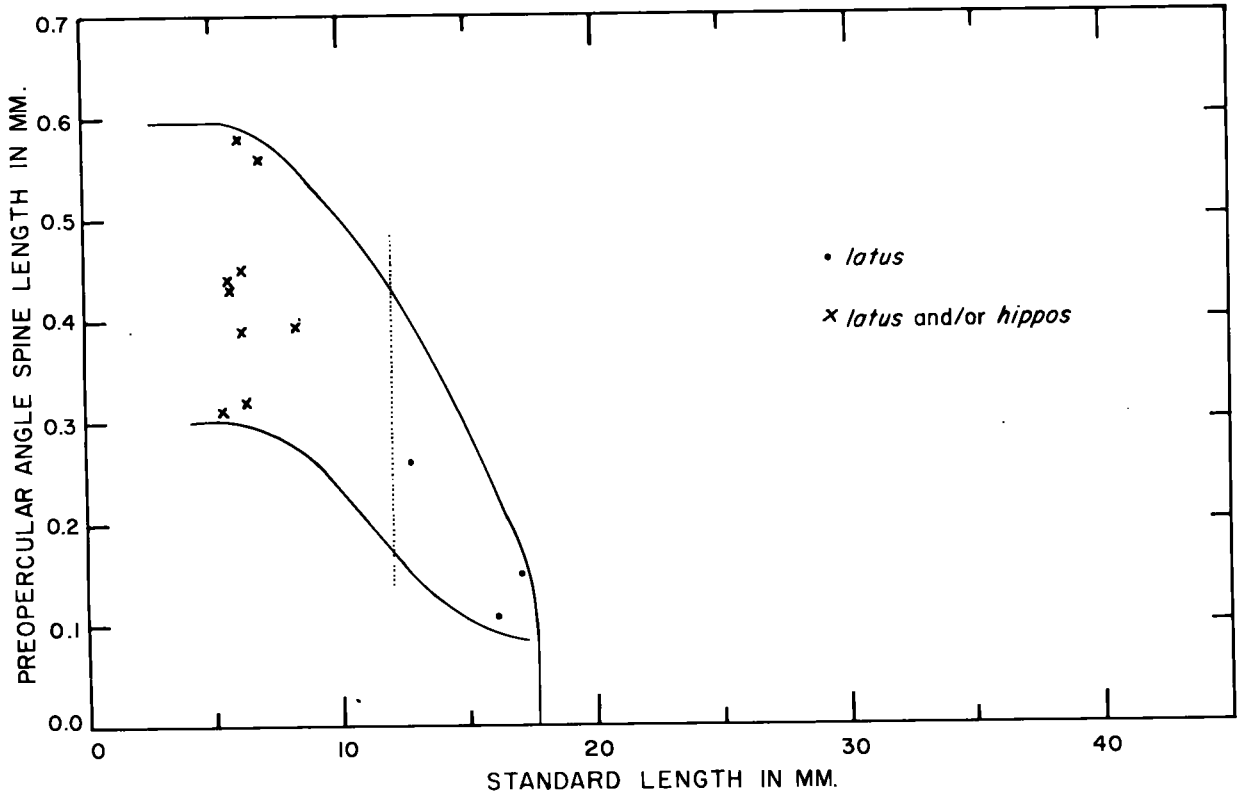

FIGURE 79.—*Caranx latus* and *Caranx* sp. ("*latus* and/or *hippos*"): Relation of length of preopercular-angle spine to standard length. Dotted line separates the two forms.

(North Edisto River, S. C.), specimens taken by SAFI (St. Simons Island and Turtle River, Ga.), UF specimens examined (St. Augustine Inlet, Vilano Beach, and St. Lucie Inlet, Fla.), and a CBSFP specimen examined (Hog Island, Bahamas) (tables 2 and 19). The specimens recorded on this chart are all juveniles. If any of the "*latus* and/or *hippos*" larval specimens recorded on figure 95 are this species, then the period of larval development of *latus* probably takes place offshore and, in this area, in association with the Gulf Stream. The 17.1-mm. juvenile *latus* taken at the 100-fathom line off Cape Lookout, N. C., contributes to this theory. The 16.1-mm. specimen from St. Lucie Inlet, Fla., distracts from it; but in that area the Gulf Stream is moving close to the coast, and this specimen could have been carried inshore by the current. The small juveniles reported by Nichols (1939: 6) from about 37°N., 69°W., were more than 300 miles offshore in the Gulf Stream. The several records of juvenile *latus* above 20 mm. standard length for the northern Bahamas and Atlantic coast of the United States, and the scarcity of records of capture of juveniles above this size in offshore waters, indicates that the species in this area adopts an inshore habitat at about 20 mm. or slightly larger. I have examined 11 juveniles 20 to 38 mm. taken by the *Oregon* in the Gulf of Mexico from 7 localities ranging from about 47 to 65 miles offshore, and there are several published records of larger juveniles and adults being taken inshore from the Gulf. Unless the habits and habitats differ greatly in the Gulf and in the Atlantic Ocean, the evidence indicates that the larvae and small juveniles are probably associated with offshore currents, and when about 16 to 20 mm. some, at least, migrate inshore.

The species occurs seasonally but not abundantly on the Atlantic coast of the United States. Presumably there is a migration southward or to warmer offshore waters during the colder months. Fowler (1905b: 258) listed the most northern inshore record for *latus* at Squan River, N. J. Dr. J. E. Böhlke stated in a personal communication that Dr. Fowler had said this specimen came from the mouth of the Manasquan River.

A possible brackish or even fresh-water affinity of this species may account for a juvenile inshore movement. Meek (1914: 121) recorded a specimen of about 139 mm. (converted) from "swift clear water at the foot of rapids." Breder (1934: 70) reported specimens 92 to 180 mm. from a fresh-water lake on Andros Island, Bahamas. Referring to the related if not identical Pacific form, *C. sexfasciatus*, Herre (1956: 1035) stated that it not only entered fresh water but remained there until it was a year or a year-and-a-half old.

Spawning

The spawning season that contributes young *latus* to this area may be estimated, from the smallest specimens taken in May (17.1 mm.) and September (21.8 mm.) to extend from about mid-March to mid-July (fig. 80). Erdman (1956: 320) noted *latus* in spawning condition during June in Puerto Rico.

If the "*latus* and/or *hippos*" specimens represent this species, in part or entirely, a limited spawning may occur in the Atlantic off the southeastern United States; but the major spawning areas for *latus* would be to the south of this area. If the larval existence is in offshore currents, as suggested previously, then spawning probably occurs in this type of environment. Breder (1951: 170) described a peculiar pattern of activity attributed to spawning behavior of five *latus* (under the name of *C. sexfasciatus*) in captivity at Bimini, Bahamas, on June 8.

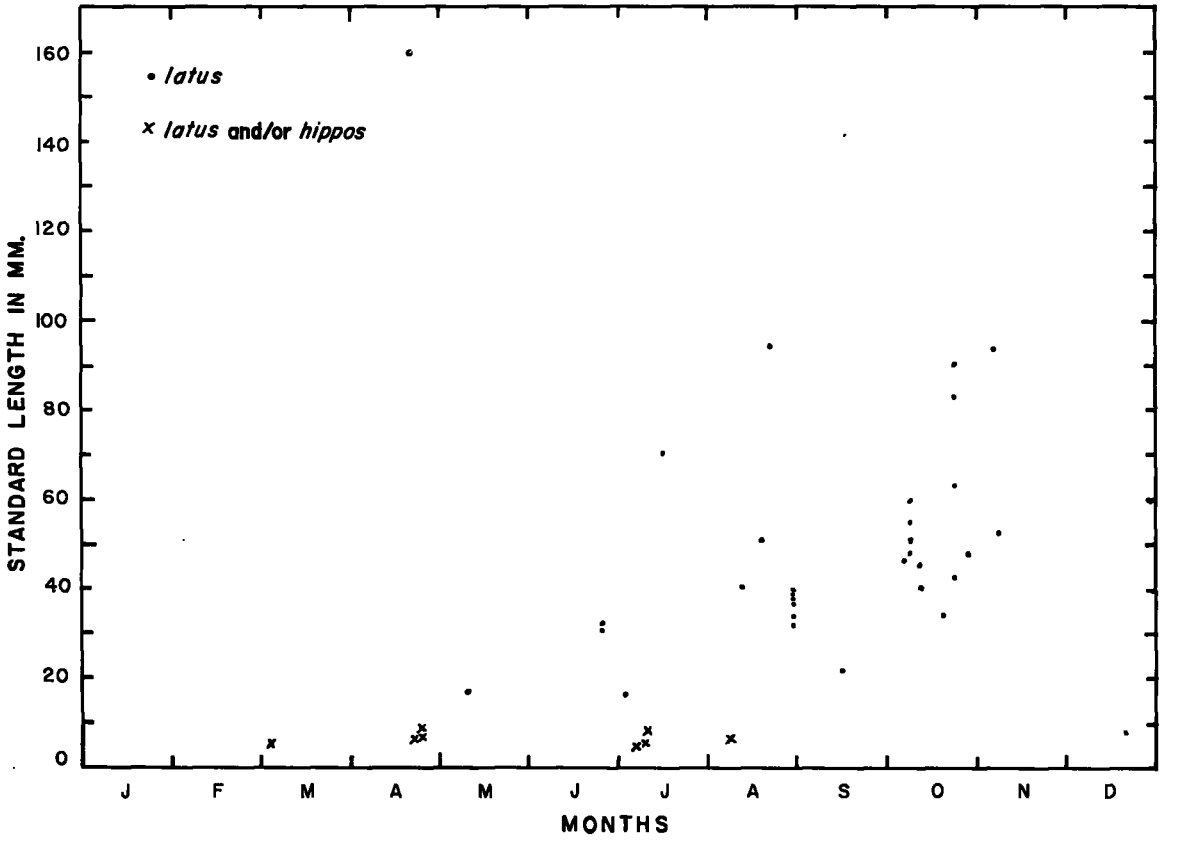

FIGURE 80.—*Caranx latus* and *Caranx* sp. ("*latus* and/or *hippos*"): Size distribution, by months, of specimens taken off the southeastern Atlantic coast of the United States.

TABLE 19.—Caranx latus: *Location and date of capture, number and size range of 106 specimens examined*

[See pp. 417 and 419, for explanation of abbreviations used; measurements in standard length]

Location	Date captured	Collection	Number of specimens	Size (mm.)
ATLANTIC OCEAN:				
Playa Baracoa, Cuba	Nov. 16, 1954	UF 5355	1	140
Spanish Wells, Bahamas	July 4, 1903	USNM 53108	1	38.1
Clarence Harbor, Bahamas	July 14, 1903	USNM 53107	1	64
24°04′ N., 79°15′ W	July 24, 1957	SAFI, *Combat* 448	2	25–30
Hog Island, Bahamas	Aug. 19, 1955	CBSFP Acct. No. 251	10	42.5–94
Do	Aug. 15, 1955	CBSFP Acct. No. 248	6	41.5–59
Rose Island, Bahamas	July 31, 1955	CBSFP Acct. No. 235	15	35–55
26°27′ N., 76°44′ W	June 13, 1954	SAFI, *Gill* 7, Std	1	40
26°54′ N., 79°07′ W	Aug. 29, 1954	SAFI, *Gill* 8, Settlement Point, Bahamas	5	31.9–39.6
St. Lucie Inlet, Martin County, Fla	July 2, 1954	UF 4291	1	16.1
Sebastian Inlet, Indian River, Fla	Nov. 7, 1956	MI	1	52
Vilano Beach, Fla	July 15, 1950	UF 3324	1	70
St. Augustine Inlet, Fla	Oct. 19, 1930	UF 2964	1	33.8
St. Augustine, Fla	Oct. 23, 1953	UF 3021	4	42.5–90.5
30°59′N., 79°14′W. to 30°59′N., 79°36.5′W	Sept. 15, 1954	SAFI, *Gill* 8, Reg. 29 to Reg. 30	1	21.8
Turtle River, Glynn County, Ga	Oct. 7, 1955	SAFI	4	48–59.5
St. Simons Island, Ga	Oct. 5, 1955	do	1	45.5
Do	May 2, 1957	do	1	41
Do	Oct. 11, 1957	do	1	45
Jekyll Island Causeway, Ga	do	do	1	40
North Edisto River, S. C	Nov. 4, 1954	BBL	1	93.5
Folly Island, S. C	Oct. 28, 1929	ChM 29.234.2	1	48.5
34°03.5′ N., 76°15′ W	May 9, 1953	SAFI, *Gill* 2, Reg. 71	1	17.1
Cape Lookout, N. C	Aug. 9, 1913	USNM 111779	1	38.3
Beaufort, N. C	July-Aug. 1904	USNM 51937	1	44.5
Do	Aug. 17, 1905	USNM 111777	1	58
36°48′ N., 68°55′ W	Aug. 27–28.	BOC (no number)	2	13–16.4
Woods Hole, Mass	1876	USNM 164529	1	36.5
Bermuda		USNM 164922	2	104–110
Do	Sept. 1862	MCZ 28979	2	37–57.5
Do	1904	MCZ 32076	1	77
GULF OF MEXICO:				
Havana fish market, Cuba	Jan. 7, 1956	SAFI	1	146
Tortugas, Fla		USNM 154694	1	118
Do		USNM 116859	5	38.8–113
One mi. off Garden Key, Tortugas, Fla	Aug. 1954	ANSP Acct. No. 215	1	55.5
Ponce Park, Fla	Nov. 24, 1908	USNM 62650, *Orian*	1	71.5
28°17′ N., 88°37′ W	Aug. 25, 1955	GFEGR, *Oregon* 1380	1	23.5
28°20′ N., 87°37′ W	July 21, 1956	UF 3925, *Oregon* 1585	1	31.5
28°45′ N., 88°03′ W	July 24, 1956	UF 3922, *Oregon* 1590	1	37
28°50′N., 87°58′ W	do	UF 3926, *Oregon* 1589	3	20–26
Do	do	UF 3923, *Oregon* 1591	1	22.5
Do	July 26, 1956	UF 3924, *Oregon* 1593	1	32.5
29°01′ N., 87°48′ W	Aug. 22, 1955	GFEGR, *Oregon* 1374	3	37.5–38.5
CARIBBEAN SEA:				
Tortuguero Lagoon and River, Costa Rica	Dec. 1, 1956	UF (uncataloged)	5	44.5–56
Bequia Is., Grenadines, B.W.I	Apr. 6–10, 1952	ANSP Acct. No. 165	1	49
Jamaica	Mar. 1–11, 1884	USNM 132225, *Albatross*	1	59.5
Palisadoes, Kingston, Jamaica	June 15, 1957	UF (uncataloged)	1	116
Kingston Harbor, Jamaica	June 25, 1957	do	2	148–156
Great Salt Pond, Jamaica	do	do	3	131–172

Caranx hippos (Linnaeus)

(Figures 81–85)

Scomber hippos Linnaeus, 1766, p. 494 (Charleston, S. C., vicinity).

Scomber carangus Bloch, 1787, pl. CCCXL (East and West Indies).

Caranx erythrurus Lacépède, 1802, p. 58 (key).

Caranx erithrurus Lacépède, 1802, p. 68 (South Carolina).

Caranx daubentonii Lacépède, 1802, p. 58 and 71 (Martinique).

Caranx carangua Lacépède, 1802, p. 59 and 74 (Martinique).

Tricopterus carangus, Rafinesque, 1810, p. 41.

Caranx carangus, Cuvier, *in* Cuvier and Valenciennes, 1833, p. 91 (Brasil; Cayenne; Porto-Rico; Havana; Martinique; Goree).

Caranx xanthopygus Cuvier, *in* Cuvier and Valenciennes, 1833, p. 109 (Isle de France).

Caranx ekala Cuvier, *in* Cuvier and Valenciennes, 1833, p. 117 (Malabar and Bombay).

Caranx antillarum Bennett, 1840, p. 282 (West Indies).

Caranx defensor DeKay, 1842, p. 120, pl. XXIV, fig. 72 (New York).

Caranx chrysos (*non* Mitchill), Baird, 1855, p. 336 (*fide* Bean, 1888, p. 139; Great Egg Harbor Bay, N. J., and Greenport, Long Island, N. Y.).

Carangus esculentus Girard, 1859, p. 23, pl. XI, figs. 1 to 3 (Brazos Santiago and mouth of Rio Grande, Texas).

Carangus hippos, Gill, 1862, p. 36.

Carangus chrysos (*non* Mitchill), Gill, 1863, p. 434 (eastern coast of United States).

Carangus carangus, Poey, 1866, p. 14 (Cuba) [Fowler (1936: 692) cites an earlier use of this name by "Griffith, 1834, The Class Pisces, *in* Cuvier Animal Kingdom, X p. 325."].

Carangus hyppos, Poey, 1868, p. 365 (Cuba).

Paratractus hippos, Abbott, 1868, p. 813.

Caranx caninus Günther, 1869, p. 432 (Pacific coast of Panama).
Carangus hippus, Jordan and Gilbert, 1879, p. 376 (Beaufort, N. C.).
Caranx hippus, Jordan and Gilbert, 1882a, p. 269 (Lake Borgne, La.).
Caranx hippos, Jordan and Gilbert, 1882b, p. 970 (key).
Caranx hippos hippos, Nichols, 1920c, p. 45 (Atlantic coast of United States; Gulf of California).
Caranx hippos tropicus Nichols, 1920c, p. 45 (Para, Brazil; ? Congo River, Africa).
Caranx hippos caninus, Nichols, 1937a, p. 58 (Gulf of California; Galapagos).

Nomenclature

Caranx hippos (Linnaeus) may be regarded as a circumtropical species until comparative studies of adequate samples of forms variously attributed to and inadequately separated from this species have been made with respect to worldwide distribution. Subspecific designations are as yet incomplete and uncertain and may be disregarded.

Many incomplete comparisons and opinions have been published in reference to this species. It is apparently a composite of the following nominal populations: *C. hippos hippos* of the Western Atlantic (excluding Brazil); *C. h. tropicus* Nichols of Brazil, the Eastern Atlantic, and the Mediterranean; *C. h. caninus* Günther of the Eastern Pacific; and *C. carangus* (Bloch) of the Western Pacific and the Indian Ocean. Varying expressions on these relationships are given by Gilbert and Starks (1904: 77), Fowler (1919a: 254), Nichols (1920c: 45; 1936: 119; 1937a: 58; and 1939: 7), Meek and Hildebrand (1925: 351), Weber and de Beaufort (1931: 246 and 258), Walford (1937: 72), Hildebrand (1939: 38), and Tortonese (1955: 194).

The relation of *Caranx hippos* to *C. ignobilis* (Forskål) and *C. sansun* (Forskål) of the Indo-Pacific is poorly known.

Material

Measurements and counts were taken on a series of 94 specimens from 15.3 to 830 mm. standard length, and meristic values were recorded for an additional 39 specimens within this size range. The 178 specimens identified are listed in table 23.

The smallest specimen of *hippos* previously reported (Nichols 1939: 7) from the Western Atlantic—13 mm. standard length, from *Atlantis* station 1952, Feb. 15, 1934, BOC 3418—is no longer available. An 18.7-mm. specimen, which evidently was not examined by Nichols, seems

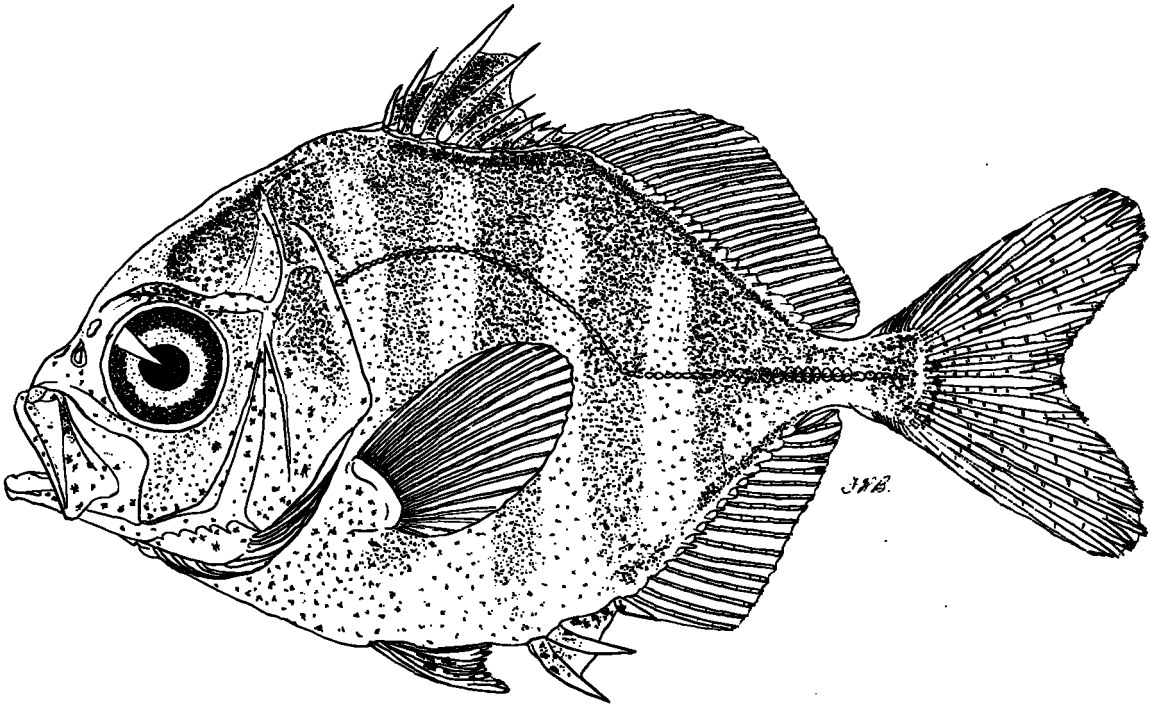

FIGURE 81.—*Caranx hippos* juvenile, 15.3 mm. standard length (UF 3815).

to be the only one in the Bingham Oceanographic Collection bearing the above BOC number, *Atlantis* station number, and date.

A 12.7-mm. specimen from the stomach of a *Sphyraena barracuda* (Walbaum) taken in the Berry Islands, Bahamas, by the *Gill*, is tentatively identified as *hippos*. The specimen was only slightly digested, but some of the characters that would associate it with the 15.3-mm. *hippos* had been destroyed. It is included only on the graphs of figures 8, 88, and 94.

Three specimens of *latus* from Bermuda, MCZ 28979 and 32076, apparently reported by Barbour (1905: 119) as *hippos*, are discussed under *C. latus* in Material, page 491. This disposed of one of the two records I have found of *hippos* from

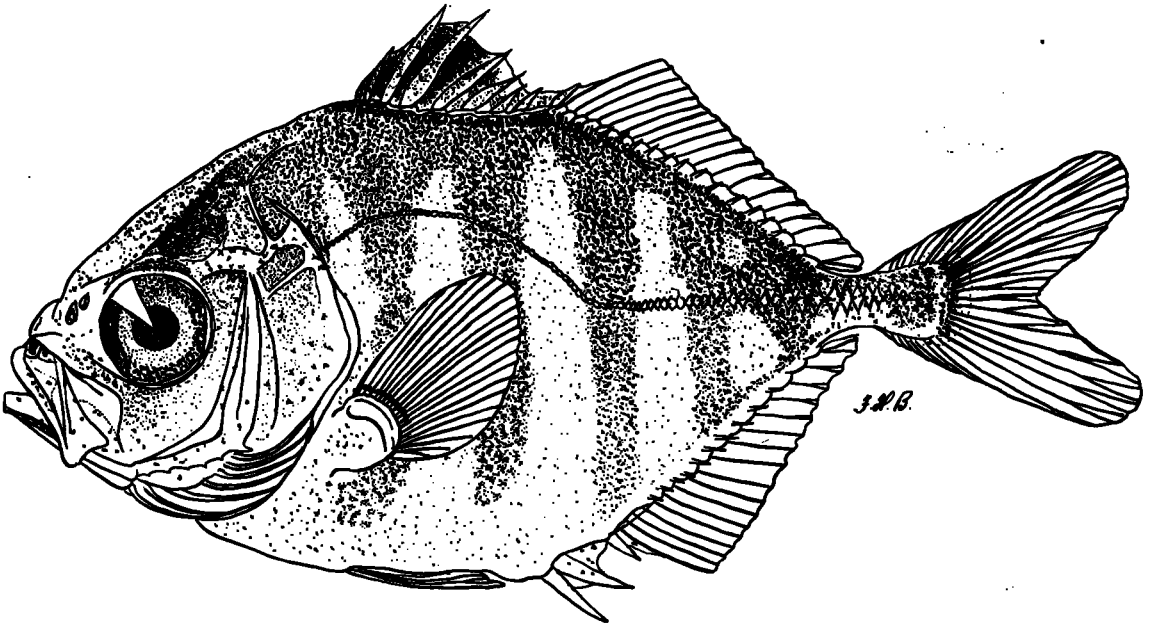

FIGURE 82.—*Caranx hippos* juvenile, 20.4 mm. standard length (UF 3803).

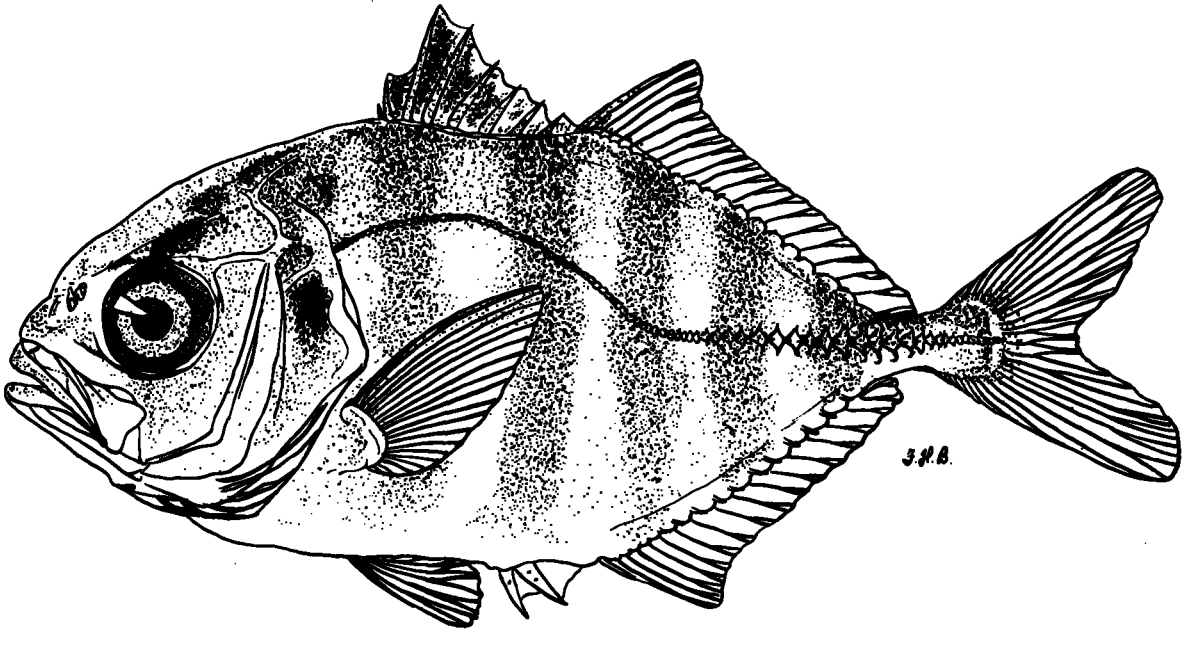

FIGURE 83.—*Caranx hippos* juvenile, 32.6 mm. standard length (SAFI, Sapelo Marsh, Ga.).

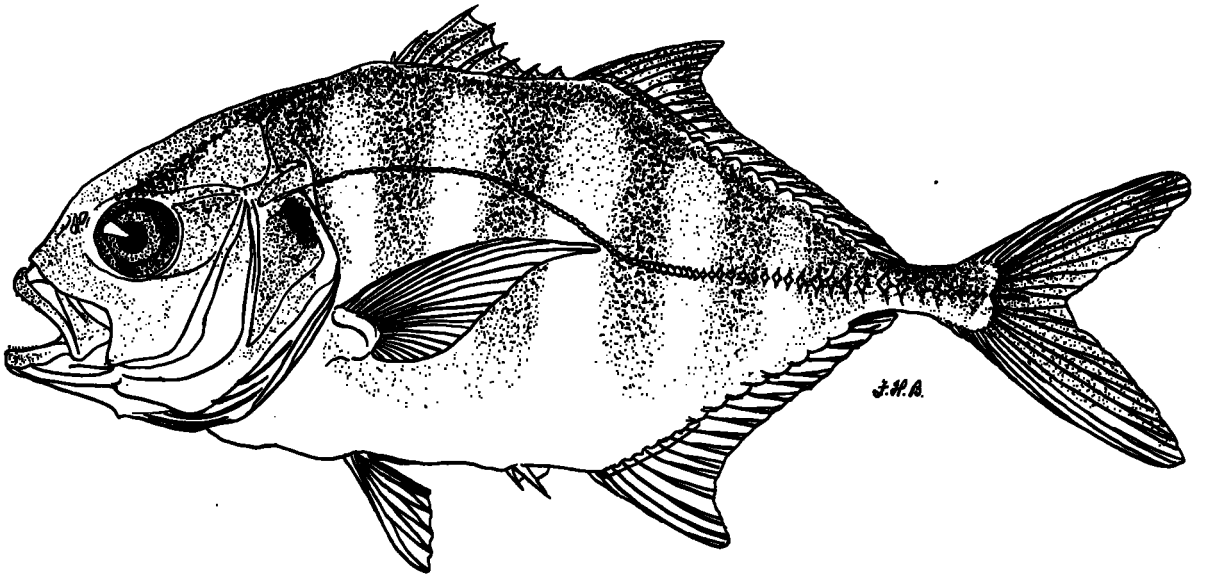

FIGURE 84.—*Caranx hippos* juvenile, 80.5 mm. standard length (SAFI, Sapelo Marsh, Ga.).

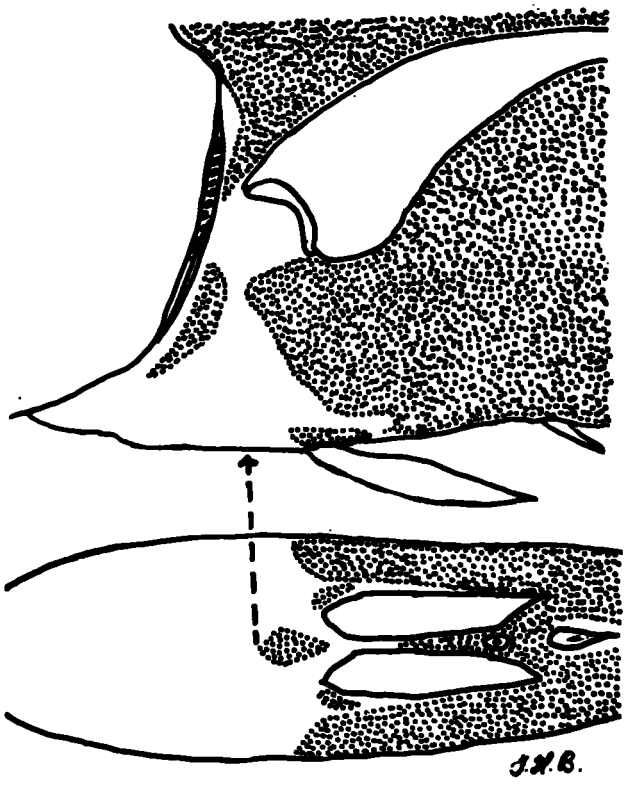

FIGURE 85.—*Caranx hippos:* Lateral view (above) and ventral view (below) of chest region of the 80.5-mm. standard length specimen of figure 84, showing scaled areas (stippled).

Bermuda. The other record, by Günther (1880: 9) of the synonymous *C. carangus* (Bloch), is doubtful, since only the name is listed, and during that era Günther's references to *carangus* and *hippos* were usually meant by him to apply to a *Caranx* with a fully scaled chest, as *latus* or *sexfasciatus*.

Morphological values of the one specimen of *lugubris* available for study are included and distinguished on the graphs with *hippos*.

Characters

Scales on chest.—The chest is unscaled at all sizes except for a small patch of scales which forms at about 25 mm. standard length and is centered in front of the pelvic fins (fig. 85). Four other patches of scales are present in the general area of the chest (at 80.5 mm.; larger sizes not examined): along each cleithrum and laterally along the insertion of each pelvic fin (fig. 85). All other Western Atlantic species of *Caranx* have completely scaled chests.

Dorsal spines.—VIII and I. The third spine is the longest at all sizes. An interspinous membrane connects the first and second dorsal fins (eighth and ninth spines) to about 80 mm. standard length (figs. 81 to 83). The membrane connecting the seventh and eighth spines dis-

appears at about 120 mm. On 770-mm., 795-mm., and 830-mm. specimens, only the first six spines are connected, and the seventh and eighth spines are completely covered by an overgrowth of skin. Ginsburg (1952: 94) described a similar spine condition for a specimen of about 585 mm. (converted).

The regression of length of the third dorsal spine on standard length is shown in figure 86 and table 20. A line fitted to this regression for specimens from 15.3 to 110 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.11-mm. increase in spine length per 1.0-mm. increase in standard length). The position of the coordinates of the "*latus* and/or *hippos*" specimens may indicate that a faster spine growth rate prevails for specimens below approximately 15 mm. The position of the coordinates of the four largest specimens of *hippos* in figure 86 below the extension of the calculated regression line and of the coordinates of specimens up to 795 mm. (fig. 90) suggests that a decrease in spine growth rate occurs between approximately 250 mm. and 300 mm

TABLE 20.—Caranx hippos: *Statistics describing regressions of body parts on standard length*

$\bar{x}$=mean of independent variable x
$\bar{y}$=mean of dependent variable y
N=number of specimens
b=rate of increase of y
a=y-intercept of regression line
$Sy \cdot x$=standard deviation from regression (standard error of estimate)

Independent variable x	Dependent variable y	Size range of specimens (mm.)	$\bar{x}$	$\bar{y}$	N	b	a	$Sy \cdot x$
Standard length	Dorsal-fin spine length (3d)	15.3–110	41.62	5.54	60	0.108	1.052	0.601
Do	Dorsal soft-ray length (1st)	15.3–164	58.77	9.41	67	.189	2.098	2.159
Do	Pectoral length	15.3–43.7	28.92	6.61	43	.265	−1.045	.441
Do	do	43.7–283	125.78	40.85	33	.386	−7.647	2.131
Do	Body depth	15.3–164	56.79	23.99	77	.370	2.996	.934
Do	Head length	15.3–164	57.26	18.60	76	.302	1.305	.811
Do	Eye diameter	15.3–51.0	30.23	3.72	51	.093	.917	.224
Do	do	51.0–162	108.65	9.46	24	.063	2.603	.500
Do	Snout length	15.3–164	57.26	4.70	76	.084	−.091	.445

Anal spines.—II and I. The first spine averages longer than the second from 15.3 to 20.4 mm. standard length; above 23 mm. the second spine is the longer. An interspinous membrane connects the second and third spines to about 25 mm. (figs. 81 and 82).

Dorsal soft-rays.—19 to 21 (table 21). Nichols and Roemhild (1946, fig. 1) indicated 2 specimens out of 42 with only 18 dorsal soft-rays; the other 40 were within my range. The posterior rays are branched at 15.3 mm. standard length (fig. 81). The extension of the anterior 5 rays to produce the fin lobe has begun by 25 mm. and is advanced by 80.5 mm. (figs. 83 and 84). The second ray averages the greatest length to about 27 mm.; above 27 mm., the first ray is longest. The third spine averages a greater length than the longest soft-ray to about 34 mm.; above 34 mm., the ray is longer (fig. 86).

The regression of length of the first dorsal soft-ray on standard length is shown in figure 86 and table 20. A line fitted to this regression for specimens from 15.3 to 164 mm. standard length indicates that a proportional rate of increase is maintained for the two variates from about 25 to 164 mm. (0.19-mm. increase in soft-ray length per 1.0-mm. increase in standard length). The alinement of the coordinates of specimens of *hippos* smaller than 20 mm. and of the "*latus* and/or *hippos*" specimens suggests that a slower soft-ray growth rate prevails below approximately 25 mm. The position of the coordinates of larger specimens (fig. 90) suggests that soft-ray growth may continue at the same proportional rate up to 830 mm.

TABLE 21.—Caranx hippos: *Correlation of the numbers of dorsal and anal soft-rays of 132 specimens*

[The upper number in each block is the count obtained for that combination, and the number in parentheses below is the approximate percentage of that count in the total sample]

ANAL SOFT-RAYS	DORSAL SOFT-RAYS 19	20	21
16	19 (14.4)	62 (47.0)	2 (1.5)
17	3 (2.3)	39 (29.5)	7 (5.3)

Anal soft-rays.—16 or 17 (table 21). Ginsburg (1952: 93) and Nichols and Roemhild (1946, fig. 1) gave a range of 15 to 17. The figure of

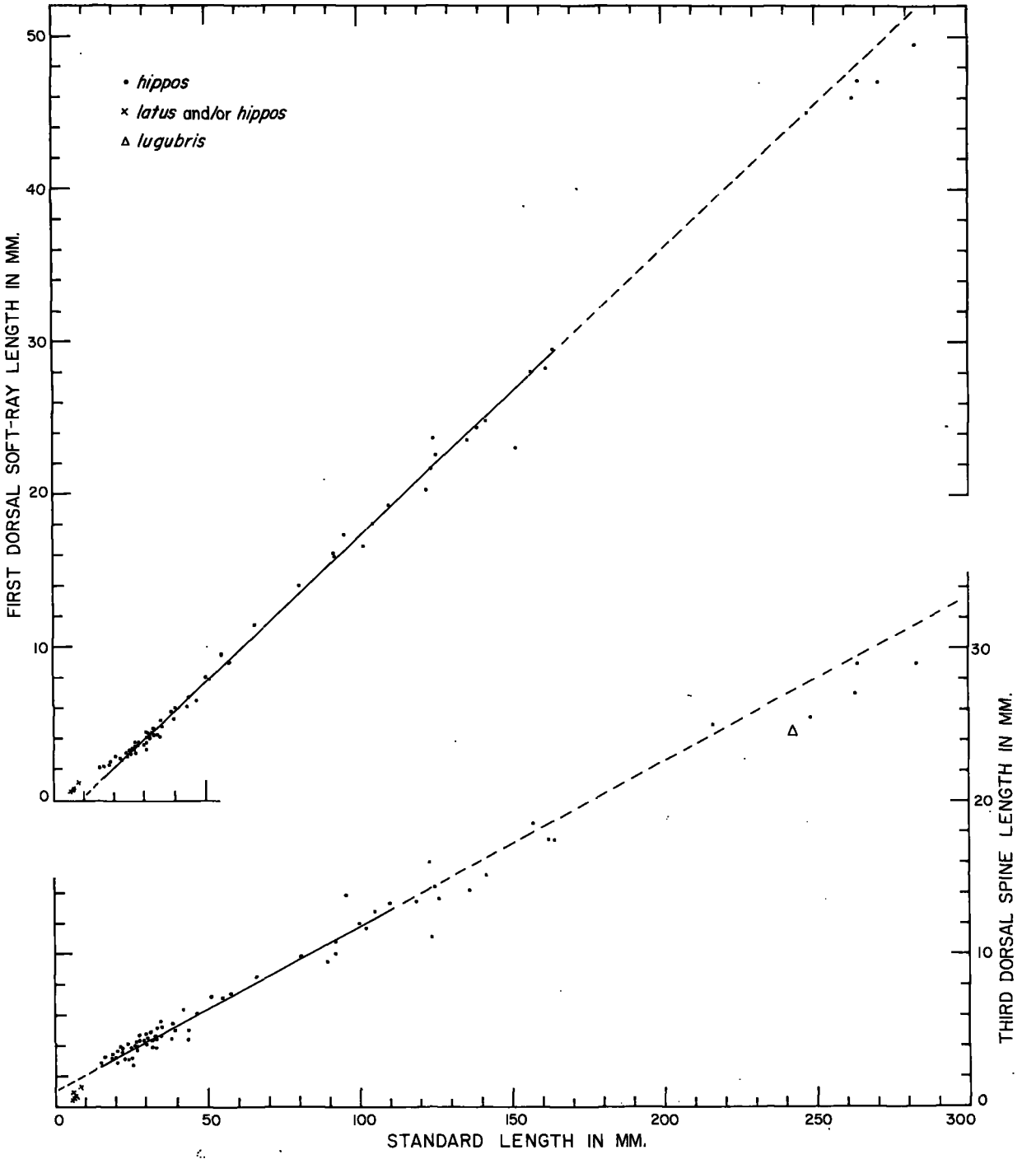

FIGURE 86.—*Caranx hippos*, *C. lugubris*, and *Caranx* sp. ("*latus* and/or *hippos*"): Relation of length of first dorsal soft-ray and of third dorsal spine to standard length.

dorsal and anal soft-ray relationships given by Nichols and Roemhild sustains the same modal value that my specimens exhibited (table 22). Branching and lobation occur as in the second dorsal fin. The first and second rays are longest and nearly equal to about 32 mm. standard length; above 32 mm., the first ray is longest. The longest dorsal ray averages longer than the first anal ray. The second anal spine is two-thirds as long as the longest anal soft-ray at 15.3 mm., one-half as long at 60 mm., about one-fourth as long at 164 mm., less than one-fifth as long at 432 mm., and about one-ninth as long at 830 mm.

Interneural and interhemal spines.—The posterior lateral projections of these spines are well developed and extend above the body surface along the bases of the dorsal and anal soft-rays at 15.3 mm. (fig. 81). They are also developed on the damaged 12.7-mm. specimen. At 164 mm. they are still externally visible, principally along the posterior bases of the fins, but are not projecting in a 248-mm. specimen.

Caudal.—9+8 principal rays; about 9 or 8+8 secondary rays. Branching of the principal rays has occurred by 15.3 mm. (fig. 81).

Pectoral.—I–19 or 20. The full complement of rays has formed by 20.4 mm. standard length. The distal end of the fin is rounded from 15.3 mm. to about 27 mm., after which it becomes pointed and falcation begins (figs. 81 to 83). Falcation is pronounced by 80.5 mm. (fig. 84).

The regression of pectoral length on standard length is shown in figure 87 and table 20. Two lines were fitted to this regression: for specimens from 15.3 to 43.7 mm. and from 43.7 to 283 mm. standard length. An extension of the lower line intersects the upper line at approximately 54 mm. indicating an inflection occurs at about 54 mm. and that a faster pectoral growth rate prevails above that size. The proportional rates of increase for the two variates are 0.27-mm. (below 54 mm.) and 0.39-mm. (above 54 mm.) increase in pectoral length per 1.0-mm. increase in standard length. Comparison of the upper regression line with specimens of *hippos* up to 830 mm. (fig. 91) suggests that a decrease in the pectoral growth rate occurs at some size around 300 mm.

Pelvic.—I–5. The soft-rays are branched and segmented at 15.3 mm. standard length.

Body depth.—Depth at first anal spine averages less than depth at pelvic from 15.3 mm. to about 30 mm. standard length, is about equal from 30 to 90 mm., and is greater above 90 mm. The coordinates for body depth at pelvic on standard length for specimens smaller than 30 mm. are plotted in figure 8.

The regression of body depth at pelvic on standard length is shown in figure 88 and table 20. A line fitted to this regression for specimens from 15.3 to 164 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.37-mm. increase in body depth per 1.0-mm. increase in standard length). The alinement of the coordinates of the specimens in the *"latus* and/or *hippos"* series suggests that a faster body-depth growth rate occurs below about 10 or 12 mm. The position of the coordinates of the six largest specimens in figure 88 below the extension of the calculated regression line and of the coordinates of specimens up to 830 mm. (fig. 90) suggests that a decrease in body-depth growth rate occurs at some size around 164 mm.

Head.—The regression of head length on standard length is shown in figure 88 and table 20. A line fitted to this regression for specimens from 15.3 to 164 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.30-mm. increase in head length per 1.0-mm. increase in standard length). Comparison of the extension of the calculated regression line with coordinates of larger specimens (fig. 91) suggests that head growth may continue at the same proportional rate up to 830 mm.

Eye.—The regression of eye diameter on standard length is shown in figure 89 and table 20. Two lines were fitted to this regression: for specimens from 15.3 to 51.0 mm. standard length and from 51.0 to 162 mm. The lines intersect at approximately 55 mm., indicating that an inflection occurs at about that size and that a slower eye growth rate prevails above that size. The proportional rates of increase for the two variates are 0.09-mm. (below 55 mm.) and 0.06-mm. (above 55 mm.) increase in eye diameter per 1.0-mm. increase in standard length. The position of the coordinates of the *"latus* and/or *hippos"* specimens suggests that a faster eye growth rate may prevail below approximately 15 mm. The position of the coordinates of the four largest specimens in figure 89 below the extension

489286 O—59——7

of the calculated regression line and of the coordinates of specimens up to 830 mm. (fig. 90) suggests that a decrease in eye growth rate occurs between approximately 200 mm. and 250 mm.

Snout.—The regression of snout length on standard length is shown in figure 89 and table 20. A line fitted to this regression for specimens from 15.3 to 164 mm. standard length shows a proportional rate of increase for the two variates within this size range (0.08-mm. increase in snout length per 1.0-mm. increase in standard length). Comparison of the extension of this calculated regression line with larger specimens (fig. 91) suggests that the snout growth may continue at the same proportional rate up to 830 mm.

Gill rakers.—Lower limb, 16 to 19; upper limb, 6 to 9; total, 22 to 27 (table 22). Of the 105 specimens examined that were more than 20 mm. standard length, all but 2 (25 mm. and 33.5 mm.) had one or more shorter or rudimentary gill

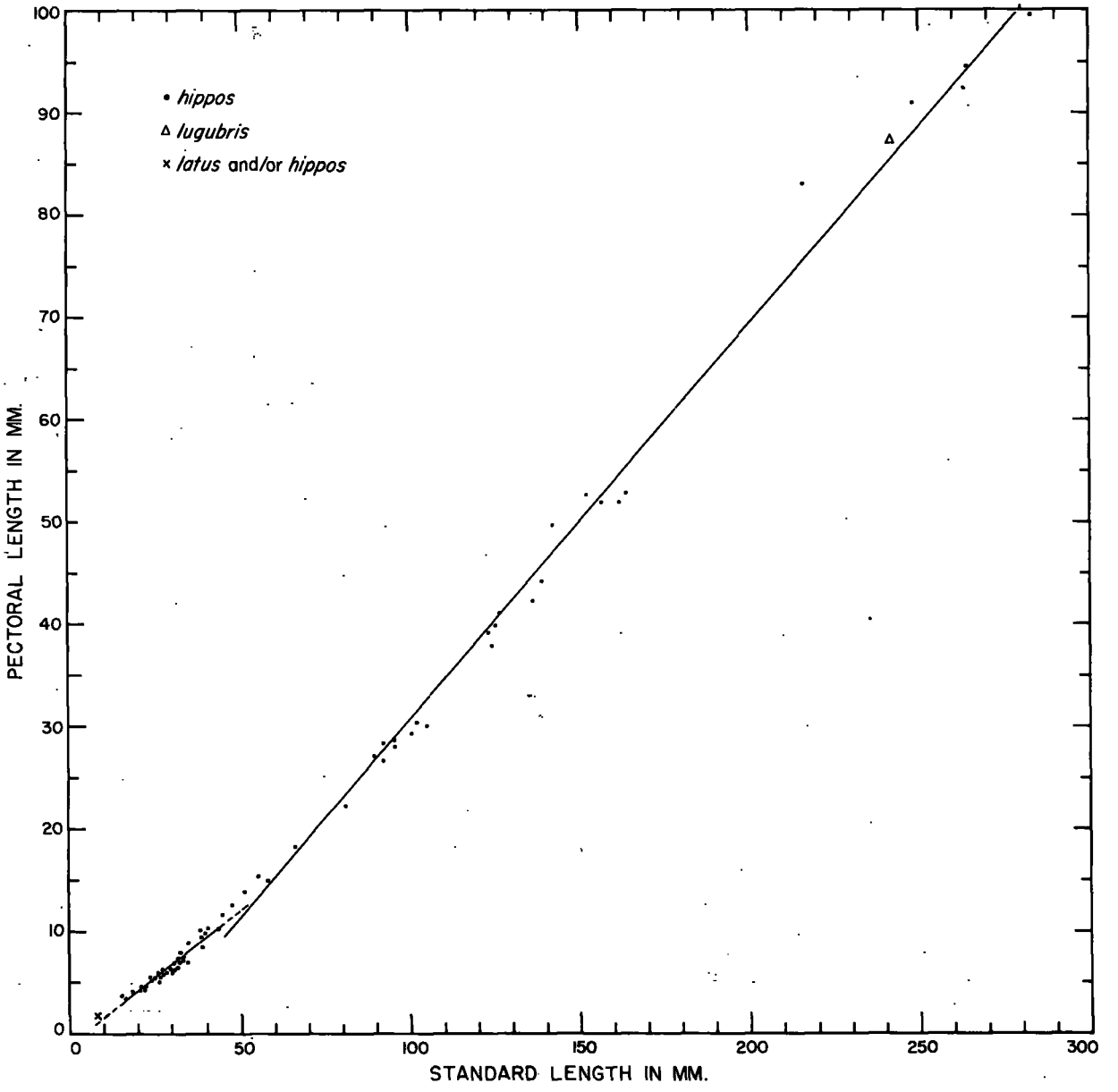

FIGURE 87.—*Caranx hippos*, *C. lugubris*, and *Caranx* sp. ("*latus* and/or *hippos*"): Relation of pectoral length to standard length.

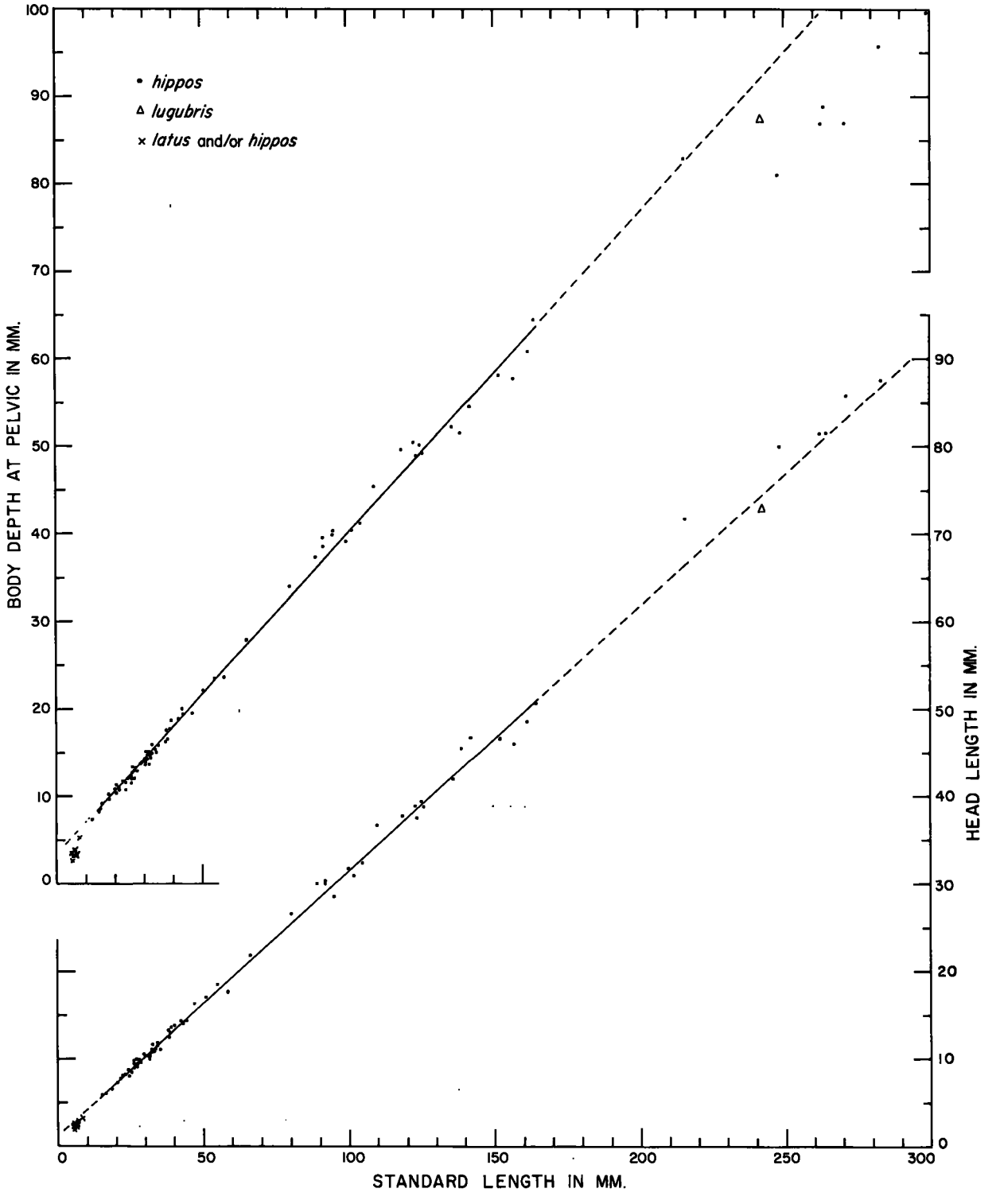

FIGURE 88.—*Caranx hippos*, *C. lugubris*, and *Caranx* sp. ("*latus* and/or *hippos*"): Relation of body depth at pelvic and of head length to standard length.

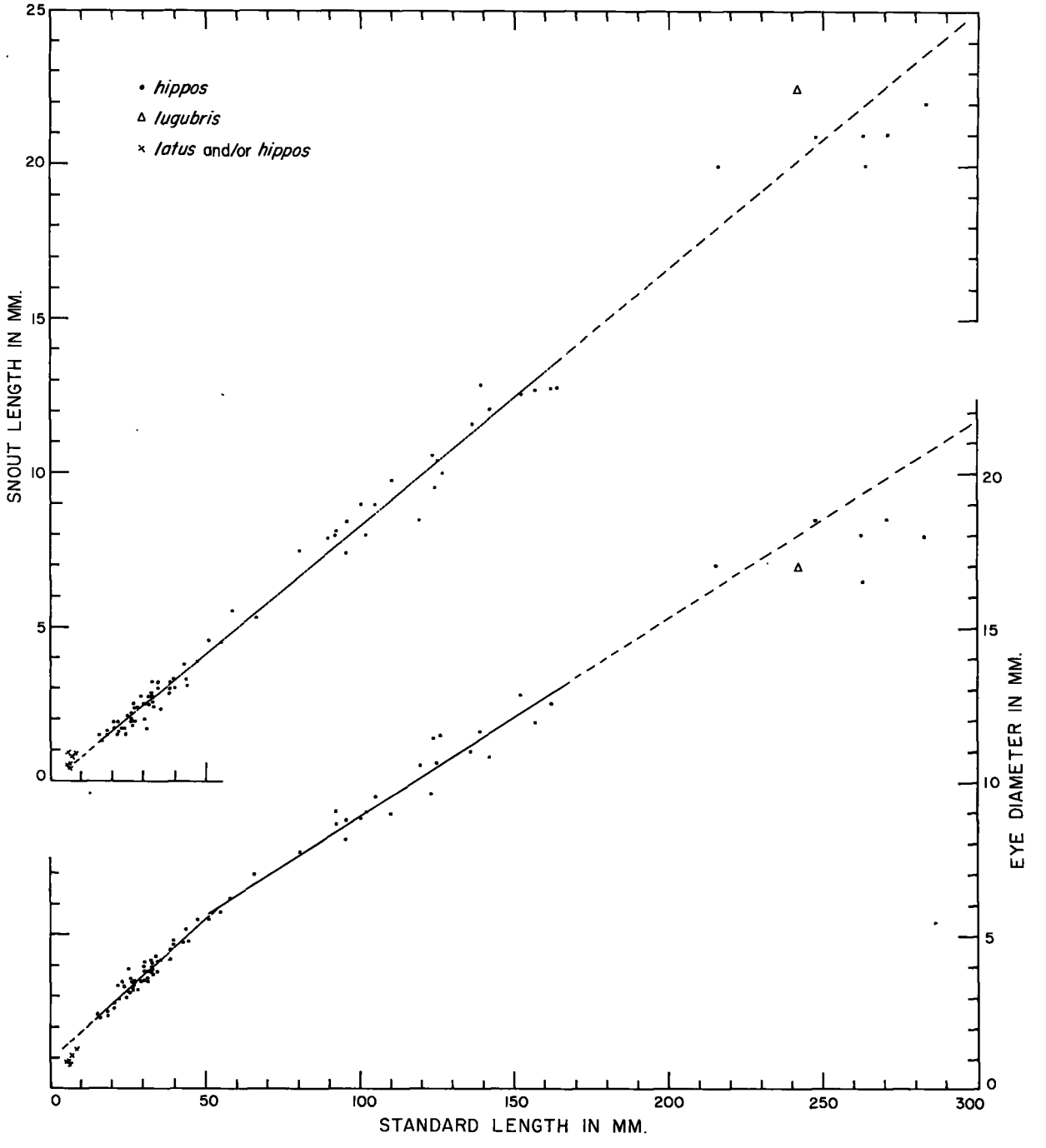

FIGURE 89.—*Caranx hippos*, *C. lugubris*, and *Caranx* sp. (*"latus* and/or *hippos"*): Relation of snout length and of eye diameter to standard length.

rakers at the origin of both limbs. A 152-mm. specimen had 6 rudimentary gill rakers (total of 9) on the upper limb. All others had from 1 to 4 rudiments on the lower limb and from 1 to 5 on the upper limb. Within the size ranges specified, the following modal numbers of rudimentary gill rakers were obtained: 20–50 mm., 1 lower, 2 upper; 50–164 mm., 2 lower, 3 to 4 upper; 248–432 mm., 3 lower, 4 upper; 795 mm., 4 lower, 4 upper; and 830 mm., 4 lower, 5 upper. Ginsburg (1952: 93)

reported the inner 3 to 5 gill rakers on the upper limb to be rather abruptly shorter or tuberclelike, and 2 or 3 tubercles present on the lower limb. This illustrates that the number of rudimentary gill rakers at the origins of both limbs increases with an increase in body length.

Nichols (1937a: 59) used the number of lower-limb gill rakers exclusive of rudiments to separate a small number of specimens of *C. h. hippos* of the Atlantic and *C. h. caninus* of the Pacific for sizes over 100 mm. In view of the association of the number of rudimentary gill rakers and body size, this separation may be incomplete. Meek and Hildebrand (1925: 351) found Pacific specimens of the species to average a slightly larger number of gill rakers than Atlantic specimens, but they also omitted rudimentary gill rakers from the counts.

TABLE 22.—Caranx hippos: *Correlation of the numbers of lower-limb to upper-limb gill rakers of 105 specimens*

[The upper number in each block is the count obtained for that combination, and the number in parentheses below is the approximate percentage of that count in the total sample]

UPPER-LIMB GILL RAKERS	LOWER-LIMB GILL RAKERS 16	17	18	19
6	13 (12.4)	19 (18.1)	1 (1.0)	
7	13 (12.4)	45 (42.9)	9 (8.5)	1 (1.0)
8	1 (1.0)	1 (1.0)	1 (1.0)	
9			1 (1.0)	

Scutes.—Range of the mean number of scutes in fish measuring approximately 100 to 430 mm. standard length: about 26 to 35 (fig. 92). Ginsburg (1952: 93) gave a range of 24 to 39 scutes

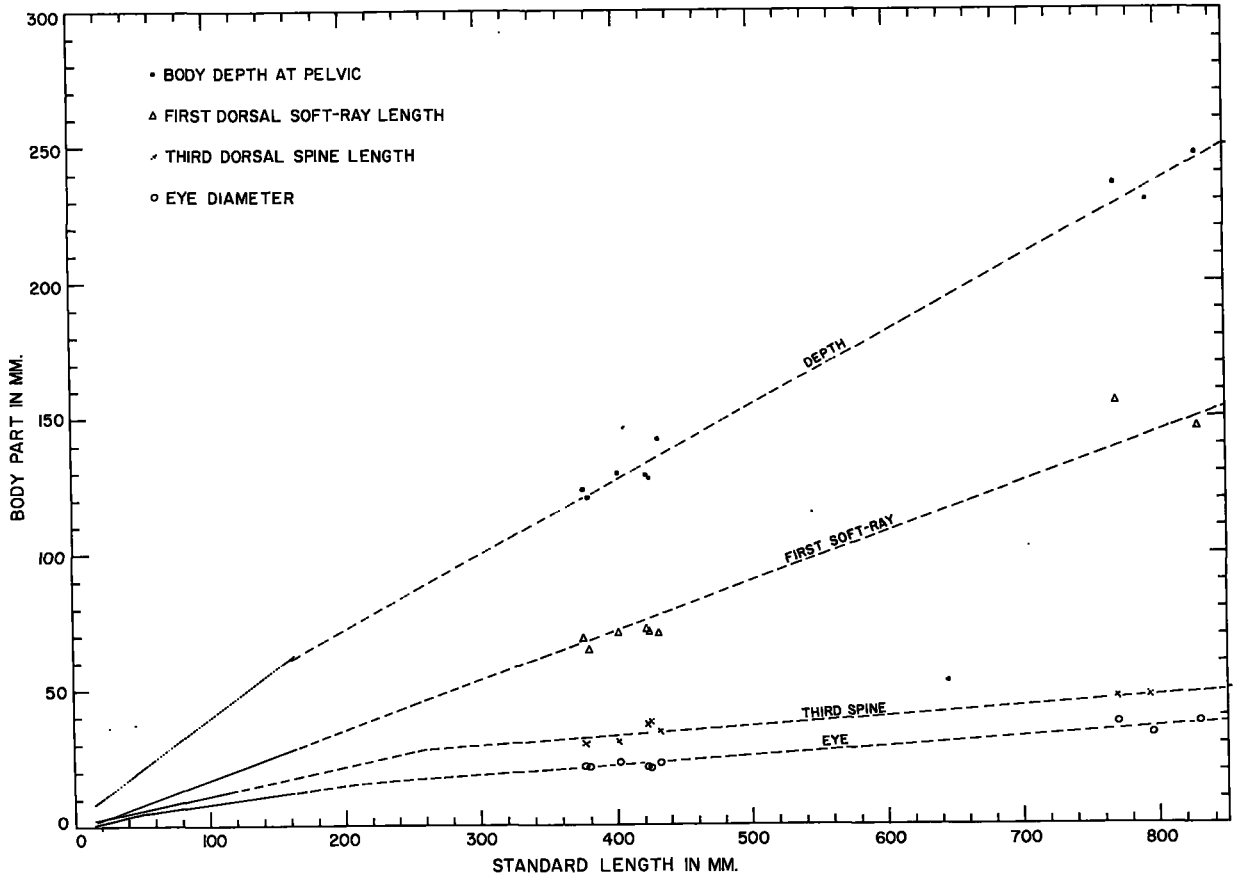

FIGURE 90.—*Caranx hippos:* Relation of body depth at pelvic, of length of first dorsal soft-ray, of length of third dorsal spine, and of eye diameter to standard length, showing calculated regression lines (solid lines) for specimens smaller than 300 mm. standard length and coordinates of and estimated regression lines (dashed lines) fitted to specimens from 377 to 830 mm. standard length.

489286 O—59——8

for specimens of about 57 to 600 mm. (converted) from the Atlantic, Gulf, and Caribbean. Schultz (1949: 124), listing *hippos* from Venezuela, gave an upper limit of 40 scutes. These values obviate the character used to separate proposed Atlantic and Pacific subspecies given by Nichols (1937a: 59), who gave a range for specimens over 100 mm. standard length of 27 to 33 scutes for *C. h. hippos* and 33 to 40 for *C. h. caninus*. Some of the scutes have completed their individual development at 16.1 mm. and nearly all by 100 mm. The mean numbers of scutes of the three largest specimens examined, 770 mm., 795 mm., and 830 mm., were 30, 23.5, and 24.5, respectively. The two lowest scute counts were obtained on the two largest specimens—this is probably caused by the terminal scutes losing their posterior spines with growth and consequently being omitted from the count.

Lateral line.—Range of mean lateral-line ratio from approximately 55 to 430 mm. standard length: about 1.15 to 1.55 (fig. 93). The mean lateral-line ratio–standard length relation has appreciable variation, but the ratio tends to increase up to about 60 mm. and to become constant or to decrease slightly above this size. Nichols (1937a: 58) gave ratios of 1.1 to 1.2 for specimens 109 to 145 mm., and he (1937c: 1) gave ratios of 1.1 to 1.3 for specimens 23 to 65 mm. His values are accommodated by the perimeters of figure 93 but average lower than those I obtained. The mean lateral-line ratios of the three largest specimens examined, 770 mm., 795 mm., and 830 mm., were 0.97, 1.47, and 1.15, respectively. The value for the 770-mm. specimen was the lowest that was obtained.

Preopercular spines.—Preopercular spines were present on specimens from 12.7 to 22.1 mm. standard length, but absent on specimens of 21.0

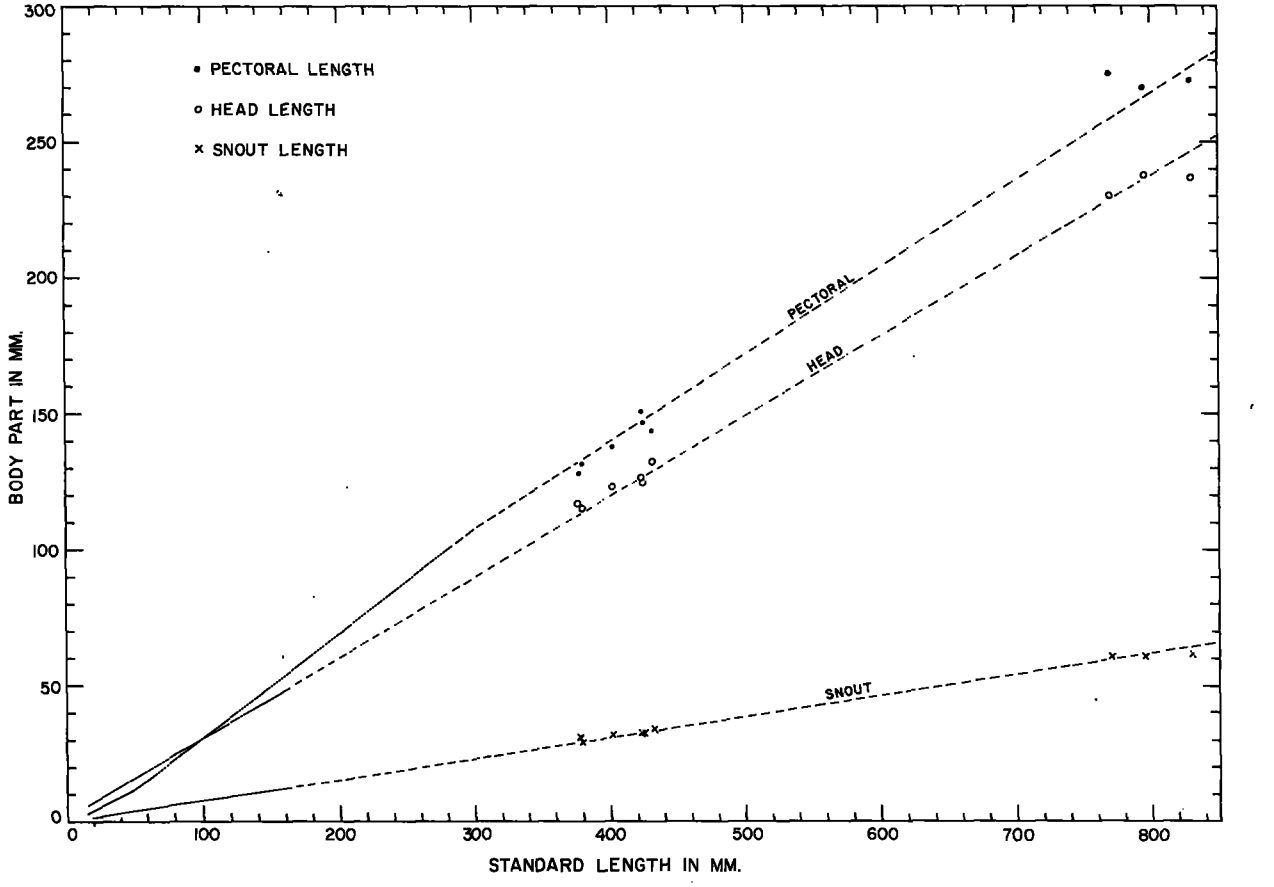

FIGURE 91.—*Caranx hippos:* Relation of pectoral length, of head length, and of snout length to standard length, showing calculated regression lines (solid lines) for specimens smaller than 300 mm. standard length and coordinates of and estimated regression lines (dashed lines) fitted to specimens from 377 to 830 mm. standard length.

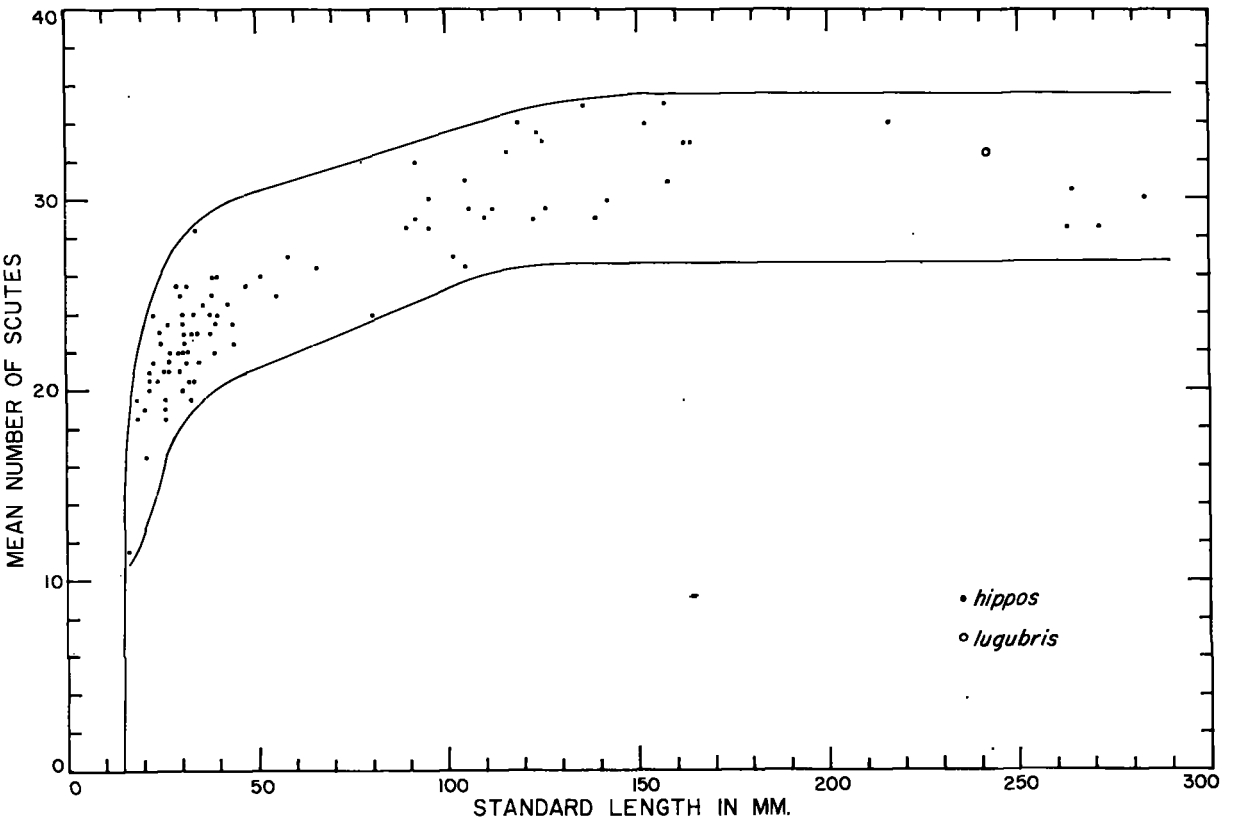

FIGURE 92.—*Caranx hippos* and *C. lugubris:* Relation of the mean number of scutes to standard length.

mm. and 22.0 mm. and at 22.5 mm. and above. The lengths of the preopercular-angle spine associate with the probable trend of decrease in spine length of the "*latus* and/or *hippos*" group (fig. 94). Preopercular upper-limb spines were absent in all specimens. Preopercular lower-limb spines, missing on the damaged 12.7-mm. specimen, numbered 3 at 20.4 mm.; 4 at 18.6 mm., 21.8 mm., and 22.1 mm.; 5 at 18.7 mm. and 20.8 mm.; and 6 at 15.3 mm. and 16.3 mm. (table 1).

Pigmentation.—Three of the juvenile complement of five (rarely four or six) body bars are present at 15.3 mm.; the fourth and fifth bars are an undivided pigment mass at this size. The covering of the brain case above the eye and the upper portion of the operculum possess pigment accumulations. A pigmented area of the body at the upper edge of the operculum has probably been termed an additional body bar by some authors. The first dorsal is densely pigmented, the pigment extending to the eighth spine. Pigment spots are present on the anal spines and their interspinous membranes and on the pelvic fins. The other fins are unpigmented (fig. 81).

Five body bars are present on a 16.3-mm. specimen. With rare exceptions, probably due to fading after preservation, the bars are present on specimens up to 164 mm.; and specimens 248 mm. and above lack bars. The bars are slightly wider than the interspaces. They extend nearly to the base of the anal fin to about 60 mm., and begin to shorten toward the straight lateral line above this size (figs. 81 to 84). An area of pigmentation develops on the top of the peduncle at about 30 mm. (fig. 83) and is very dark on specimens of more than 100 mm.

The pigment area over the eye elongates posterodorsally to form the nuchal band between 20 mm. and 30 mm. A pigmented area below the eye suggests a bending and continuation of the nuchal band through the eye (figs. 82 and 83). Massing of pigment on the operculum between 20 mm. and 30 mm. forms the opercular spot (figs. 83 and 84).

Pigmentation on the first dorsal fin decreases

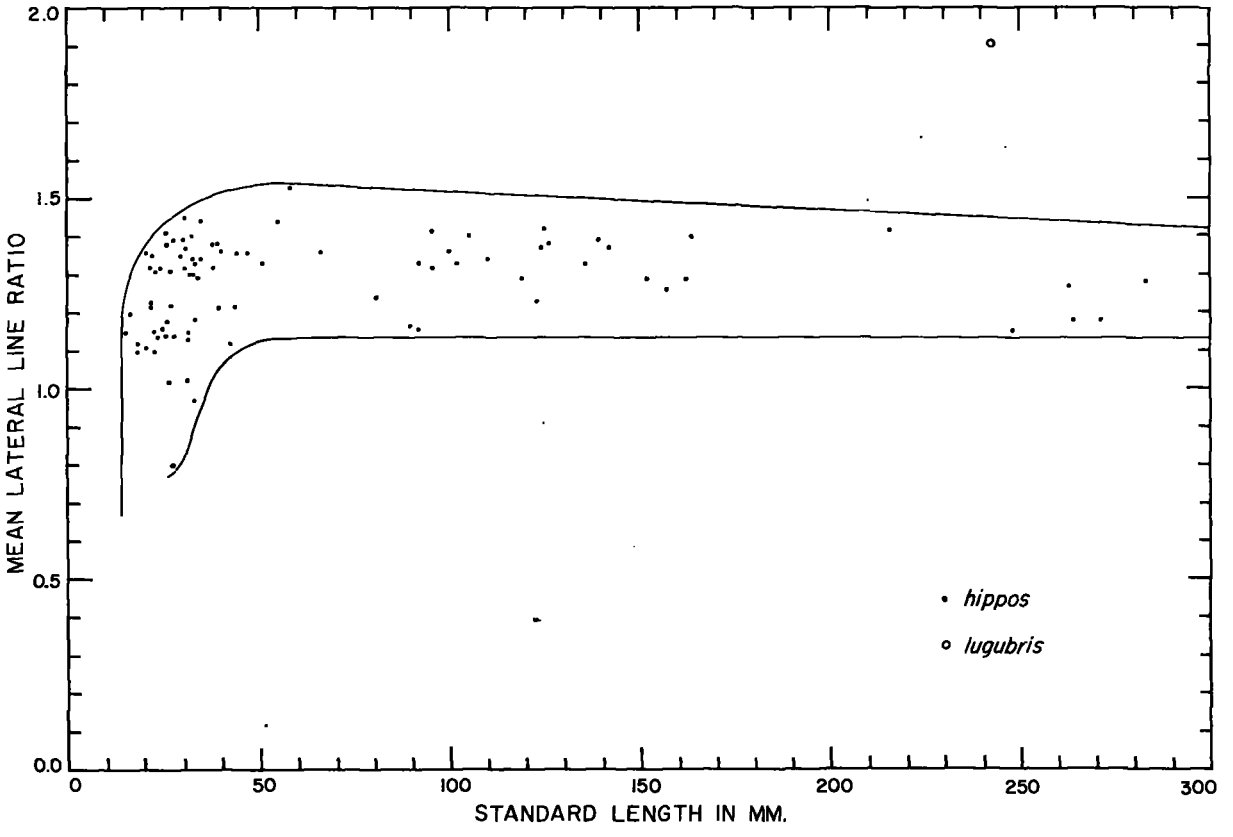

FIGURE 93.—*Caranx hippos* and *C. lugubris:* Relation of the mean lateral-line ratio to standard length.

above 30 mm. Pigment appears on the second dorsal fin at about 30 mm. (fig. 83) and migrates to the edge of the fin along the ninth spine and the tips of the soft-rays by about 40 to 50 mm. (fig. 84). The anal soft-rays and their connecting membranes are pigmented, and the pigment spots on the anal spines and their membranes disappear above 35 mm. The pelvic is unpigmented above 20 mm. The pectoral spot develops midway along the lower rays of the fin at about 120 mm. and 140 mm. Pigmentation of the caudal rays develops at about 30 mm. (fig. 83).

Distribution off Southeastern Atlantic Coast of the United States

Specimens have been reported from the following specific localities within this area: Gulf Stream off Bimini, Bahamas, by Nichols (1937b: 237); Biscayne Bay, Fla., by McCormick, *in* Smith (1896: 175); Eden, Stuart, and Lake Worth on Indian River, Fla., by Evermann and Bean (1898: 236); Indian River, Fla., by Goode (1882: 34); New Smyrna, Fla., by Lönnberg (1894: 122); mouth of St. Johns River, Fla., by Goode (*circa* 1897: 112); James Island Creek, Sullivans Island, Porcher's Bluff, Seabrook's Beach, Edisto Island, Morris Island, Magnolia Beach, and Magnolia Bluff, S. C., by Fowler (1945: 190, ChM specimens); Pamlico Sound, N. C., by Higgins and Pearson (1927: 42); and Beaufort, N. C., by Yarrow (1877: 208), Bean (1881: 90), Linton (1905: 365), Smith (1907: 205), and Nichols (1938b: 1).

Figure 95 shows the location of specimens taken on the *Gill* cruises (dip-netted off Cape Hatteras, N. C., and from the stomach of a *Sphyraena barracuda* above Great Harbor Key, Berry Islands, Bahamas, and from the stomach of a *Thunnus atlanticus* (Lesson) from northwest of the Berry Islands), specimens taken by the *Combat* off southern Florida, USNM specimens examined (Cape Lookout, N. C., and St. Andrews Sound, Ga.), ChM specimens examined (at and below Charleston, S. C., the same specimens reported by Fowler 1945: 190), and specimens in the SAFI collection (Jekyll Island, Jekyll Causeway Marsh, Doboy Sound, St. Simons Island, Sapelo Marsh, and off

Brunswick, Ga., and Mayport, Fla.) (tables 2 and 23). Of the records of capture of *hippos* shown on the chart, that at Mayport, Fla., is composed of fish 248 to 432 mm. standard length which may have been adult; and the others were juveniles.

In the waters of the Atlantic Ocean and the Gulf of Mexico off the coast of the United States, I believe that *hippos* has an offshore larval existence that may be associated with offshore currents; it may migrate inshore during the early juvenile stage; and it probably selectively inhabits inshore waters during the late juvenile stage. The following evidence supports this theory:

1. Some or all of the "*latus* and/or *hippos*" specimens taken offshore (fig. 95) may be *hippos*.

2. An 18.7-mm. specimen and the 12.7-mm. early juvenile reported by Nichols (1939: 7), BOC 3418, were taken from 11°15′ N., 81°50′ W., about 98 miles offshore east of Port Limon, Costa Rica.

3. Three of the smaller juveniles examined (15.3 mm., 16.3 mm., and 20.4 mm.) were taken at two stations, about 39 miles and 51 miles offshore, east of Tampico, Mexico.

4. Four small juveniles (18 to 21 mm.) were taken about 52 miles offshore southeast of South Pass, La. (Mississippi Delta).

5. The foregoing records of early juveniles are all from offshore waters (the small specimen from the stomach of a barracuda taken in the Bahamas is not conclusive in speculation on habitat).

6. No records of larvae or of juveniles smaller than 21 mm. standard length exist for inshore waters, and no such small specimens other than those previously listed were available from the many collections canvassed. Absence of larval *hippos* and of juveniles smaller than 21 mm. in the many inshore collections that have been made would seem to preclude their presence in inshore waters. Collections of the *Gill* were concentrated in waters off the southeastern Atlantic States from near the beaches to beyond the axis of the Gulf Stream and furnished only one record of *hippos*, an early juvenile taken inshore. SAFI collections have been maintained biweekly in the vicinity of Brunswick, Ga., at surf, marsh, and river stations, and collections here yielded only juvenile *hippos* 21 mm. and larger, although other

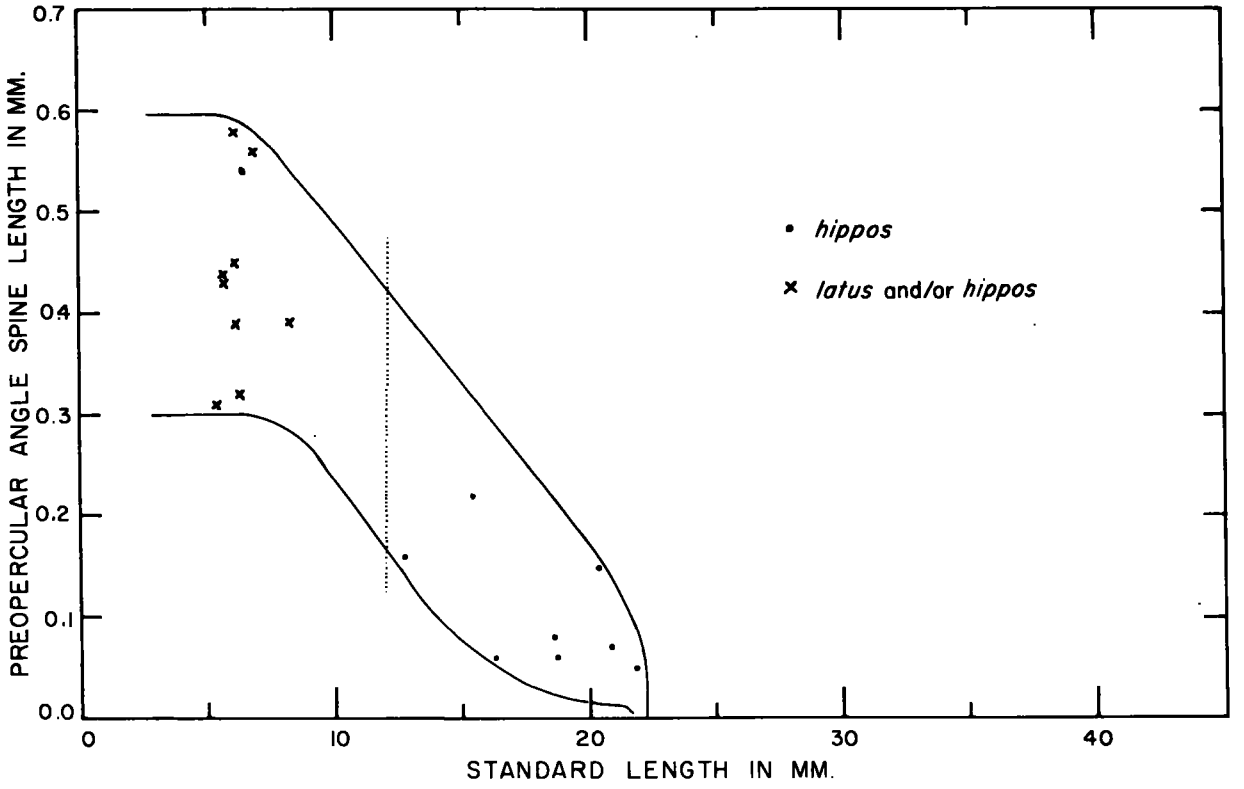

FIGURE 94.—*Caranx hippos* and *Caranx* sp. ("*latus* and/or *hippos*"): Relation of length of the preopercular-angle spine to standard length. Dotted line separates the two forms.

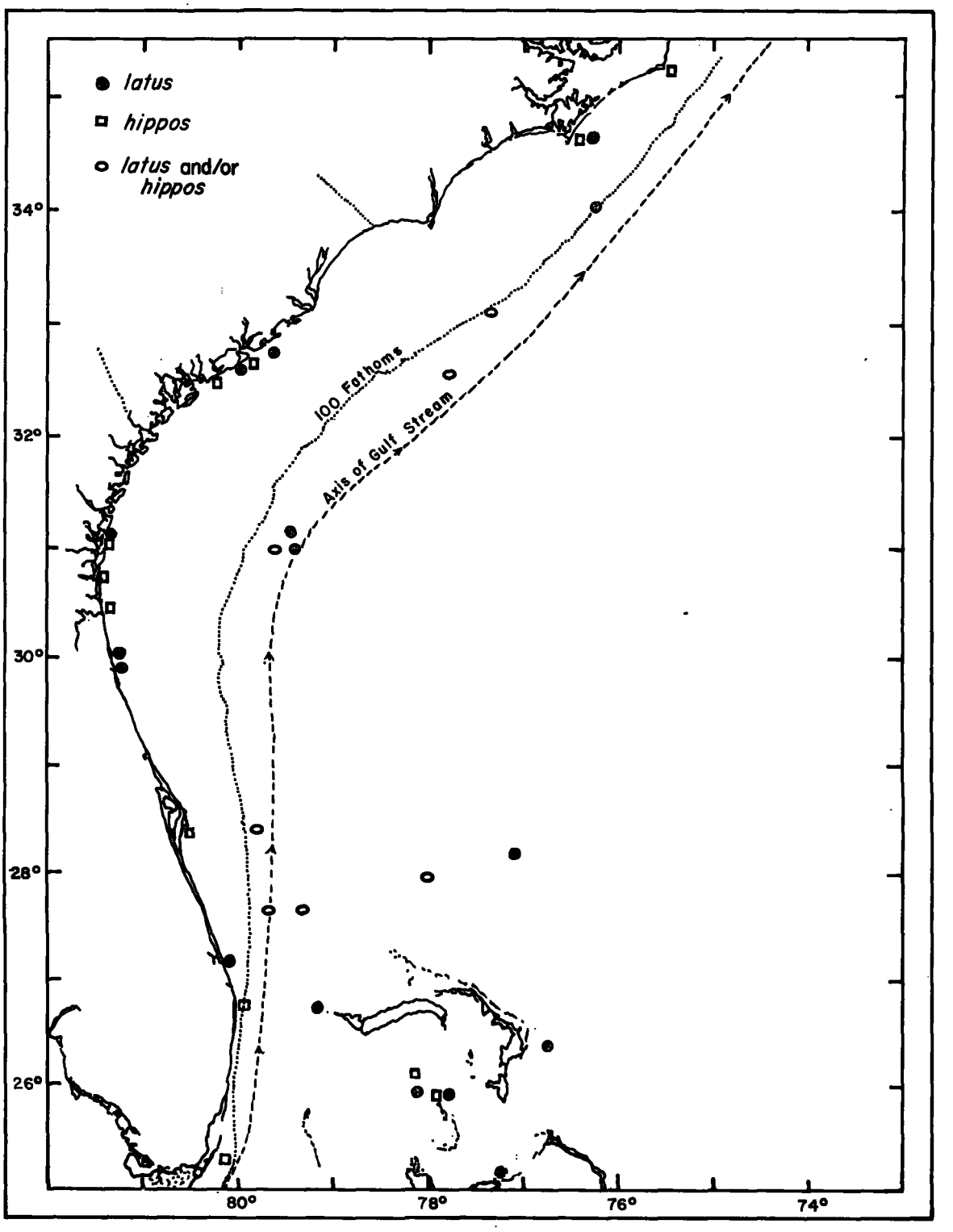

FIGURE 95.—*Caranx hippos*, *C. latus*, and *Caranx* sp. (*"latus* and/or *hippos"*): Locations of capture off the southeastern Atlantic coast of the United States.

small carangids (*Trachinotus* and *Oligoplites*) down to 10 mm. standard length were frequently seined.

7. Thirty-two early juveniles (24 to 39 mm.) were taken from about 52 to 66 miles offshore east to south-southeast of South Pass, La., in 1955 and 1956 at 10 collecting stations of the M/V *Oregon*. Ten of these were taken with four of the smaller specimens (18 to 21 mm.) previously described.

8. There are many records of capture of larger juvenile *hippos* from inshore waters along the Atlantic and Gulf coasts of the United States. A 21.0-mm. specimen from St. Simons Island, Ga., a 22.0-mm. specimen from Magnolia Beach, S. C., and a 22.5-mm. specimen from Plantation Key, Fla., are the smallest juveniles from inshore waters that I have examined. Smith (1898: 98) recorded young an inch long from Woods Hole, Mass., about July 1 (1 inch total length converts to about 21.5 mm. standard length; but, since Smith's measurements apparently were not critical, the young he reported may have been more than 21.5 mm.). Juvenile specimens about 39 to 41 mm. (converted) were reported by Vladykov (1935: 4) from Musquodoboit Harbor, Nova Scotia, in summer (the most northern record for the genus in the Western Atlantic).

9. The distribution records of juvenile and adult *hippos* in the Western Atlantic, Gulf of Mexico, and Caribbean point to a habitat association with continental waters or larger islands. While commonly reported from the eastern coasts of North, Central, and South America and from the Greater Antilles, the only records from the Bahamas are from the analysis of the stomach contents of two large fish and a report by Nichols (1921a: 22) from Turk Island.

There is a possible association between an expected movement of early juveniles to inshore waters and the loss or absorption of the preopercular spines. Specimens as large as 20.8 mm., 21.8 mm., and 22.1 mm. standard length taken from offshore waters still possessed small preopercular spines, while the smallest specimens

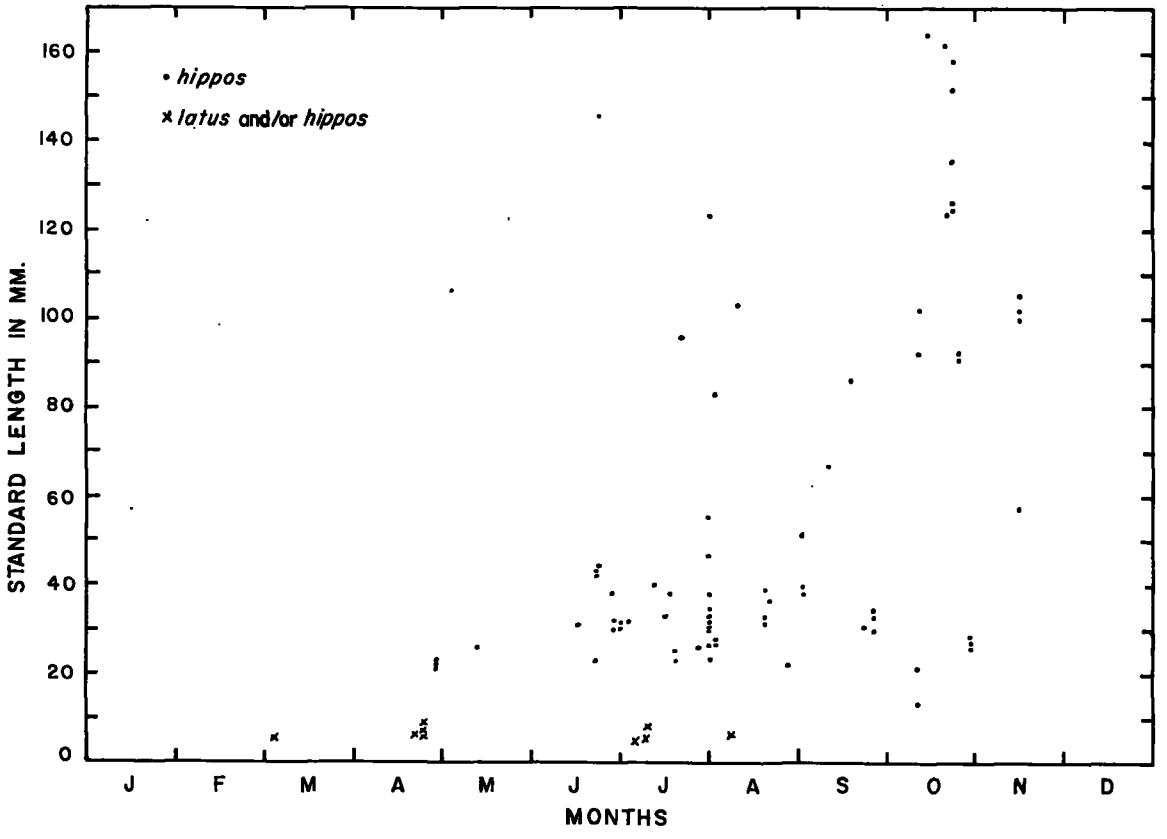

FIGURE 96.—*Caranx hippos* and *Caranx* sp. ("*latus* and/or *hippos*"): Size distribution, by months, of specimens taken off the southeastern Atlantic coast of the United States.

TABLE 23.—Caranx hippos: *Location and date of capture, number and size range of 178 specimens examined*

[See pp. 417 and 419 for explanation of abbreviations used; measurements in standard length]

Location	Date captured	Collection	Number of specimens	Size (mm.)
ATLANTIC OCEAN:				
Plantation Key, Fla.	June 12, 1956	UF 7089	2	22.4–23.5
25°16′ N., 80°07′ W.	July 26, 1957	SAFI, *Combat* 457	1	26
26°47′ N., 79°53′ W.	July 28, 1957	SAFI, *Combat* 459	1	38
Indian River, Fla.	July 3, 1954	UF 4709	1	32.1
Cape Canaveral Anchorage, Fla.	Apr. 29, 1957	SAFI, *Combat*	3	22.3–22.9
Mayport, Fla.	Apr. 25, 1956	SAFI	11	248–432
Cumberland River Sound, Ga.	Oct. 23, 1930	USNM 119238	2	91.5–92
St. Andrews Sound, Ga.	Nov. 19, 1956	SAFI	1	105
Off Jekyll Island, Ga.	Sept. 5, 1956	do	2	118–141
Commercial trawling area, Brunswick, Ga.	Oct. 4–5, 1956	do	1	158
Do	Oct. 13–14, 1955	do	1	164
Do	Oct. 20, 1955	do	2	124–162
Do	Nov. 13, 1956	do	2	106–116
Jekyll Island Causeway, Ga.	Sept. 26, 1957	do	2	33.5–34
Do	Oct. 25, 1957	do	2	25.5–26
St. Simons Sound, Ga.	July 20, 1957	do	1	95.5
Do	Oct. 16, 1957	do	1	170
Off Parsons Creek, Brunswick, Ga.	Nov. 7, 1956	do	1	112
Off St. Simons Island, Ga.	Oct. 3, 1956	do	1	158
Do	Oct. 23, 1955	do	5	125–157
St. Simons Island, Ga.	June 22, 1955	do	1	23.1
Do	July 10, 1956	do	1	25.9
Do	Aug. 19, 1955	do	2	30.6–38.7
Do	Aug. 27, 1957	do	1	22.0
Do	Sept. 7, 1956	do	1	30
Do	Sept. 26, 1957	do	1	30
Do	Sept. 29, 1956	do	2	34–37.5
Do	Oct. 11, 1956	do	1	29.5
Do	Oct. 11, 1957	do	2	92–102
Do	Oct. 25, 1957	do	1	29
Do	do	do	3	21.0–32
Do	Oct. 29, 1954	do	3	25.9–28
Do	Nov. 16, 1955	do	4	58–105
Do	Nov. 20, 1956	do	1	33.5
Doboy Sound, Ga.	Aug. 2, 1957	do	1	83
Do	Aug. 9, 1957	do	1	103
Sapelo Marsh, Ga.	Aug. 19, 1955	do	1	32.6
Do	Sept. 19, 1955	do	1	30.5
South end of Edisto Island, S. C.	Sept. 25, 1933	ChM 33.284.4	1	30.5
Seabrook's Beach, S. C.	June 30, 1932	ChM 32.100.5	2	30–32.1
Morris Island, S. C.	July 19, 1934	ChM 34.190.1	2	23.3–25
James Island Creek, S. C.	June 16, 1936	ChM 38.180	1	30.9
Sullivans Island, S. C.	Aug. 20, 1931	ChM 31.192	1	36.2
Porcher's Bluff, S. C.	Sept. 2, 1931	ChM 31.196.11	3	39.4–50.5
Do	Sept. 10, 1931	ChM 31.208.2	1	66
Magnolia Beach, S. C.	Aug. 1, 1934	ChM 34.239.5	11	23–123
Do	Oct. 1934	ChM 34.316.9	1	110
Isle of Palms, S. C.	Sept. 8, 1950	ChM (no number)	1	27.6
Murrell's Inlet, S. C.	July 13, 1943	USNM 132083	1	39.9
35°14′ N., 75°34′ W.	May 11, 1953	SAFI, *Gill* 2, Cape Hatteras Bight	1	26.2
Fort Macon, Beaufort, N. C.	Aug. 2, 1915	USNM 111778	2	26.7–27.5
Do	July 16, 1913	USNM 111781	1	32.7
Do	June 30, 1932	USNM 111782	3	24.6–31.4
North River at bridge, Beaufort, N. C.	June 21, 1932	USNM 111783	3	42.5–44
Beaufort, N. C.	July 18, 1913	USNM 111780	1	38.2
Do		USNM 86257	2	95.5–119
Below Yorktown, Va.	Oct. 11–13, 1921	USNM 144025	1	95.5
Woods Hole, Mass.		USNM 20672	2	33.5–35.2
GULF OF MEXICO:				
22°30′ N., 96°57′ W.	May 24, 1954	UF 3803, *Oregon* 1070	1	20.4
22°43′ N., 97°10′ W.	do	UF 3815, *Oregon* 1072	2	15.3–16.3
Havana market, Cuba	Jan. 7, 1956	SAFI	1	216
Tortugas, Fla.	June-Aug., 1926	USNM 164530	1	33
Do	June 30, 1932	USNM 164531	3	24.6–31.4
Off Cape Sable, Fla.		USNM 39874	1	89.5
Bayport, Fla.	Sept. 25, 1954	UF 3743	2	139–142
28°17′ N., 88°37′ W.	Aug. 25, 1955	GFEGR, *Oregon* 1380	2	30–35
28°21′N., 88°42′ W.	Dec. 5–6, 1956	SAFI, *Oregon* 1614	4	23.5–30.5
28°47′ N., 87°56′ W.	July 23, 1956	UF 3923, *Oregon* 1589	2	26–28
28°47′ N., 87°57′ W.	Aug. 15, 1955	GFEGR, *Oregon* 1367	2	28.5–33.5
28°47′ N., 87°58′ W.	July 24, 1956	UF 3929, *Oregon* 1591	4	28–31.5
28°48′ N., 87°50′ W.	Aug. 14, 1955	GFEGF, *Oregon* 1365	14	18–31.5
28°50′ N., 87°58′ W.	July 26, 1956	UF 3927, *Oregon* 1593	6	24.5–34
28°50′ N., 87°50′ W.	Aug. 13, 1955	GFI, *Oregon* 1363	1	24.5
28°55′ N., 87°30′ W.	June 21, 1957	SAFI, *Oregon* 1835	3	30.5–31.5
28°55′ N., 87°50′ W.	Aug. 10, 1955	GFEGR, *Oregon* 1356	1	24.5
28°55′ N., 87°57′ W.	Aug. 21, 1955	GFEGR, *Oregon* 1372	2	27.8–38.7
29°01′ N., 87°48′ W.	Aug. 22, 1955	GFEGR, *Oregon* 1374	2	29.6–34.2
Destin, Fla.	Sept. 3, 1957	SAFI	3	770–830
East Beach, Galveston, Texas.	May 24, 1956	GFI	1	26
Aransas County, Texas.	June 7, 1954	UF 4259	2	24–27
Do	June 8, 1954	UF 4241	2	30.5–39.3
30°00′ N., 87°43′ W.	June 19, 1957	SAFI, *Oregon* 1831	3	20.1–26.1
CARIBBEAN SEA:				
11°15′ N., 81°50′ W.	Feb. 15, 1934	BOC 3418, *Atlantis* 1952	1	18.7

taken inshore, 21.0 mm., 22.0 mm., and 22.5 mm., did not have these spines. The angle produced by the preopercular-angle spine was present on the 21.0-mm. specimen, but the spine was completely covered by skin.

Records of juvenile and adult *hippos* from inshore waters along the Atlantic coast of the United States from April through November and the scarcity of such records from December through March indicate that the species either migrates to the south during the colder months or moves to warmer, offshore waters.

An affinity to brackish or even fresh water may account for an inshore migration of early juvenile *hippos*. The species has been recorded from Homosassa Springs, Fla., in water of very low salinity, by Carr, *in* Gunter (1942: 311) and by Herald and Strickland (1949: 109); and juveniles and adults were recorded from Texas by Gunter (1945: 57) in waters ranging in salinity from 4.8 to 36.4 parts per thousand.

Spawning

The spawning season that contributes young *hippos* to this area may be estimated, from the smallest specimens taken in May (26.2 mm.) and in October (12.7 mm.), to extend from early March to early September (fig. 96; tables 2 and 23).

Hildebrand (1939: 26) recorded specimens with "large or developing roe" from the Gatun Locks on the Atlantic side of the Panama Canal. These specimens were taken February 20 to 24. A sample from a group of more than 500 fish from the middle locks was composed of 11 males, about 540 to 690 mm. (converted), only 4 of which had undeveloped testes, and 8 females, about 524 to 768 mm. (converted). A sample from about 250 fish from the lowest chamber of the canal consisted of 4 males, about 528 to 650 mm. (converted), and 7 females, about 595 to 784 mm. (converted). This evidences that females may average a larger size than males. Beebe and Tee-Van (1928: 107) recorded a female of about 406 mm. (converted) from Haiti taken March 11 in which "the eggs were well-developed, and the ovary measured 110 by 60 mm." Erdman (1956: 320) noted *hippos* in spawning condition in May at Puerto Rico. Evermann and Bean (1898: 236), writing of the fishes of Indian River, Fla., said of *hippos*, "It probably spawns in salt-water lagoons and bays during the summer, as schools of young have been seen going out in the fall." Actually, the place of spawning is unknown. An offshore larval existence, as previously discussed, indicates an offshore spawning. If the larvae are associated with a northward movement in the Gulf Stream, many of the juveniles that have been taken on the Atlantic coast of the United States may have been spawned to the south of this area.

Caranx dentex (Bloch and Schneider)

(Figure 97)

? *Scomber adscensionis* Osbeck, 1771, p. 94 (Ascension Island).
Scomber cordila (*non* Linnaeus), Bonnaterre, 1788, p. 139, pl. LVIII, fig. 229 (America).
Scomber dentex Bloch and Schneider, 1801, p. 30 (Brazil).
Trachurus imperialis Rafinesque, 1810, p. 42 (Palermo).
Caranx luna Geoffroy Saint-Hilaire, 1809, pl. XXIII (Egypt).
Citula banksii Risso, 1826, p. 422, pl. 6, fig. 13 (Nicè).
Caranx dentex, Cuvier, *in* Cuvier and Valenciennes, 1833, p. 87 (Rio-Janiero, Brasil).
Caranx solea Cuvier, *in* Cuvier and Valenciennes, 1833, p. 86 (Brasil).
Caranx analis Cuvier, *in* Cuvier and Valenciennes, 1833, p. 88 (Sainte-Helene).
Selenia luna, Bonaparte, 1846, p. 75.
Caranx guara (*nomen nudum*, based on the French vernacularism of Bonnaterre, 1788) Jordan and Evermann, 1896, p. 926 (tropical Atlantic; Mediterranean; coasts of Africa, Brazil, and Madeiras; South Pacific; doubtless in West Indies).
Caranx cheilio Snyder, 1904, p. 524, pl. 8, fig. 14 (Honolulu market).
Carangus cheilio, Jordan and Evermann, 1905, p. 196, pl. 33, fig. 1 (Honolulu market).
Uraspis cheilio, Jordan, 1925, p. 16 (Honolulu market).
Caranx ascensionis (Osbeck), Fowler, 1928, p. 145 (in part; Honolulu and ? Johnson material; excluding other records and synonymy; not pl. XII B).
Caranx adscensionis (Osbeck), Smith, 1949, p. 215 (Cape and Natal, South Africa; all tropical waters).

Nomenclature

The name that has most commonly been applied to this species for the past 50 years, *Caranx guara* (Bonnaterre), is invalid. Linnaeus (1758: 298; 1766: 493) described *Scomber cordyla*, which is currently recognized under the name of *Megalaspis cordyla* (Linnaeus), an Indo-Pacific species with dorsal and anal finlets. Bonnaterre (1788: 139) described *Scomber cordila*, associated it with the vernacular name of "Le Guare," and referred this to page 492 of Linnaeus' Systema Naturae (1766). This indicates that Bonnaterre's *cordila* is a trans-

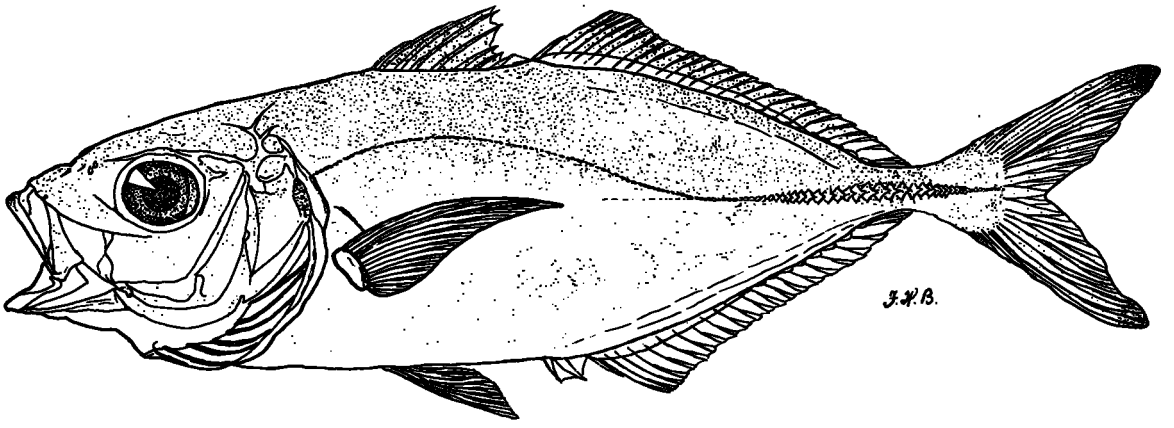

FIGURE 97.—*Caranx dentex* juvenile, 89.5 mm. standard length (AMNH 19994).

literation of Linnaeus' *cordyla*, although the specimen described by Bonnaterre may have been *C. dentex*. In synonymizing *C. dentex* (Bloch and Schneider) with Bonnaterre's description, Jordan and Evermann (1896: 926) lifted the vernacular name to apply to the species, calling it *Caranx guara* (Bonnaterre). This was pointed out by Dr. John C. Briggs, University of Florida, in a personal communication and by Padoa, *in* Padoa et al. (1956: 554).

Nichols (1951: 4) placed *Caranx cheilio* Snyder in the synonymy of *C. dentex* (under the name of *C. guara*), and specifically distinguished these from *C. georgianus* Cuvier (= *C. chilensis* Gay).

Recent authors have used *Caranx ascensionis* (Osbeck) as Fowler (1936: 699) or *C. adscensionis* (Osbeck) as Smith (1949: 215), to designate this species. Jordan and Evermann (1896: 926) included *Scomber adscensionis* Osbeck 1771 in questionable synonymy of *C. dentex*, under the name of *C. guara*, and stated that Osbeck's description might apply to *Selar crumenophthalmus* (Bloch) or *C. ruber*. I have not seen Osbeck's description, but according to Fowler (1936: 701) Osbeck gives the following characters: "Dorsal VIII–25; anal 25; pectoral 20; ventral 5; scutes 27, 49. Body narrow. Head obtuse. Mouth oblong, lower jaw longer. Teeth small. Pectoral bent. Ventral half of pectoral. Body grayish above, white below. Length 304 mm." This insufficient description cannot specifically designate any species of carangid. Instead, the identical number of dorsal and anal soft-rays, admittedly a possible miscount, discredits any possible identity with the genus *Caranx*. Published accounts and my observations indicate that *Caranx* species always have more dorsal soft-rays than anal soft-rays (from 2 to 5 more in Western North Atlantic species).

Material

Four specimens were examined (the smallest that could be located): 87 mm., 89.5 mm., 108 mm., and 132 mm., AMNH 19990, 19991, and 19994, from Bermuda. The following brief descriptions apply mainly to these specimens. Measurements are recorded on the graphs with *crysos*, the species they most closely resemble meristically.

Two specimens of *bartholomaei* from Boca Chica, Key West, Fla., ANSP 70973–74, at least one of which was identified as *dentex* (under the name of *guara*) by Fowler (1945: 292, fig. 307), and two specimens of *bartholomaei* from northwest of Cay Sal Bank, ANSP 72693, which Fowler (1950: 70, fig. 3) identified as *dentex* (under the name of *guara*), are discussed under *bartholomaei* (p. 472).

Three specimens reported as young *dentex* from New Orleans by Günther (1860: 441) are not this species, but are probably *ruber* and are discussed under that species (p. 458).

Characters

Dorsal spines.—VIII and I. The third spine is the longest. Lengths of the third spine are shown in figure 25. The first and second dorsal fins are not connected by an interspinous membrane.

Anal spines.—II and I. The second spine is longer than the first. The second and third spines are not connected by an interspinous membrane.

Dorsal soft-rays.—25 or 26 (fig. 1). Bean

(1906: 47) listed 27 rays; Tortonese (1952: 302) gave a range of 24 to 27. The first ray is the longest, except in the 89.5-mm. specimen, which has a distorted first ray. Lengths of the first soft-ray are shown in figure 25. The first ray is shorter than the third dorsal spine.

Anal soft-rays.—21 to 23 (fig. 1). Tortonese (1952: 302) gave a range of 20 to 22. The first and second rays are the longest and nearly equal, and are shorter than the first dorsal soft-ray.

Interneural and interhemal spines.—Posterior lateral projections of these spines are not extended above the body surface (as occurs in *latus* and *hippos*).

Caudal.—9+8 principal rays; about 9+10 secondary rays.

Pectoral.—I–19 or 20. Falcation is pronounced. Pectoral lengths are shown in figure 26.

Pelvic.—I–5.

Body depth.—The depth at pelvic and depth at first anal spine are similar at 87 mm. and 89.5 mm.; the latter is slightly greater at 108 mm. and 132 mm. Measurements of depth at pelvic are shown in figure 27.

Head.—Measurements of head length are shown in figure 27.

Eye.—Measurements of eye diameter are shown in figure 28.

Snout.—Measurements of snout length are shown in figure 28.

Gill rakers.—Lower limb, 26 to 28; upper limb, 11 to 13; total, 37 to 41 (fig. 2). Meek and Hildebrand (1925: 349) gave a count of 21 lower-limb gill rakers, exclusive of rudiments, for a specimen 515 mm. total length; Tortonese (1952: 302), also working with larger specimens and presumably excluding rudiments, gave a range of 21 to 25. The terminal gill raker at the origin of the lower limb of the 132-mm. specimen is the only one that is appreciably shorter or rudimentary. Judging from this specimen and the two accounts cited, the terminal gill rakers tend to become rudimentary with an increase in body size, and complete counts including rudiments might be expected to be higher than indicated by Meek and Hildebrand or by Tortonese.

Scutes.—Range of mean number of all specimens: 22 to 29 (fig. 29). Tortonese (1952: 302) gave a range of 23 to 30.

Lateral line.—Range of mean lateral-line ratio: 0.87 to 0.83 (fig. 30).

Preopercular spines.—None.

Pigmentation.—The four specimens are very faded. The only distinctive pigmentation is the very dark tip of the upper caudal lobe of the 89.5-mm. specimen (end of upper lobe missing from 87-mm. specimen). In addition, the two smaller specimens appear vaguely dark above the lateral line (fig. 97).

Beebe and Tee-Van (1933: 103), Bean (1906: 47), Meek and Hildebrand (1925: 349), and Jordan and Evermann (1896: 927) described a black opercular spot, but no records exist of body bars.

Distribution

C. dentex has not been reliably reported from the Atlantic and Gulf coasts of the United States nor from the eastern coast of Central America, the Bahamas, or the Lesser Antilles. Two records exist from the Greater Antilles, at Port-au-Prince, Haiti, by Fowler (1952b: 99) and from Puerto Rico by Erdman (1956: 327); from Bermuda by Günther (1880: 9), Bean (1906: 47), Beebe and Tee-Van (1933: 103), Nichols (1919: 98; and 1921b: 45), and Mowbray (1949: 13); from Brazil (Fowler 1941b: 154, see synonymy), the Azores and West Africa (Fowler 1936: 699, see synonymy), the Mediterranean by Tortonese (1952: 310), and from the Pacific and Indian Oceans by many authors. This is an offshore species, frequently associated with offshore islands.

Spawning

The time and place of spawning are unknown. The 87-mm. specimen is the smallest that I have been able to obtain. Schnakenbeck (1931: 18, figs. 13 to 16) questionably identified 5-mm. and 6-mm. total length specimens from the Mediterranean as this species, but they can not adequately be associated with *dentex*.

Caranx lugubris Poey

(Figure 98)

Scomber ascensionis (*non* Osbeck), Bloch and Schneider, 1801, p. 33 (Ascension Island).

Caranx ascensionis (*non* Osbeck), Cuvier, *in* Cuvier and Valenciennes, 1833, p. 102 (Ascension Island).

Caranx lugubris Poey, 1860, p. 222 (Cuba).

Caranx frontalis Poey, 1860, p. 222 (Cuba).

Carangus lugubris, Poey, 1866, p. 14.

Carangus ascensionis (*non* Osbeck), Streets, 1877, p. 88 (Fanning Islands).

Caranx ishikawai Wakiya, 1924, p. 193, pl. XXVI (Bonnin Islands; Formosa).

Caranx tenebrosus Jordan, Evermann, and Wakiya, *in* Jordan, Evermann, and Tanaka, 1927, p. 656 (Sulphur Bay, Clarion Island, Revillagigedo Islands).

Xurel lugubris, Jordan, Evermann, and Clark, 1930, p. 273 (tropical Atlantic; West Indies).

Xurel tenebrosus, Jordan, Evermann, and Clark, 1930, p. 273 (South Seas; Revillagigedos; Hawaii).

Caranx adscensionis (*non* Osbeck), Harry, 1953, p. 128 (Raroia, Tuamotu Archipelago).

Nomenclature

Caranx lugubris Poey has been recognized as an Atlantic and Pacific species since Jordan and Gilbert (1883: 201) compared specimens from both oceans. Interoceanic comparisons of specimens have also been made by Meek and Hildebrand (1925: 352) and Woods, *in* Schultz et al. (1953: 514). These three studies were made with small numbers of specimens, and all workers noted slight differences in Atlantic and Pacific forms. It is possible that comparisons of larger numbers of specimens will determine specific or subspecific differences, but at this time the Atlantic and Pacific forms should be considered merely as conspecific.

Material

Only one specimen was examined: USNM 167425, from Onotoa, Gilbert Islands, 242 mm. standard length. This is the smallest USNM specimen so identified and the smallest available from the many collections that were canvassed. Presumably it could be the same specimen collected and described by Randall (1955: 88), but his minimum length of three specimens taken does not quite coincide with mine, and some of his ranges differ from the counts I obtained on the one specimen. The measurements of this specimen are included and distinguished on the graphs with *hippos*.

Comparison of figure 98 with the photograph of a larger specimen (exact size not given, but between 343 and 545 mm. standard length) in Schultz et al. (1953, pl. 46, A) shows that the larger fish has a more-indented profile in front of the eye, shorter dorsal and anal fin lobes, and is narrower and more elongated from the origins of the soft-rayed fins to the caudal base. These are believed to be normal growth changes. An elongation of the posterior part of the body also occurs in comparable-sized specimens of *hippos*.

The specimen identified as *lugubris* from Tortugas, Fla., by Longley, *in* Longley and Hildebrand (1941: 78), was not this species. It probably was *Uraspis heidi* Fowler and is discussed under the account of that species (p. 526).

Characters

Dorsal spines.—VIII and I. The third spine is the longest, 24.5 mm. (fig. 86). The eighth and ninth spines are not connected.

Anal spines.—II and I. The second spine, 10.3 mm., is longer than the first and both are well separated from the third.

Dorsal soft-rays.—22. Meek and Hildebrand (1925: 352) and Woods, *in* Schultz et al. (1953: 514) gave a range of 21 or 22. Walford (1937: 76) gave a range of 21 to 23. The first ray is the longest, 75.7 mm. This measurement is too large to be placed on the graph of the first dorsal soft-

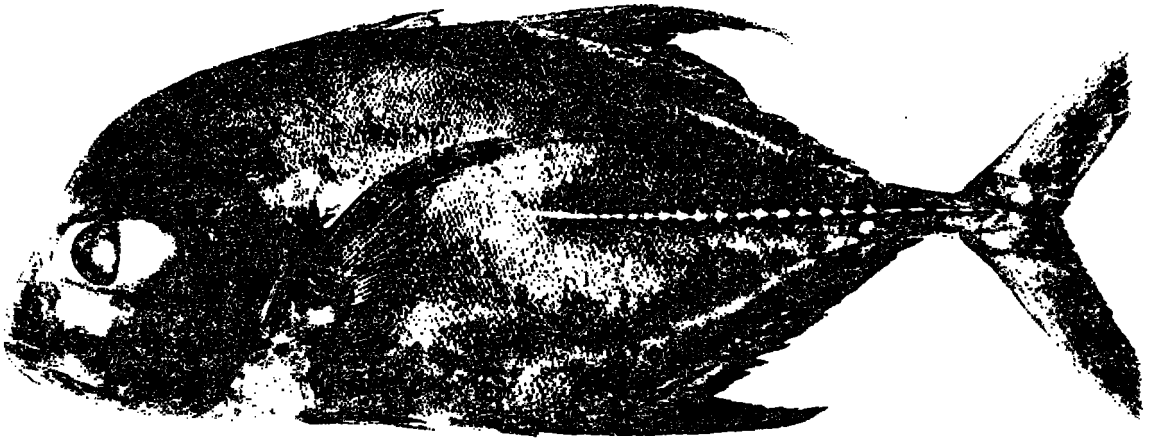

FIGURE 98.—*Caranx lugubris*, 242 mm. standard length (USNM 167425).

ray–standard length relation of *hippos*; it exceeds the first dorsal soft-ray length of a comparable 248-mm. *hippos* by 30 mm.

Anal soft-rays.—19. A range of 17 to 19 was given by Meek and Hildebrand (1925: 353). Woods, *in* Schultz et al. (1953: 514) gave a range of 17 to 20. Poey (1875: 76) gave the following combined counts for 5 specimens: D.21, A.18 (2); D.21, A.19(1); and D.22, A.18(2). The first ray is the longest, 61 mm.

Interneural and interhemal spines.—Posterior lateral projections of these spines do not extend above the body surface on the specimen examined.

Caudal.—9+8 principal rays; secondary rays not discernible without dissection.

Pectoral.—I–19. 87.5 mm. (fig. 87).

Pelvic.—I–5. 32.5 mm.

Body depth.—Depth at first anal spine (100 mm.) is greater than depth at pelvic (94 mm.) (fig. 88).

Head length.—73 mm. (fig. 88).

Eye diameter.—17 mm. (fig. 89).

Snout length.—22.5 mm. (fig. 89).

Gill rakers.—Upper limb, 6; lower limb, 20. One gill raker at the origin of the lower limb and two gill rakers on the upper limb are small or rudimentary. Meek and Hildebrand (1925: 352) gave a range on the lower limb of 17 or 18 exclusive of rudiments. Woods and Kanazawa (1951: 632) gave a count of 7+1+19 (7+20 by my combination). Woods, *in* Schultz et al. (1953: 514) gave a (combined) range of 7+20 or 21.

Scutes.—Right side, 32; left side, 33 (fig. 92). Meek and Hildebrand (1925: 352) gave a range of 26 to 30 for six specimens of 335 to 500 mm. total length. Woods and Kanazawa (1951: 632) recorded 27 for a specimen of 635 mm. standard length. Woods, *in* Schultz et al. (1953: 514) gave a range of 29 to 33 for specimens 343 to 535 mm. standard length.

Lateral line.—Mean lateral-line ratio: 1.91 (fig. 93). Woods, *in* Schultz et al. (1953: 514) gave a range for this ratio of 1.36 to 1.70.

Preopercular spines.—None.

Pigmentation.—Head, body, and fins almost uniformly brown with a black tint (fig. 98). Woods and Kanazawa (1951: 632) described the color in alcohol-preserved specimens as rich dark brown and the fresh color as grayish brown to blackish. Jordan and Evermann (1896: 925) described the color as sooty black.

Distribution

This species has not been reliably reported from the Atlantic or Gulf coasts of the United States. Poey's type specimen (1860: 222) was from Cuba, and Howell y Rivero (1938: 187) reported on the type of the synonymous *C. frontalis* Poey from Cuba. Additional Cuban records were given by Jordan (1886b: 36) and Meek and Hildebrand (1925: 352). The species has been reported from Bermuda by Woods and Kanazawa (1951: 631); from West Caicos Island, Bahamas, by Parr (1930: 45); from Puerto Rico by Erdman (1956: 327); and from Trinidad by Nichols and Murphy (1914: 263). It has been recorded by Springer and Bullis (1956: 74) from the *Oregon* collections in the Gulf of Mexico from about 110 miles and 125 miles north of Yucatan and from about 50 miles south of South Pass, La. It has been listed from Brazil by Fowler (1941b: 154, see synonymy), the Eastern Atlantic by Fowler (1936: 699, see synonymy), and from the Pacific and Indian Oceans by many authors.

Spawning

The time and place of spawning are unknown. The specimen of 635 mm. standard length reported by Woods and Kanazawa (1951: 631) from offshore Bermuda, August 8, was described as a ripe male.

Hemicaranx fasciatus (Cuvier)

Caranx fasciatus Cuvier, *in* Cuvier and Valenciennes, 1833, p. 70 (Gulf of Mexico off Mexico).
Caranx secundus Poey, 1860, p. 223 (Cuba).
Carangops secundus, Poey, 1866, p. 15 (Cuba).
Hemicaranx secundus, Jordan and Evermann, 1896, p. 914 (Cuba).
Xurel fasciatus, Jordan, Evermann, and Clark, 1930, p. 272 (Cuba; Atlantic coast of Mexico).

Since one objective of this study is to consider the species of *Caranx* that might occur off the southeastern Atlantic coast of the United States, and because the last major taxonomic treatment of *Hemicaranx fasciatus* (Jordan, Evermann, and Clark, 1930: 272) would cause it to be considered in the genus *Caranx*, a brief notation of its relationships is necessary.

Caranx fasciatus was described by Cuvier, *in* Cuvier and Valenciennes (1833: 70) from a drawing by Mocigno and Sesse of a specimen from the Atlantic off Mexico. *Caranx secundus*, described

from Cuba by Poey (1860: 223), was placed in the synonymy of *Xurel fasciatus* (Cuvier) by Jordan, Evermann, and Clark (*op. cit.*) and by Howell y Rivero (1938: 187). However, Jordan and Evermann's genus *Xurel* (1927: 505) is taxonomically unsound and has been disregarded, and most of the species placed in this genus have been returned to the genus *Caranx*. This would superficially indicate that *C. fasciatus* Cuvier should be in the genus *Caranx*.

Mrs. M. M. Dick, Museum of Comparative Zoology, kindly examined Poey's cotypes of *C. secundus* and furnished information on four of the characters commonly used to separate the genera *Caranx* and *Hemicaranx*. In one character there is a resemblance to *Caranx:* the greatest width of the maxillary is greater than the diameter of the pupil; however, this character may be expected to vary with growth. The other three characters are all of *Hemicaranx* affinity: there are no vomerine teeth; all teeth in the jaws are approximately equal in size, none enlarged; and there are no bilaterally paired fleshy keels on the peduncle. In view of the evidence, this form should be currently considered as *Hemicaranx fasciatus* (Cuvier). Cuvier is recognized as the sole author of the name in accord with Bailey (1951: 249).

A comparison of Poey's cotypes with *Hemicaranx amblyrhynchus* (Cuvier) of comparable sizes, if available, should be made to determine the relationship of these two forms.

Uraspis heidi Fowler

Uraspis heidi Fowler, 1938, p. 150 (Manasquan, N. J.). ? *Caranx lugubris* (*non* Poey), Longley, *in* Longley and Hildebrand, 1941, p. 78 (Long Key, Tortugas, Fla.).

Only two definite published records exist for this species: the type, 273 mm. standard length (320 mm. total length), from Manasquan, N. J., Sept. 3, 1938, was described by Fowler (1938: 150) and later illustrated (1952a, fig. 1). The species was corroborated and further described by Ginsburg (1952: 99, pl. 5, fig. b) from a specimen 207 mm. total length, from *Oregon* station 131, 29°20′ N., 88°35.5′ W., about 25 miles east of Pass a Loutre, La., Sept. 24, 1950.

A third known specimen, from off North Carolina in September 1954, is cataloged as USNM 163884. It agrees with the foregoing descriptions: standard length 192 mm.; total length 238 mm. Dorsal VIII, I–29. Anal I, I–22 (first anal spine covered by skin). Pectoral I–22. Gill rakers 6+14 (both sides). Scutes 36 (both sides; about 25 of the scutes on each side have forward-directed spines).

The specimen identified by Longley, *in* Longley and Hildebrand (1941: 78) as *C. lugubris* was probably this species. He described the specimen, about 80 mm. long and found in the waste of Long Key (Tortugas, Fla.) tern colony, as having strongly antrorse or forward-directed spines on the scutes of the posterior half of the straight lateral line, a leaden color, and a shorter snout and larger head than possessed by other *Caranx* species at Tortugas. All of these characters are distinctive of *U. heidi* and, since the specimen is apparently no longer available, Longley's record should be placed in the questionable synonymy of *U. heidi*.

LITERATURE CITED

Abbott, Charles Conrad.
*1868. Catalogue of vertebrate animals of New Jersey. Rept. State Geologist of New Jersey, Appendix E, Fishes, pp. 751–830.

Ahlstrom, Elbert H., and Orville P. Ball.
1954. Description of eggs and larvae of jack mackerel (*Trachurus symmetricus*) and distribution and abundance of larvae in 1950 and 1951. Fish. Bull., U. S. Fish and Wildlife Serv., 56(97): 207–245, figs. 1–28.

Anderson, William W.
1957. Early development, spawning, growth and occurrence of the silver mullet (*Mugil curema*) along the South Atlantic coast of the United States. Fish. Bull., U. S. Fish and Wildlife Serv., 57(119): 397–414, figs. 1–22.

Anderson, William W., Jack W. Gehringer, and Edward Cohen.
1956. Physical oceanographic, biological, and chemical data, South Atlantic coast of the United States, M/V *Theodore N. Gill* Cruise 1. U. S. Fish and Wildlife Serv., Spec. Sci. Rept.—Fish. No. 178, pp. 1–160, figs. 1–4.

Bailey, Reeve M.
1951. The authorship of names proposed in Cuvier and Valenciennes' "Histoire Naturelle des Poissons." Copeia, 1951(3): 249–251.

Baird, Spencer F.
1855. Report on the fishes observed on the coasts of New Jersey and Long Island during the summer of 1854, by Spencer F. Baird, Assistant Secretary of the Smithsonian Institution. Ninth Ann. Rept. Smithsonian Inst. (1854), pp. 317–352, *337.

Note.—References preceded by an asterisk were not seen.

BAPAT, S. V., and R. RAGHU PRASAD.
1952. On some developmental stages of *Caranx kalla* Cuv. & Val. Jour. Bombay Nat. Hist. Soc., 51(1): 111–115, figs. 1–4.

BARBOUR, THOMAS.
1905. Notes on Bermudian fishes. Bull. Mus. Comp. Zool., 46(7): 109–134, pls. 1–4.

BAUGHMAN, J. L.
1947. Fishes not previously reported from Texas, with miscellaneous notes on other species. Copeia, 1947(4): 280.

BEAN, BARTON A.
1891. Fishes collected by William P. Seal in Chesapeake Bay, at Cape Charles City, Virginia, September 16 to October 3, 1890. Proc. U. S. Natl. Mus., 14(843): 83–94.
1905. Fishes of the Bahama Islands, *in* The Bahama Islands, pp. 293–325, pls. LII–LXI. Johns Hopkins Press, Baltimore.

BEAN, TARLETON H.
1881. Check-list of duplicates of North American fishes distributed by the Smithsonian Institution in behalf of the United States National Museum, 1877–1880. Proc. U. S. Natl. Mus. (1880), 3(127): 75–116.
1888. Report on the fishes observed in Great Egg Harbor Bay, New Jersey, during the summer of 1887. Bull. U. S. Fish Comm. (1887), 7: 129–154, pls. I–III.
1906. A catalogue of the fishes of Bermuda, with notes on a collection made in 1895 for the Field Museum. Field Mus. Nat. Hist., Zool. Ser., 7(2): 1–72, figs. 1–14.

BEEBE, WILLIAM, and GLORIA HOLLISTER.
1935. The fishes of Union Island, Grenadines, British West Indies, with the description of a new species of star-gazer. Zoologica, 19(6): 209–224, fig. 27.

BEEBE, WILLIAM, and JOHN TEE-VAN.
1928. The fishes of Port-au-Prince Bay, Haiti, with a summary of the known species of marine fish of the Island of Haiti and Santo Domingo. Zoologica, 10(1): 1–279, text-figs.
1933. Field book of the shore fishes of Bermuda. G. P. Putnam's Sons, N. Y., xiv–337 pp., text-figs. and pls.

BENNETT, FREDERICK DEBELL.
*1840. Narrative of a whaling voyage round the globe. 2 vols. R. Bentley, London.

BEN-TUVIA, ADAM.
1953. Mediterranean fishes of Israel. Sea Fish. Res. Sta., Israel Dept. Fish., Bull. No. 8, pp. 1–40, figs. 1–20.

BIGELOW, HENRY, and WILLIAM C. SCHROEDER.
1953. Fishes of the Gulf of Maine. First revision. Fish. Bull., U. S. Fish and Wildlife Serv., 53(74): 1–577, figs. 1–288.

BLEGVAD, H.
1944. Fishes of the Iranian Gulf. Danish Sci. Invest. in Iran, Pt. 3, pp. 1–247, figs. 1–135, pls. I–XII.

BLOCH, MARC ELIESER.
*1787. Naturgeschichte der ausländischen Fische. Berlin, Pt. 2, xii–260 pp., Atlas of 216 colored plates.
1793. Naturgeschichte der ausländischen Fische. Berlin, Pt. 7, xii–144 pp., pls. CCCXXV–CCCLX.

BLOCH, MARC ELIESER, and JOHANN GOTTLOB SCHNEIDER.
*1801. Systema Ichthyologiae inconibus cx illustratum. Berolini, lx–584 pp., 110 col. pls.

BONAPARTE, CHARLES LUCIEN.
*1846. Catalogo metodico dei pesci Europei. Napoli, 97 pp.

BONNATERRE, JOSEPH P.
1788. Tableau encyclopedique et methodique des trios regnes de la nature . . . Ichthyologie. Paris, vi-215 pp., 102 pls.

BREDER, CHARLES M., JR.
1925. Notes on fishes from three Panama localities: Gatun Spillway, Rio Tapia and Caledonia Bay. Zoologica, 4 (4): 137–158, figs. 33–38.
1926. Fish notes for 1925 from Sandy Hook Bay. Copeia, 1926 (153): 121–128.
1934. Ecology of an oceanic fresh-water lake, Andros Island, Bahamas, with special reference to its fishes. Zoologica, 18(3): 57–88, figs. 26–35.
1951. A note on the spawning behavior of *Caranx sexfasciatus*. Copeia, 1951(2): 170.

CARVALHO, J. PAIVA.
1941. Nota preliminar sobre a fauna ictiologica do litoral sul do Estado de São Paulo. Boletim de Industria Animal, Brazil, No. 150, N. S., 4(3/4): 27–81.

CASTELNAU, FRANCIS L. DE.
*1855. Animaux nouveaux ou rares l'Expedition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro a Lima, et de Lima au Para; executee . . . pendant les années 1843 a 1847. 14 vols. Paris.

CHACKO, P. I.
1950. Marine plankton from the waters around the Krusadi Island. Proc. Indian Acad. Sci., 31(3): 162–174.

CUVIER, GEORGES, and ACHILLE VALENCIENNES.
1833. Histoire naturelle des poissons, 9: 1–512, pls. 246–279. F. G. Levrault, Paris.

DEKAY, JAMES E.
1842. Zoology of New-York, or the New-York fauna. Part IV. Fishes. 415 pp.; Atlas 79 pls., 250 figs. Albany, N. Y.

ERDMAN, DONALD S.
1956. Recent fish records from Puerto Rico. Bull. Marine Sci. Gulf and Caribbean, 6(4): 315–340.

EVERMANN, BARTON WARREN, and BARTON APPLER BEAN.
1898. Indian River and its fishes. Rept. U. S. Fish Comm. (1896), Pt. 22, pp. 227–248.

EVERMANN, BARTON W., and OLIVER P. JENKINS.
1891. Report upon a collection of fishes made at Guaymas, Sonora, Mexico, with descriptions of new species. Proc. U. S. Natl. Mus., 14(846): 121–165, pls. 1–2.

FOWLER, HENRY W.
1905a. New, rare or little-known scombroids. No. II. Proc. Acad. Nat. Sci. Phila. (1905–1906), 57: 56–88, figs. 1–5.
1905b. The fishes of New Jersey. Ann. Rept. New Jersey State Mus., Pt. II, pp. 35–477, text-figs., pls. 1–103.
1915. Cold-blooded vertebrates from Florida, the West Indies, Costa Rica, and eastern Brazil. Proc. Acad. Nat. Sci. Phila. (1916), 67: 244–269, figs. 1–4.
1919a. The fishes of the United States Eclipse Expedition to West Africa. Proc. U. S. Natl. Mus., 56(2294): 195–292, figs. 1–13.
1919b. Notes on tropical American fishes. Proc. Acad. Natl. Sci. Phila., 71: 128–155.
1928. The fishes of Oceania. Mem. B. P. Bishop Mus., 10: 1–540, figs. 1–82, pls. I–XLIX.
1936. Marine fishes of West Africa. Bull. Amer. Mus. Nat. Hist., 70(Pt. 2): 607–1493, figs. 276–567.
1938. Description of a new carangid fish from New Jersey. Proc. Acad. Nat. Sci. Phila., 90: 149–151.
1940. The fishes obtained by the Wilkes Expedition, 1838–1842. Proc. Amer. Philos. Soc., 82(5): 733–800, figs. 1–76.
1941a. Notes on Florida fishes with descriptions of 7 new species. Proc. Acad. Nat. Sci. Phila., 93: 81–106, figs. 1–17.
1941b. A list of the fishes known from the coast of Brazil. Arquivos de Zoologia do Estado de Sao Paulo, 3(Art. 6): 115–184.
1944. Results of the Fifth George Vanderbilt Expedition (1941). The fishes. Monogr. Acad. Nat. Sci. Phila., No. 6, pp. 57–529, figs. 1–268, pls. 1–20.
1945. A study of the fishes of the southern Piedmont and coastal plain. Monogr. Acad. Nat. Sci. Phila., No. 7, v–408 pp., pl.-figs. 1–313.
1950. Results of the Catherwood-Chaplin West Indies Expedition, 1949. Part III. The fishes. Proc. Acad. Nat. Sci. Phila., 102: 69–93, figs. 1–50.
1952a. A list of the fishes of New Jersey, with off-shore species. Proc. Acad. Nat. Sci. Phila., 104: 89–151, 1 fig.
1952b. The fishes of Hispaniola. Mem. de la Soc. Cubana de Hist. Nat., 21(1): 83–115, pls. 20–26.
1953. The shore fishes of the Colombian Caribbean. Caldasia, 6(27): 43–73.

GEOFFROY SAINT-HILAIRE, ÉTIENNE FRANCOIS.
1809. Poissons du Nil, de la mer Rouge et de la Mediterranee, *in* Description de l'Egypt . . . Histoire naturelle, vol. 1, Pt. 1, pp. 1–52, 27 pls.

GILBERT, CHARLES H.
1900. Results of the Branner-Agassiz Expedition to Brazil. III. The fishes. Proc. Washington Acad. Sci., 2: 161–184, pl. IX.

GILBERT, CHARLES H., and EDWIN C. STARKS.
1904. The fishes of Panama Bay. Mem. California Acad. Sci., 4: 1–304, pls. I–XXXIII, pl.-figs. 1–62.

GILL, THEODORE NICHOLS.
1857. On the fishes of New York. Ann. Rept. Smithsonian Inst. (1856), pp. 253–269.
1862. Catalogue of the fishes of the eastern coast of North America, from Greenland to Georgia. Proc. Acad. Nat. Sci. Phila. (1861), Ser. 2, vol. 13, Appendix, pp. 1–63.
1863. Synopsis of the carangoids of the eastern coast of North America. Proc. Acad. Nat. Sci. Phila. (1862), ser. 2, pp. 430–443.
1873. Catalogue of the fishes of the east coast of North America. Rept. U. S. Comm. Fish and Fisheries (1871–72), pp. 779–822.
1883. On the family and subfamilies of Carangidae. Proc. U. S. Natl. Mus., 5(304): 487–493.

GINSBURG, ISAAC.
1952. Fishes of the family Carangidae of the northern Gulf of Mexico and three related species. Publ. Inst. Marine Sci., 2(2): 43–117, pls. 1–7.

GIRARD, CHARLES.
1859. United States and Mexican Boundary Survey under the order of Lt. Col. W. H. Emory, Major First Cavalry, and the United States Commissioner. Ichthyology of the boundary. Rept. U. S. and Mexican Boundary Survey, 2: 1–77, 41 pls.

GOODE, G. BROWN.
1879. A preliminary catalogue of the fishes of the St. John's River and the east coast of Florida, with descriptions of a new genus and three new species. Proc. U. S. Natl. Mus. (1880), 2(73): 108–121.
1882. The carangoid fishes of the United States—pompanoes, crevalles, amber-fish, etc. Bull. U. S. Fish Comm. (1881), 1: 30–43.

GOODE, G. BROWN, and TARLETON H. BEAN.
1880. Catalogue of a collection of fishes obtained in the Gulf of Mexico, by Dr. J. W. Velie, with descriptions of seven new species. Proc. U. S. Natl. Mus., 2(98): 333–345.
1882. A list of the species of fishes recorded as occurring in the Gulf of Mexico. Proc. U. S. Natl. Mus., 5(281): 234–240.

GRAY, JOHN EDWARD.
1854. Catalogue of fish collected and described by L. G. Gronow now in the British Museum. xiv–193 pp. London.

GUDGER, EUGENE WILLIS.
1929. On the morphology, coloration and behavior of seventy teleostean fishes of Tortugas, Florida. Carnegie Inst. Washington Pub. No. 391, pp. 149–204, pls. I–IV.

GUNTER, GORDON.
1935. Records of fishes rarely caught in shrimp trawls in Louisiana. Copeia, 1935(1): 39–40.
1942. A list of fishes of the mainland of North and Middle America recorded from both freshwater and sea water. Amer. Midland Nat., 28(2): 305–326.
1945. Studies on marine fishes of Texas. Pub. Inst. Marine Sci., 1(1): 1–190.

GÜNTHER, ALBERT.
1860. Catalogue of the Acanthopterygian fishes in the collection of the British Museum. Vol. 2, xxi–548 pp. London.
1869. An account of the fishes of the States of Central America, based on collections made by Capt. J. M. Dow, F. Goodman, Esq., and O. Salvin, Esq. Trans. Zool. Soc. London, 6 (Pt. 7): 377–494, pls. LXIII–LXXXVII.
1880. Report on the shore fishes procured during the voyage of H. M. S. *Challenger* in the years 1873–1876. Rept. Sci. Results Voyage H. M. S. *Challenger*, Zool., 1 (6): 1–82, pls. 1–32.

HARRY, ROBERT R.
1953. Ichthyological field data of Raroia Atoll, Tuamotu Archipelago. Atoll Res. Bull., No. 18, pp. 1–190.

HERALD, EARL L., and ROY R. STRICKLAND.
1949. An annotated list of the fishes of Homosassa Springs, Florida. Quart. Jour. Florida Acad. Sci. (1948), 11 (4): 99–109.

HERRE, ALBERT W. C. T.
1956. Marine fishes in freshwater. Science, 123 (3206): 1035.

HIGGINS, ELMER, and JOHN C. PEARSON.
1927. Examination of the summer fisheries of Pamlico and Core Sounds, N. C., with special reference to the destruction of undersized fish and the protection of the gray trout, *Cynoscion regalis* (Bloch and Schneider). Rept. U. S. Comm. Fish., Appendix II, Doc. No. 1019, pp. 29–65, figs. 1–15.

HILDEBRAND, SAMUEL F.
1939. The Panama Canal as a passageway for fishes, with lists and remarks on the fishes and invertebrates observed. Zoologica, 24 (Pt. 1): 15–45, pls. I and II.

HOLBROOK, JOHN EDWARDS.
1860. Ichthyology of South Carolina. Vol. I, vii–205 pp., pls. I–XXVIII. University Press, Cambridge.

HOLLISTER, GLORIA.
1941. Caudal skeleton of Bermuda shallow water fishes. V. Order Percomorphi: Carangidae. Zoologica, 26 (Pt. 1, No. 8): 31–45, figs. 1–20.

HOWELL Y RIVERO, LUIS.
1938. List of the fishes, types of Poey, in the Museum of Comparative Zoology. Bull. Mus. Comp. Zool., 82 (3): 169–227.

JONES, S.
1950. Bibliography of breeding habits and development of estuarine and marine fishes of India. Jour. Zool. Soc. India, 3 (1): 121–139.

JORDAN, DAVID STARR.
1881. Description of a new species of *Caranx* (*Caranx beani*) from Beaufort, North Carolina. Proc. U. S. Natl. Mus., 3 (178): 486–488.
1886a. Notes on fishes collected at Beaufort, North Carolina, with a revised list of the species known from that locality. Proc. U. S. Natl. Mus., 9 (550): 25–30.

JORDAN, DAVID STARR—Continued
1886b. List of fishes collected at Havana, Cuba, in December, 1883, with notes and descriptions. Proc. U. S. Natl. Mus., 9 (551): 31–55.
1887. Notes on typical specimens of fishes described by Cuvier and Valenciennes and preserved in the Musée d'Histoire Naturelle in Paris. Proc. U. S. Natl. Mus., 9 (593): 525–546.

JORDAN, DAVID STARR, and ALVIN SEALE.
1906. The fishes of Samoa: Description of the species found in the Archipelago, with a provisional check list of the fishes of Oceania. Bull. U. S. Bur. Fish. (1905), 25: 173–455, figs. 1–111, pls. XXXVII–LIII.

JORDAN, DAVID STARR, and BARTON WARREN EVERMANN.
1896–1900. The fishes of North and Middle America: A descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, North of the Isthmus of Panama. Bull. U. S. Natl. Mus., No. 47: 1896, Pt. I, lx–1240 pp.; 1898, Pt. III, xxiv, 2183a–3136 pp.; 1900, Pt. IV, ci, pp. 3137–3313, pls. I–CCCXCII, figs. 1–958.
1903. Notes on a collection of fishes from the island of Formosa. Proc. U. S. Natl. Mus., 25 (1289): 315–368, figs. 1–29.
1905. The aquatic resources of the Hawaiian Islands. Part I. The shore fishes of the Hawaiian Islands, with a general account of the fish fauna. Bull. U. S. Fish Comm. (1903), 23 (Pt. I): i–xxviii, 1–574, figs. 1–229, pls. 1–65, col. pls. I–LXXIII.
1927. New genera and species of North American fishes. Proc. California Acad. Sci., ser. 4, 16 (15): 501–507.

JORDAN, DAVID STARR, BARTON WARREN EVERMANN, and HOWARD WALTON CLARK.
1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Rept. U. S. Comm. Fish. (1928), Appendix X, pp. 1–670. [Reprint, 1955.]

JORDAN, DAVID STARR, BARTON WARREN EVERMANN, and SHIGEHO TANAKA.
1927. Notes on new or rare fishes from Hawaii. Proc. California Acad. Sci., ser. 4, 16 (20): 649–680, pls. 22–24.

JORDAN, DAVID STARR, and CHARLES HENRY GILBERT.
1879. Notes on the fishes of Beaufort Harbor, North Carolina. Proc. U. S. Natl. Mus., 1 (55): 365–388.
1882a. Notes on fishes observed about Pensacola, Florida, and Galveston, Texas, with description of new species. Proc. U. S. Natl. Mus. (1883), 5 (282): 241–307.
1882b. Synopsis of the fishes of North America. Bull. U. S. Natl. Mus., No. 16, lvi–1018 pp.
1883. A review of the American Caranginae. Proc. U. S. Natl. Mus. (1884), 6 (367): 188–207.
1884. Note on *Caranx ruber* and *Caranx bartholomaei*. Proc. U. S. Natl. Mus., 7 (403): 32–33.

JORDAN, ERIC KNIGHT.
1925. Notes on the fishes of Hawaii, with descriptions of six new species. Proc. U. S. Natl. Mus., 66 (2570): 1–43, pls. 1–2.

KENDALL, WILLIAM C.
1908. Fauna of New England. 8. List of the Pisces. Occas. Papers Boston Soc. Nat. Hist., 7: 1–162.

LACÉPÈDE, BERNARD GERMAINE ÉTIENNE.
1802. Histoire naturelle des poissons. Tome 3, pp. 1–558, pls. 1–34. Paris.

LATHAM, ROY.
1918. Notes on fishes at Orient, Long Island, in 1917. Copeia, 1918 (57): 53–56.
1920. 1919 fish notes from Orient, Long Island. Copeia, 1920 (87): 91–92.

LEE, THOMAS.
1889. List of fish taken by steamer *Albatross* among Bahama Islands and at Nassau fish-market during March and April 1886. Rept. U. S. Fish Comm. (1886), Pt. 14, pp. 669–672.

LEIM, A. H.
1930. Unusual fishes and other forms in Nova Scotian waters. Proc. and Trans. Nova Scotian Inst. Sci., 17 (Pt. 4): xlvi (abstract).

LINNAEUS, CARL.
1758. Systema naturae. L. Salvii, Holmiae, ed. 10, vol. 1, ii–824 pp.
1766. Systema naturae. L. Salvii, Holmiae, ed. 12, vol. 1, 531 pp.

LINTON, EDWIN.
1905. Parasites of fishes of Beaufort, North Carolina. Bull. U. S. Bur. Fish. (1904), 24: 321–428, pls. I–XXXIV.

LONGLEY, WILLIAM H., and SAMUEL F. HILDEBRAND.
1941. Systematic catalogue of the fishes of Tortugas, Florida, with observations on color, habits, and local distribution. Carnegie Inst. Washington Publ. 535, 34: 1–331, pls. 1–34.

LÖNNBERG, AXEL JOHAN EINAR.
1894. List of fishes observed and collected in South Florida. Oefvers. Svenska Vet. Akad. Förh., 51: 109–131. Stockholm.

LÜTKEN, CHRISTIAN FREDERICK.
1880. Spolia Atlantica. Bidrag til Kundskab om Formforandringer hos Fiske under deres Vaext og Udvikling, saerligt hos nogle af Atlanterhavets højsøfiske. K. Danske Vidensk. Selsk. Skr., V, 12: 409–613, 11 figs., pls. I–V.

MARTIN, W. R.
1949. The mechanics of environmental control of body form in fishes. Univ. Toronto Studies, Biol. Ser., No. 58, pp. 1–91, figs. 1–24.

MATHER, FRANK J., III
1954. Northerly occurrences of warmwater fishes in the Western Atlantic. Copeia, 1954 (4): 292–293.

MEEK, SETH EUGENE.
1914. An annotated list of fishes known to occur in the fresh waters of Panama. Field Mus. Nat. Hist., Zool. Ser., 10 (10): 101–134.

MEEK, SETH E., and SAMUEL F. HILDEBRAND.
1925. The marine fishes of Panama. Pub. Field Mus. Nat. Hist., Zool. Ser., 15 (Pt. II): xv–xix, 331–707, pls. XXV–LXXI.

METZELAAR, JAN.
1919. Report on the fishes, collected by Dr. J. Boeke, in the Dutch West Indies, 1904–1905, with comparative notes on marine fishes of tropical West Africa. Rapport Viss. Ind. Zee. Kolonie Curacao, 2 (Pt. 2): 1–316, figs. 1–64.

MIRANDA RIBEIRO, ALPIO DE.
1918. Fauna Brasiliense (Peixes). Tomo V. Eleutherobranchios, Aspirophoros. Physoclisti. Archivos do Museu Nacional do Rio de Janeiro, 21: 7–227.

MITCHILL, SAMUEL LATHAM.
1815. The fishes of New York, described and arranged. Trans. Lit. Philos. Soc. New York, 1: 355–492, pls. I–VI.

MOWBRAY, LOUIS S.
1949. The commercial and game fishing industries of Bermuda. Paper prepared for Gulf and Caribbean Fish. Inst., Miami, Fla., Nov. 1949, 19 pp., 5 figs. Hamilton, Bermuda.

MURPHY, R. C., and FRANCIS HARPER.
1915. Ichthyological notes from Montauk, Long Island. Copeia, 1915 (23): 41–43.

NICHOLS, JOHN TREADWELL.
1912. Notes on Cuban fishes. Bull. Amer. Mus. Nat. Hist., 31 (Art. 18): 179–194.
1919. On *Caranx guara* from Bermuda. Copeia, 1919 (76): 98–99.
1920a. *Caranx bartholomaei* and *ruber* compared. Copeia, 1920 (81): 28–29.
1920b. On *Caranx crysos*, etc. Copeia, 1920 (81): 29–30.
1920c. On the range and geographic variation of *Caranx hippos*. Copeia, 1920 (83): 44–45.
1921a. A list of Turk Islands fishes, with a description of a new flatfish. Bull. Amer. Mus. Nat. Hist., 44 (Art. II): 21–24, pl. III.
1921b. Species of Northwest and Atlantic *Caranx*. Copeia, 1921 (98): 45–51.
1935. Skipjacks. Nat. Hist., 36: 268.
1936. On *Caranx ignobilis* (Forskål). Copeia, 1936 (2): 119–120.
1937a. On *Caranx hippos* (Linnaeus) from Ecuador. Copeia, 1937 (1): 58–59.
1937b. Young *Caranx ruber* (Bloch). Copeia, 1937 (4): 236–237.
1937c. Notes on carangin fishes. I—On young *Caranx hippos* (Linnaeus). Amer. Mus. Novitates, No. 967, pp. 1–5.
1938a. Notes on carangin fishes. III—On *Caranx sexfasciatus* Quoy and Gaimard. Amer. Mus. Novitates, No. 998, pp. 1–6.
1938b. Notes on carangin fishes. IV.—On *Caranx crysos* (Mitchill). Amer. Mus. Novitates, No. 1014, 4 pp., figs. 1–2.

NICHOLS, JOHN TREADWELL—Continued
1939. Young *Caranx* in the western North Atlantic. Bull. Bingham Oceanogr. Coll., 7 (Art. 2): 1–9.
1951. Notes on carangin fishes. 8. On *Caranx guara* and *Caranx georgianus*. Amer. Mus. Novitates, No. 1527, pp. 4–6.

NICHOLS, JOHN TREADWELL, AND C. M. BREDER, JR.
1927. The marine fishes of New York and Southern New England. Zoologica, 9 (1): 1–192, figs. 1–263.

NICHOLS, JOHN TREADWELL, and JANET ROEMHILD.
1946. Fin-count variation in *Caranx hippos* (Linnaeus). Marine Life, Occas. Papers, 1 (5): 15–17, fig. 1.

NICHOLS, JOHN TREADWELL, AND ROBERT CUSHMAN MURPHY.
1914. Fishes from South Trinidad Inlet. Bull. Amer. Mus. Nat. Hist., 33 (Art. 20): 261–266, figs. 1–3.
1944. A collection of fishes from the Panama Bight, Pacific Ocean. Bull. Amer. Mus. Nat. Hist., 83 (Art. 4): 221–260, figs. 1–6, pls. 15–18.

OSBECK, PEHR.
*1771. A voyage to China and the East Indies. 2 vols. B. White, London.

PADOA, A., L. SANZO, A. SPARTA, M. VIALLI, and E. TORTONESE.
1956. Fauna e flora del Golfo di Napoli. 38. Monografia: Uova, larvae e stadi giovanili di Teleostei. Pub. Sta. Zool. Napoli, 3 (2): 457–1064, figs. 287–831, pls. XXXVI–LI.

PARR, ALBERT EIDE.
1930. Teleostean shore and shallow-water fishes from the Bahamas and Turks Island. Bull. Bingham Oceanogr. Coll., 3 (Art. 4): 1–148, figs. 1–38.

POEY, FELIPE.
1860. Memorias sobre la historia natural de la Isla de Cuba, acompañadas de sumarios Latinos y extractos de Frances, 2: 97–336, pls. 10–12, 14. Habana.
1861. *Ibid.* 2: 337–442, pls. 13, 15–19. Habana.
1866. Repertorio fiscio-natural de la Isla de Cuba, 2 (1): 1–24. Habana.
1868. Synopsis Piscium Cubensium. Repertorio fiscio-natural de la Isla de Cuba, 2 (13–20): 279–484. Habana.
1875. Enumeratio Piscium Cubensium. Anales Soc. Esp. Hist. Nat. (Madrid), 4 (1): 75–161 (consecutive page nos. 1–88), pls. 5–8.

POZZI, AURELIO J., and LUIS F. BORDALE.
1935. Cuadro sistematico de los peces marinos de la Republica Argentina. Anales Soc. Cient. Argentina, Entrega IV, Tomo CXX, pp. 145–189.

RAFINESQUE, CONSTANTINE SAMUEL.
*1810. Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia, con varie osservazioni sopra i medisimi. 105 pp., 20 pls. Palermo.

RANDALL, JOHN E.
1955. Fishes of the Gilbert Islands. Atoll Res. Bull., No. 47, xi–246 pp., 1 chart.

RISSO, ANTOINE.
*1826. Histoire Naturelle des principales productions de l'Europe meridionale. Vol. 3, p. 422. Paris.

ROSEN, NILS.
1911. Contributions to the fauna of the Bahamas. III. The fishes. Lunds Univ. Arsskrift., afd. 2, bd. 7, nr. 5, pp. 46–72, 1 pl.

ROXAS, HILARIO A., and ANTOLIN G. AGCO.
1941. A review of Philippine Carangidae. Philippine Jour. Sci., Manila, 74 (1): 1–82, pls. 1–12.

SCHNAKENBECK, W.
1931. Carangidae. Rept. Danish Oceanogr. Exped. 1908–1910 to the Mediterranean and adjacent seas, No. 10, vol. 2 (Biol.), A. 14, pp. 1–20, figs. 1–19.

SCHULTZ, LEONARD P.
1949. A further contribution to the ichthyology of Venezuela. Proc. U. S. Natl. Mus., 99 (3235): 1–211, figs. 1–20, pls. 1–3.

SCHULTZ, LEONARD P., EARL S. HERALD, ERNEST A. LACHNER, ARTHUR D. WELANDER, and LOREN P. WOODS.
1953. Fishes of the Marshall and Mariana Islands. Vol. I. Families Asymmetrontidae through Siganidae. Bull. U. S. Natl. Mus., No. 202, xxxii–685 pp., figs. 1–90, pls. 1–74.

SHAPIRO, SIDNEY.
1943. The relationship between weight and body form in various species of scombroid fishes. Zoologica, 28 (Pt. 2, No. 12): 87–104, figs. 1–12.

SMITH, HUGH M.
1896. Notes on Biscayne Bay, Florida, with reference to its adaptability as the site of a marine hatching and experiment station. Rept. U. S. Fish Comm. (1895), Pt. 21, pp. 169–191.
1898. Fishes found in the vicinity of Woods Hole. Bull. U. S. Fish Comm. (1897), 17: 85–111, 1 text-fig., pl. 3.
1907. The fishes of North Carolina. North Carolina Geol. and Economic Survey, vol. 2, xi–453 pp., figs. 1–188, pls. 1–21.

SMITH, JAMES L. B.
1949. The sea fishes of southern Africa. Central News Agency, Ltd., Cape Town, xvi–550 pp., 1232 text-figs., 103 col. pls. [Hafner Publishing Co., New York.]

SNYDER, JOHN OTTERBEIN.
1904. A catalogue of the shore fishes collected by the Steamer *Albatross* about the Hawaiian Islands in 1902. Bull. U. S. Fish. Comm. (1902), 22: 513–538.

SPIX, JOHANN BAPTIST VON, and LOUIS AGASSIZ.
1829–1831. Selecta genera et species piscium quos in itinere per Brasiliam annis MDCCCXVII–MDCCCXX . . . Monachii, 1829; xvi–82 pp., pls. 1–48; 1831: 83–138 pp., pls. 49–101.

SPRINGER, STEWART, and HARVEY R. BULLIS, Jr.
1956. Collections by the *Oregon* in the Gulf of Mexico: List of crustaceans, mollusks, and fishes identified from collections made by the exploratory fishing vessel *Oregon* in the Gulf of Mexico and adjacent seas, 1950 through 1955. U. S. Fish and Wildlife Serv., Spec. Sci. Rept.: Fish. No. 196, pp. 1–134.

STEINDACHNER, FRANZ.
1894. Die Fische Liberia's. Notes Leyden Mus., 16 (1): 1–96, 4 pls.

STREETS, THOMAS H.
*1877. Contributions to the natural history of the Hawaiian and Fanning Islands and Lower California, made in connection with the United States North Pacific Surveying Expedition. 1873–75. Bull. U. S. Natl. Mus., No. 7, 172 pp.

TORTONESE, ENRICO.
1952. Monografia dei Carangini viventi nel Mediterraneo (Pisces Perciformes). Ann. Mus. Stor. Nat. Genova, 65: 259–324, figs. 1–19.
1955. Note intorno ai Carangidi del Mediterraneo. Estratto dall' Arch. Oceanogr. e Limn., 10 (3): 185–195, figs. 1–3.

VLADYKOV, V. D.
1935. Some unreported and rare fishes for the coast of Nova Scotia. Proc. Nova Scotian Inst. Sci., 19 (Pt. 1): 1–8.

WAKIYA, YOJIRO.
1924. The carangoid fishes of Japan. Ann. Carnegie Mus., 15 (2–3): 139–244, pls. XV–XXXVIII.

WALFORD, LIONEL A.
1937. Marine game fishes of the Pacific Coast—Alaska to the Equator. xxix–207 pp., 469 pls., text-figs. Univ. California Press, Berkeley.

WEBER, MAX, and L. F. DE BEAUFORT.
1931. The fishes of the Indo-Australian Archipelago. VI. Perciformes (continued). xii–448 pp., figs. 1–81. E. J. Brill Ltd., Leiden.

WOODS, LOREN P., and ROBERT H. KANAZAWA.
1951. New species and new records of fishes from Bermuda. Fieldiana, Zool., 31 (53): 629–644, figs. 134–137.

YARROW, HARRY CRECY.
1877. Notes on the natural history of Fort Macon, N. C., and vicinity. (No. 3). Proc. Acad. Nat. Sci. Phila., 29: 203–218.

ADDENDA

Subsequent to submission of the manuscript for publication, additional specimens were examined and records obtained that warrant comment.

Six specimens of *crysos* between 210 mm. and 240 mm. standard length, that were caught from a pier at Pensacola Beach, Fla., July 1, 1958, had enlarged gonads (3 males and 3 females); but the gonads were not as large or as well-developed as *crysos* taken offshore in the Gulf of Mexico. Body bars were visible on the two smallest fish, 210 mm. and 220 mm., when they were caught, but the fish were dead and the bars had disappeared within 5 minutes after the fish had been pulled out of the water.

An 11.0-mm. specimen of *ruber* (SAFI collection) is slightly smaller than the smallest specimen previously known to be available. It is similar in proportions and pigmentation to the 12.4-mm. *ruber* of figure 34.

Comparison of measurements of four large specimens of *latus*, 259 mm. (UF collection), 319 mm. (CNHM 39717), 478 mm. (CNHM 46773), and 602 mm. standard length (CNHM 46772), with growth trends of the smaller specimens indicates that: The third dorsal spine length-standard length regression is generally stable from about 130 to 319 mm. standard length, but a decrease in spine growth rate has occurred by 478 mm. The first dorsal soft-ray length-standard length regression is essentially unchanged from 40 to 602 mm. The body depth at pelvic-standard length regression is changed with a decrease in depth growth rate occurring between 170 mm. and 259 mm. The snout length-standard length regression remains generally stable from 16 to 602 mm. The eye diameter-standard length regression is apparently changed between 170 mm. and 259 mm. with a subsequently slower eye growth rate.

The recent acquisition of three small specimens, 11.0 mm. (SAFI collection), 12.8 mm. (UF collection), and 14.2 mm. standard length (SAFI collection), will be useful in later analysis of differences in larval and early juvenile *latus* and *hippos*; but a larger series still is needed: (1) The 11.0-mm. specimen is identified as *Caranx* sp. ("*latus* and/or *hippos*"). Depth at pelvic, 6.2 mm. Third dorsal spine length, 1.94 mm. Second anal spine length, 1.0 mm. Preopercular-angle spine length, 0.35 mm. Dorsal and anal soft-rays, 20 and 16. Preopercular upper-limb and lower-limb spines, 0 and 4. The straight part of the lateral line is prominent, but the curved part is indistinct. No "completely developed scutes" are present. The interneural and interhemal spines have not protruded above the body surface. The body is densely pigmented except for areas below and beneath the pectoral,

pigmented between spines 1 and 5, there are a few melanophores between spines 5 and 7, and the fin is unpigmented between spines 7 and 8. (2) The 12.8-mm. specimen is questionably identified as *hippos*. Depth at pelvic, 7.45 mm. Preopercular-angle spine length, 0.44 mm. Dorsal and anal soft-rays, 20 and 16. Preopercular upper-limb and lower-limb spines, 0 and 5. The lateral line is formed. No "completely developed scutes" are present. Projections of the interneural and interhemal spines have protruded above the body surface. The first three body bars are present, but the fourth and fifth are represented by a single broad pigment mass. (3) The 14.2-mm. specimen is identified as *hippos* because of its similarity to the 15.3-mm. specimen of *hippos* previously discussed, especially in body depth at pelvic (7.8 mm.) and mean lateral-line ratio (0.97). Preopercular-angle spine length, 0.27 mm. Dorsal and anal soft-rays, 20 and 17. Scutes, 9 right side and 10 left. Preopercular upper-limb and lower-limb spines, 0 and 5. The five body bars are completely formed.

The 12.8-mm. specimen is questionably identified as *hippos* only because it cannot be adequately distinguished from *latus*. This is the smallest specimen of either of these species to be recorded from inshore waters. It was seined from the surf on Plantation Key, Fla. If, as suspected, *Caranx* of this small size normally inhabit offshore waters, this specimen probably was carried inshore by currents from the nearby Gulf Stream.

A 65.5-mm. standard length specimen of *dentex* (CNHM 4936) from Bermuda has been examined, and is the smallest juvenile of this species to be reported. Dorsal and anal soft-rays, 26 and 23. Gill rakers, 14 + 27. Scutes, 30 right side and 26 left. Third dorsal spine length, 8 mm. First dorsal soft-ray broken, but apparently was shorter than third dorsal spine. Mean lateral-line ratio, 0.80. All counts and measurements of this specimen correspond to trends or ranges of other specimens of *dentex* examined and reported in the literature, except that its upper-limb gill-raker count (14) extends the range for this character. Pigmentation had faded completely.

Measurements of the 650-mm. standard length specimen of *lugubris* (CNHM 48389) from Bermuda, previously described by Woods and Kanazawa (1951: 631), and of the 602-mm. specimen of *latus* (CNHM 46772), were compared with the estimated regression lines on the graphs accommodating the large specimens of *hippos* (figs. 90 and 91). The following comparative features were indicated for these three species around the 600- to 650-mm. size range: First dorsal soft-ray length (*lugubris*, 168 mm.; *latus*, 114 mm.) and depth at pelvic (*lugubris*, 240 mm.; *latus*, 185 mm.): *latus* and *hippos* are similar, but *lugubris* has a much longer soft-ray and greater depth than either of these. Third dorsal spine length (*lugubris*, 58 mm.; *latus*, 49 mm.) and snout length (*lugubris*, 65 mm.; *latus*, 54 mm.): *lugubris* has a longer spine and snout than *hippos*, and *latus* may be intermediate between the two in these characters. Eye diameter (*lugubris*, 36 mm.; *latus*, 47 mm.): *latus* has an appreciably larger eye than the other two. Head length (*lugubris*, 183 mm.; *latus*, 190 mm.): the three species are generally similar, but *latus* may have a significantly longer head than *lugubris*, with *hippos* intermediate between these two. Pectoral length (*lugubris*, 233 mm.; *latus*, 202 mm.): the three species are generally similar in this character. The mean lateral-line ratio of the 650-mm. *lugubris* (1.64) is distinct from the predicted range of *hippos*, but is within that of *latus*.

A recent publication by McKenney, Alexander, and Voss (1958, Bull. Marine Sci. Gulf and Caribbean, 8 (2): 167–200, figs. 1–7) described juvenile *crysos* and larvae, identified as this species, as small as 2.6 mm. (snout to tip of urostyle). Their series of 148 specimens is fairly complete from 3.8 mm. to over 50 mm., but there is a small discontinuity in their series between 3.8 mm. and the three smallest larvae, 2.6 mm., 2.7 mm., and 2.8 mm. No indication is given as to how these larvae may be distinguished from other carangid larvae. Their figures and descriptions bear several minor discrepancies to my figures and accounts for *crysos*. Differences in pigmentation descriptions might be due to fading or individual variation. Development of their 4.2-mm. larva (their fig. 1c) had not progressed to the stage of the 3.8-mm. specimen (my fig. 16) that I suspect to be a larval *crysos*. They noted that the preopercular spines reach their greatest relative size in the 4.0- to 5.0-mm. group and then decline in importance—my less-complete data had suggested that the preopercular-angle spine ceased to increase in length at some size around 7 mm. (fig. 31) and

that the number of upper-limb and lower-limb spines began to decrease in number at about 20 to 25 mm. (table 1). They stated that the terminal dorsal and anal soft-rays were not formed on some specimens until the fish were 6.0 mm. long, but that one 5.0-mm. specimen had these rays—my data indicated that the adult complement of all fin rays had begun ossification by about 8.0 mm. Their ranges of dorsal and anal soft-rays coincided with my tabulations. They mentioned that the procumbent spine of the dorsal fin is an interneural spine (see under Definitions, p. 420). A useful listing of stomach contents of the larval and juvenile specimens is given. The authors suggested that *crysos* may spawn throughout the year with the main spawning occurring from January through August—specimens taken off the southeastern Atlantic coast had produced my estimation that the spawning season contributing young *crysos* to this area extended from April into September. They listed specimens of 12.1 to 24.2 mm. from inshore at Matecumbe Key, Fla.—these are the smallest *crysos* to be recorded from inshore waters, but they could have been carried inshore from the nearby Gulf Stream (Florida Current) by temporary currents.

Specimens were obtained from the following sources in addition to those previously acknowledged: Earl E. Deubler, Jr., University of North Carolina (UNC); Donald C. Scott, University of Georgia (UG); Loren P. Woods, Chicago Natural History Museum (CNHM); Bernard Lewis, Institute of Jamaica (IJ).

SPECIMENS EXAMINED

Caranx crysos

Atlantic Beach, Carteret Co., N. C., 27 Oct. 1956, (1 specimen), 126 mm. standard length, UNC 806, group No. 42.—30°00′ N., 80°10′ W., *Silver Bay* sta. 476, 18 June 1958, (1) 14.5 mm., SAFI collection.—29°54′ N., 80°11′ W., *Silver Bay* sta. 481, 19 June 1958, (7) 15.5 to 25 mm., SAFI.—29°48′ N., 80°12′ W., *Silver Bay* sta. 470, 17 June 1958, (2) 17.5 mm. and 22 mm., SAFI.—29°38′ N., 80°14′ W., *Silver Bay* sta. 460, 13 June 1958, (6) 14.4 to 31 mm., SAFI.—29°38′ N., 80°09′ W., *Silver Bay* sta. 471, 17 June 1958, (8) 13.1 to 25 mm., SAFI.—Gulf of Mexico, *Oregon* sta. 2198, (15) 20.5 to 50 mm., SAFI.

Caranx ruber

32°13.5′ N., 64°32.5′ W., off Bermuda, 6 Aug. 1948, (1) 94 mm., CNHM 49168.—30°00′ N., 80°10′ W., *Silver Bay* sta. 476, 18 June 1958, (6) 32 to 63 mm., SAFI.—29°54′ N., 80°11′ W., *Silver Bay* sta. 481, 19 June 1958, (9) 14.1 to 20 mm., SAFI.—29°48′ N., 80°12′ W., *Silver Bay* sta. 470, 17 June 1958, (13) 11.0 to 53.5 mm., SAFI.—29°38′ N., 80°16′ W., *Silver Bay* sta. 461, 13 June 1958, (2) 24.5 mm. and 25.5 mm., SAFI.—29°38′ N., 80°14′ W., *Silver Bay* sta. 460, 13 June 1958, (5) 15.5 to 22.5 mm., SAFI.—29°38′ N., 80°09′ W., *Silver Bay* sta. 471, 17 June 1958, (17) 14.8 to 59 mm., SAFI.—29°19′ N., 79°58′ W., *Silver Bay* sta. 454, 12 June 1958, (2) 20 mm. and 23 mm., SAFI.—27°53′ N., 79°09′ W., *Silver Bay* sta. 442, 9 June 1958, (5) 20 to 25 mm., SAFI.—Gulf of Mexico, *Oregon* sta. 2196, (7) 18.5 to 23 mm., SAFI.—Gulf of Mexico, *Oregon* sta. 2198, (22) 19 to 74 mm., SAFI.—Southwest Cays, Glover Reef, Caribbean Sea, 16 Jan. 1940, (1) 160 mm., CNHM 39813.

Caranx bartholomaei

Flatts Inlet, Bermuda, (1) 61 mm., CNHM 48629.—Offshore between Beaufort Inlet and Cape Lookout, N. C., Sept. 1956, (1) 156 mm., UNC 896.—30°00′ N., 80°10′ W., *Silver Bay* sta. 476, 18 June 1958, (3) 20.5 to 38.5 mm., SAFI.—29°38′ N., 80°16′ W., *Silver Bay* sta. 461, 13 June 1958, (1) 24 mm., SAFI.—29°38′ N., 80°09′ W., *Silver Bay* sta. 471, 17 June 1958, (3) 28.5 to 33.5 mm., SAFI.—29°22′ N., 80°05′ W., *Silver Bay* sta. 227, 24 Nov. 1957, (1) 24 mm., SAFI.—East end of Kingston Harbor, Jamaica, 14 May 1957, (1) 62.5 mm., UF collection.

Caranx sp. ("*latus* and/or *hippos*")

29°48′ N., 80°12′ W., *Silver Bay* sta. 470, 17 June 1958, (1) 11.0 mm., SAFI.

Caranx latus

Flatts Inlet, Bermuda, (1) 52 mm., CNHM 48629.—Richardson's Cove, Bermuda, 2 Sept. 1948, (2) 55 mm. and 64 mm., CNHM 48356.—Flatts Inlet, Bermuda, 31 Jan. 1933, (1) 41.5 mm., CNHM 48652.—Little River at Calabash, N. C., 23 Oct. 1957, (2) 40 mm. and 61 mm., SAFI.—St. Simons Island, Ga., 18 Aug. 1958, (1) 65 mm., SAFI.—Jekyll Causeway, Brunswick, Ga., 4 Aug. 1958, (2) 114 mm. and 124 mm., SAFI.—Garden Key, Tortugas, Fla., 20 Mar. 1951, (7) 116 to 155 mm., UG collection.—Alacran Rocks, Campeche Banks, Gulf of Mexico, *Oregon*, 27 Aug. 1951, (1) 478 mm., CNHM 46773.—Alacran Rocks, Campeche Banks, *Oregon*, 27 Aug. 1951, (1) 602 mm., CNHM 46772.—Southwest Cays, Glover Reef, Caribbean Sea, 16 Jan. 1940, (1) 319 mm., CNHM 39717.—Runaway Bay, Eaton Hall, Jamaica, about 12 June 1958, (1) 259 mm., UF collection.

Caranx hippos ?

Plantation Key, Fla., 12 June 1956, (1) 12.8 mm., UF collection.

Caranx hippos

Great Egg Harbor, N. J., 10 July 1958, (2) 34 mm. and 41 mm., SAFI.—Ocean View, Va., (1) 105 mm., CNHM 1164.—Little River at Calabash, N. C., 23 Oct. 1957, (2) 35.5 mm. and 50 mm., SAFI.—East shore of Scuppernong River, Albemarle Sound, about 3.5 miles northwest of Columbia, N. C., 7 Aug. 1956, (1) 60 mm., UNC 345.—Jeremy Creek, McClellansville, S. C., 21 Aug. 1956, (2) 126 mm. and 127 mm., SAFI.—Jeremy Creek, Cape Romain, S. C., 2 Nov. 1956, (2) 45.5 mm. and 53.5 mm.,

SAFI.—Mays River drainage, 5 miles west of Bluffton, S. C., 16 July 1956, (1) 83 mm., SAFI.—Atlantic Ocean off St. Catherines, Blackbeard, and Sapelo Islands, Ga., 15 Oct. 1949, (2) 110 mm. and 119 mm., UG coll. No. 125.—St. Simons Island, Ga., 3 July 1958, (4) 25 to 30.5 mm., SAFI.—St. Simons Island, Ga., 18 Aug. 1958, (11) 25.5 to 36 mm., SAFI.—Jekyll Causeway, Brunswick, Ga., 20 June 1958, (12) 25 to 38 mm., SAFI.—Same area, 3 July 1958, (3) 42 to 47 mm., SAFI.—Same area, 21 July 1958, (1) 50 mm., SAFI.—Same area, 1 Aug. 1958, (1) 68 mm., SAFI.—Same area, 3 Aug. 1958, (4) 87.5 to 109 mm., SAFI.—Same area, 4 Aug. 1958, (11) 95 to 111 mm., SAFI.—Same area, 2 Sept. 1958, (1) 43.5 mm., SAFI.—Cumberland River, near Cumberland Island, Ga., 21 Aug. 1958, (1) 104 mm., SAFI.—Halifax River, at Karona Crossing, Fla., 28 June 1957, (1) 36 mm., SAFI.—North River, Vilano Beach, near St. Augustine, Fla., 21 Aug. 1950, (1) 32 mm., UG coll. No. 180A.—30°00′ N., 80°10′ W., *Silver Bay* sta. 476, 18 June 1958, (1) 15.5 mm., SAFI.—29°56′ N., 80°10′ W., *Silver Bay* sta. 483, 20 June 1958, (1) 28 mm., SAFI.—29°54′ N., 80°11′ W., *Silver Bay* sta. 481, 19 June 1958, (1) 27 mm., SAFI.—29°48′ N., 80°12′ W., *Silver Bay* sta. 470, 17 June 1958, (2) 16.7 mm. and 16.9 mm., SAFI.—29°38′ N., 80°09′ W., *Silver Bay* sta. 471, 17 June 1958, (5) 17.6 to 20.2 mm., SAFI.—29°38′ N., 80°14′ W., *Silver Bay* sta. 460, 13 June 1958, (1) 14.2 mm., SAFI.—Garden Key, Tortugas, Fla., 20 Mar. 1951, (1) 163 mm., UG coll. No. 196.—Ft. Pickens, Santa Rosa Island, Fla., 5 July 1958, (4) 32.5 to 38.5 mm., SAFI.—Ocean Springs vicinity, Miss., (1) 114 mm., UG coll. No. 506.—28°17′ N., 87°52′ W., *Oregon* sta. 1145, 26 July 1954, (1) 28 mm., CNHM 61349.—27°34′ N., 89°00′ W., *Oregon* sta. 1134, 22 July 1954, (5) 19 to 27 mm., CNHM 61348.—Porto Bello, Panama, 24–28 Apr. 1911, (1) 105 mm., CNHM 20335.—Simmons Bay, St. Thomas, Jamaica, 4 Oct. 1951, (1) 103 mm., IJ collection.—Pernambuco, Brazil, (1) 94.5 mm., CNHM 3830.—Santos, Brazil, (1) 147 mm., CNHM 3362.

Caranx dentex

Bermuda, (1) 65.5 mm., CNHM 4936.

Caranx lugubris

South of Ariadne Bank, offshore, Bermuda, 5 Aug. 1948, (1) 650 mm., CNHM 48389.

○

Blank page retained for pagination

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

LIFE HISTORY OF THE THREESPINE STICKLEBACK *Gasterosteus aculeatus* Linnaeus IN KARLUK LAKE AND BARE LAKE KODIAK ISLAND, ALASKA

BY JOHN GREENBANK AND PHILIP R. NELSON

FISHERY BULLETIN 153

From Fishery Bulletin of the Fish and Wildlife Service

VOLUME 59

UNITED STATES GOVERNMENT PRINTING OFFICE • WASHINGTON • 1959

For sale by the Superintendent of Documents, U. S. Government Printing Office
Washington 25, D. C. - Price 25 cents

Library of Congress catalog card for this bulletin:

Greenbank, John.

Life history of the threespine stickleback *Gasterosteus aculeatus* Linnaeus in Karluk Lake and Bare Lake, Kodiak Island, Alaska, by John Greenbank and Philip R. Nelson. Washington, U. S. Govt. Print. Off., 1959.

iii, 537–559 p. illus., map, diagrs., tables. 26 cm. (U. S. Fish and Wildlife Service. Fishery bulletin 153)

"From Fishery bulletin of the Fish and Wildlife Service, volume 59."

Bibliography: p. 558–559.

1. Three-spined stickleback. I. Nelson, Philip R., joint author. II. Title. (Series: U. S. Fish and Wildlife Service. Fishery bulletin, v. 59, no. 153)

[SH11.A25 vol. 59, no. 153] Int 59–54

U. S. Dept. of the Interior. Library
for Library of Congress

Library of Congress catalog card for the series, Fishery Bulletin of the Fish and Wildlife Service:

U. S. *Fish and Wildlife Service.*

Fishery bulletin. v. 1–

Washington, U. S. Govt. Print. Off., 1881–19

v. in illus., maps (part fold.) 23–28 cm.

Some vols. issued in the congressional series as Senate or House documents.

Bulletins composing v. 47– also numbered 1–

Title varies: v. 1–49, Bulletin.

Vols. 1–49 issued by Bureau of Fisheries (called Fish Commission, v. 1–23)

1. Fisheries—U. S. 2. Fish-culture—U. S. I. Title.

SH11.A25 639.206173 9–35239 rev 2*

Library of Congress [r55e1]

CONTENTS

	Page
Introduction	537
History and literature	537
Description of the waters	537
Biology of the stickleback	540
Morphological variation	541
Numbers	543
Habitat	544
Age, size, and growth	544
Reproduction	550
Physiology and behavior	554
Food habits	555
Role as prey	556
Relation to red salmon	557
Summary	557
Literature cited	558

ABSTRACT

The threespine stickleback occurs in large numbers in Karluk Lake, Kodiak Island, Alaska, an important water in studies of red salmon production. The life history of the stickleback in Karluk and Bare Lakes presents many interesting phases. It has few lateral plates, which is characteristic of the fresh-water sticklebacks. It has a lifespan of about two-and-one-quarter years and in that period spawns once, or twice at the most. Structurally, the stickleback is hermaphroditic. It feeds on planktonic invertebrates and insect larvae. A possible interrelationship between stickleback and juvenile red salmon is that both consume the same kinds of food. Both species are preyed on by the Arctic charr.

LIFE HISTORY OF THE THREESPINE STICKLEBACK *Gasterosteus aculeatus* Linnaeus IN KARLUK LAKE AND BARE LAKE, KODIAK ISLAND, ALASKA

By John Greenbank[1] and Philip R. Nelson, *Fishery Research Biologists*, BUREAU OF COMMERCIAL FISHERIES

Over a period of many years, investigations have been made by the U. S. Fish and Wildlife Service at Karluk Lake and Bare Lake on Kodiak Island, Alaska. These have covered, primarily, the production of red (sockeye) salmon. They have embraced many biological and limnological factors which are related to salmon production, including the presence in these waters of other fishes whose life histories are interrelated with that of the red salmon.

One of these species is the threespine stickleback, *Gasterosteus aculeatus* Linnaeus, which occurs in large numbers in these lakes. As a part of the field studies, stickleback specimens were collected, seine hauls that captured sticklebacks were recorded, stomach samples were analyzed, fish samples for age determination were taken, and numerous observations of habits were made.

Most of the fieldwork on the sticklebacks was done by Nelson, and crews under his supervision. Greenbank has analyzed and evaluated the data. We present this report as a summary of our knowledge of the stickleback in these waters and its relation to red salmon production, and as a contribution to the life history of the species.

C. Y. Conkle, Robert F. Raleigh, C. S. Thompson, Carl E. Abegglen, and others assisted in the collection of specimens and information. The drawings were made by R. J. Kramer; the photograph for figure 13 was taken by Fred Rabe. Information on the Karluk Lake sticklebacks was furnished by C. E. Walker of the Fisheries Research Institute.

HISTORY AND LITERATURE

The threespine stickleback is widespread and easily observed and has been studied by many workers through the centuries. A large number of references exist in the published literature. Many of these, however, consist of little more than notes regarding such things as nest-building behavior.

Leiner (1929, 1930, and 1934) has studied the species intensively. Bertin (1925) published a monograph on sticklebacks. Many of his conclusions have been objected to by later workers, but at least he stimulated research and thought.

M. J. Heuts has made a thorough study of the threespine stickleback in Western Europe and has published (1947, 1947a, and 1949) important papers on variation, physiology, and genetics.

Wunder (1928, 1930) published the results of studies and experiments concerning behavior. The reproduction of the stickleback has been described by Craig-Bennett (1931) and others. Food studies have been made by Markley (1940) and by Hynes (1950). Age and growth of three species of sticklebacks in the British Isles have been worked out by Jones and Hynes (1950).

In North America, few papers have dealt at length with the life history of the stickleback. Cox (1922) reviewed the various species of sticklebacks of the Hudson Bay region; Myers (1930) made a study of races of the threespine stickleback in California and Lower California; and Vrat (1949) reported on the reproduction of the threespine stickleback in California.

DESCRIPTION OF THE WATERS

The southwestern section of Kodiak Island (fig. 1), in which Karluk Lake and Bare Lake lie, is a low plain with numerous mountains rising from it. The coastline is broken by many bays. The drainage pattern is involved. The vegetation is tundralike, composed of grasses, various flowering plants, willows, and alder, with cottonwood and birch trees irregularly distributed along the stream courses.

The area lies in a temperate climate, with much cloudy weather and a mean annual rainfall of about 50 inches. The air temperature ranges

[1] Present address: State Teachers College, Kirksville, Mo.

NOTE:—Approved for publication February 2, 1958. Fishery Bulletin 153.

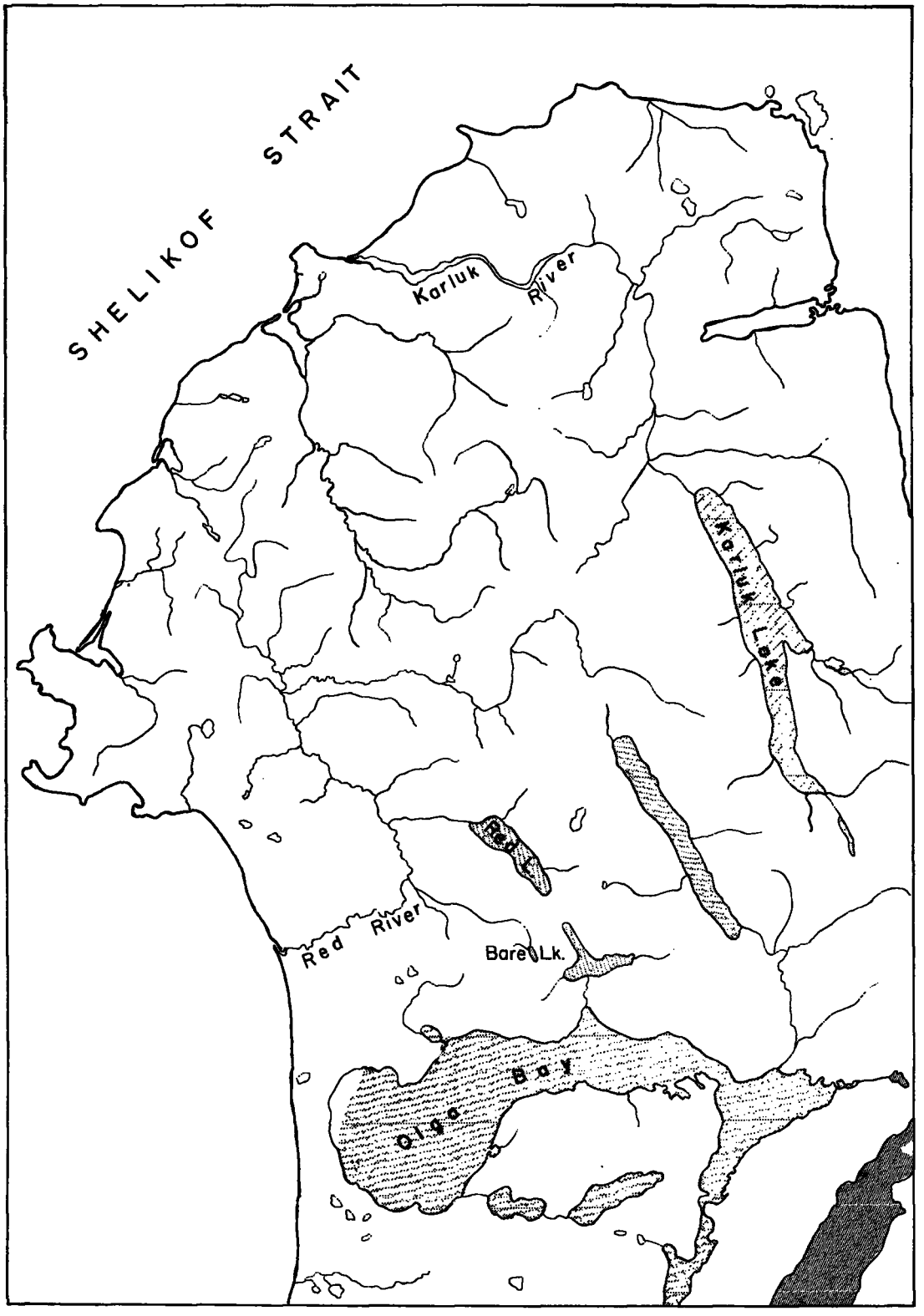

FIGURE 1.—Western Kodiak Island.

from below −18° C. in winter to above 29° C. in summer.

Karluk Lake is drained by Karluk River, which flows some 23 miles and empties into Karluk Lagoon, and thence into the ocean. Several small streams plus the drainage of two small lakes, Thumb and O'Malley, flow into Karluk Lake.

The physical and chemical characteristics of Karluk Lake have been described by Juday et al. (1932). The lake lies at an elevation of 350 feet above sea level. It is 12 miles long; its greatest width is 2 miles, and its area 15 square miles. It has relatively little shoal area, only 10 percent of the total area being less than 30 feet deep. The maximum depth is 410 feet. The beaches are of gravel and rubble, the predominant rock material being shale. The water is clear, has a pH ranging from 7.0 to 8.7, and is low in carbonate and in total dissolved minerals. It contains an abundance of dissolved oxygen at all depths throughout the summer.

Bare Lake is only 15 miles from Karluk Lake but belongs to another drainage. It is drained by a small stream, Bare Creek, that flows into Red River.

Bare Lake is 380 feet above sea level. It is slightly less than 1 mile long; its greatest width is 1,600 feet, and its area about 120 acres. The maximum depth is 25 feet and the mean depth 13 feet. The bottom is gravel and rubble on the shoals and soft mud in the deeper area. The chemical characteristics are similar to those of Karluk Lake.

In both Karluk Lake and Bare Lake, vegetation is sparse. The predominant forms are water moss, *Fontinalis;* quillwort, *Isoëtes;* and water buttercup, *Ranunculus.* There are scattered patches of filamentous algae, and in Karluk Lake there are beds of sparse *Potamogeton.*

Juday et al. (1932) have described the plankton of Karluk Lake, and Nelson and Edmondson (1955) that of Bare Lake. Bottom-dwelling animals are few in numbers of species. Diptera larvae, especially of Chironomidae, are abundant in places, and there are larvae of caddis flies (Trichoptera), mayflies (Ephemeroptera), and other insects. Included also are pea clams (Pelecypoda) and snails (Gastropoda).

The fishes of Bare Lake consist of seven species: red salmon (*Oncorhynchus nerka*), coho salmon (*Oncorhynchus kisutch*), and king salmon (*Oncorhynchus tshawytscha*); rainbow or steelhead trout (*Salmo gairdnerii*), Dolly Varden charr (*Salvelinus malma*), threespine stickleback (*Gasterosteus aculeatus*), and a fresh-water sculpin (*Cottus aleuticus*).

Karluk Lake has, in addition to these species, arctic charr (*Salvelinus alpinus*) and chum salmon (*Oncorhynchus keta*). Pink salmon (*Oncorhynchus gorbuscha*) spawn in Karluk River and a few enter the lake. Small numbers of the ninespine stickleback (*Pungitius pungitius*) have been seen in Karluk Lake (Charles E. Walker, private communication, 1956).

Karluk Lake has been the site of extensive biological investigations. These date back to 1889, when Tarleton H. Bean made a reconnaissance survey of the lake. Various scientists visited Karluk Lake in the years between 1900 and 1920. Henry O'Malley and Charles H. Gilbert made a survey of the salmon spawning grounds in 1921.

In 1926, a party led by Willis H. Rich conducted a limnological study of the lake including a physical survey (Juday et al., 1932). Studies of the lake, especially of its red salmon runs, have been carried out on a year-to-year basis since then.

A weir for counting adult red salmon ascending the Karluk River was installed near the mouth of the river in 1921. It was moved in 1942 about 13 miles upriver, and moved again in 1945 to its present location just below the outlet of Karluk Lake. The current investigations include counts and estimates of adult salmon entering the lake, of spawning salmon in the tributary streams, and of young salmon leaving the lake to go to the ocean. Studies also are being made of certain aspects of the life history of the red salmon and of the limnology of the lake.

Bare Lake was selected by the Fish and Wildlife Service (Nelson and Edmondson, 1955) for experiments in lake fertilization, because it represents the waters of the area and yet is small enough to be worked on feasibly. Preliminary surveys were conducted in 1949, and each summer, starting with 1950, the lake has been treated with commercial fertilizer. Various limnological

observations have been made as a means of assessing the effectiveness of fertilization in increasing lake productivity.

BIOLOGY OF THE STICKLEBACK

Since it was named and described by Linnaeus in 1758, *Gasterosteus aculeatus* has had a long and involved nomenclatural history. Specific and subspecific names have been based in the main on variations in the numbers of bony plates and of fin rays, on length of spines, and on selection of environment.

The threespine stickleback in Karluk and Bare Lakes is of the partially armored form. For present purposes, we shall not assign to it a name designating a subspecies or variety, but shall simply refer it to the species *Gasterosteus aculeatus*.

The ninespine stickleback, *Pungitius pungitius* (Linnaeus), is the only other member of the family which occurs in the waters of the North Pacific area, and it is found only in small numbers in Karluk Lake.

The sticklebacks as a group (family Gasterosteidae) differ considerably in morphology and appearance from even their nearest relatives among the fishes. They are small fish and have as a distinguishing character a number of isolated (free) stout spines in front of the dorsal fin. These spines are short but sharp pointed. At the posterior side of each spine is a small, triangular fin membrane. The dorsal spines can be erected or depressed by the fish and will lock weakly in the erect position. There is one short anal spine, and the pelvic fin consists of one heavy spine and one or two rudimentary rays. There are no scales, but some of the species have bony plates.

Gasterosteus aculeatus, the threespine stickleback, is a moderately slender, streamlined fish. The snout is somewhat pointed. The caudal peduncle is slender, the tail shallowly forked (fork length of fish equals approximately 0.97 times total length). The anal fin originates well back of the dorsal fin (almost even in *Pungitius pungitius*). The species is extremely variable in numbers of lateral bony plates and fin rays. Figure 2 represents an adult threespine stickleback from Karluk Lake.

The color varies with the locality and the type of water. Except for spawning males, dull tones predominate. Generally the upper surfaces are olive, greenish, or brown, the colors becoming lighter on the sides. The ventral surface is light yellow, white, or silver. Dark-brown pigmentation occurs in small indefinite blotches and in a variable pattern of transverse patches along the sides. The fins are pale. The rays of the pectoral fin are outlined by lines of small dots of black pigment. The breeding female in Karluk and Bare Lakes does not assume any bright coloration. The male, in breeding season, from the snout to the back of the pelvic fin, is red to yellowish-salmon colored. The color tones are clear but not bold. Bluish tints may appear along the sides and on the face. Vrat (1949) mentions the iridescent blue-green color in the iris of the eye of the breeding male and indicates that this color is noticeable for a period of many days or weeks. We have found this condition to hold for the Kodiak Island sticklebacks.

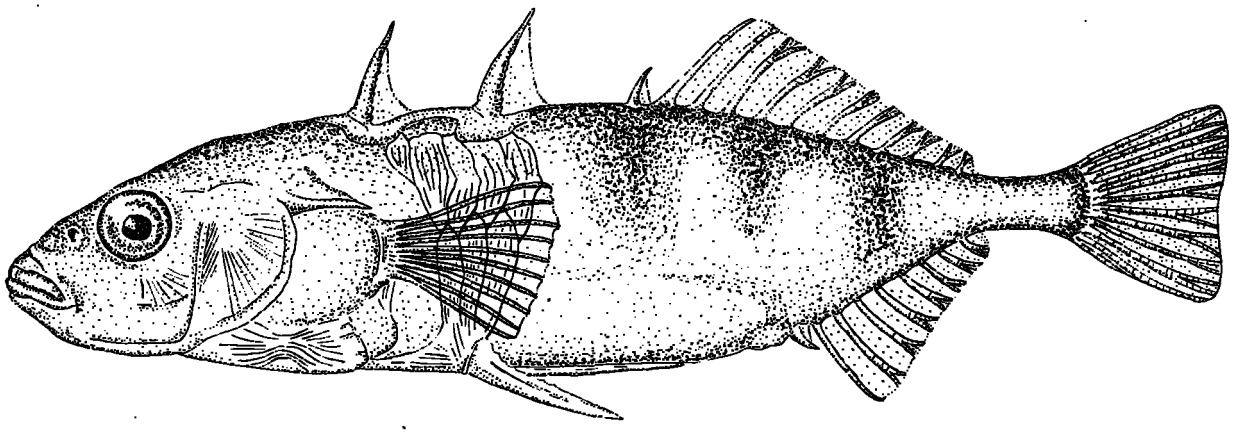

FIGURE 2.—Adult threespine stickleback (*Gasterosteus aculeatus*).

When the female is approaching the time of spawning, the belly becomes distended visibly. In the early part of the year, before the breeding characters are evident, the two sexes look much alike.

Morphological Variation

Throughout its geographical range, the species *Gasterosteus aculeatus* is subject to a large amount of morphological variation. There are minor differences in color and color pattern and in body shape. More pronounced variations occur in numbers of vertebrae, fin rays, and lateral bony plates.

Within the species, the number of lateral plates varies from none to about 35. Most of the long list of specific, subspecific, and racial names which have been used have to do with the degree of armature.

It has long been recognized that populations which are year-round inhabitants of fresh waters have few plates, while those that live in salt water, and enter fresh water only for spawning, are many-plated. Bertin (1925) made an analytical study of populations of threespine stickleback throughout Europe and came to the conclusion that the number of bony plates is directly correlated with the salinity of the environment, and that a continuous gradation occurs from water of high salinity to fresh water.

However, Heuts (1947, 1947a) presents strong evidence that such a clinal gradation does not exist. The European stickleback populations are, instead, of two types, one of which shows a strong mode at about 5 to 7 plates, the other having a mode at around 32 plates. Within a given population, individuals with an intermediate number of plates may occur, but there are no populations which consist only or largely of fish with intermediate plate numbers. Therefore, Heuts concludes that individuals with an intermediate number indicate only a skewed distribution curve of one type or the other and not a genotypical intermediacy.

On the Atlantic coast of North America, both the form with many plates and that with few are present (Bigelow and Schroeder, 1953). As in Europe, the fish with strong armature are to be found in salt water, while the fresh-water populations generally have few plates. The same situation occurs also along the Pacific coast of North America.

The geographic pattern of variability in Alaskan waters has not been worked out thoroughly. Marine collections have been few, and in many fresh waters the species has been recorded without reference to which of the two forms was present. It is likely that there are many bodies of fresh water, particularly those close to the sea, in which both the many-plated and the partially plated forms may occur, at least for part of the year. An instance is Chignik Lake on the south side of the Alaska Peninsula (private communication from Fredrik Thorsteinson of the Fisheries Research Institute, 1956).

There is very little, if any, migration of the Karluk and Bare Lakes sticklebacks to and from the ocean. No substantial numbers of sticklebacks have been observed in movement in Bare Creek or upper Karluk River. There is no evidence of a sea-run stock of sticklebacks in either lake. The number of lateral plates on all specimens examined does not exceed nine.

Plates and fin rays were counted on a total of 200 fish from each of the 2 lakes. The total for each lake was made up of 4 subsamples of 50 fish each, taken in different years (table 1).

Each subsample probably included individuals of at least 2 age groups; therefore, there is considerable overlapping of year classes. However, as there is little if any exchange of stock with outside populations, the genetic makeup of the population of the lake should be about the same from one year to the next.

TABLE 1.—*Subsamples of fish taken in different years from Karluk and Bare Lakes*

Karluk Lake	Subsample *a*	1956
	b	1949
	c	1949
	d	1948
Bare Lake	Subsample *w*	1956
	x	1954
	y	1950
	z	1951

An additional sample consisted of 50 specimens from O'Malley River, a tributary to Karluk Lake. This sample was taken in 1951.

The lateral plates were counted on the left side of the fish under low-power magnification. The point of a scalpel was used to lift the edge of each plate, so that none would be missed in counting. The first (most anterior) plate is

small and sometimes hard to find. Fin rays were counted in the dorsal and anal fins and both pectoral fins. In counting the (soft) rays, each element was counted as one ray. The last (most posterior) two elements in the dorsal and anal fins are well separated at the visible base of the fin, not jointed or branched as in some groups of fishes, and hence were counted as separate rays.

Numbers of lateral plates are shown in table 2. The Karluk Lake fish have from 5 to 9 plates, with no specimen having 4. The mean for 200 specimens is 6.55. The fish from Bare Lake have from 4 to 7 plates, no individuals having 8 or 9. The mean for 200 specimens is 5.22.

Between the various pairs of subsamples from Karluk Lake, there are significant differences (for the most widely separated pair, subsamples *c* and *d*, $t=8.0$ and $P<0.001$). The subsamples were captured at different places on a large lake and probably represent separate subpopulations.

TABLE 2.—*Number of lateral plates on stickleback from Karluk and Bare Lakes*

Subsample	Number of plates						Mean	σ	σ_M
	4	5	6	7	8	9			
Karluk Lake:									
Subsample *c*	----	1	12	31	6	----	6.84	0.64	0.09
a	----	----	18	26	4	2	6.80	.75	.11
b	----	2	25	15	4	4	6.66	.97	.14
d	----	10	35	5	----	----	5.90	.54	.08
Total	----	13	90	77	14	6	6.55	.84	.06
O'Malley River	----	5	26	14	5	----	6.38	0.80	0.11
Bare Lake:									
Subsample *w*	6	19	21	4	----	----	5.46	.81	.12
x	8	24	18	----	----	----	5.20	.69	.10
y	6	29	14	1	----	----	5.20	.66	.09
z	13	22	15	----	----	----	5.04	.75	.11
Total	33	94	68	5	----	----	5.22	.74	.05

The means for the samples of 200 fish each from the 2 lakes differ by 1.33. The difference is highly significant ($t=16.8$; $P<0.001$).

For the sample from O'Malley River, the mean number of lateral plates lies between the extremes for Karluk Lake.

The number of dorsal spines has a high degree of constancy. Of 400 specimens from the 2 lakes, 391 had 3 spines, only 9 (2.2 percent) had 4 spines, and none had 5 or 2. The fourth spine, when present, may be small and near the last spine, or it may be almost as long as the middle spine and be inserted midway between the last 2 of the 3 normal spines (fig. 3). The fourth spine was not found to occupy a position anterior to the first normal spine or between the first two.

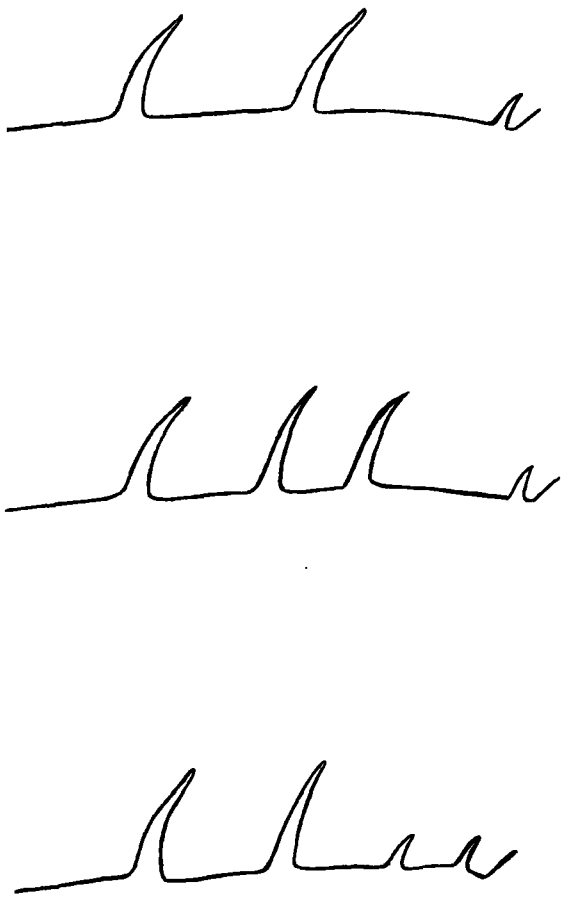

FIGURE 3.—Insertion of dorsal spines. Top, normal position of 3 spines. Center, fourth spine about the same size as, and inserted just posterior to, the second spine. Bottom, fourth spine small and inserted just anterior to third spine.

Counts of rays of the dorsal, anal, and pectoral fins are summarized in tables 3–5. In the numbers of dorsal and anal fin rays, there are differences, of varying degrees of significance, between the means of various subsamples from a given lake. These differences, however, definitely are overshadowed by the differences between the means of Karluk Lake and Bare Lake. In each of the latter instances, there is almost one fin ray difference, the mean number for Bare Lake being lower than that for Karluk Lake. The mean for the O'Malley River sample falls between the means for Karluk and Bare Lakes, for dorsal and for anal rays.

TABLE 3.—*Number of dorsal fin rays on sticklebacks from Karluk and Bare Lakes*

Subsample	Number of rays							Mean	σ	σ_M
	8	9	10	11	12	13	14			
Karluk Lake:										
Subsample *c*			3	20	23	3	1	11.58	0.77	0.11
a			3	26	19	2		11.40	.66	.09
d			6	25	16	3		11.32	.76	.11
b			6	29	13	2		11.22	.70	.10
Total			18	100	71	10	1	11.38	.74	.05
O'Malley River		3	11	19	16	1		11.02	0.93	0.13
Bare Lake:										
Subsample *x*		3	27	18	2			10.38	.66	.09
w		6	22	21	1			10.34	.71	.10
y		3	30	16	1			10.30	.61	.09
z	1	2	28	16	3			10.36	.74	.10
Total	1	14	107	71	7			10.34	.68	.05

TABLE 4.—*Number of anal fin rays on sticklebacks from Karluk and Bare Lakes*

Subsample	Number of rays					Mean	σ	σ_M
	6	7	8	9	10			
Karluk Lake:								
Subsample *c*		3	26	19	2	8.40	0.66	0.09
a	1	5	27	15	2	8.24	.76	.11
b		4	34	11	1	8.18	.59	.08
d		9	32	9		8.00	.60	.08
Total	1	21	119	54	5	8.20	.67	.05
O'Malley River	1	5	33	11		8.08	0.63	0.09
Bare Lake:								
Subsample *z*	2	25	20	3		7.48	.67	.09
w	2	25	22	1		7.44	.61	.09
x	3	31	16			7.26	.56	.08
y	3	34	12	1		7.22	.57	.08
Total	10	115	70	5		7.35	.62	.04

TABLE 5.—*Number of pectoral fin rays on sticklebacks from Karluk and Bare Lakes*

Location	Number of rays			Mean
	9	10	11	
Karluk Lake	12	374	14	10.00
Bare Lake	6	378	16	10.02

The ranges of the counts differ also. For dorsal rays (table 3), the fish in Karluk Lake range from 10 to 14 with no individuals having 8 or 9. The Bare Lake counts range from 8 to 12, and no individuals have 13 or 14. For anal rays (table 4), the ranges are 6 to 10, and 6 to 9, for Karluk Lake and Bare Lake, respectively.

Heuts (1949) shows, for *Gasterosteus aculeatus* in Europe, a negative correlation between the number of dorsal and anal rays and the water temperature during development of the embryo. The water temperatures at the time of embryological development, in Karluk and Bare Lakes, are not known with any degree of accuracy.

For the sample from both lakes, there is a significant positive correlation between the number of dorsal rays and the number of anal rays in an individual fish. The figures for Karluk Lake are $r=0.46$, $P<0.005$; for Bare Lake, $r=0.22$, $P<0.005$.

The number of pectoral fin rays is remarkably constant (table 5). Of 800 fins counted (both fins of each of 400 fish), only 48 (6.0 percent) had more or fewer than 10 rays. The data are too few to yield information on correlation between numbers in the left and right pectoral fins.

Numbers

Almost every published account of the threespine stickleback in any location describes it in such terms as abundant, plentiful, or numerous. Low egg counts per female, and the fact that it spawns only once or, at the most, twice during its life, are balanced by a high rate of survival of young and the adaptability of the species to various physical conditions and types of food.

No quantitative estimates of stickleback populations have been made for Karluk and Bare Lakes. During three summers, a considerable number of fish marked by fin clipping were released in Bare Lake, but recoveries were inadequate to produce a reliable estimate of population numbers. Nelson and Edmondson (1955) state that the stickleback is the most abundant fish species in Bare Lake, and it may be so in Karluk Lake. Morton,[2] on the basis of fyke net catches, believed the stickleback outnumbered by far the juvenile red and coho salmon in the littoral zone in Karluk Lake.

Over almost any shoal of either lake, on almost any day in summer, sticklebacks may be seen in widely varying numbers. Usually they are more or less evenly distributed over a considerable area and are not in tightly packed clumps or streams. A single haul with a 70-foot beach seine, sweeping some 200 square yards, often catches from 300 to 1,500 sticklebacks. Large concentrations have been observed at the mouths of tributaries

[2] The ecology of two Alaskan charrs as shown by their parasites. By William Markham Morton. Master's thesis, University of Washington, Seattle. Typewritten, 31 pp., 1942.

to Karluk Lake, presumably fish in spawning migration.

The degree of fluctuation of numbers from year to year is not known. Certain beach locations in Bare Lake were seined several times each summer in the years 1951–55. The catches varied widely, from less than 50 to more than 4,000 (table 6). No attempt has been made to make a statistical analysis of the variance or to arrive at a measure of its significance; since many external factors, such as light and wave action, are involved. Assuming that these factors averaged out to some extent, there is indication that a population peak was reached in 1953.

The proportionate strength of the different year classes cannot be estimated, since seine hauls may not constitute random samples of the population.

TABLE 6.—*Seine hauls, southwest corner Bare Lake, and catch of sticklebacks per haul*

Date	Catch [1]	Average for year	Date	Catch [1]	Average for year
1951			*1955*		
July 8	1,000	500	May 23	1,300	500
July 22	350		June 7	400	
Aug. 25	400		June 24	600	
Sept. 12	150		July 12	700	
1952			July 18	250	
June 25	1,000	300	July 30	----------	
July 8	100		Aug. 10	----------	
July 29	50		Aug. 17	100	
Sept. 11	50		Aug. 27	150	
1953			Sept. 6	1,300	
May 23	150	1,300	*1956*		300
June 8	1,700		May 30	250	
June 27	4,300		June 20	500	
July 24	1,400		July 10	400	
Aug. 12	250		July 23	250	
Aug. 26	150		Aug. 4	200	
1954			Aug. 28	150	
May 23	850	450			
June 7	950				
June 24	300				
June 26	800				
July 12	650				
July 26	50				
July 29	[2]				
Aug. 7	----------				
Aug. 10	700				
Aug. 17	----------				
Aug. 27	250				
Sept. 28	250				

[1] Figures rounded to nearest 50.
[2] Dash indicates fewer than 25.

Habitat

Essentially, the stickleback in Bare and Karluk Lakes is an inhabitant of the shallow waters. A few fish, but no large numbers, have been observed on the surface of Karluk Lake at a considerable distance from the shore. Morton caught 12 sticklebacks in one set of a fyke net at a depth of 80 feet in Karluk Lake, but did not take any sticklebacks in a set at 200 feet. Similarly, C. E. Walker (private communication) reports having taken sticklebacks in Karluk Lake in a fyke net set at a depth of 30 feet but not in a net set at 126 feet.

Presumably, food is more readily obtainable along the shoals; although plankton animals, which comprise a substantial part of the stickleback diet, are plentiful in at least the upper layers of the water in the center of the lake. It is probable, also, that conditions of light, temperature, and shelter are not as suitable to the stickleback in the lower levels as in the surface water. Bigelow and Schroeder (1953, p. 309) state that *Gasterosteus aculeatus* in the North Atlantic Ocean often is picked up far from land, but nearly always on the surface, usually in patches of weeds.

There is little aquatic vegetation on the shoals of Karluk and Bare Lakes. Often, when disturbed, the sticklebacks dart to the bottom to hide among rocks and moss. Much of the time they stay in open water and depend for protection on their appearance and behavior. Weeds, where present, furnish feeding opportunity in the way of insect larvae and small Crustacea and Mollusca attached to the plants.

Age, Size, and Growth

In the published literature to date, the most comprehensive work on age determination in sticklebacks, which has come to our attention, is that of Jones and Hynes (1950). These authors determined age by means of the otoliths and drew up growth-rate tables and curves for three species of sticklebacks from the Birket River in England.

We have examined otoliths of about 250 sticklebacks from Bare Lake and Karluk Lake. Also, we have drawn up length-frequency histograms for about 65 samples as described below. The information obtained by the two methods is in good agreement and provides a reasonably reliable estimate of age and growth.

In preparing and examining the stickleback otoliths, we have followed essentially the technique used by Jones and Hynes. Only fresh fish,

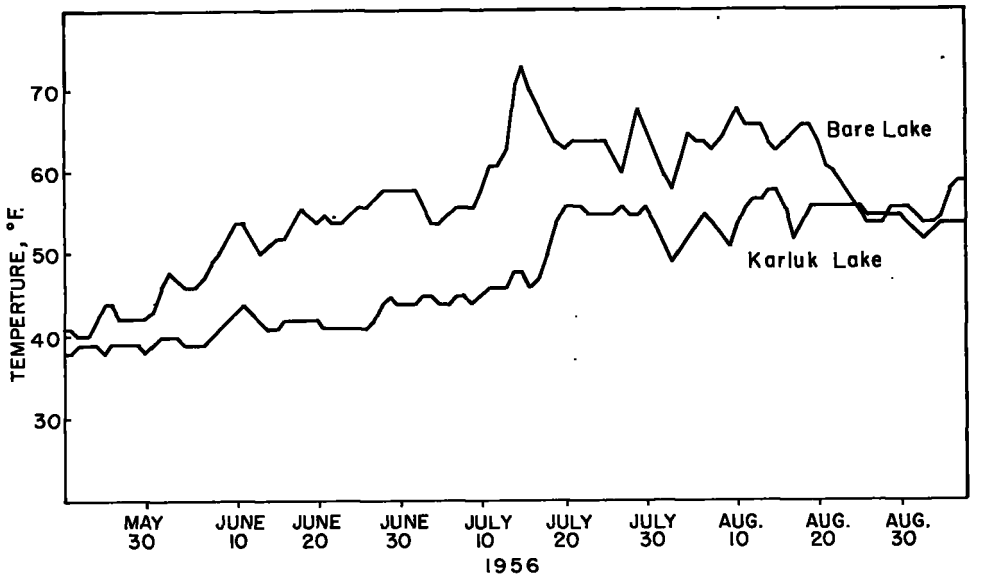

FIGURE 4.—Water temperatures, surface, summer of 1956. Upper curve, Bare Lake. Lower curve, Karluk Lake. Curves smoothed slightly.

or those preserved in alcohol, can be used, as formalin destroys the otoliths in only a few weeks.

The standard length in millimeters, and the sex and state of maturity are recorded for each fish. Then, working under a low-power microscope, the top of the skull is sliced off, and the otoliths are extracted by sharp-pointed forceps. Only the sagitta, the largest of the three otoliths to be found in each side of the skull, is used. Both sagittae from one fish are treated and mounted together.

The otoliths (sagittae) are placed in 65 percent alcohol, where they are cleaned of bits of tissue. Then they are put into pure creosote for from 5 to 15 minutes for clearing. Finally, they are mounted in Canada balsam or some other clear mounting fluid. They are read under a magnification of about 40 diameters, using a strong light reflected from the surface of the otolith, with a black mat background.

For a description of the appearance of the otolith and an interpretation of its markings, we quote Jones and Hynes.

> The sagitta first appears when the fish is about 6 mm. long, i. e., a few days after its emergence from the nest; the otolith is then a small body either uniformly transparent or more or less opaque. By the end of June the center is usually completely formed. Otoliths in this state or in an earlier state of development were designated S—. During June or early July the first transparent (S) ring appears, followed by the opaque zone (+) which is visible in some fish in July and in all by September. At first the opaque zone is narrow, but it rapidly increases in width during the summer. From September until the following June the otoliths of all fish in their first year read S+, i. e., they consist of center, one transparent ring and an opaque zone. Thereafter the S ring becomes evident in July, not June or July as in young fish: This may be due to the fact that it is not so easy to see the S ring on the edge of the larger otoliths. The opaque zone (+) begins to be visible in August or September, and is present in all fish by October.

This delineation appears to hold true for the Kodiak Island sticklebacks with minor variations. In the otoliths from the Bare Lake and Karluk Lake fish, the transparent rings apparently form during a rather short period in June and early July. In about early August, the material which gives cloudiness starts to be deposited, Seemingly (although it is difficult to be certain), this material accumulates to some extent in the outer portion of the previously clear zone, as well as in a newly formed zone. Thus the result is that the apparent clear bands are narrower than the cloudy bands.

At any rate, in age determination each opaque ring (outside of the centrum and first transparent ring) is read as one winter (although the opaque band actually starts to form in late summer or early fall). For example, the otolith of a fish

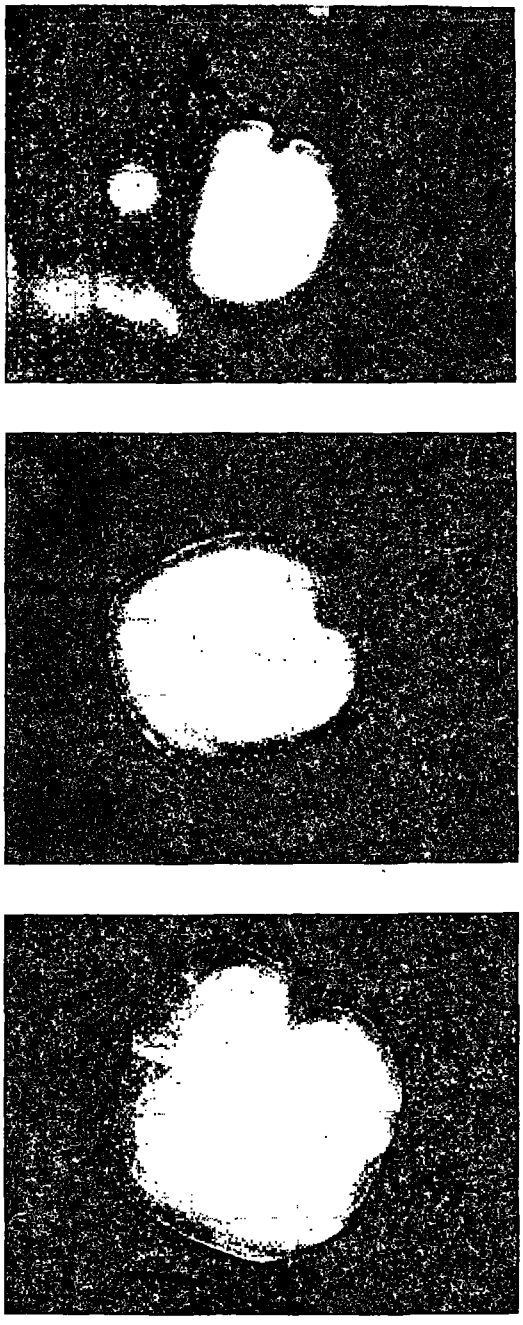

FIGURE 5.—Stickleback otoliths: Top, otolith from fish age 2–3 months; Middle, otolith from 1-year-old fish; Bottom, otolith from 2-year-old fish.

1 year old, taken in June, would show in order: centrum, first transparent ring, first opaque ring, and, at the outer edge, the beginning of the second transparent ring. The same fish, if captured in September of the same year, would have two transparent rings, and the second opaque ring would be forming at the edge. Shown in figure 5 are photographs of otoliths taken from fish of a few months, 1 year, and 2 years of age.

As mentioned by Jones and Hynes, the times of formation of the light and dark rings in the otolith are not the same for all species of fish. In certain fishes, such as *Clupea harengus*, the transparent ring appears to be formed in winter and the opaque ring in the summer, the reverse of *Gasterosteus*.

Our samples for length-frequency determination were taken by seining, which is probably more nearly nonselective as to size than any other method available to us. However, it may be that a completely random sample of the population cannot be obtained, since the sticklebacks may sort and distribute themselves by size to some extent. It is believed though that size selectivity in the sampling is more or less smoothed out by the large number of samplings.

Samples in Bare Lake were taken at intervals of 1 to 2 weeks during the summers (approximately June 1 to September 1) of 1950–56, inclusive, and in Karluk Lake during the summers of 1948 and 1949. In Bare Lake almost all of the sampling was done in one area, the beach at the southwest corner of the lake. In Karluk Lake most of the samples were taken around or near Camp Island on the east side of the lake.

Each sample consisted of from 100 to 400 fish. Standard length of each fish was measured in millimeters. A length-frequency histogram was drawn for each sample expressed in percentage of the total number of fish in the sample. For the Bare Lake samples, the lengths were grouped in 2-mm. intervals; for the samples from Karluk Lake, in 3-mm. intervals. The histograms showing the sequence of samples from Bare Lake for one summer (1954) are presented in figure 6. In figure 7 the sequence for Karluk Lake in the summer of 1949 is shown.

Standard lengths may be converted to fork lengths or total lengths (all of these terms are well defined in recent literature) by use of the following factors: F. L./S. L.=1.17, and T. L./S. L.=1.21.

Jones and Hynes (op. cit.) give a summary of the information regarding age and size of the threespine stickleback. Various authors have

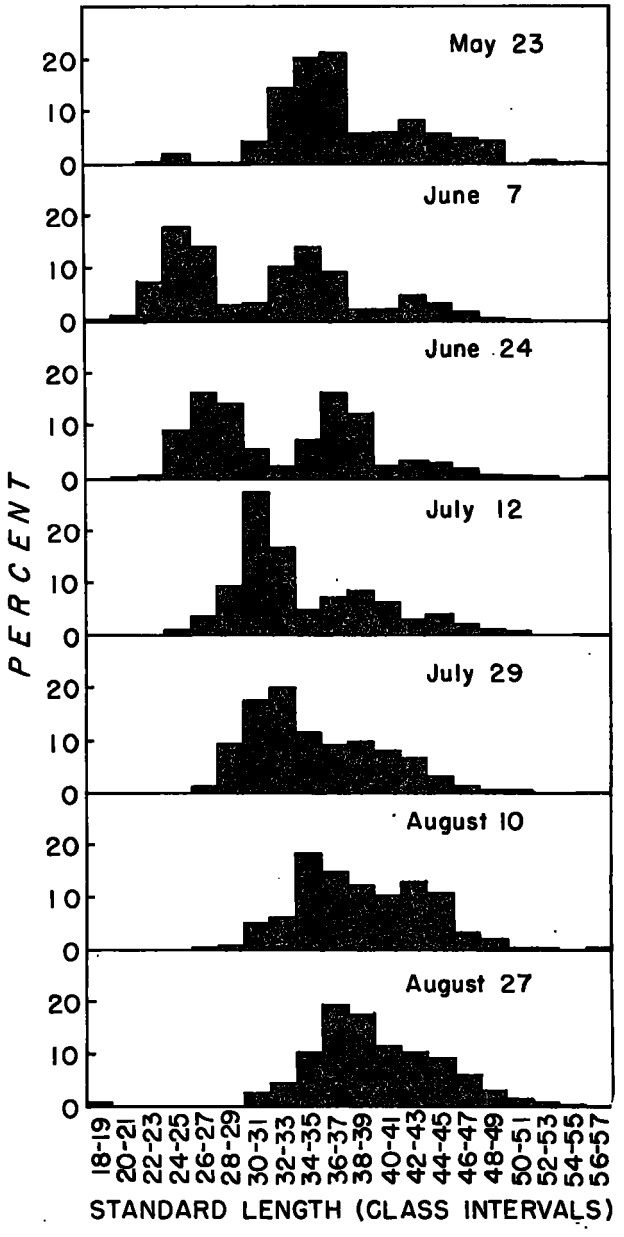

FIGURE 6.—Length-frequency histograms, sticklebacks from Bare Lake, 1954. Each diagram represents a sampling of 100–400 fish on a given date. Vertical ordinate, percent of total sample. Horizontal ordinate, standard length group.

placed the lifespan of the species at from 1 to 4 years. Some have said that the fish breeds only once, others that it may breed in each of 2 or 3 successive years. No doubt there is considerable variation, which is due to differences in race or strain or to environmental differences.

In the Birket River sticklebacks (*Gasterosteus aculeatus*), Jones and Hynes found the maximum lifespan to be 3 years plus. The fish at the end of the first summer of life (i. e., when a few months old) averaged about 24 mm., standard length. At the end of the second summer, the average was about 34 mm., and at the end of the third summer about 40 mm. Most of the growth occurred during the summer. Maximum size achieved was about 65 mm.

Assuming that our interpretation of the otoliths is correct, the sticklebacks in Karluk and Bare Lakes have a lifespan of about two and one-fourth years. Most of the 2-year-old fish die shortly after spawning, as indicated by the successively smaller numbers of large fish in the samples as the summer progresses. A very few otoliths appeared to show an extra winter ring. It may be that an occasional fish survives the third winter.

In the samples from Bare Lake in the summer of 1954 (fig. 6), at the time of the first sampling on May 23, very few young-of-the-year fish were present. The frequency mode at about 35 mm. apparently represented 1-year-old fish, the 2-year-old fish being much fewer and showing a broad frequency mode at about 45 mm.

In the next sample, taken on June 7, the small fish predominate, with a mode at about 25 mm. The fish of the other two size groups (age classes) have fallen off in comparative numbers. Successive samples throughout the remainder of the summer show: (1) a fairly rapid increase in size of the fish of the year; (2) a somewhat slower but steady growth of the 1-year-old and 2-year-old fish; and (3) a reduction in numbers of the older fish, especially of the 2-year-old group, probably caused by their death and disappearance from the population.

The same picture holds good for the summers of 1951 and 1953, with certain variations, probably caused in part by differences in spawning dates and hence in the growth achieved in the first summer. In the 1953 samples the 1-year-old group appeared in weak numbers throughout the summer, possibly indicating poor survival through the preceding winter.

In Karluk Lake in 1949 (fig. 7), the first sample of the summer was taken on June 23. The young-of-the-year group was almost or entirely

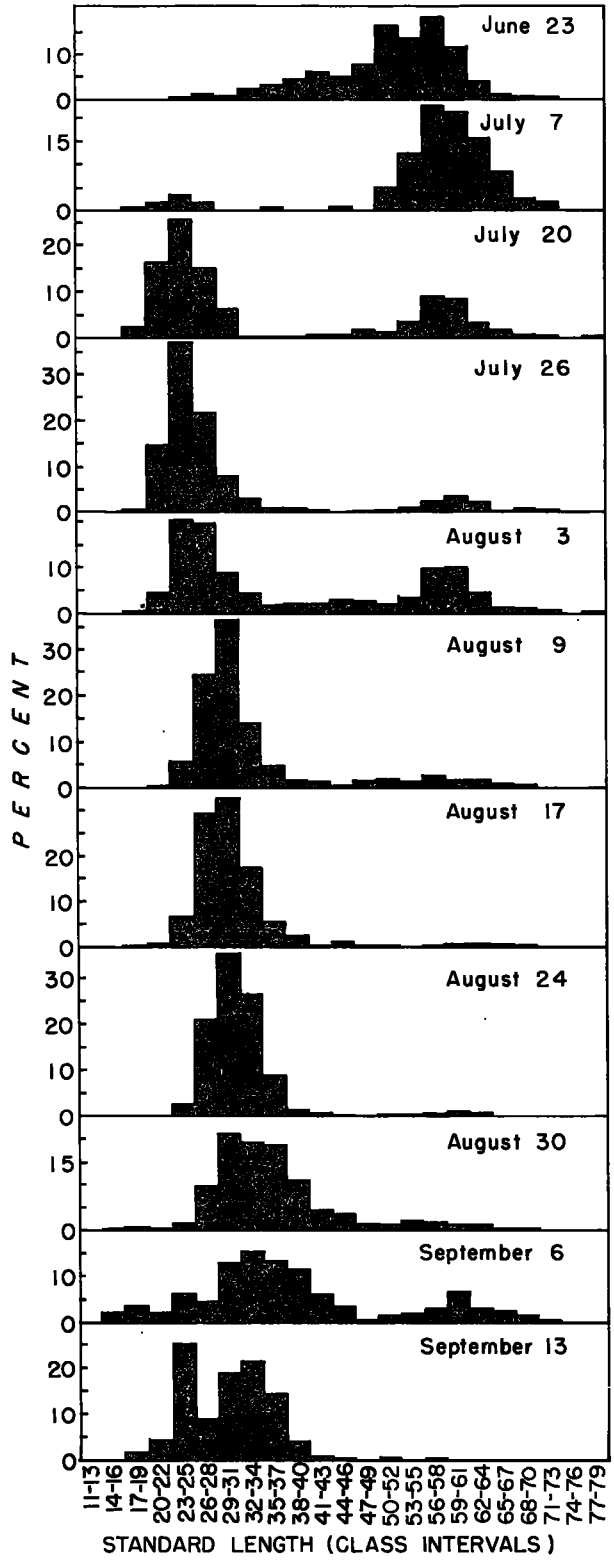

FIGURE 7.—Length-frequency histograms, sticklebacks from Karluk Lake, 1949. Arrangement as in figure 6.

absent. It is thus indicated that the sticklebacks probably spawn later in Karluk Lake than in Bare Lake, presumably because the water warms up later in Karluk Lake. The next sample, taken on July 7, contained a few small fish, and by July 20, the young fish predominated in numbers. From that date through the remainder of the summer, the young-of-the-year were the group with by far the largest numbers in the samples. The older fish steadily dwindled in numbers, except for a showing such as that on September 6, possibly occasioned by nonrandom sampling. Apparently, as in Bare Lake in 1953, the Karluk Lake stickleback population in the summer of 1949 was weak in 1-year-old fish; although, because of overlapping in size, some of the apparent modes may have been composed of fish from two age groups.

The Karluk Lake samples for September 6 and September 13, 1949, show an apparent bimodality for the young-of-the-year group, probably caused by the appearance of a late hatched brood.

The figures in table 7 represent peaks (apparent modes) in the length-frequency histograms for the sampling dates for Bare Lake. Each vertical column thus portrays the growth of a certain year class (fish hatched in the summer of a certain year), assuming that the peaks represent the average length of the fish of a particular age group at a given time.

These data are plotted in figure 8 as points on growth curves. Each curve in this figure represents the growth of the fish of a given year class. The early growth, in the first few weeks after hatching, cannot be shown, as the fish were not available in the areas sampled. Spawning no doubt takes place at different times in different years, and the young fish thus get a slower or faster start and achieve a different average length at the end of the first summer. Thus in 1954 the hatching probably was early, and the first summer's growth was greater than in most other years. Carrying over this increased growth, the fish of this year class were somewhat larger than normal at the start of the next summer.

The growth curves for the year classes of 1951, 1952, and 1953 fall close together (fig. 8). A curve representing the average or composite for these 3-year classes is redrawn in figure 9. Superimposed on it are symbols, each of which repre-

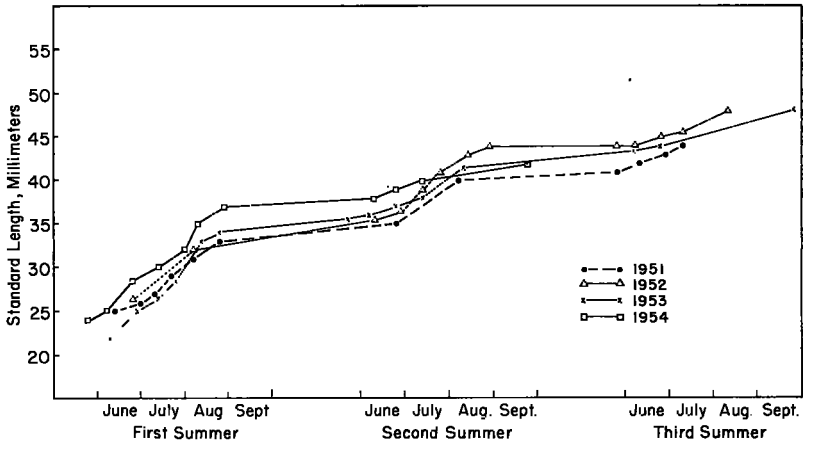

FIGURE 8.—Growth of Bare Lake sticklebacks. Each curve represents a year class. Points on curves derived from modes of length-frequency histograms.

sents a fish whose age was determined by otolith reading.

In these symbols, the sexes are separated for the fish in their third summer (2 years old). The females attain a somewhat larger size than the males.

The fact that the curve, which presumably indicates average sizes, does not pass through the median of the lengths indicated by the otolith readings may be due to an unconscious tendency on the part of the technician to select usually the larger fish in a given size-group for otolith samples.

In a similar diagram for the Karluk Lake sticklebacks (fig. 10), the symbols represent mean lengths of fish of length-frequency modes (for samples through the summers of 1948 and 1949), and the curve indicates the regression line as drawn by visual inspection. The vertical bars show the ranges of lengths of fish the ages of which were determined by otolith reading. Samples for otolith determinations were available only for dates in mid-July (1956).

As shown in figures 8–10, the Karluk Lake and Bare Lake sticklebacks do most of their growing from June 1 to September 1 and make comparatively little growth through the fall, winter, and spring.

The sticklebacks in Bare Lake average from 32 to 35 mm. in standard length at the end of

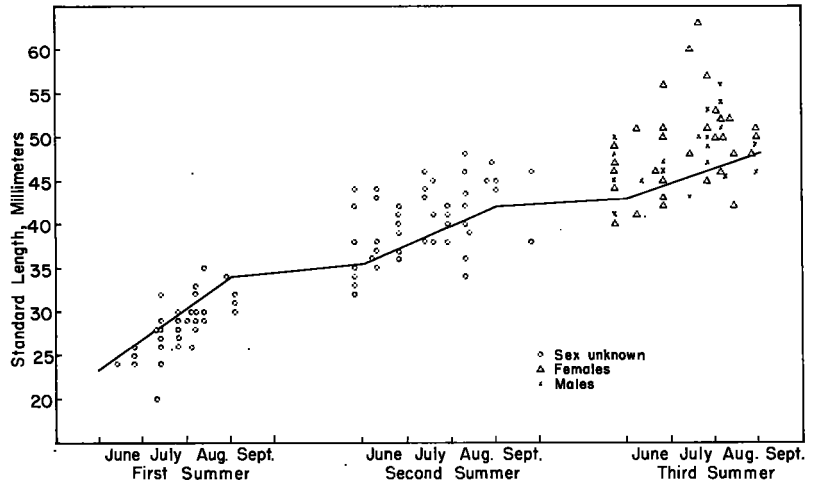

FIGURE 9.—Growth of Bare Lake sticklebacks. Curve is composite of growth of 3-year classes (from figure 8). Scattered points represent ages and lengths of individual fish determined by otolith reading.

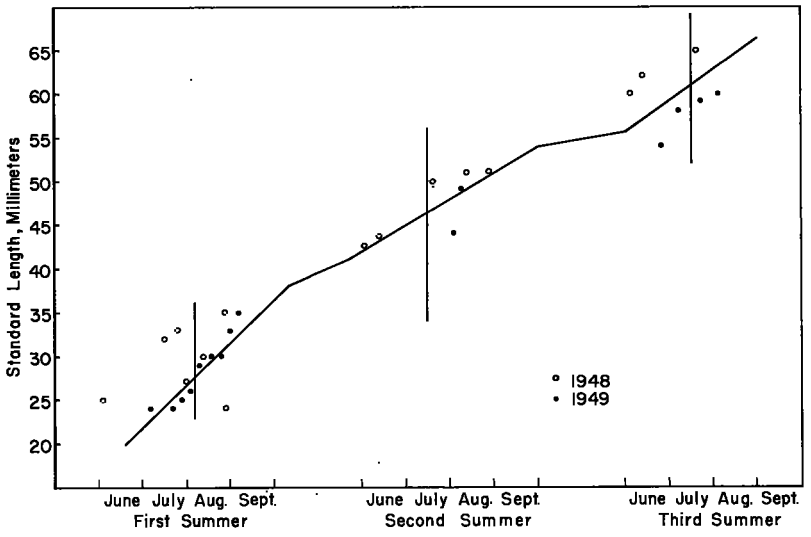

FIGURE 10.—Growth of Karluk Lake sticklebacks. Scattered points, modes from length-frequency histograms, 1948 and 1949. Curve drawn by inspection. Vertical bars, range of lengths from otolith readings.

TABLE 7.—*Bare Lake, average standard length of sticklebacks on various dates*

[Each entry in table represents a peak [mode] on length-frequency diagram of a sample taken on that date]

Sampling date		Year class					
Year	Date	1954	1953	1952	1951	1950	1949
1951	June 13				24	34	40
	June 29				25	35	41
	July 8				27	36	41
	July 22				30	39	44
	Aug. 7				31	39	
	Aug. 25				33	41	
	Sept. 12					42	
1952	June 25			26	35	41	
	Aug. 6			32	40	45	
1953	May 23				42		
	June 8		22	35	41		
	June 27		25	36	43		
	July 11		28	39	44		
	July 24		29	41			
	Aug. 12		34	43			
	Aug. 26		34	44			
1954	May 23	24	35	42			
	June 7	25	35	43			
	June 24	27	36	43			
	July 12	30	38	45			
	July 29	32					
	Aug. 10	35	43	48			
	Aug. 27	37					
1955	June 7	38	44				
	June 24	39	45				
	July 12	40	44				
	July 18	40					
	Sept. 25	42	48				

the first summer, depending somewhat on the date of hatching. At the end of the second summer (about 16 months after hatching), the average length is about 42 to 44 mm. At the start of the third summer, the average is about the same, and at the end of August of that summer, the few fish of that age group still alive are from 45 to 60 mm. long. The largest individual stickleback measured from Bare Lake was 69 mm. standard length (3.3 inches total length).

In Karluk Lake growth in the early part of the first summer is somewhat less than in Bare Lake because of later hatching. However, the growth thereafter is faster in Karluk Lake, and the maximum size achieved is greater. At the end of the first summer, the average standard length of the Karluk Lake fish is about 32 mm. At the end of the second summer it is about 50 mm. At the end of August in the third summer, the average for the fish of that age group still alive is about 60 to 65 mm. The maximum size recorded for Karluk Lake is 78 mm. standard length (3.8 inches total length).

The growth rate of the Karluk Lake and Bare Lake sticklebacks is greater than that of those in Birket River (Jones and Hynes, 1950), but the latter attain about the same maximum size, since they live 1 year longer. Sticklebacks of various populations from salt and fresh waters in western Europe (Heuts 1947a) ran up to 70 mm. standard length in maximum size.

Reproduction

The stickleback in Karluk and Bare Lakes spawns at the age of 1 or 2 years. It is strongly indicated that those fish of either sex which spawn at the age of 2 years die within a few weeks after spawning. In the late summer many

spawned sticklebacks are found along the shores of the lakes or at the outlets. These fish are either dead or in a weak, emaciated condition.

The proportion of sticklebacks that spawn at age 1 year is not known with certainty. Judging from egg development in females (ages obtained by reading otoliths of 1-year-olds), fewer than one-half spawn at 1-year-old. Moreover, it is not known whether a stickleback that spawns at 1 year dies, or lives another year without spawning again, or spawns again the next year.

Bertin (1925) believed that the life cycle of the stickleback in Europe is accomplished in 1 year (in other words, that the fish spawn at the age of 1 year), and that the fish die after breeding. He stated, however, that in some localities the fish may live longer. Leiner (1934) wrote that *Gasterosteus aculeatus* breeds at least 2 or 3 times during its life. Jones and Hynes (1950) found the sticklebacks in England to live 3 years and to show gonad maturation from the first year, but did not indicate how many times the fish spawns during its life.

The sexually mature sticklebacks are structurally hermaphroditic. Schneider (1904) reported an instance of hermaphroditism in *Gasterosteus* in which one of the paired gonads contained both ovarian and testicular tissue. C. W. Huver in 1955 discovered that the sticklebacks at Bare Lake and Karluk Lake have gonads of both sexes present in the same fish, and Greenbank in 1956 examined a large number of mature specimens and found all of them to show this condition. In the ripe male (fig. 11), the testes are enlarged to occupy at least one-third of the abdominal cavity. Between the testes and the other organs, there is a thin septum. Against the ventral side of this septum lie the paired ovaries. These are 8 to 12 mm. long. They contain no cells which can be identified under low-power magnification as ova. No staining or sectioning has been done.

The oviduct is Y-shaped and apparently enters the cloaca separately from the vas deferens. The cloaca is simple and is continuous with the hind gut. There is a single external opening.

Just anterior to the cloaca and ventral or slightly lateral to the posterior portion of the gut, there is a pear-shaped, thin-walled sac some 8 to 12 mm. long. This sac, as spawning time approaches, becomes filled with a clear, viscous fluid, presumably the material which is used to cement the nest.

The ovaries of the ripe female (fig. 12) occupy a large proportion of the abdominal space. There is a septum as in the male. The testes are not prominent but definitely are discernible as ribbonlike structures and readily distinguishable from the darker streak of the kidney. No cytological examination of the testes has been made. The vas deferens and the oviduct apparently enter the cloaca separately as in the male.

A female stickleback, 70 mm. standard length, captured in Karluk Lake on July 25, 1956, had ovaries well distended with eggs. Among the eggs were several which were well eyed (fig. 13). While it may be possible that sperm cells had entered the cloaca from the water outside and had made their way up the oviduct, there is the possibility that the spermatozoa were derived from testicular material in the same fish.

Aside from the change in coloring in the male discussed earlier, and a visible swelling of the ripe female, secondary sex characters attendant on maturity are lacking.

There is little agreement in the literature about the time of spawning of *Gasterosteus aculeatus* or external factors with which it may be related. Roule (1945) states that the stickleback spawns in the latter part of spring or the first part of summer. Carl (1953) says that the spawning period is prolonged from the first week in April to the first week in September. In the estuaries and streams tributary to the Gulf of Main (Bigelow and Schroeder, 1953), the fish is said to spawn probably in May to June.

Eechhoudt (1947) was able to induce a considerable degree of sexual development in the stickleback by exposure to artificial light. Apparently this development did not reach the point of actual spawning.

We do not have information to fix the spawning date of the sticklebacks in Karluk and Bare Lakes with any degree of precision. In Karluk Lake in 1948 stickleback eggs were recovered from a stickleback stomach on June 7. On the other hand, females still carrying ripe eggs were taken from Karluk Lake as late in the summer

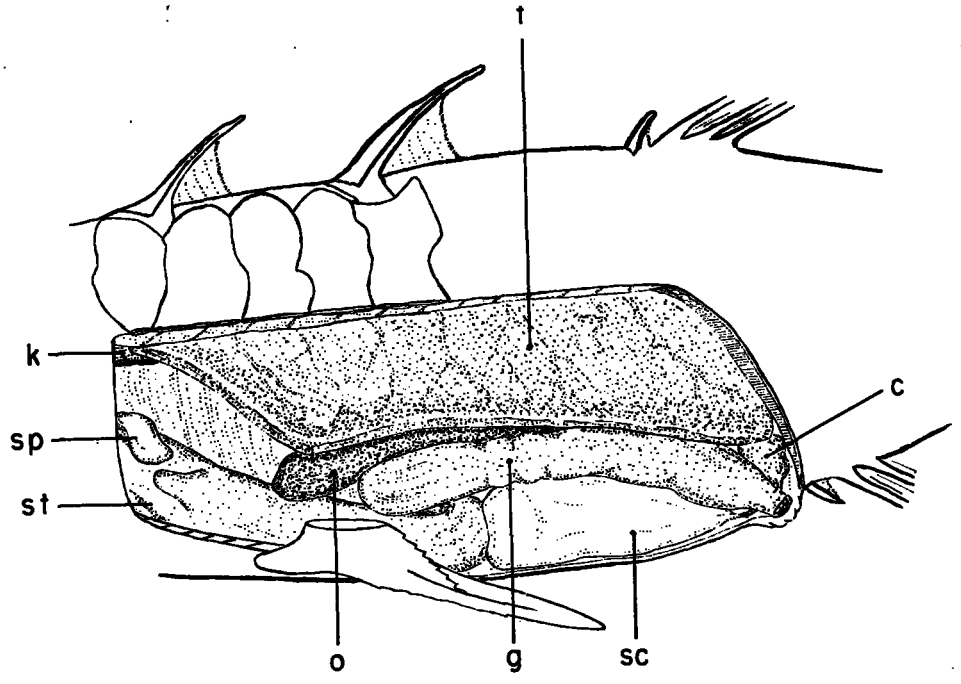

FIGURE 11.—Internal anatomy of normal, sexually mature, male stickleback showing presence of ovaries. c=cloaca; g=gut; k=kidney; o=ovary; sc=sac; sp=spleen; st=stomach; t=testis.

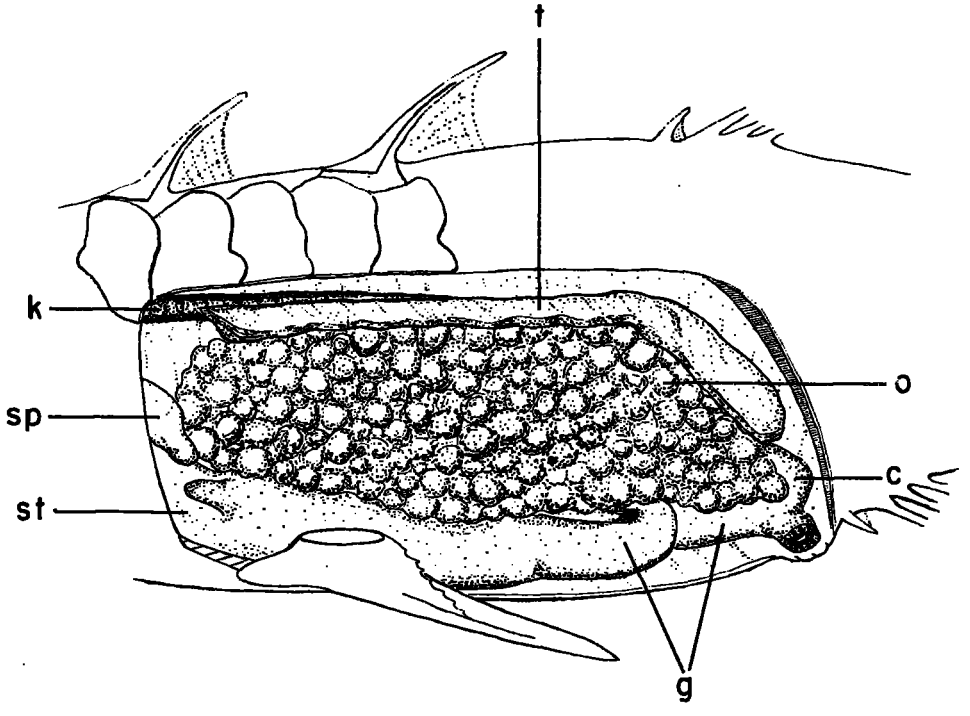

FIGURE 12.—Internal anatomy of normal, ripe, female stickleback showing presence of testes. c=cloaca; g=gut; k=kidney; o=ovary; sp=spleen; st=stomach; t=testis.

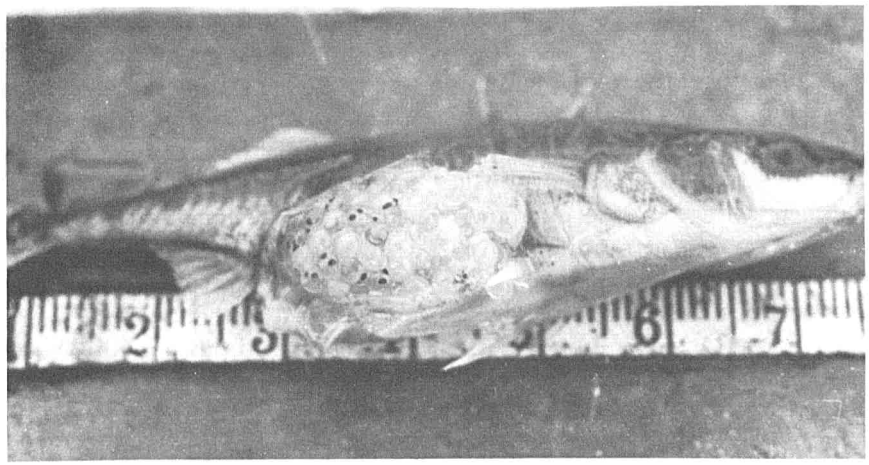

FIGURE 13.—Dissection of female stickleback with eyed eggs in ovary.

[of 1949] as August 3. Morton [3] found stickleback eggs in the stomachs of charrs taken in Karluk Lake in June, July, and August, but not in those taken in April, May, and September.

A collection of sticklebacks, made along the shore of Karluk Lake on July 15, 1956, had a few spawned-out females, but most of the females were ripe with eggs. Observations on July 25 showed many females still to be carrying eggs. But a collection made on August 6 had no fish with ripe eggs, all the large females having spawned.

In Bare Lake we have taken ripe females as early as May 23 [1954] and as late as July 29 [1952]. Specimens less than 20 mm. standard length were captured on June 7, 1954. Judging from the size of the young-of-the-year in June and July (fig. 6), many of the sticklebacks in Bare Lake presumably spawn in May.

A collection from Bare Lake on July 23, 1956, had a few fish still gravid with eggs, but most of the mature fish were spent. On August 1 all the larger fish in a collection were spawned out. A nest with eyed eggs in it was found on August 4, and on August 15 a young stickleback was taken.

These scanty data indicate that perhaps the stickleback spawns earlier in Bare Lake than in Karluk Lake. Such should not be the case if light (length of day) were the sole factor controlling spawning date. Bare Lake, being small and shallow, warms faster in the early summer and maintains a higher surface water temperature through the summer than does Karluk Lake (fig. 4). It is suggested that water temperature may influence the time of spawning.

Spawning takes place in Bare Lake in shoal water around the shores of the lake. In Karluk Lake, too, many sticklebacks utilize the lake shore for spawning. Congregations of possibly hundreds of thousands of sticklebacks have been noted by C. E. Walker at the lower ends of Lower Thumb and O'Malley Rivers, the two principal tributaries of Karluk Lake, from early May until June 1950. Walker states (private communication) that the fish ascended these streams to Thumb and O'Malley Lakes, where they spawned.

The literature contains many references to the nest-building habits of the stickleback. In some waters the male constructs an elaborate nest of small sticks, twigs, or pieces of vegetation held together by a sticky substance presumably secreted by the kidney (Wunder 1930; and others). However, Vrat (1949) reports that the sticklebacks which he studied in California did not use leaves or twigs in their nests. These nests took the form of a hole in the sand, excavated by the male and shaped by strokes of his head.

The nests in Karluk and Bare Lakes are well hidden and camouflaged. The very few that we have been able to discover did not contain sticks or plant material but appeared to be made mostly

[3] Food studies of the Dolly Varden (*Salvelinus malma*) and arctic charr (*Salvelinus alpinus*) at Karluk, Alaska, from 1939 through 1941. By William Markham Morton. (In preparation.)

of sand grains. We have not observed the male in the process of nest-building.

As stated in the literature the male, having constructed the nest, induces one or more females to enter it and lay eggs which he immediately fertilizes. He then maintains a guard over the eggs and newly hatched young, and perhaps provides aeration by his swimming or fanning movements.

In Karluk Lake many stickleback eggs have been found more or less scattered through aquatic vegetation. Possibly these eggs were deposited free, without construction of nests.

At Bare Lake, in 1955, C. W. Huver stripped eggs from female sticklebacks, fertilized them with macerated testes from mature males, and succeeded in hatching them in a bowl floated in a tub. At a water temperature varying from 9° to 16° C., the eggs were eyed in 9 days and started hatching at 14 days.

The embryological development of the threespine stickleback has been studied by Vrat (1949), who published a series of drawings of various stages. The development follows a pattern typical in teleost fishes.

Physiology and Behavior

The literature, at least in North America, contains little information regarding physiological responses, tolerances, and adaptations of the three-spine stickleback. It is believed to be a hardy fish in many respects. For instance, it is known to survive over winter in shallow lakes in northern temperate and subarctic zones, where the chemical conditions become severe. Dissolved oxygen sinks to a trace, and dissolved carbon dioxide and other gases build up considerable tensions. The mechanism for survival is not known; presumably it combines a greatly reduced metabolic rate with the ability to extract oxygen at low pressure.

The threespine stickleback has been used, particularly in Europe, as an aquarium fish. Possibly it would be a satisfactory subject for tank and jar experiments on physiological responses and adaptations. However, Cope et al. (1949) state that "Sticklebacks could not stand holding in the live jars, and mortalities were high at 24 hours." These authors used *Gasterosteus aculeatus* for some experiments in tolerance to certain insecticides. They found the stickleback to be more tolerant to emulsions of DDT, benzene hexachloride, chlorinated camphene, and chlordan than were salmonid fishes (the criterion of tolerance being the amount of agitation after 15-minute test periods). However, in certain tests with acetone solutions of pyrethins they noted that the sticklebacks "were rendered helpless within the time of treatment, while only a few salmonids were so affected." They suggest that selective poisoning might possibly be used in control of sticklebacks. Jones (1935, 1938, 1939, 1947) has made extensive use of *Gasterosteus aculeatus* as a test fish, particularly in determining the toxicity of various metals to fish.

The sticklebacks in Karluk and Bare Lakes apparently suffer a heavy mortality after spawning. The physiology of this post-spawning mortality is not known. Feeding apparently continues until the time of spawning but perhaps ceases with spawning. The dead, spawned-out fish picked up along shores are extremely emaciated.

Except for spawned-out fish, nutrition is satisfactory. All individuals are in reasonably plump condition throughout the summer. Nothing is known concerning diseases in the Karluk and Bare Lake sticklebacks.

These fish harbor various parasites. One of these is the ligualid cestode, *Schistocephalus*, the plerocercoids of which lie in the abdominal cavity of the fish. Crustacea are the host of the initial larval stage, and fish-eating birds, such as mergansers, of the adult tapeworm. At least 20 percent of the adult sticklebacks are infested. These cestode larvae reach 20 mm. or more in length, and one larva can fill all the available space in the fish and cause a visible distension of the abdomen. A few of the infested fish have from 2 to 8 of the worms each.

Morton (1942) states that the stickleback in Karluk Lake carries in its intestines the larva of a proteocephalid cestode, presumably *Proteocephalus arcticus* Cooper. The adult worm is found in the intestine of the lake charr, *Salvelinus alpinus*, which feeds on the stickleback.

Also reported by Morton, a larval cestode of the Dyphyllobothriid type, provisionally called *Dibothrium fasteni*, is found in the stickleback as well as in the lake charr and in young red

salmon. It occurs either free or in a cyst on the viscera. Presumably it is the worm, the adult form of which has been reported from bears and mergansers as *Diphyllobothrium.*

A nematode, identified by Morton [4] as *Dacnitis laevis* Zschokke and Heitz, is fairly common in the stomach and intestine of the stickleback, usually occurring in small numbers. This worm is found in both species of charr (*Salvelinus alpinus* and *S. malma*). Morton reports also an acanthocephalan worm, *Neoechinorhynchus rutili* (Müller), in the Karluk Lake stickleback and states that Meyer (1932) has found this worm in sticklebacks (*Gasterosteus*) in Europe.

A parasitic copepod, identified by Wilbur M. Tidd as *Ergasilus cotti* Kellicott, is found on the Karluk Lake sticklebacks. A large proportion of the fish carry from 1 to 5 of these copepods each, attached to the skin at the base of the pelvic or dorsal fins or more often in the gill chamber and gills.

Bigelow and Schroeder (1953) state that the stickleback "is a proverbially pugnacious fish, using its spines with good effect as weapons of offense and defense, even on fishes much larger than itself." We have not observed any demonstration of this pugnacity in the sticklebacks in Karluk and Bare Lakes. As will be discussed under food habits, the stickleback in these waters is not known to feed on other fishes large or small. It is preyed upon by the arctic charr, but the act of capturing a stickleback by a charr has not been observed. We may surmise that the act takes so little time that the stickleback has no opportunity for defensive action. Juvenile red salmon have been found with sticklebacks in their mouths or stomachs, but the act of capture has not been observed.

According to our observation, the stickleback depends to a large extent for protection on a sort of camouflage. In clear, calm water, over a shoal, it will lie at the surface, perfectly motionless for many minutes at a time. In such a position, it resembles a floating stick or twig.

It is possible that the male stickleback makes effective use of his spines in chasing females into the nest and in guarding the nest after the eggs are laid.

[4] See footnote 2, p. 543.

Food Habits

Norman (1936), Jordan (1905), and others have remarked on the voracity of *Gasterosteus aculeatus* and stated that it is strongly predaceous on the eggs and young of other fishes. However, Markley (1940) found the sticklebacks of Sacramento River (sample taken in October) to be feeding mainly on insects and other invertebrates, especially amphipods. Carl (1953) examined a small number of stickleback stomachs from Cowichan Lake, British Columbia, and found zooplankton (Cladocera, copepods, amphipods) and insect larvae to be the chief items in the diet. Bigelow and Schroeder (1953) list as food for the threespine stickleback in the Gulf of Maine copepods, isopods, small shrimp, young squid, diatoms, small fish fry, and fish eggs. It is evident that the stickleback will eat a wide variety of (animal) foods depending on what is available.

Stomach examinations of sticklebacks in Karluk and Bare Lakes are summarized in tables 8–10. The larvae and pupae of chironomid flies (Diptera) were found, often in considerable numbers, in a large percentage of the stomachs. Other insects, such as caddis-fly larvae and damselfly and stonefly nymphs, occurred irregularly.

Also of importance were copepods, of the genera *Diaptomus* and *Cyclops;* and Cladocera, of the genera *Daphnia* and *Bosmina.* Stomachs were examined that contained well over 200 invertebrate plankters of 1 one more of these 4 genera.

TABLE 8.—*Contents of stickleback stomachs, Bare Lake, 1951*

[Numbers in parentheses are range of number of organisms per stomach]

Food	Date					
	June 13	June 29	July 8	Aug. 7	Sept. 12	Totals
Number of stomachs containing food	15	14	17	17	16	79
Number of stomachs containing—						
Chironomids	14 (4–124)	9 (5–88)	11 (1–11)	9 (1–104)	2 (2–3)	45
Other insects	7	8	5	13	5	38
Copepods	14 (7–63)	10 (2–36)	16 (1–16)	10 (1–108)	16 (7–242)	66
Cladocera	2 (1–2)	3 (1–5)	15 (1–112)	9 (2–218)	13 (11–229)	42
Ostracods	3 (1–2)	3 (1–2)	5 (1–11)	1 (1)	6 (1–121)	18
Rotifers	1 (1)	-------	9 (2–15)	-------	-------	10
Clams	1 (9)	1 (1)	-------	1 (5)	3 (1–7)	6
Stickleback eggs	4 (1–3)	2 (1–11)	-------	-------	-------	6

TABLE 9.—*Contents of stickleback stomachs, Karluk Lake*

[Numbers in parentheses are range of number of organisms per stomach]

Food	Date							
	June 4, 1948	June 7, 1948	June 13, 1948	July 25, 1948	July 7, 1949	Aug. 9, 1949	Sept. 13, 1949	Totals
Number of stomachs containing food	11	23	50	15	68	25	25	217
Number of stomachs containing—								
Chironomids	7 (4-14)	10	9		31	2	3	62
Other insects	1				4			5
Copepods	10 (11-20)	23	22	9 (1-71)	59 (1-276)	24	25	172
Cladocera	3	20		13 (1-182)	31	23	25	115
Ostracods	3 (1)	2	2	5 (1-22)	9 (1-134)	1	1	23
Rotifers	2	13	24		1	1		41
Clams					2			2
Stickleback eggs		1		5 (1-38)	23 (5-58)	1		30

TABLE 10.—*Contents of stickleback stomachs from fish of three size groups, Karluk Lake, July 7, 1949*

Food	Standard length of fish, mm.		
	31-45	46-60	61-75
Number of stomachs containing food	21	23	24
Number of stomachs containing—			
Chironomids	11	10	10
Other insects		1	3
Copepods	20	19	20
Cladocera	14	14	3
Ostracods	1	2	6
Rotifers		1	
Clams		2	
Stickleback eggs		3	20

Ostracods and rotifers were present. Several stomachs contained pea clams, sometimes in large enough numbers to constitute considerable bulk. Other food items, encountered only occasionally, included snails, leaches, planarians, and water mites. Vegetation or phytoplankton, in identifiable form, was never or scarcely ever present.

Several stomachs contained fish eggs, easily identifiable as stickleback eggs. No other fish material was found.

Some changes in the feeding habits throughout the summer may be noticed (tables 8 and 9). Chironomids were fewer in the stomachs in the latter part of the season. Various plankton invertebrate species fluctuated in numbers in the stickleback diet, probably in relation to fluctuations of numbers of these species present in the water.

There are also differences in the food selected by fish of various size groups (table 10). Fewer of the large fish were feeding on Cladocera, more of them on ostracods. Stickleback eggs were found in only the larger fish. Possibly the eggs are too large to be swallowed by the small fish. Or perhaps the larger fish were in a nesting area and thus had ready access to eggs.

Role as Prey

Several species of fish present in Karluk and Bare Lakes may be predators on the stickleback. The arctic charr (*Salvelinus alpinus*), which does not occur in Bare Lake, is a year-round resident in Karluk Lake in substantial numbers. According to Morton [5] and DeLacy [6], this charr feeds on sticklebacks and stickleback eggs, especially in the months of June and July. In the study of the food habits of the arctic charr, in the Wood River drainage in western Alaska, it was found that the charr consumed large numbers of sticklebacks, particularly when young red salmon were not readily available.

The Dolly Varden charr (*Salvelinus malma*) is said by Morton not to utilize sticklebacks in Karluk Lake. Of 60 stomachs of Dolly Varden taken in Bare Lake in the period June–August 1956, only 3 contained stickleback. It is likely that sticklebacks are eaten to some extent by the fingerling coho salmon and the rainbow trout, especially during the winter, when food items such as insects are not available in large numbers. Baxter (1956) found the stickleback to be an important item in the diet of the rainbow trout in a lake near Anchorage, Alaska. Also, the

[5] See footnote 2, p. 543.

[6] Contributions to the life histories of two Alaskan charrs. *Salvelinus malma* (*Walbaum*) and Salvelinus alpinus (Linnaeus). By Allan Clark DeLacy. Doctoral thesis, University of Washington, Seattle. (Typewritten) 114 pp., 1941.

sculpin *Cottus aleuticus* may eat stickleback eggs and small sticklebacks.

Sticklebacks are eaten by several kinds of birds including probably mergansers (Munro and Clemens, 1937), gulls, loons, and kingfishers. The quantitative relationships are not known. Of some significance to the overall ecology of the lake may be the fact that the stickleback carries one or more species of internal parasites which are transmitted to other fish or to birds.

The stickleback has been used to some extent in northwestern Europe in the production of fish oil and meal, and in Russia and possibly in northwestern Alaska for human food. It has been reported that sticklebacks on Kodiak Island sometimes are used for dog food, and are consumed by humans on occasion. For these uses the fish are stored in frozen blocks.

Relation to Red Salmon

Aside from such intangible things as dual occupation of and competition for space, the relation between the stickleback and the production of young red salmon involves four possible major factors: the predation of the stickleback on the salmon, food competition between the stickleback and the young salmon, the use of stickleback fry or eggs as food for the salmon, and the role of the stickleback in the diet of charr and other predators on the salmon.

Predatory habits of the stickleback have been mentioned by various authors. Kincaid (1919) makes the (unsupported) statement: "The damage done by the stickleback is out of proportion to his size, as he is able to kill the fry of larger fish, notably the salmon, for which reason the stickleback is known locally as the Salmon Killer." We have no evidence of sticklebacks in Karluk and Bare Lakes feeding on red salmon eggs or fry. We have not examined any stickleback stomachs taken in the spring while the salmon fry were very small. Rounsefell (1958), states that: "there seems to be little evidence that they [sticklebacks] are actual predators (on young salmon)." Rounsefell cites White (1930) who performed experiments on the consumption of brook trout (*Salvelinus fontinalis*) fry by large trout of the same species and by adult threespine sticklebacks. The results of White's experiments showed the stickleback to be an almost negligible factor in the loss of trout fry. Rounsefell comments, "Salmon fry are much larger than the fry of the brook trout, so that there would seem to be even less chance of any destruction."

The feeding habits of the young red salmon in Karluk Lake are not fully known. It is probable that the fry eat insects and plankton animals, but the larger juveniles may eat a few small fish. Therefore, although there may be some points of difference, the food habits of the small red salmon and the sticklebacks are similar in large measure. Both fishes eat insect larvae (mainly chironomids) and plankton crustaceans. The diet is suited to the fare. Whether and to what extent the consumption of part of the available food supply by the stickleback has an adverse effect on red salmon production is not a matter easy to assess.

As we have suggested above, small sticklebacks may be an item in the food supply of the salmon fingerlings, especially the larger smolts. However, data for making a quantitative estimate of the effect on salmon production are lacking.

Certain predators, in particular the arctic charr, have been shown to utilize sticklebacks for food. This use of sticklebacks may in some measure relieve predation on the young red salmon and possibly be a favorable factor in the production of salmon smolts. However, relationships between predators and prey are complex and not understood fully. A reduction in numbers of sticklebacks present in Karluk Lake might mean that more salmon would be eaten by the charrs. Or it might mean only that the charr population would decline, because the total food supply had decreased, and thus the number of salmon smolts eaten by chars might remain substantially the same.

SUMMARY

The threespine stickleback, *Gasterosteus aculeatus*, is found in large numbers in Karluk Lake and Bare Lake in southwestern Kodiak Island, Alaska. Its presence may have a relation to the production of red salmon (*Oncorhynchus nerka*) in these waters.

This species of stickleback has a wide distribution in the subarctic and temperate zones of the northern hemisphere. It has had a history

of much confusion in classification and nomenclature, largely because of wide variations in morphological characters from one locality or one type of environment to another. The stickleback in Karluk and Bare Lakes is of the partially naked (few lateral plates) form, which is characteristic of populations that reside permanently in fresh water. Counts of lateral plates and fin rays show the populations of the two lakes to be discrete.

Estimates of numbers of fish in the stickleback populations are difficult to make. Sticklebacks appear to be more numerous in Karluk and Bare Lakes than any other species. There is evidence of considerable fluctuation in numbers from year to year.

The sticklebacks are often to be found in large numbers along the shoals and have been observed on the surface in the center of the lake and in small numbers in deep water. Apparently there is little or no movement to and from the ocean, but spawning runs ascend the two main tributaries of Karluk Lake to Thumb and O'Malley Lakes.

The species is at least moderately hardy and resistant to adverse conditions. It carries several species of parasites in these waters, notably the pleroceroid of a cestode (*Schistocephalus*) which has a plankton crustacean (Cladocera) as its initial host and a bird as the final host.

The sexually mature fish have both male and female gonads. The male has paired ovaries and the female a mass of testicular tissue. A large female from Karluk Lake had several eyed eggs in the ovary.

Spawning takes place in early summer. In some years a part of the spawning occurs as late as August. In these waters the male does not use plant material to any great extent in constructing the nest (as has often been reported in the literature), but makes a nest of sand cemented together with a secretion from within his body and more or less buried in sand and gravel in shoal water. Sticklebacks may spawn also in weed beds, with little or no nest construction.

The lifespan is about two and one-fourth years. A standard length of 60 to 65 mm. is attained in Bare Lake and up to 80 mm. in Karluk Lake. Spawning may occur only once during life or at most twice. At least part of the fish die within a few weeks after spawning.

The principal foods for the stickleback in both lakes are midge fly (Chironomid) larvae, and plankton crustacea (Copepods, Cladocera, Ostracoda). Minor items include other insects, water mites, rotifers, small clams, snails, leeches, and stickleback eggs. Stomachs examined at various times during the summer did not contain eggs or fry of fish other than sticklebacks. The period covered by these examinations included the spawning time of the red salmon, but not the time of emergence of red salmon fry.

The stickleback is a component of the food of the arctic charr, which is a predator also on young red salmon. Birds, rainbow trout, and possibly large juvenile coho salmon eat sticklebacks. Small sticklebacks may be used to a small extent as food by the larger juvenile red salmon.

The principal means by which the stickleback in Karluk and Bare Lakes may influence red salmon production include competition with young salmon for food and by reducing predator pressure on red salmon by furnishing food to the charr. Quantitative information is insufficient to assess accurately the benefit or harm to salmon production caused by the stickleback population.

LITERATURE CITED

BAXTER, RAE.
1956. Effectiveness of gill nets and sport fish tackle in sampling fish populations. Quart. Progress Report, Federal Aid in Fish Restoration; U. S. Fish and Wildlife Service and Alaska Game Commission, June 30, 1956. 149 pp., mimeographed.

BERTIN, LEÓN.
1925. Recherches bionomiques, biométriques et systématiques sur les épinoches. Ann. Inst. Océanogr. Monaco, vol. 2, pp. 1–208.

BIGELOW, HENRY B., and WILLIAM C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U. S. Fish and Wildlife Service, vol. 74, Fishery Bulletin 53, pp. 1–577.

CARL, G. CLIFFORD.
1953. Limnobiology of Cowichan Lake, British Columbia. Jour. Fish. Res. Bd. Canada, vol. 9, pp. 417–449.

COPE, OLIVER B., CLAUDE M. GJULLIN, and ALF STORM.
1949. Effects of some insecticides on trout and salmon in Alaska, with reference to blackfly control. Trans. Amer. Fish. Soc., vol. 77, pp. 160–177.

COX, PHILIP.
1922. Results of the Hudson Bay expedition, 1920. II. The Gasterosteidae of Hudson Bay. Contrib. to Can. Biol., 1921, No. 10, pp. 149–153.

CRAIG-BENNETT, M. A.
1931. The reproductive cycle of the three-spined stickleback, *Gasterosteus aculeatus*, Linn. Philos. Trans. Royal Soc. London, series B, vol. 219, pp. 197–279.

EECHHOUDT, JEAN-P. VANDEN.
1947. Recherches sur l'influence de la lumiére sur le cycle de l'épinoche (*Gasterosteus aculeatus*). Ann. Soc. Roy. Zool. Belgique, vol. 77, pp. 83–89.

HEUTS, M. J.
1947. Experimental studies on adaptive evolution in *Gasterosteus aculeatus* L. Evolution, vol. I, pp. 89–102.
1947a. The phenotypical variability of *Gasterosteus aculeatus* (L). populations in Belgium. Verhand. Akad. Wetensch. van Belgie, vol. 9, No. 25, pp. 1–63.
1949. Racial divergence in fin ray variation patterns in *Gasterosteus aculeatus*. Jour. Genetics, vol. 49, pp. 183–191.

HYNES, H. B. N.
1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. Jour. An. Ecol., vol. 19, pp. 36–58.

JONES, J. R. E.
1935. The toxic action of heavy metal salts on the three-spined stickleback (*Gasterosteus aculeatus*). Jour. Exp. Biol., vol. 12, pp. 165–173.
1938. The relative toxicity of salts of lead, zinc, and copper to the stickleback (*Gasterosteus aculeatus* L.) and the effect of calcium on the toxicity of lead and zinc salts. Jour. Exp. Biol., vol. 15, pp. 394–407.
1939. The relation between the electrolytic solution pressures of the metals and their toxicity to the stickleback (*Gasterosteus aculeatus* L.). Jour. Exp. Biol., vol. 16, pp. 425–437.
1947. The oxygen consumption of *Gasterosteus aculeatus* L. in toxic solutions. Jour. Exp. Biol., vol. 23, pp. 298–311.

JONES, J. W., and H. B. N. HYNES.
1950. The age and growth of *Gasterosteus aculeatus*, *Pygosteus pungitius* and *Spinachia vulgaris*, as shown by their otoliths. Jour. An. Ecol., vol. 19, pp. 59–73.

JORDAN, DAVID STARR.
1905. A guide to the study of fishes. New York, Henry Holt & Co., 2 vols.

JUDAY, C., WILLIS H. RICH, and G. I. KEMMERER.
1932. Limnological studies of Karluk Lake, Alaska, 1926–1930. Bull. Bur. Fish., Bulletin 12 (vol. 42), pp. 407–436.

KINCAID, TREVOR.
1919. An annotated list of Puget Sound fishes. Wash. State Dept. Fish., pp. 1–51.

LEINER, M.
1929. Ökologische Studien an *Gasterosteus aculeatus*. Zeitschr. Wiss. Biob. A. Morphol. u. Ökol. Tierre., vol. 14, pp. 360–399.
1930. Forsetzung der ökologischen Studien an *Gasterosteus aculeatus*. Z. morph. Ökol. Tiere., vol. 16, pp. 499–540.
1934. Die drei europaischen Stichlinge (*Gasterosteus aculeatus* L., *Gasterosteus pungitius* L. und *Gasterosteus spinachia* L.) und ihre Kreuzungsprodukte. Z. Morph. Ökol. Tiere., Vol. 28, pp. 107–154.

MARKLEY, MERLE H.
1940. Notes on the food habits and parasites of the stickleback *Gasterosteus aculeatus* Linn. in the Sacramento River, California. Copeia, 1940 (No. 4), pp. 223–225.

MEYER, A.
1932. Acanthocephala. Bronn's Klassen u Ordnung Tier-Reichs. Vermes Askhelminthen. Vol. 4 (Abt. II, Buch 2, Lief 1), pp. 1–332.

MYERS, GEORGE S.
1930. The killifish of San Ignacio and the Sticklebacks of San Ramon, Lower California, Proc. Calif. Acad. Sci., vol. 19, pp. 95–104.

MUNRO, J. A., and W. A. CLEMENS.
1937. The American merganser in British Columbia and its relation to the fish population. Biol. Bd. Canada, Bulletin 55, pp. 1–50.

NELSON, PHILIP R., and W. T. EDMONDSON.
1955. Limnological effects of fertilizing Bare Lake, Alaska. U. S. Fish and Wildlife Service, Fishery Bulletin 102 (vol. 56), pp. 415–436.

NORMAN, J. R.
1936. A history of fishes. 2d ed. London, Benn. 463 pp.

ROULE, LOUIS.
1945. Les poissons et le monde vivant des eaux. Paris, Librairie Delagrave. 10 vols.

ROUNSEFELL, GEORGE A.
1958. Factors causing decline in sockeye salmon of Karluk River, Alaska. U. S. Fish and Wildlife Service, Fishery Bulletin 130 (vol. 58), pp. 83–169.

SCHNEIDER, G.
1904. Ueber einen Fall von Hermaphroditismus bei *Gasterosteus aculeatus*. Helsingfors Medd. Soc. Faun. et Fl. Fenn., vol. 30, pp. 7–8.

VRAT, V.
1949. Reproductive behaviour and development of the three-spined stickleback (*Gasterosteus aculeatus*) of California. Copeia, 1949, pp. 252–260.

WHITE, H. C.
1930. Trout fry planting experiments in Forbes Brook, Prince Edward Island, in 1928. Contrib. Can. Biol. and Fish., vol. 5, pp. 203–211.

WUNDER, W.
1928. Experimentelle Unterschungen an Stichlingen (Kämpfe, Nestbau, Laichen, Brutpflege). Zool. Anz. (Suppl.) 3 (Verh. Deutsch. Zool. Ges. 32), pp. 115–127.
1930. Experimentelle Untersuchgen am drei-stachligen Stichling (*Gasterosteus aculeatus* L.) während der Lachzeit. Z. Morph. Ökol. Tiere., vol. 16, pp. 453–498.

U.S. GOVERNMENT PRINTING OFFICE : 1959 O - 489027

Blank page retained for pagination

UNITED STATES DEPARTMENT OF THE INTERIOR • Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE • Arnie J. Suomela, *Commissioner*

LIFE HISTORY OF THE SEA LAMPREY OF CAYUGA LAKE, NEW YORK

By ROLAND L. WIGLEY

FISHERY BULLETIN 154

From Fishery Bulletin of the Fish and Wildlife Service

VOLUME 59

PUBLISHED BY U.S. FISH AND WILDLIFE SERVICE • WASHINGTON • 1959

PRINTED AT U.S. GOVERNMENT PRINTING OFFICE, WASHINGTON

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington 25, D.C. Price 40 cents

Wigley, Roland L

Life history of the sea lamprey of Cayuga Lake, New York. Washington, U. S. Govt. Print. Off., 1959.

iv, 561–617 p. illus., map, diagrs., tables. 26 cm. (U. S. Fish and Wildlife Service. Fishery bulletin 154)

"From Fishery bulletin of the Fish and Wildlife Service, volume 59." Bibliography: p. 616–617.

1. Lampreys. I. Title. (Series: U. S. Fish and Wildlife Service. Fishery bulletin, v. 59, no. 154)

[SH11.A25 vol. 59, no. 154] Int 59–88

U. S. Dept. of the Interior. Library
for Library of Congress

Library of Congress catalog card for this bulletin:

U. S. ***Fish and Wildlife Service.***
Fishery bulletin. v. 1–
Washington, U. S. Govt. Print. Off., 1881–19

v. in illus., maps (part fold.) 23–28 cm.

Some vols. issued in the congressional series as Senate or House documents.
Bulletins composing v. 47– also numbered 1–
Title varies: v. 1–49, Bulletin.
Vols. 1–49 issued by Bureau of Fisheries (called Fish Commission, v. 1–23)

1. Fisheries—U. S. 2. Fish-culture—U. S. I. Title.

SH11.A25 639.206173 9–35239 rev 2*

Library of Congress [r55e‡]

Library of Congress catalog card for the series, Fishery Bulletin of the Fish and Wildlife Service:

CONTENTS

	Page
Establishment of the sea lamprey in Cayuga Lake	561
Size, growth, and morphometry of the sea lamprey	562
Length composition	562
Weight composition	563
Growth of parasitic-phase sea lampreys	565
Comparison with size in other landlocked populations	567
Length-weight relation of adults	567
Morphometry	569
Seasonal changes and sexual differences in body proportions	569
Morphometric comparison of Cayuga Lake and Seneca Lake sea lampreys	572
Spawning migration	576
Tributaries of Cayuga Lake	576
Water conditions in Cayuga Inlet	576
Migratory behavior	576
Population estimates of spawning adults	578
1950	578
1951	579
1952	581
Rate of upstream movement	581
Barriers to upstream migration	582
Sex ratio	584
Size of upstream migrants	586
Body color	586
Spawning habits	587
Nest building	587
Time of construction and location of nests	588
Spawning	589
Fecundity	590
Postspawning habits and morphological changes	592
Loss of body weight and length	593
Egg development and habits of ammocoetes	593
Egg development	593
Habits of ammocoetes	594
Food and feeding	595
Duration of larval life	595
Transformation and downstream movement	602
Parasitic habits	602
Sea lamprey parasitism on like trout in Cayuga and Seneca Lakes	603
Loss of body weight resulting from sea lamprey attacks	604
Length of trout and incidence of sea lamprey attacks	607
Annual variations in incidence of sea lamprey attacks	608
Incidence of sea lamprey parasitism in various parts of Cayuga Lake	609
Seasonal trends in feeding activity of sea lampreys	611
Comparison of sea lamprey parasitism in Seneca and Cayuga Lakes	611
Location of attachment on the fish's body	612
Sea lamprey parasitism on the white sucker	612
Parasites and predators of the lamprey	612
Parasites	613
Predators	613
Control methods	613
Summary	614
Literature cited	616

ABSTRACT

A life history study of the sea lamprey, *Petromyzon marinus* Linnaeus, in Cayuga Lake, N.Y., was conducted during 1950, 1951, and 1952. One of the major objectives was to obtain biological data concerning this endemic stock of sea lampreys for comparison with the newly established stocks in the Great Lakes.

Sexually mature sea lampreys captured on their spawning migration in Cayuga Inlet were the basis of much of this study. Such items as meristic counts, body proportions, body color, sex ratios, lengths and weights, fecundity, rate of upstream travel, effect of dams in retarding upstream movement, nesting habits, parasites, predators, estimates of abundance, and morphological changes were based on mature upstream migrants. Sea lampreys were procured by weir and trap operations and captured by hand. Tagging and marking programs each spring made it possible to determine movements and morphological changes of individual lampreys, in addition to estimating the number of upstream migrants.

Growth of parasitic-phase sea lampreys was estimated from measurements of specimens captured in Cayuga Inlet and Cayuga Lake proper.

The incubation period of lamprey eggs and the habits of ammocoetes and transforming lampreys were ascertained from specimens kept in hatchery troughs and raceways. Length-frequency and weight-frequency distributions, together with the length-weight regression, of ammocoetes from Cayuga Inlet were utilized for estimating the duration of their larval life.

Lake trout, *Salvelinus n. namaycush* (Walbaum), from Cayuga Lake and Seneca Lake were the subject of an inquiry into the effects of sea lamprey attacks. Incidence of sea lamprey attacks on the white sucker, *Catostomus c. commersoni* (Lacépède), was investigated.

Three methods are suggested for reducing the number of sea lampreys in Cayuga Lake.

LIFE HISTORY OF THE SEA LAMPREY OF CAYUGA LAKE (N.Y.)

By Roland L. Wigley, *Fishery Research Biologist*, BUREAU OF COMMERCIAL FISHERIES

In recent years the sea lamprey, *Petromyzon marinus* Linnaeus, has attracted the attention of commercial fishermen, sportsmen, and fishery biologists because of the destruction of food and game fishes attributed to this parasite. It was the invasion and rapid multiplication of the sea lamprey in the upper Great Lakes, coincident with the drastic decline of food fishes, especially lake trout in Lake Huron and Lake Michigan, which stimulated interest in the life-history study of the sea lamprey. One phase of the Great Lakes sea lamprey investigation was to obtain detailed information on biological characteristics of an endemic sea lamprey population in order to make comparisons with the newly expanding Great Lakes population.

Cayuga Lake has been inhabited by a thriving sea lamprey population for centuries. In addition to offering a natural habitat of limited size, Cayuga Lake has only one tributary that is extensively used by the sea lamprey for spawning. Thus, a study of the Cayuga Lake sea lamprey was undertaken in order to obtain comparative data and basic information pertaining to the life cycle of the sea lamprey.

The year 1875 marks the beginning of scientific inquiry into the taxonomic status and life history of the Cayuga Lake sea lamprey. In the spring of that year, a large male lamprey was captured in Cascadilla Creek, a tributary of Cayuga Lake near Ithaca. This specimen was unusually large and its coloration and large ropelike dorsal ridge were greatly different from immature specimens previously taken from the lake. Wilder studied this specimen and, after he obtained others, named it *Petromyzon marinus dorsatus* (Jordan and Gilbert, 1883).

Meek (1889) summarized observations on spawning habits and gave some data on size composition and sex ratio of the 1886 spawning run in Cayuga Inlet. Surface (1898, 1899) reported considerable information on natural enemies, host species, and control methods. Gage (1893, 1928) contributed much to our knowledge of the sea lamprey of Cayuga Lake. His studies encompassed the anatomical and physiological aspects as well as its life history. His works have long been considered an authoritative source of information concerning the sea lamprey.

Profs. Edward C. Raney, Dwight A. Webster, and John C. Ayers, Department of Conservation, Cornell University, guided and assisted in the organization of this study. William F. Carbine, Dr. James W. Moffett, Dr. Ralph Hile, Dr. Vernon C. Applegate, and other members of the Great Lakes fishery investigations, the U.S. Fish and Wildlife Service, generously provided equipment, technical advice, and aid in preparing the manuscript. Members of the New York State Conservation Department, especially Dr. U. B. Stone, W. G. Bentley, and Dr. R. M. Roecker, aided in collecting lamprey data; C. W. Lyon, J. P. Galligan, Dr. R. D. Suttkus, Dr. R. M. Yerger, and many other associates assisted with the fieldwork; and Douglas S. Robson gave statistical advice.

ESTABLISHMENT OF THE SEA LAMPREY IN CAYUGA LAKE

Prior to 1921, the known range of the sea lamprey in North America extended from the Maritime Provinces of Canada southward along the Atlantic coast to northern Florida, and westward up the St. Lawrence drainage into Lake Ontario and four inland lakes in New York State. In recent times (1921 and later) this range has been extended westward throughout the Great Lakes. Detailed information on this invasion has been recorded by Hubbs and Pope (1937), Radforth (1944), MacKay and MacGillivray, (1949), Shetter (1949), Trautman (1949), Applegate (1950), and Loeb and Hall (1952).

Early accounts in the literature (Goode 1884) describe the capture of large numbers of sea lampreys in some New England rivers for utilization as food, and indicate that at one time they were abundant in that region. The sea lamprey is

anadromous, and until several decades ago was considered to be primarily a marine species. In recent years it has been demonstrated that lampreys can adapt themselves successfully to a lake-stream habitat where conditions are suitable, as is evidenced by their recent success in the upper Great Lakes. Moreover, several lakes in New York, including Cayuga Lake, have supported landlocked populations of sea lampreys for centuries

During the Pleistocene period, when the glacial Great Lakes were forming, glacial Cayuga Lake was also passing through some profound alterations. Changes in the outlet drainage of glacial Cayuga Lake are of primary importance in this discussion of the sea lamprey's establishment in Cayuga Lake.

Marine-dwelling sea lampreys may have penetrated into Cayuga Lake through any one of three drainages.

1. The drainage of glacial Cayuga Lake southward into the Susquehanna River. This outlet opened up relatively early in the formative period of the Great Lakes, but was later cut off by a lower level drainage opened to the north and east through the Syracuse, Mohawk, and St. Lawrence outlets.

2. At a later date, the Syracuse outlet (via the Hudson River) may have permitted access to glacial Cayuga Lake.

3. A still later development was the final disappearance of the ice in the St. Lawrence Valley which permitted an arm of the sea to extend up the St. Lawrence into Lake Champlain. This situation would have permitted passage of the sea lamprey from the Atlantic Ocean, via the "Champlain Sea," into glacial Lake Iroquois and on into Cayuga Lake. Another alternative passage in existence during this same time was from the Atlantic Ocean to the Hudson-Champlain estuary, to the Mohawk outlet, into glacial Lake Iroquois, and into Cayuga Lake.

Because the first two routes mentioned above would have permitted the sea lamprey to establish itself in all the Great Lakes, which did not occur until approximately the present century, it would appear that the third route was the most probable path of entrance. The fact that Niagara Falls would have blocked their movement into Lake Erie, and the other upper Great Lakes, lends credence to the belief that the sea lamprey entered Cayuga Lake by way of the "Champlain Sea" or the Hudson-Champlain estuary and Mohawk outlet. Presumably, a sufficient supply of large host fishes in the lake made possible the establishment of a landlocked form of the sea lamprey.

To date, size is the only morphological difference recorded between the marine form and the landlocked form. The landlocked sea lamprey in Cayuga Lake attains approximately one-half to two-thirds the length of the marine form.

SIZE, GROWTH, AND MORPHOMETRY OF THE SEA LAMPREY

Length Composition

The sea lamprey of Cayuga Lake has often been termed the dwarf form of the species. A misconception of its relatively small size was one of the principal factors that prompted many authors to consider it a separate subspecies.

During the 3-year period 1950–52 the mean total length of 3,363 sea lampreys captured in Cayuga Inlet was 15.4 inches; extreme lengths were 8.4 and 21.4 inches. Only unspent, upstream migrants are considered in this discussion. A summary of length measurements, recorded in table 1, is listed according to sex and year of capture. To facilitate a comparison of mean values and their associated variation, these data are diagramed in figure 1. These diagrams are a modification of the type originally employed by Hubbs and Perlmutter (1942). The significance of differences between samples can be judged by com-

TABLE 1.—*Summary of length measurements of sea lampreys captured in Cayuga Inlet*

Year and sex	Number of specimens	Length (inches)			
		Mean	Range	Standard deviation	Standard error
1950					
Male	153	15.2	9.0–19.5	1.72	0.139
Female	92	14.8	10.7–18.7	1.54	.160
Total	508	15.0	8.4–20.7	1.84	.081
1951					
Male	961	15.3	11.0–20.8	1.61	.052
Female	591	15.2	11.3–20.2	1.54	.063
Total	1,917	15.3	11.0–20.8	1.56	.036
1952					
Male	519	15.9	11.1–21.0	1.24	.054
Female	419	15.8	11.5–21.4	1.86	.091
Total	938	15.9	11.1–21.4	1.75	.057

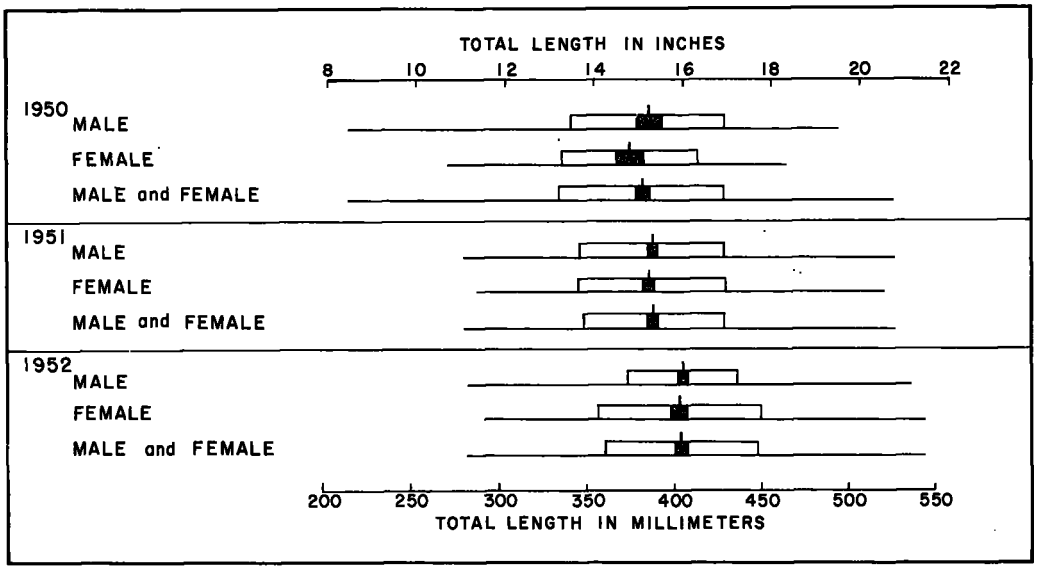

FIGURE 1.—Length composition of Cayuga Lake sea lampreys. The horizontal line represents the total range of variation; the mean is indicated by a vertical bar; the hollow rectangle on each side of the mean represents one standard deviation; the solid rectangle on each side of the mean represents twice the standard error.

paring the standard errors. If the solid rectangles, which represent twice the standard error, of the two samples are of nearly equal length and overlap one another by 10 percent or less, the difference between the means may be considered significant; that is, the probability that the two samples came from the same statistical population is 0.08 or less.

Annual mean lengths for the sexes combined, together with the estimated abundance of sea lampreys, were as follows:

Year	Total length (inches)	Estimated abundance [1]
1950	15.0	10–15,000
1951	15.3	9,390
1952	15.9	4,435

[1] Refer to p. 578 for details pertaining to population estimates.

For 1950, the mean length was calculated from measurements of 508 lampreys. These lampreys were taken relatively early in the migratory period and are thought to be biased in favor of large specimens. Mean lengths for 1951 and 1952 were determined from samples taken regularly throughout the entire migratory period. The 1,917 specimens measured in 1951 represent 20 percent of the estimated spawning population for that year. The 938 specimens measured in 1952 represent 21 percent of the total number in the run.

Mean length of Cayuga Lake sea lampreys increased slightly during the period 1950–52. The successive annual increases in length, 0.3 and 0.6 inch, were statistically significant. In these three years body length was inversely related to the total number of lampreys in each year class.

Total lengths of male lampreys consistently averaged longer than those of females. This difference was small, however, between 0.1 and 0.4 inch, and was not statistically significant.

The histogram of the length composition of adult Cayuga Lake sea lampreys (fig. 2) is based on length measurements of 1,917 specimens captured on their spawning migration in Cayuga Inlet during the spring of 1951.

Weight Composition

The average weight of 3,135 adult sea lampreys captured in Cayuga Inlet in 1950–52 was 4.5 ounces. Extreme weights were 1.4 and 12.1 ounces. A summary of weight measurements (table 2) is recorded according to the year of capture and sex. Diagrams of these data in figure 3 facilitate a comparison of the groups. Only unspent upstream migrants are included in this discussion.

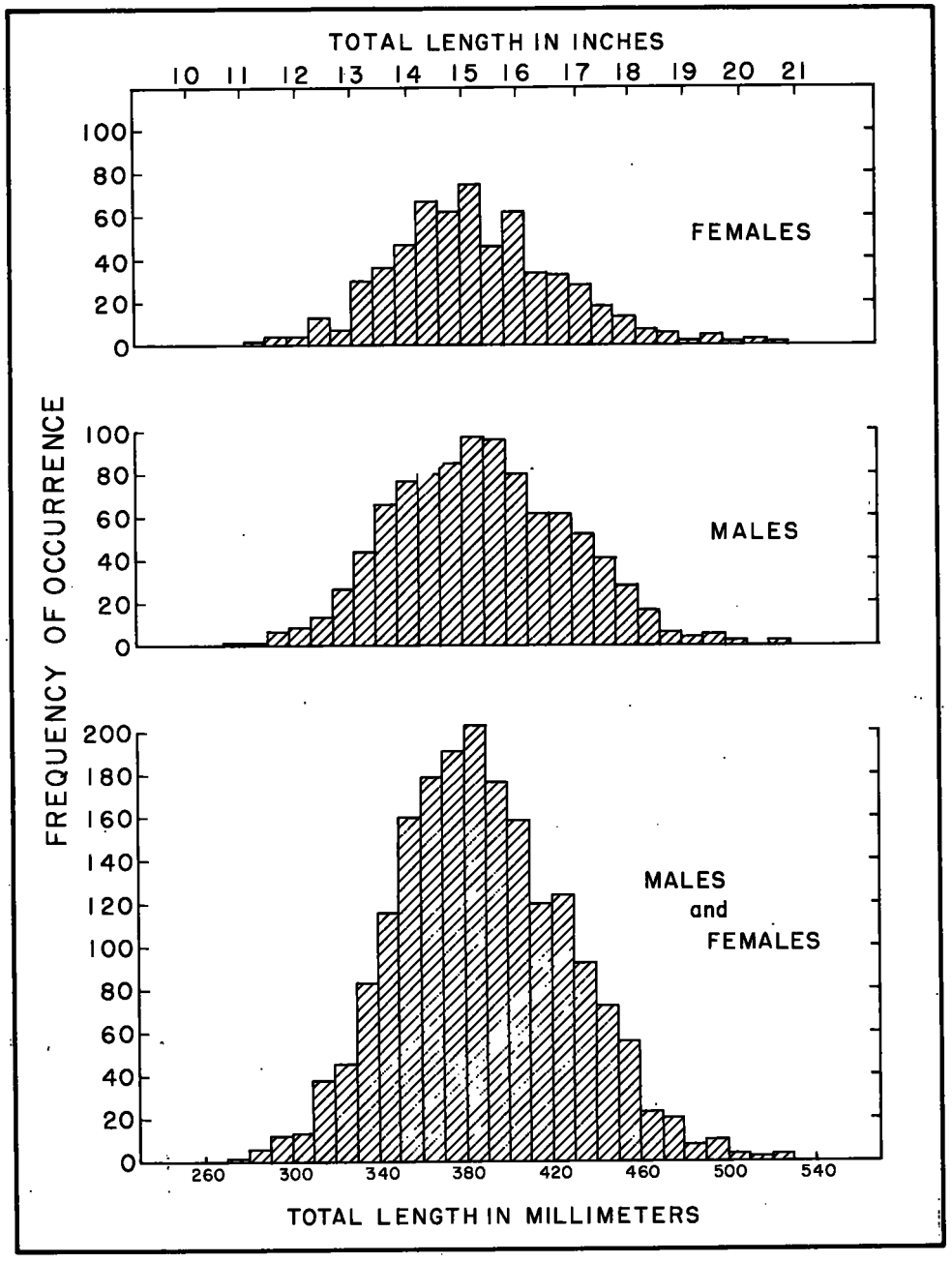

FIGURE 2.—Length-frequency distribution of adult sea lampreys taken in Cayuga Inlet, 1951.

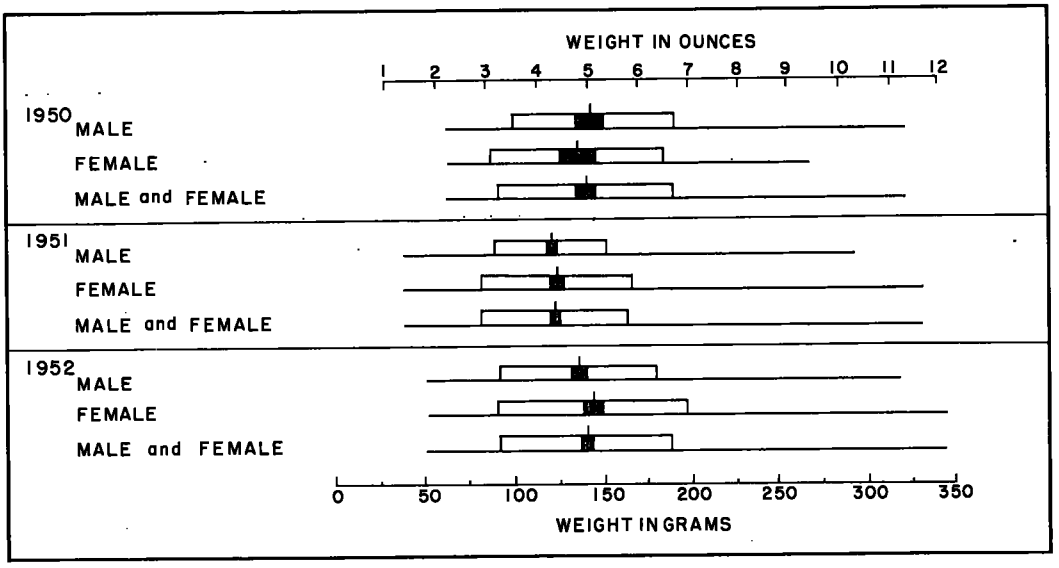

FIGURE 3.—Weight composition of Cayuga Lake sea lampreys. (Description of symbols is given in the caption of fig. 1.)

TABLE 2.—*Summary of weight measurements of sea lampreys captured in Cayuga Inlet*

Year and sex	Number of specimens	Weight (ounces)			
		Mean	Range	Standard deviation	Standard error
1950					
Male	153	4.8	2.2- 9.5	1.81	0.146
Female	92	5.1	2.2-11.3	1.91	.199
Total	245	5.0	2.2-11.3	1.95	.124
1951					
Male	961	4.4	1.4-11.7	1.22	.039
Female	604	4.3	1.4-10.3	1.65	.067
Total	1,968	4.3	1.4-11.7	1.63	.037
1952					
Male	507	5.1	1.8-12.1	1.73	.077
Female	416	4.8	1.8-11.2	2.08	.102
Total	922	4.9	1.8-12.1	1.90	.063

Annual mean body weights for the sexes combined, together with the estimated abundance of lampreys follow.

Year	Mean weight (ounces)	Estimated abundance [1]
1950	(5.0)	10-15,000
1951	4.3	9,390
1952	4.9	4,435

[1] Refer to p. 578 for details pertaining to population estimates.

Mean weight for the 1950 sample, shown in parentheses, was based on 245 specimens, which is approximately 2 percent of the estimated number in the spawning migration. Since they were taken during the early part of the migratory period, it is believed that this sample is biased in favor of unusually large specimens. Mean weights for 1951 and 1952 represent specimens taken throughout the migratory period, and each year 21 percent of the estimated total number were weighed.

The mean weight of sea lampreys differed significantly from year to year. Except for 1950, a biased value, these variations appear to be inversely related to their abundance.

No significant difference could be detected between weights of male and female specimens. In the seasons during which representative samples were measured, however, the females were heavier than males.

During the spring of 1951 a total of 1,968 sea lampreys from Cayuga Inlet were weighed. These data are depicted in figure 4 to illustrate the weight composition of the adult population of Cayuga Lake sea lampreys.

Growth of Parasitic-Phase Sea Lampreys

Evidence has been presented by Applegate (1950) that the sea lamprey in Lakes Huron and Michigan spend between 12 and 20 months in the parasitic phase of life in the lakes proper. Applegate's conclusion was based on measurements of specimens taken from the lakes throughout a 1½-year period. In the spring the newly transformed lampreys and the large mature individuals that were ready to enter the tributaries for spawning differed markedly in size. After the spawning

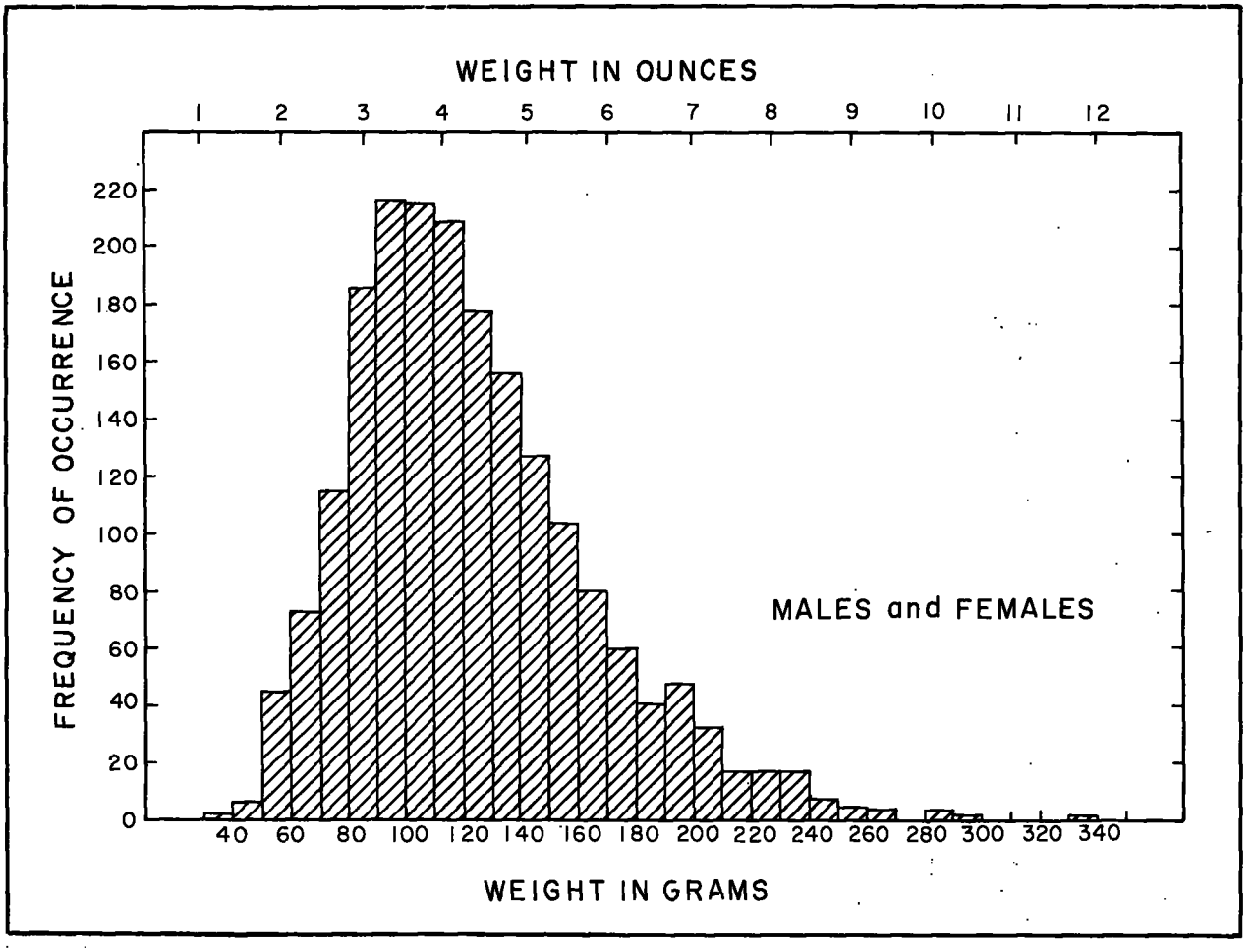

FIGURE 4.—Weight-frequency distribution of adult sea lampreys taken in 1951.

season only the small newly transformed lampreys were found in the lake.

Parasitic-phase sea lampreys taken from Cayuga Lake show the same trend of growth as Lake Huron and Lake Michigan specimens (table 3). These lampreys were captured during the gill-netting of lake trout in 1948–51. Some lampreys were entangled in the net and others adhered to the netted trout. Since both large and small lampreys are caught by this method, these specimens are considered to be representative of the population. Lampreys captured during the several years have been combined because of the small number taken in any one season.

The mean length of parasitic-phase sea lampreys in Cayuga Lake increased from 5.5 inches in March to 15.4 inches in April–May, 13 to 14 months later (table 3). Data given here include adequate

TABLE 3.—*Lengths of parasitic-phase sea lampreys from Cayuga Lake*

Month of capture	Number of specimens	Length (inches)		
		Mean	Minimum	Maximum
August–March [1]	68	5.5	4.6	6.4
April	2	6.1	6.0	6.2
May	2	9.5	8.2	10.8
June	2	11.3	10.5	12.0
July	5	10.3	8.4	12.9
August	7	13.1	11.5	14.5
September	13	12.5	8.4	18.0
October	38	13.9	9.1	19.5
November	1	19.1	19.1	19.1
January	2	15.7	14.6	16.7
April–May [2]	3,363	15.4	8.4	21.4

[1] Recently transformed lampreys captured in Cayuga Inlet.
[2] Mature lampreys captured on their spawning migration in Cayuga Inlet.

samples of newly transformed specimens and adults captured just before spawning. Mean lengths of sea lampreys captured between these two periods exhibited a distinct, if irregular, upward trend. The irregularities can be attributed to the small number of specimens representing most months.

Length-frequency distributions of parasitic-phase sea lampreys taken from Cayuga Lake and Seneca Lake during September and October combined (table 4) offer further strong evidence that only one year class is included in the samples. This finding substantiates the contention that the sea lamprey lives only 1 year (approximately) in the parasitic, feeding stage of life in the lake.

TABLE 4.—*Length-frequency distributions of sea lampreys from Cayuga and Seneca Lakes*

Total length (inches)	Frequency		Total length (inches)	Frequency	
	Cayuga Lake	Seneca Lake		Cayuga Lake	Seneca Lake
8.0– 8.9	1		16.0–16.9	6	16
9.0– 9.9	4		17.0–17.9	2	8
10.0–10.9	6		18.0–18.9	2	6
11.0–11.9	5	2	19.0–19.9	1	3
12.0–12.9	12	5	20.0–20.9		2
13.0–13.9	11	8			
14.0–14.9	9	10			
15.0–15.9	15	15	Mean length	13.7	15.5

Comparison With Size in Other Landlocked Populations

In the two preceding sections evidence was offered that size of Cayuga Lake sea lampreys was inversely related to lamprey abundance. Actually, this relation is more likely to be dependent on the ratio of the number of lampreys to the number of lake trout. This view is supported by comparisons of the sizes of sea lampreys from several areas where some measure of the lamprey-trout ratio is available.

Seneca Lake (N.Y.) is known to have few sea lampreys in relation to the number of lake trout (p. 611). A summary of lengths and weights of a series of sea lampreys from Seneca Lake and a series from Cayuga Lake, all captured during September and October (table 5), shows that the Seneca Lake sea lampreys averaged 1.8 inches (13 percent) longer and 2 ounces (59 percent) heavier than Cayuga Lake specimens.

In Lake Huron the abundance of lake trout has decreased disastrously; at the same time, the numbers of sea lampreys have increased (Hile 1949; Hile, Eschmeyer, and Lunger, 1951). Both factors operating simultaneously tend to reduce the lamprey-lake trout ratio at a rapid rate. As a result, both the length and weight of Lake Huron sea lampreys have decreased. During the 5-year period 1947–51 the average lengths of the upstream migrants in Carp Creek, a Lake Huron tributary, diminished from 17.4 to 15.8 inches (Applegate, Smith, McLain, and Patterson, 1952). The mean length of adult sea lampreys from the Ocqueoc River, another Lake Huron tributary, decreased from 17.1 inches in 1949 to 16.2 inches in 1951 (Applegate 1950; Applegate et al., 1952). Substantial reductions in weight accompanied the decreases in length. It would thus appear that Lake Huron sea lampreys are fast approaching the size of Cayuga Lake specimens, and are already smaller than those from Seneca Lake (table 6).

TABLE 5.—*Summary of lengths and weights of sea lampreys from Cayuga Lake and Seneca Lake*

Locality and years	Number of specimens	Length (inches)			Number of specimens	Weight (ounces)		
		Mean	Minimum	Maximum		Mean	Minimum	Maximum
Cayuga Lake 1948–50	74	13.7	8.4	19.5	44	3.4	1.4	9.2
Seneca Lake 1949–51	74	15.5	11.3	19.7	75	5.4	1.3	9.9

TABLE 6.—*Mean lengths and weights of sea lampreys from Cayuga Lake, Seneca Lake, and Lake Huron, 1951*

Item	Cayuga Lake Cayuga Inlet, April–May	Lake Huron [1]		Seneca Lake, lake proper, September–October [2]
		Carp Creek, April–August	Ocqueoc River, April–August	
Length (inches)	15.3	15.8	16.2	15.5
Weight (ounces)	4.3	4.1	4.6	5.4

[1] Applegate, Smith, McLain, and Patterson, 1952
[2] Seneca Lake specimens would probably attain a length greater than 17 inches and increase considerably in weight by April.

Length-Weight Relation of Adults

Length and weight of 1,906 adult migrant sea lampreys captured in Cayuga Inlet during April and May 1951 are from fresh specimens shortly after capture. This number includes both males and females and represents 20 percent of the estimated number of lampreys in the spawning migration. Lengths and weights (table 7) were derived from specimens sorted into 5-mm. length groups. The regression of weight on length is illustrated in figure 5.

The length-weight relation of Cayuga Lake sea lampreys is remarkably similar to that found by

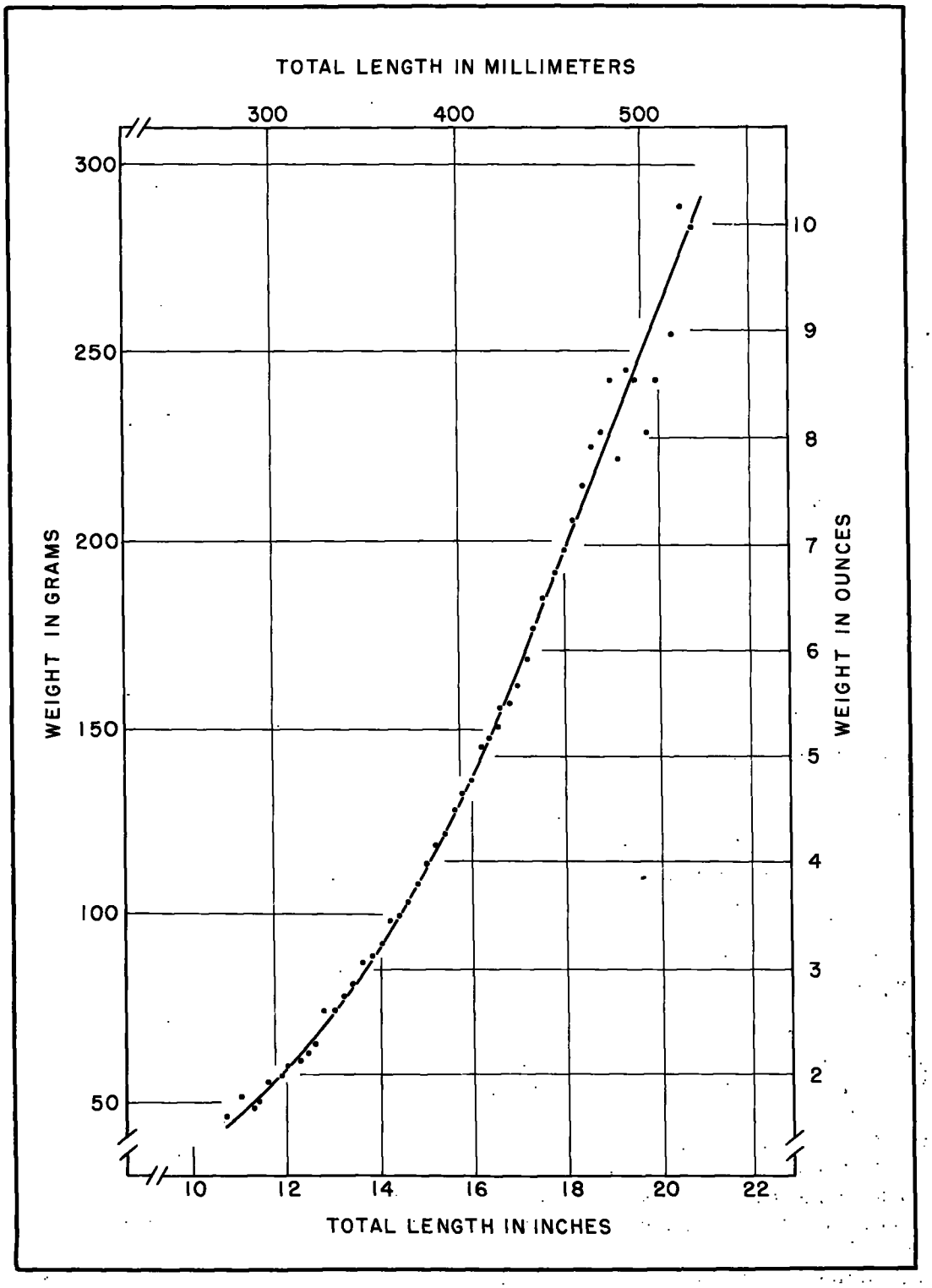

FIGURE 5.—Length-weight relation of adult sea lampreys from Cayuga Inlet, 1951.

Applegate (1950) for Lake Huron specimens. At a length of 10–12 inches their weight increased at a rate of approximately one-half ounce per inch of length. When they reached a length of 18–20 inches their weight increased at a rate of 1 ounce per inch. There was little difference in the length-weight relation between sexes.

TABLE 7.—*Length-weight relation of mature sea lampreys from Cayuga Inlet, April and May 1951*

Number of specimens	Mean length (inches)	Mean weight (ounces)	Number of specimens	Mean length (inches)	Mean weight (ounces)
1	10.7	1.62	79	16.0	4.78
1	11.1	1.80	68	16.2	5.10
2	11.3	1.71	52	16.4	5.18
6	11.5	1.76	69	16.6	5.46
6	11.7	1.94	56	16.8	5.50
10	11.9	2.00	53	17.0	5.69
5	12.0	2.09	42	17.2	5.92
13	12.3	2.16	39	17.4	6.22
17	12.5	2.22	36	17.6	6.50
22	12.7	2.29	29	17.8	6.74
18	12.9	2.62	26	18.0	6.96
44	13.1	2.61	19	18.2	7.25
38	13.3	2.76	11	18.4	7.56
53	13.5	2.80	12	18.6	7.90
63	13.7	3.06	9	18.8	7.68
72	13.9	3.12	3	19.0	8.47
75	14.0	3.24	6	19.1	7.78
88	14.2	3.44	8	19.4	8.65
92	14.4	3.49	2	19.5	8.52
96	14.6	3.62	2	19.7	8.02
78	14.8	3.82	2	20.0	8.47
118	15.0	3.99	1	20.1	11.67
89	15.2	4.15	1	20.3	8.96
94	15.4	4.27	1	20.5	10.16
77	15.6	4.50	2	20.7	9.91
100	15.8	4.66			

Detailed data, not given here, revealed a rather wide variation in weight among individuals of the same length and sex. The range was approximately an ounce for specimens 12 inches long and increased to 4 ounces for 20-inch specimens.

Morphometry

Taxonomists frequently employ body proportions as an aid in determining the taxonomic status of many animal groups, including the lampreys. Inasmuch as body proportions differ between the sexes and change with age and size, it becomes necessary first to determine the extent of these differences before valid comparisons between taxonomic categories can be undertaken. From the systematist's point of view it is just as important to know which characteristics remain constant as to know the degree of variation of the changing characteristics.

The methods of measurement and much of the terminology are those described by Hubbs and Trautman (1937).

Seasonal changes and sexual differences in body proportions

In this discussion, each of the principal sections of the sea lamprey's body has been dealt with separately to describe the relative size and sexual dimorphism during three significant periods of its life: September–October, May, and June. In September to October the sea lamprey is considered to have reached "normal" adult form. Changes accompanying sexual maturity become evident during May. By June, gross morphological modifications that are typical of spawning adults have been attained.

All measurements of body parts have been expressed as thousandths of the total length. Separate tables (nos. 8–12) have been compiled for each body section. The data in these tables are listed according to sex and collecting period, and include a frequency distribution, mean values, and measures of variation. (See figure 6.) It should be kept in mind that changes in proportional measurements of a particular body section that ostensibly appear to be increases or decreases in size, may be the result of changes in other body sections that affect the total body length.

Length over gill openings.—Length over the gill openings was the only body section that differed significantly between the sexes during the September–October period; males had the larger component (table 8). During May and June there was no difference between the sexes in this characteristic. As the season progressed, the relative length over

TABLE 8.—*Relative length over gill openings of Cayuga Lake sea lampreys in 3 collecting periods*

[Expressed as thousandths of the total length]

Relative length over gill openings	September–October			May			June		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
80–89	8	9	17						
90–99	27	12	39	12	9	21			
100–109	2	2	4	15	7	22	27	13	40
110–119				1		1	29	16	45
120–129								3	3
Mean ratio	93	88	91	101	99	100	110	111	110
Standard deviation	4.2	6.9	5.9	3.6	4.1	4.6	5.9	5.7	5.8
Standard error	0.7	1.4	0.8	0.7	1.0	0.7	0.8	1.0	0.6
Number of specimens	37	23	60	28	16	44	56	32	88
Mean total length (inches)	13.7	13.6	13.7	15.9	14.8	15.5	14.5	13.3	14.1

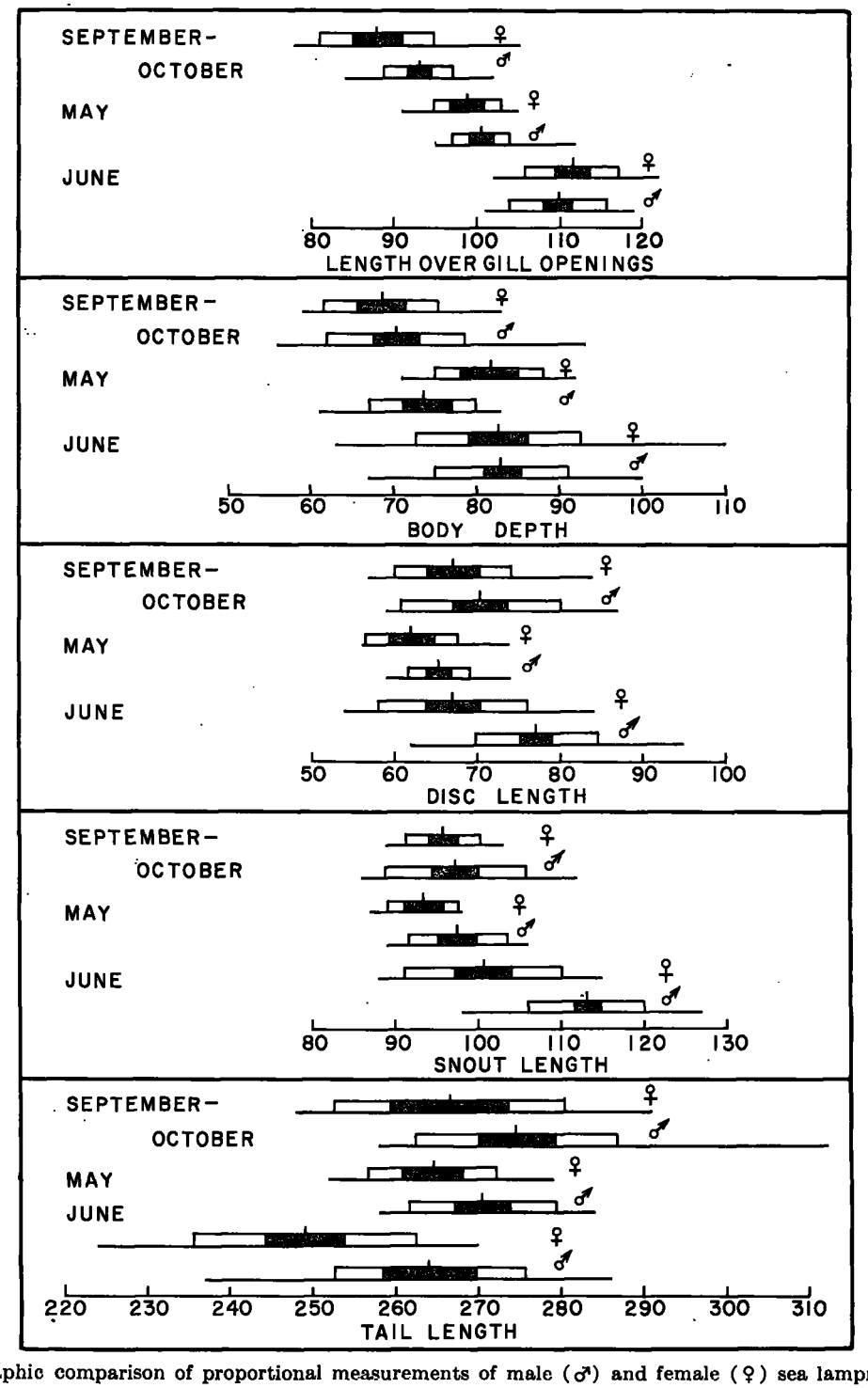

FIGURE 6.—Graphic comparison of proportional measurements of male (♂) and female (♀) sea lampreys captured in Cayuga Lake and Cayuga Inlet. Measurements are given in thousandths of the total length. (Description of symbols in caption of fig. 1.)

the gill openings increased from about ninety one-thousandths of the total body length in September–October to approximately one hundred and ten one-thousandths in June.

Body depth.—Body depth of male and female specimens was approximately equal in September–October and June, but in May, before egg deposition, the females were considerably deeper bodied than males (table 9). Males increased in body depth at a nearly constant rate from September–October through June. However, the females increased in depth very rapidly prior to spawning (May), but changed very little thereafter.

Disc length.—Males and females had discs (mouths) of about the same relative size during September–October and May (table 10). In June, the proportional disc length of male specimens was considerably larger than that for females. The disc size remained nearly constant throughout the entire year except for a slight decrease in both sexes in May and a great enlargement in male specimens in June. This difference was distinct enough to be useful in the field as an aid in determining sexes.

Snout length.—Length of the snout changed in much the same manner as the disc length (table 11). Only in June did the proportional snout length differ greatly between the sexes; in this month the males possessed the larger snouts. Only minor seasonal changes were evident except for the June specimens, at which time the size of the snout of males increased considerably.

TABLE 9.—*Relative body depth of Cayuga Lake sea lampreys in 3 collecting periods*

[Expressed as thousandths of the total length]

Relative body depth	September–October			May			June		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
50–59	1	1	2	------	------	------	------	------	------
60–69	19	13	32	7	------	7	3	2	5
70–79	13	8	21	17	6	23	14	10	24
80–89	3	1	4	4	9	13	32	14	46
90–99	1	------	1	------	1	1	8	3	11
100–109	------	------	------	------	------	------	1	1	2
110–119	------	------	------	------	------	------	------	1	1
Mean ratio	70	68	69	73	81	76	83	83	83
Standard deviation	8.4	6.9	8.5	6.3	6.6	7.4	8.1	10.0	8.8
Standard error	1.4	1.4	1.1	1.2	1.6	1.1	1.1	1.8	0.9
Number of specimens	37	23	60	28	16	44	58	31	89
Mean total length (inches)	13.7	13.6	13.7	15.9	14.8	15.5	14.5	13.4	14.1

TABLE 10.—*Relative length of the disc of Cayuga Lake sea lampreys in 3 collecting periods*

[Expressed as thousandths of the total length]

Relative length of disc	September–October			May			June		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
50–59	2	3	5	1	4	5	------	8	8
60–69	18	12	30	24	12	36	7	10	17
70–79	11	7	18	3	------	3	32	12	44
80–89	6	1	7	------	------	------	16	2	18
90–99	------	------	------	------	------	------	3	------	3
Mean ratio	70	67	69	65	62	64	77	67	73
Standard deviation	9.7	7.2	9.0	3.8	5.6	3.0	7.5	9.0	9.4
Standard error	1.6	1.5	1.2	0.7	1.4	0.5	1.0	1.6	1.0
Number of specimens	37	23	60	28	16	44	58	32	90
Mean total length (inches)	13.7	13.6	13.7	15.9	14.8	15.5	14.5	13.3	14.1

TABLE 11.—*Relative length of the snout of Cayuga Lake sea lampreys in 3 collecting periods*

[Expressed as thousandths of the total length]

Relative length of snout	September–October			May			June		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
80–89	6	1	7	1	2	3	------	3	3
90–99	17	18	35	18	14	32	------	10	10
100–109	12	4	16	9	0	9	18	14	32
110–119	2	------	2	------	------	------	30	4	34
120–129	------	------	------	------	------	------	10	------	10
Mean ratio	97	96	97	97	93	96	113	101	109
Standard deviation	8.5	4.7	6.9	6.0	4.3	5.2	6.9	9.5	10.4
Standard error	1.4	1.0	0.9	1.1	1.1	0.8	0.9	1.7	1.1
Number of specimens	37	23	60	28	16	44	58	31	89
Mean total length (inches)	13.7	13.6	13.7	15.9	14.8	15.5	14.5	13.3	14.1

Tail length.—Tail length of male lampreys averaged larger than that for females during each collecting period (table 12). The differences were not large, however, until June. As the seasons progressed from fall to spring, the relative tail length consistently decreased. Tail length was the only body section in which relative size decreased. From September–October to May the change was small, but a marked decrease took place between May and June, especially in females.

Summary.—Sexual dimorphism during September–October was exhibited only by the length over the gill openings. In May, only body depth showed any appreciable differences in the sexes.

In the June collections the disc length, snout length, and tail length showed distinct differences between males and females.

Seasonal changes in the various body sections were somewhat erratic. In general, the relative size of all body sections except tail length tended to increase as the seasons progressed from September–October through June. The tail length decreased during this period.

TABLE 12.—*Relative length of the tail of Cayuga Lake sea lampreys during 3 collecting periods*

[Expressed as thousandths of the total length]

Relative length of tail	September–October			May			June		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
220–229								4	4
230–239							1	1	2
240–249		2	2				5	11	16
250–259	4	4	8	1	5	6	10	9	19
260–269	4	4	8	11	6	17	23	6	29
270–279	11	2	13	12	5	17	17	1	18
280–289	8	3	11	4		4	2		2
290–299		1	1						
300–309									
310–319	1		1						
Mean ratio	274	266	272	271	264	269	264	249	259
Standard deviation	12.2	14.1	14.0	8.8	7.9	9.2	10.8	13.3	14.9
Standard error	2.3	3.5	2.1	1.6	2.0	1.4	1.4	2.4	1.6
Number of specimens	28	16	44	28	16	44	58	32	90
Mean total length (inches)	14.3	14.3	14.3	15.9	14.8	15.5	14.5	13.3	14.1

Morphometric Comparison of Cayuga Lake and Seneca Lake Sea Lampreys

Sea lampreys from Seneca Lake superficially appeared to be longer and proportionately greater in body girth than specimens from Cayuga Lake. Even though the two lakes are connected by the Seneca River (Barge Canal), because of the location of the interconnecting river in relation to the deepwater areas of the lake, it was thought that little interchange of sea lampreys takes place between the two. In view of these conditions it was desirable to make a taxonomic comparison of specimens from the two lakes. Body proportions and the number of teeth [3] and myomeres were compared.

Body proportions.—Measurements of the following body sections were taken from collections of sea lampreys captured in both lakes during September and October: body depth, disc length, snout length, length over the gill openings, and tail length (tables 13 and 14; fig. 7). Comparison of these data revealed a very close agreement in the relative size of snout length, length over gill openings, and tail length in specimens from the two lakes. Distinct differences between the two samples were disclosed in the relative length of the disc and body depth.

In the previous section it was shown that disc length decreased proportionately with normal (nonbreeding) growth, and that body depth increased proportionately with normal growth. Since the Seneca Lake specimens were larger and their body proportions were consistent with changes accompanying additional growth—i.e., disc length was smaller and body depth greater—these differences were considered to be of environmental rather than genetic origin.

TABLE 13.—*Relative body depth, disc length, snout length, and length over gill openings of sea lampreys from Cayuga Lake and Seneca Lake*

[Expressed as thousandths of the total length]

Length classes	Body depth		Disc length		Snout length		Length over gill openings	
	Cayuga Lake	Seneca Lake	Cayuga Lake	Seneca Lake	Cayuga Lake	Seneca Lake	Cayuga Lake	Seneca Lake
50–59	2		5	17				
60–69	32	2	30	46				
70–79	21	37	18	12				
80–89	4	30	7		7	8	7	23
90–99	1	5			35	54	39	46
100–109					16	13	4	3
110–119					2			1
Mean ratio	69	80	69	63	97	95	91	92
Standard deviation	8.5	6.8	9.0	5.8	6.9	5.5	5.9	5.1
Standard error	1.1	0.8	1.2	0.7	0.9	1.3	0.8	0.6
Number of specimens	60	74	60	74	60	74	60	74
Mean total length (inches)	13.7	15.5	13.7	15.5	13.7	15.5	13.7	15.5

TABLE 14.—*Relative length of tail of sea lampreys from Cayuga Lake and Seneca Lake*

[Expressed as thousandths of the total length]

Length classes	Cayuga Lake	Seneca Lake
220–229		1
230–239		
240–249	2	1
250–259	8	11
260–269	8	25
270–279	13	25
280–289	11	8
290–299	1	3
300–309		1
310–319	1	
Mean ratio	272	270
Standard deviation	14.0	13.5
Standard error	2.1	1.6
Number of specimens	44	75
Mean total length (inches)	14.3	15.5

[3] The terms "tooth" and "teeth" are used in the broadest sense of their meaning; the sea lamprey's dental armature, consisting of cornified epithelium, does not represent true teeth.

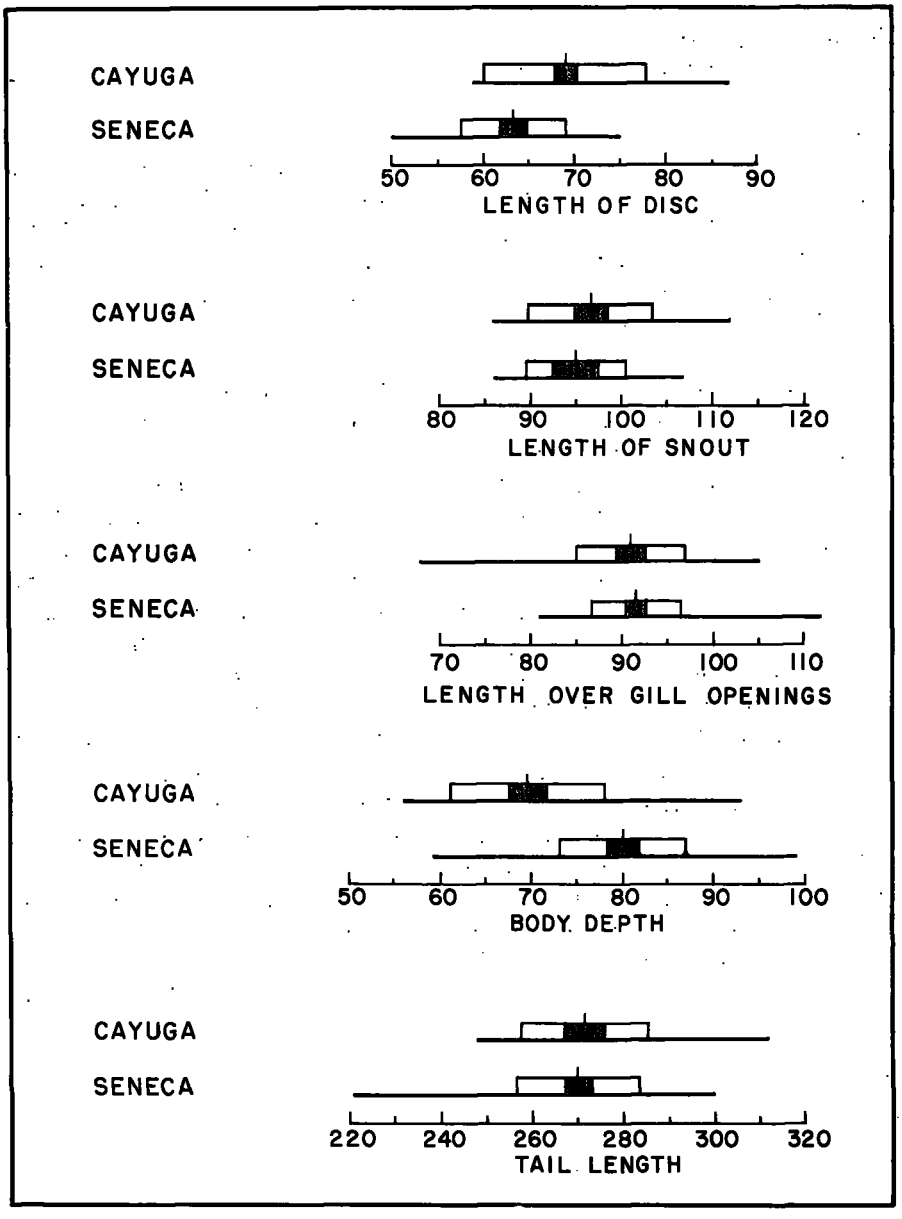

FIGURE 7.—Comparison of body sections of sea lampreys from Cayuga Lake and Seneca Lake. Measurements are given in thousandths of the total body length. (Description of symbols in caption of fig. 1.)

Teeth and myomeres.—Methods outlined by Hubbs and Trautman (1937) were followed in counting teeth and myomeres. Many of the difficulties they encountered in work on *Icthyomyzon* were present also in work on *Petromyzon*. Most troublesome was the myomere count on immature specimens, especially those that had been preserved for several years. In such specimens, the myomeres were nearly indistinguishable externally. It was necessary to slit the abdomen lengthwise, in the ventrolateral area, and count the muscle bands.

In addition to the myomeres the following series of teeth or cusps were counted: Cusps on the supraoral lamina; number of biscuspid circumorals; teeth in the anterior row; cusps on the lateral lingual lamina; cusps on the transverse lingual lamina; teeth in the lateral row; teeth in the circumoral row; and cusps on the infraoral lamina.

498325 O—59——2

Variation was nil or slight in three characters: supraoral cusps; bicuspid circumorals; and the anterior row. The number of cusps on the supraoral lamina was 2 in all of the 176 specimens from Cayuga Lake and 106 from Seneca Lake. The number of bicuspid circumorals was 8 in 171 specimens of a sample of 173 from Cayuga Lake (the other 2 counts were 6 and 9) and in all 75 from Seneca Lake. The number of teeth in the anterior row was 3 in all 73 Cayuga Lake specimens. In Seneca Lake lampreys the anterior row count was 3 in 164 of 174 specimens; 9 had a count of 4, and 1 a count of 2, which gave a mean of 3.05.

Other tooth counts exhibited greater variability (table 15; fig. 8). The number of infraoral cusps ranged from 7 to 10 in Cayuga Lake lampreys (average of 8.02) and from 6 to 10 in Seneca Lake specimens (average of 7.69). In specimens whose infraoral cusps had been worn down, the outer covering was ready to be sloughed off. Invariably the distal ends of the lamina in these specimens were so constricted as to make it difficult to count the cusps. Removal of this outer sheath, however, exposed the underlying sharp, distinct cusps that could be counted accurately.

The number of teeth in the circumoral row averaged 18.3 for both Cayuga Lake and Seneca Lake samples. The number of circumoral teeth ranged from 15 to 22 in Cayuga Lake specimens and from 16 to 20 for Seneca Lake specimens. Undoubtedly the greater number of specimens examined from Cayuga Lake (174), as opposed to 75 from Seneca Lake, contributed to the greater range of this character observed in the Cayuga Lake sample.

The number of teeth in the lateral row varied little. Cayuga Lake specimens had an average of 7.3 lateral teeth (range, 5 to 8). Seneca Lake specimens had significantly fewer teeth in the lateral row, an average of 7, with extremes of 6 and 8.

Denticulations on the lingual lamina are well developed and never seemed to be so dull or worn as the circumoral teeth. For ease and accuracy in making counts of both the transverse and lateral lingual lamina, the tongue was excised.

The number of cusps on the transverse lingual lamina of Cayuga Lake specimens ranged from 12 to 19, and averaged 14.8. In Seneca Lake specimens the count varied from 12 to 18 and averaged 14.6. This small difference between the two groups was not significant.

Cusps on the lateral lingual lamina of Cayuga Lake specimens ranged from 9 to 15 and averaged 12.6. In Seneca Lake specimens the count varied from 9 to 17, with an average of 12.5. This difference between Cayuga Lake and Seneca Lake specimens was not statistically significant.

Sea lampreys from Seneca Lake had a greater number of myomeres (average, 72.7; range, 67–76) than Cayuga Lake specimens (average 71.4; range, 68–75: table 16). This difference in number of

TABLE 15.—*Counts of cusps and laminae on sea lampreys from Cayuga Lake and Seneca Lake*

Number of cusps or laminae	Lateral lingual lamina		Transverse lingual lamina		Lateral row		Circumoral row		Infraoral cusps	
	Cayuga Lake	Seneca Lake	Cayuga Lake	Seneca Lake	Cayuga Lake	Seneca Lake	Cayuga Lake	Seneca Lake	Cayuga Lake	Seneca Lake
5					1					
6					15	14				2
7					95	52			47	24
8					63	9			81	37
9	2	1							46	10
10	2	4							2	1
11	13	24								
12	27	46	1	3						
13	27	39	11	11						
14	17	24	10	22						
15	5	2	10	23			1			
16		1	9	9			1	1		
17		1	5	4			12	2		
18			1	2			96	43		
19			1				59	26		
20							4	3		
21										
22							1			
Mean	12.6	12.5	14.8	14.6	7.3	7.0	18.3	18.3	8.0	7.7
Standard deviation	1.4	1.3	1.5	1.3	0.7	0.6	0.8	0.8	0.8	0.8
Standard error	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.1
Number of specimens	[1] 48	[1] 71	48	74	174	75	174	75	176	74

[1] Both left and right lateral lingual laminae are grouped together. The discrepancy in numbers results from broken laminae.

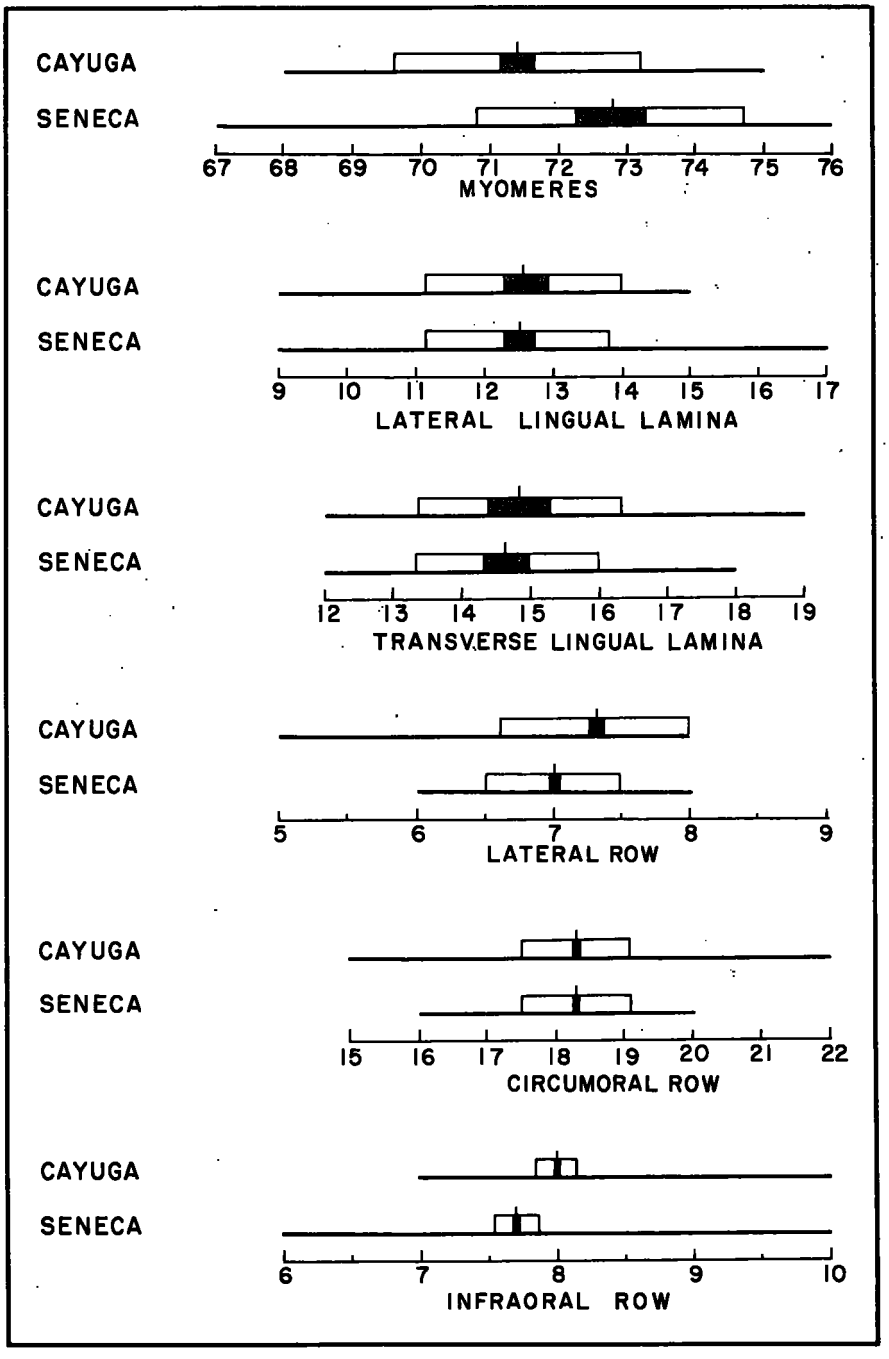

FIGURE 8.—Comparison of tooth and myomere counts of Cayuga Lake and Seneca Lake sea lampreys. (Description of symbols in caption of fig. 1.)

myomeres between the stocks is statistically significant. Even though the process of making a myomere count is slow, tedious, and subject to error, it is one of the most useful meristic characters for determining specific and infraspecific categories of lampreys.

Of all counts (teeth and myomeres) described in the preceding paragraphs, only three characters exhibited a significant difference between the Cayuga Lake and Seneca Lake stocks: number of cusps on the infraoral lamina; number of teeth in the lateral row; and the number of myomeres. A

better grasp of the magnitude of differences between Cayuga Lake and Seneca Lake stocks is gained by further analysis of these three characters.

A divergence between the two populations in number of cusps on the infraoral lamina was found to be 56.2 percent. The divergence in number of teeth in the lateral row was 62.5 percent, and the divergence in the number of myomeres was 66.8 percent. Since the number of laminae cusps, teeth, and myomeres are believed to be genetic, and since the average divergence of these characters differ at the racial level, it follows that Cayuga Lake sea lampreys are to be considered a separate race from Seneca Lake sea lampreys.

TABLE 16.—*Myomere counts on sea lampreys from Cayuga Lake and Seneca Lake*

Number of myomeres	Cayuga Lake	Seneca Lake
67		1
68	7	
69	20	
70	28	7
71	34	8
72	42	9
73	25	17
74	19	8
75	4	12
76		1
Mean	71.4	72.7
Standard deviation	1.8	2.0
Standard error	0.1	0.2
Number of specimens	179	63

SPAWNING MIGRATION

Tributaries of Cayuga Lake

Each spring the sea lampreys pass from the depths of Cayuga Lake into the tributary streams to find suitable spawning sites. Practically all the tributaries of the lake have natural barriers near the mouth, a circumstance which substantially limits the available spawning area. The only tributaries that could possibly provide an appreciable amount of nesting territory are: Sawyer Creek, Salmon Creek, Fall Creek, Cascadilla Creek, Sixmile Creek, Cayuga Inlet, Taughannock Creek, and Canoga Creek (fig. 24).

Sea lampreys have never been reported from Sawyer Creek, Salmon Creek, or Canoga Creek, nor were they found in these creeks during this study. A few adults were seen in all the remaining streams mentioned except Sixmile Creek. However, nesting or spawning lampreys were found only in Taughannock Creek and Cayuga Inlet. Just four pairs of nesting lampreys are known to have utilized Taughannock Creek, whereas each year thousands of lampreys have been observed spawning in Cayuga Inlet. Thus, Cayuga Inlet is the only tributary of Cayuga Lake that has significant value for lamprey reproduction.

Water Conditions in Cayuga Inlet

The middle and lower portions of Cayuga Inlet exhibit water conditions typical of a marginal trout stream. At the U.S. Geological Survey dam, 5 miles upstream from the lake, the waterflow varied between 63 and 18 cubic feet per second during the period April 25 to May 23, 1951 (fig. 9). The minimum and maximum morning (7 to 8 a.m.) water temperatures during this period were 42° and 64° F. Volume of flow was greatest early in the season and decreased steadily throughout the period, with the exception of a flood which occurred on May 11. As the water volume decreased the water temperature gradually increased, reaching its highest value (64° F.) on May 22, the time of lowest waterflow (18 c.f.s.).

Migratory Behavior

Sea lampreys are believed to assemble at the mouth of Cayuga Inlet in early spring (February and March). When water from Cayuga Inlet becomes warmer than the lake water, they begin moving into the deep lower portion of the inlet. They do not move into shallow waters until the evening water temperatures reach nearly 50° F., a value usually not attained until the latter part of April. The year's first specimens were captured in Cayuga Inlet on May 4, 1950,[4] April 22, 1951, and April 19, 1952.

Water temperature and lamprey activity are closely correlated. After the lampreys arrive in the shallow portions of the stream, a drop in water temperature to the low forties drastically retards activity. Upstream migration nearly ceases, and even when handled the lampreys do not react with as much vigor as they show when temperatures are higher.

Early migrants move upstream only during darkness, hiding under rocks, logs, and debris during the daylight hours. As the season progresses their aversion to light gradually disappears and

[4] Sea lampreys are believed to have arrived in Cayuga Inlet at least 1 week prior to their capture in 1950.

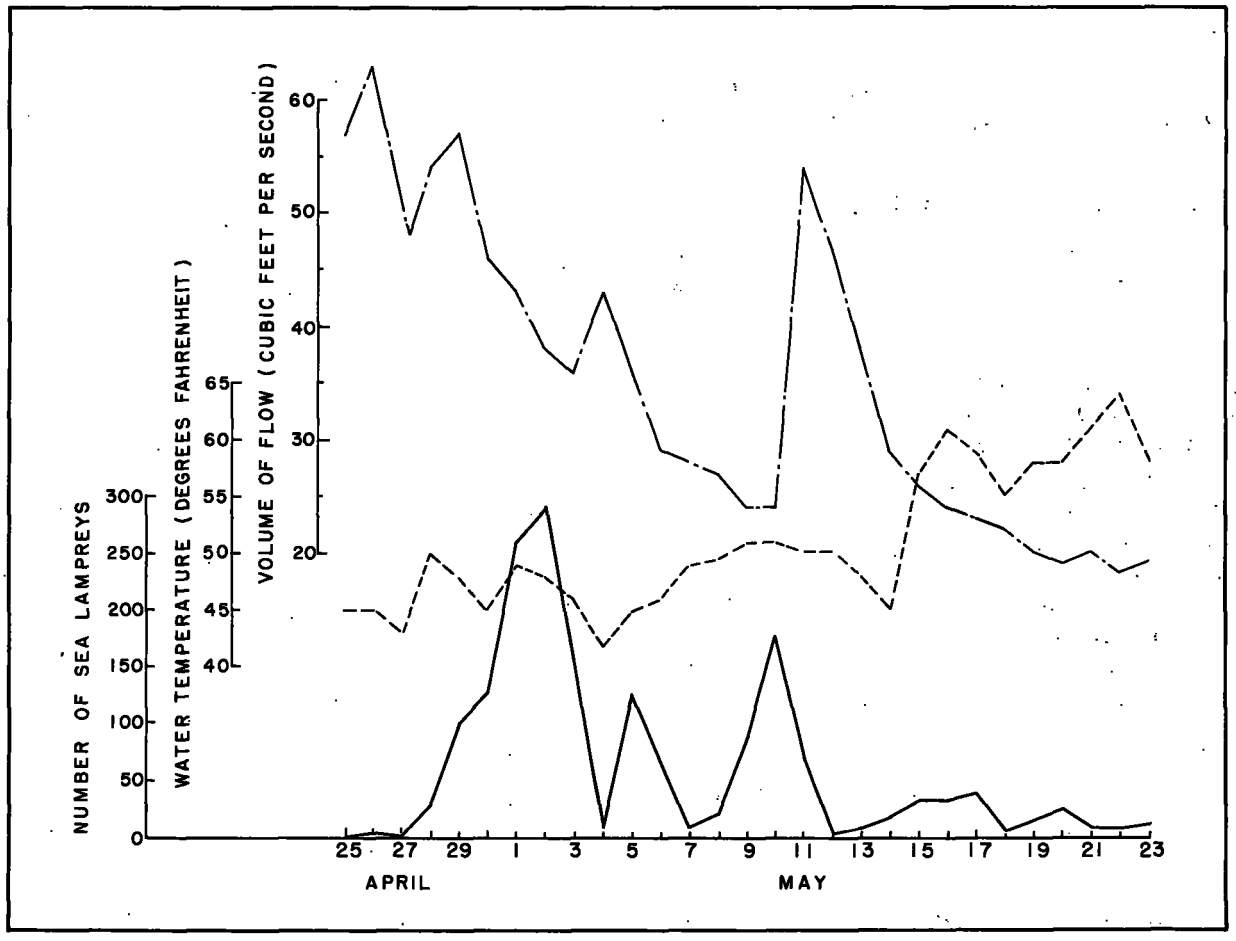

FIGURE 9.—Daily morning water temperature, average daily waterflow, and number of upstream-migrant sea lampreys captured at the U.S. Geological Survey dam, 1951.

blindness afflicts many; consequently, late arrivals move upstream during the daytime.

In favorable locations, lampreys often hide during the day in groups of several hundred. The individuals in these groups usually maintain their position by adhering with their buccal discs to solid objects below which they are hiding, or to each other. Notable exceptions were clusters of approximately 25 or 30 which were hiding during the daytime under the concrete apron (fig. 11) of the U.S. Geological Survey dam. These lampreys were packed side by side between the underside of the apron and the stream bottom, forming a mass approximately 6 inches deep and 10 inches wide. The mouths of many were plainly seen; they were open, but were not attached to any object. This behavior was observed on several occasions between May 9 and 16, 1952.

Upstream-migrant sea lampreys held in hatchery troughs invariably clung to the end of the trough where the water entered. They were so aggressive when disturbed that cover screens had to be held in place by cleats. These confined lampreys performed a search pattern of varying intensity that was closely associated with their state of nervousness. In an undisturbed group, a single lamprey left its position in the mass, backed out, slowly explored the sides of the trough, and returned to the mass. About the time one returned another backed out and explored the trough. This routine was repeated continually although not always with such precision. The number of exploring lampreys and the rapidity of their movements were in direct proportion to their state of excitement. If the group was greatly excited, all specimens frantically searched the trough for an exit.

If undisturbed for half a day or so, searches were conducted by single individuals departing at intervals of several minutes. This same type of searching activity was also performed by sea lampreys in their natural habitat in Cayuga Inlet.

Population Estimates of Spawning Adults

Each spring during the years 1950, 1951, and 1952 an estimate of the number of adult upstream-migrant sea lampreys in Cayuga Inlet was made by the mark-and-recapture method. Due to the lack of trapping devices and a suitable tag in 1950, the population estimate is questionable. Adequate facilities in 1951 and 1952 permitted the use of more accurate methods and the results were most satisfactory.

To facilitate the designation of locations in Cayuga Inlet, the stream was divided into eleven 1-mile sections assigned letters A to K from the lowermost section to the one farthest upstream. These sections conform somewhat to natural physical areas of the stream (fig. 10).

1950

It is estimated that 10,000 to 15,000 sexually mature sea lampreys entered Cayuga Inlet in the spring of 1950. This estimate is based on the results of a mark-and-recapture study in addition to three indices of abundance that are related to lamprey population density. These indices were sex ratio of lampreys in the spawning migration, size of migrant lampreys, and the incidence of lamprey attacks on lake trout. These indices of abundance were used in conjunction with accurate estimates of lamprey abundance obtained for 1951 and 1952.

A mark-and-recapture study was conducted during May 15 to May 24, 1950. Sea lampreys were captured by hand in Cayuga Inlet between Newfield station and Cayuga Lake; most were caught at the U.S. Geological Survey dam and at Newfield station. A white plastic disc 7/16-inch diameter, connected to a No. 10 Mustad-Best Kirby fishhook by a silver link, was attached to the lamprey through the median dorsal ridge just anterior to the first dorsal fin. In addition to this tag a notch was made in the dorsal fin of each specimen with a paper punch. Ninety-five marked lampreys were released in section *E*, 54 in section *A*, and 59 1½ miles downstream from section *A*. Dates and numbers of lampreys tagged and recaptured are included in table 17.

TABLE 17.—*Estimate of the number of sea lampreys in the 1950 spawning migration in Cayuga Inlet*

Date	Number lampreys captured (*A*)	Number of tagged sea lampreys at large (*B*)	Product (*AB*)	Sum of product (ΣAB)	Tagged sea lampreys recaptured: Number per day (*C*)	Tagged sea lampreys recaptured: Sum (ΣC)	Estimated population (P) [1]
May 15	186	109	20,274	20,274	1	1	20,274
May 17	50	154	7,700	27,974	1	2	13,987
May 20	96	208	19,968	47,942	----------	2	23,971
May 23	69	208	14,352	62,294	2	4	15,574
May 24	126	208	26,208	88,502	8	12	7,375
Total	527	----------	----------	88,502	----------	12	[2] 7,375

[1] $P=\frac{\Sigma AB}{\Sigma C}$.

[2] The 95-percent confidence limits are 4,210 and 12,950.

Due to a high percentage loss of tags, most of the recaptured specimens were identified from the notch made in the first dorsal fin and the wound remaining where the tag had been attached. As a result, it was impossible to determine the date they had been released. Since the date of release is a requisite for use of the Schaefer (1951) method of estimating abundance, the Schnabel method [5] was employed.

Estimates of abundance from this study varied from 7,375 to 23,971 (last column of table 17). These rather wide fluctuations in the abundance estimates are attributed to the small number of lampreys utilized in this study: total catch of 527, 208 tagged, 12 recaptured. Because of the erratic results only a very general interpretation of the data is permissible, that the 1950 migration consisted of between 7,375 and 23,971 sea lampreys.

Indices of abundance based on other characteristics of lamprey stocks that are associated with population density yielded more consistent values. The sex ratio of the 1950 spawning migration (table 26) indicates a population of 10,000–12,000 lampreys. Length composition of the 1950 spawning migration (p. 562) indicates a population of 11,000–12,000. The incidence of lamprey attacks on lake trout in 1949 (table 45) indicates a population of approximately 15,000.

The weight of evidence from both the mark-and-recapture results and the other data on density of the lamprey population support the conclusion that the 1950 spawning migration consisted of between 10,000 and 15,000 sea lampreys, and thus

[5] The formula and meaning of the letters and symbols are given in table 17.

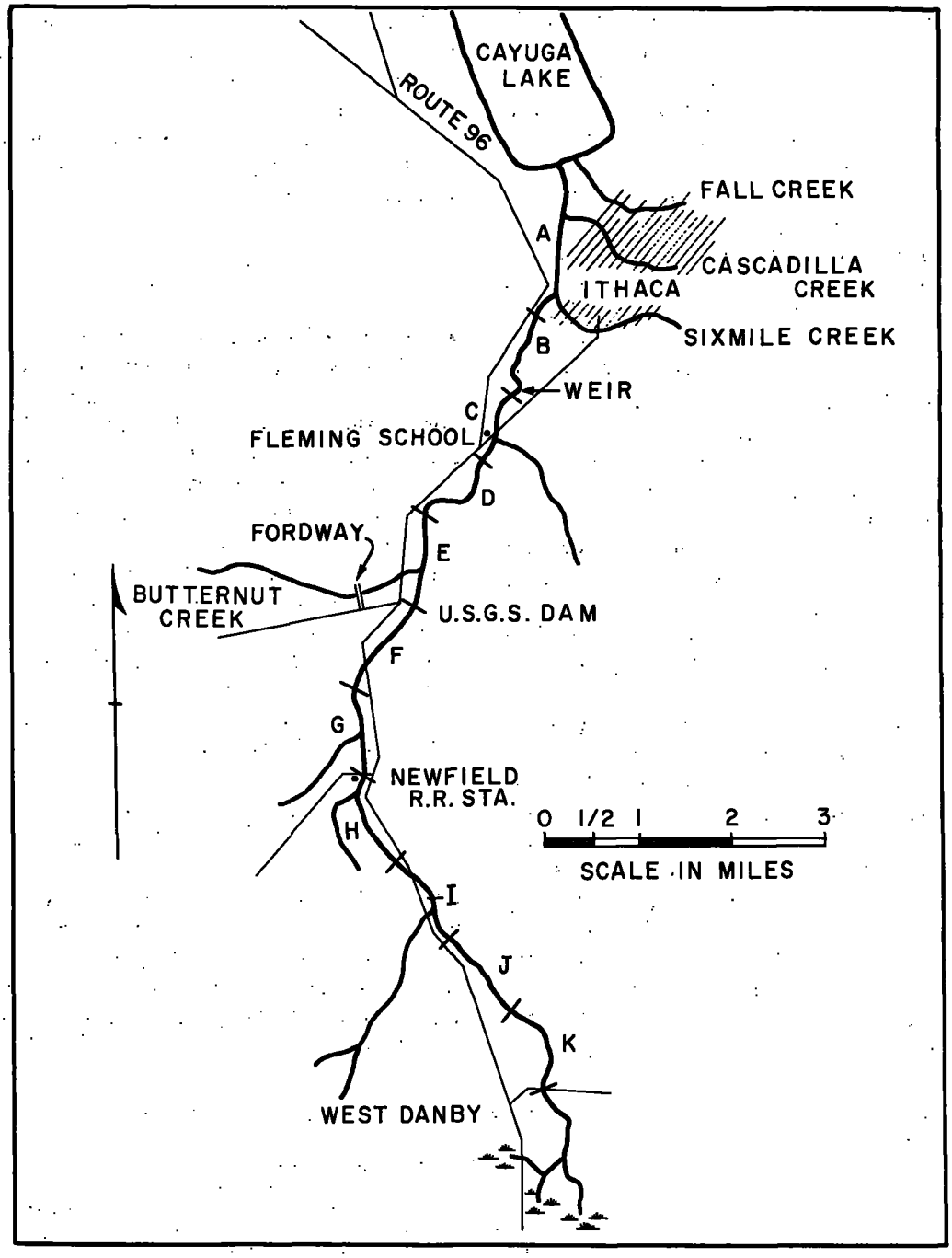

FIGURE 10.—Map of Cayuga Inlet and vicinity showing the 1-mile sections of the stream and localities mentioned in the text.

should be considered the largest migration during the 1950–52 period.

1951

The number of upstream-migrant sea lampreys that entered Cayuga Inlet in the spring of 1951 was estimated to be 9,390. This estimate is based on 960 tagged specimens and a total catch of 5,559.

During the period April 19 to June 13, migrant lampreys were captured by means of a weir, three portable lamprey traps, and by hand. The weir consisted of a barrier net placed diagonally across

the stream with a boxlike trap at the upstream end. The net, 60 feet long and 3½ feet high, was made of two layers of netting for added strength. One layer of netting was ½-inch mesh, bar measure, the other was 1½ inches, bar measure. A trap box 3 feet square, constructed of ¼-inch galvanized hardware cloth on a wooden frame, had a conical entrance on the downstream face with a 1-inch opening at the apex. Rectangular portable traps (36 ×18×18 inches), were constructed of ¼-inch galvanized hardware cloth over a wooden frame. Conical entrances at each end were 16 inches deep and had 2-inch openings at the apex. A removable top was held in place with dowels and cleats.

A Petersen tag consisting of two 7/16-inch-diameter plastic discs, one red and one white, was attached to the first dorsal fin by means of a brass pin. One disc was numbered so that identification of individual specimens was possible. Tagged specimens were released as follows: 257 in section *E*; 417 in section *A*; and 286 one and one-half miles downstream from section *A*. Date and number of lampreys tagged and captured are included in table 18.

Schaefer's method for estimating the total number of specimens in a migratory population was employed. This method is well adapted for estimating the numbers of adult lampreys on their spawning run because it takes into consideration the changing abundance of lampreys in the tributary stream during the several weekly periods of tagging and recovery. Even though a variable number of tagged or marked lampreys was released in the stream during the marking periods, this number was directly proportional to the total catch of unmarked or untagged lampreys. In table 18 is a summary, by weekly periods, of the number of lampreys tagged, number of tagged lampreys recaptured, and total number of lampreys captured.

An estimate of the number of sea lampreys on the 1951 spawning run (table 19) was computed from the formula:

$$n_{ai}=m_{ai}\frac{T_a}{m_a.}\frac{C_i}{m._i},$$

where, n_{ai}=the estimated number of lampreys based on the ath tagging period and the ith recovery period; m_{ai}=the number of lampreys tagged during the ath period of tagging and recovered during the ith period of recovery; T_a=the number of lampreys tagged during the ath tagging period; m_a=the total number of tagged lampreys recovered during each ath recovery period; C_i=the total number of lampreys recovered during the ith recovery period; $m._i$=the total number of tagged lampreys recovered during each ith recovery period. The summation of n_{ai} values gave a population estimate (N) of 9,390.

Fiducial limits at the 95-percent level were calculated from the formula:

$$P=p\pm\lambda\sqrt{\frac{N-n}{N-1}\cdot\frac{pq}{n}}$$

where, P=the population estimate at the 95-percent confidence level; N=the population estimate; p=the total number of tagged lampreys divided by the population estimate N; q=1—p; n=the total number of lampreys captured; λ=1.96 for the 95-percent confidence limits. Upper and

TABLE 18.—*Tagging-and-recapture record of sea lampreys in the 1951 spawning migration in Cayuga Inlet*

Week of capture (*i*)	Number of tagged sea lampreys recaptured				Total number of sea lampreys captured (C_i)	$C_i/m._i$
	Week tagged (*a*)				Total ($m._i$)	
	Apr. 19–25	Apr. 26–May 2	May 3–9	May 10–16		
Apr. 19–25					7	
Apr. 26–May 2		46			46	1,538 33.43
May 3–9		19	9		28	626 22.36
May 10–16	1	81	26	80	188	1,718 9.14
May 17–23		59	31	130	220	1,390 6.32
May 24–30		8	1	1	10	18 1.80
May 31–June 6		25	15	20	60	212 3.53
June 7–13		3	2	2	7	50 7.14
Total tagged lampreys recaptured ($m_a.$)	1	241	84	233	559	5,559
Total number of lampreys tagged (T_a)	6	384	176	394		
$T_a/m_a.$	6	1.59	2.10	1.69		

lower population limits were determined to be 9,897 and 8,972.

1952

The number of upstream-migrant lampreys that entered Cayuga Inlet in 1952 was estimated to be 4,435. This estimate is based on 1,773 marked specimens and a total catch of 3,413. A total of 1,234 marked specimens were recaptured.

TABLE 19.—*Estimate of the number of sea lampreys in the 1951 spawning migration in Cayuga Inlet*

Week of capture (*i*)	Calculated number of sea lampreys [1]				
	Week tagged (*a*)				Total
	Apr. 19–25	Apr. 26–May 2	May 3–9	May 10–16	
Apr. 19–25					
Apr. 26–May 2		2,445			2,445
May 3–9		675	423		1,098
May 10–16	55	1,177	499	1,236	2,967
May 17–23		593	411	1,388	2,392
May 24–30		23	4	3	30
May 31–June 6		140	111	119	370
June 7–13		34	30	24	88
Total	55	5,087	1,478	2,770	9,390

[1] Values computed from data in table 18 and the formula given on p. 580.

All lampreys utilized for this population estimate were captured at the U.S. Geological Survey dam or at Newfield station during April 30 to June 3. They were caught by a portable lamprey trap and by hand. The lampreys were marked by a system of notches made in the dorsal and caudal fins, and were all released at the U.S. Geological Survey dam. They were subsequently recaptured at the dam or upstream at Newfield station. Dates and numbers of lampreys marked and captured are included in table 20.

The Schaefer method was again used to estimate the number of lampreys. Weekly summaries of tagging and recapture are listed in table 20. In table 21 are the population estimates recorded by weekly periods. The number of lampreys in the 1952 spawning run was calculated to be 4,435, with 95-percent fiducial limits of 4,108 and 4,818.

These population estimates for the 1951 and 1952 seasons are considered to be reliable. All theoretical assumptions are believed to have been adequately fulfilled.

TABLE 21.—*Estimate of the number of sea lampreys in the 1952 spawning migration in Cayuga Inlet*

Week of capture (*i*)	Calculated number of sea lampreys [1]					
	Week tagged (*a*)					Total
	Apr. 30–May 6	May 7–13	May 14–20	May 21–27	May 28–June 3	
Apr. 30–May 6	1,529					1,529
May 7–13	482	398				880
May 14–20	278	465				743
May 21–27	79	164		221		464
May 28–June 3	30	62		481	246	819
Total	2,398	1,089		702	246	4,435

[1] Values computed from data in table 20 and the formula given on p. 580.

Rate of Upstream Movement

The tagging and recapture of many lampreys at six locations along Cayuga Inlet during the spring of 1951 provided an opportunity to measure the rate at which they proceed upstream on their spawning migration (table 22).

Sea lampreys traversed the slow-moving portions of Cayuga Inlet at a rate of 1 to 2 miles per day. Farther upstream where the current is swifter, their rate of travel decreased to approximately one-third to 1 mile per day. Actual swimming velocity under average conditions approximates 1 foot per second, but frequent "rest periods" account for a large share of their time.

When the occasion demands, the lamprey is

TABLE 20.—*Tagging-and-recapture record of sea lampreys in the 1952 spawning migration in Cayuga Inlet*

Week of capture (*i*)	Number of tagged sea lampreys recaptured					Total number of sea lampreys captured (C_i)	$C_i/m_{.i}$
	Week tagged (*a*)				Total ($m_{.i}$)		
	Apr. 30–May 6	May 7–13	May 14–20	May 21–27	May 28–June 3		
Apr. 30–May 6	334					334	1,511	4.52
May 7–13	217	148				365	817	2.24
May 14–20	130	180				310	668	2.16
May 21–27	42	72		19		133	253	1.90
May 28–June 3	17	29		44	2	92	164	1.78
Total tagged lampreys recaptured ($m_{a.}$)	740	429		63	2	1,234	3,413	
Total number of lampreys tagged (T_a)	734	515		386	138			
$T_a/m_{a.}$	0.99	1.20		6.13	69.00			

capable of swimming rapidly. Sometimes, when a group of lampreys is frightened, they scatter so swiftly that a few may wriggle onto dry land to points several feet from the shore. Also, when rapids and swift currents are encountered, they ascend quickly though not without considerable effort.

TABLE 22.—*Rate of upstream movement of sea lampreys in the 1951 spawning migration in Cayuga Inlet*

Area traveled	Number of specimens	Distance (stream-miles)	Minimum number of days	Average number of days [1]	Stream gradient
Airport to weir [2]	21	2.0	1	2.3	Very low.
USGS dam to Newfield	55	2.0	2	6.0	High.
Lighthouse to weir	6	2.2	1	2.0	Very low.
Weir to USGS dam	105	2.9	1	8.2	Medium.
Cascadilla Falls to weir	5	2.9	8	12.8	Low.
Weir to Newfield	37	4.9	4	13.9	Medium and high.
Lighthouse to USGS dam	10	5.1	4	8.6	Low and medium.

[1] Not a true average rate of upstream movement because all specimens were not always captured immediately upon entering a station.
[2] Locations mentioned in this column are identified on a map of Cayuga Inlet (fig. 10, p. 579).

Late migrants ascended the stream more rapidly than did early migrants. The average time for travel from the weir upstream 2.9 miles to the U.S. Geological Survey dam was 11 days (minimum, 2 days), during the period April 22–29. Specimens that traveled the same section of stream during May 10–15 averaged 4 days (minimum of 1 day). Daily morning water temperatures at the U.S. Geological Survey dam averaged 46° F. for the April 22–29 period and 59° F. for the May 10–15 period. The stimulating effects of increased water temperatures on the lamprey's metabolic rate and spawning urge are believed the cause of the faster rate of upstream movement during the warmer period.

Barriers to Upstream Migration

Diurnal and nocturnal observations of the sea lamprey's behavior throughout the 1951 spawning migration indicated that a "partial-barrier" dam is effective in retarding upstream movement and serves as a block to some individuals.

A small dam constructed for the U.S. Geological Survey, Water Resources Division, across Cayuga Inlet 5 miles upstream from the lake offered an excellent place for observations of the lamprey's reaction to a barrier. This dam consists of a concrete wall 30 feet long and 1 foot wide (fig. 11) with an irregular concrete apron which extends 3 to 6 feet downstream. A drop of approximately 1 foot in water level is created by the dam, but the fall varies inversely with the volume of waterflow.

When early migrants first encountered this small dam they reacted by searching actively back and forth along the base for a bypass. After several days of investigation, many proceeded downstream, and were observed as much as one-half mile below the dam, slowly moving downstream, seemingly in search of a tributary.

To learn the fate of spawning-run sea lampreys which were prevented from ascending a tributary stream, Applegate and Smith (1951) captured and tagged specimens that entered the Cheboygan River in which upstream movement was blocked by a power dam. Tag returns indicated that sea lampreys will return to the lake from which they came, and then search for another tributary.

A tagging experiment on the Cayuga Lake sea lamprey indicated a reaction similar to that found by Applegate and Smith. Recovery of tagged lampreys in Cayuga Inlet proves they will return downstream at least 1 mile. In 1951, one of 59 tagged lampreys which were captured in Cayuga Inlet and released in Fall Creek (fig. 10) was recaptured in Cayuga Inlet. This lamprey had to travel 1 mile downstream to Cayuga Lake, and one-half mile in the lake to the mouth of Cayuga Inlet. Of the 92 tagged lampreys released in Cascadilla Creek, a tributary of Cayuga Inlet, 23 (25 percent) were later recaptured in Cayuga Inlet proper. They had moved 1 mile downstream.

Early arrivals in the spawning tributary attempt to reach the headwaters, whereas late arrivals occupy the lowermost reaches of the stream. Possibly the early arrivals, which are the larger, are stronger and hence more able to progress upstream farther than late arrivals. Or, the greater amount of time available to them may permit the early migrants to travel farther.

Waterflow also is a factor in upstream movement. High waters in 1952 permitted lampreys to cross the barriers and ascend to the very headwaters of Cayuga Inlet; as a result the density of nests was low throughout the stream. In 1951, moderate waterflow made the barriers more effective. That year the density of nests was high in the lower and middle section of the inlet and practically no nesting took place in the headwaters.

With the passage of time the spawning urge becomes increasingly strong. About mid-May,

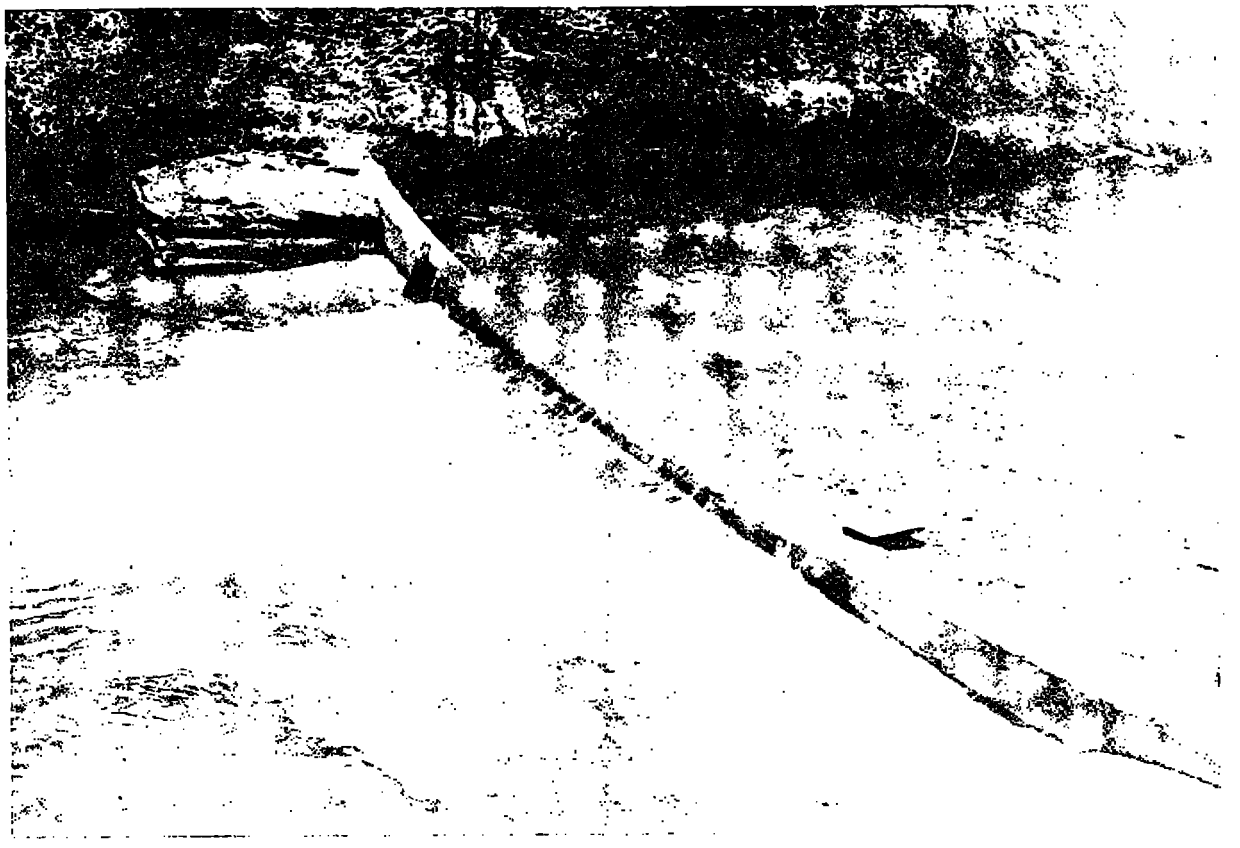

FIGURE 11.—U.S. Geological Survey Dam on Cayuga Inlet.

when the evening water temperatures approach 55°–60° F. lampreys can be found adhering to the apron below the U.S. Geological Survey dam (fig. 11). Water flowing over the dam is shallow and swift (roughly 1 to 6 inches deep, flowing at 2 feet per second), but some lampreys make their way up to the brink of the dam and rest there until capable of attempting to cross. Some individuals swim over; others slowly maneuver their body perpendicular to the current and parallel to the stream bottom, while still attached to the dam by the suctorial mouth. After sufficient rest, they quickly release their hold, swing the head upstream, and make a few very rapid swimming motions which usually carry them over the dam. Characteristically, they rest several minutes just a few feet upstream from the dam before continuing their migration.

It should be emphasized that the U.S. Geological Survey dam is by no means a complete barrier. It is surmounted by many lampreys as well as by teleost fishes. A 10-inch (estimated length) smallmouth bass, *Micropterus dolomieu*, easily swam over this dam under normal water conditions.

In 1952, between April 30 and May 6, 872 lampreys were marked and released just below the U.S. Geological Survey dam. During the 4-week period (May 7–June 3) following their release, many of these marked specimens were recaptured at the same locality where they were liberated; i.e., on the downstream side of the dam. Recorded in table 23 are the date, number, and percentage of the original number of specimens recaptured there. Since the fishing effort of the trap remained constant and the total catch decreased steadily, the decreased percentage of marked lampreys recaptured is the rate of emigration, either upstream or down. A large number of marked specimens found upstream from the dam indicates that most of the movement was upstream. Approximately 3 to 7 percent of the marked lampreys departed from below the dam each week. The most notable fact is that 10 percent of the 872 lampreys marked prior to May 6

remained below the dam for more than 4 weeks. By that time (June 3) the nesting season was well underway and upstream migration was practically nil. Thus, considering the other traits displayed by upstream-migrant sea lampreys, approximately 10 percent of the early arrivals were unable to negotiate the partial barrier created by the U.S. Geological Survey dam.

TABLE 23.—*Emigration of 872 sea lampreys marked and released below the U.S. Geological Survey dam on Cayuga Inlet, between Apr. 30 and May 6, 1952*

Recovery period	Total number of lampreys captured	Number of marked lampreys recaptured	Percentage of marked lampreys in catch
May 7–May 13	817	217	26.6
May 14–May 20	668	130	19.5
May 21–May 27	253	42	16.6
May 28–June 3	164	17	10.4

The effect of barriers on lamprey migration in Cayuga Inlet is brought out in figure 12, which shows the number of lamprey nests in each 1-mile section of Cayuga Inlet at the height of the 1951 spawning season. The numbers of nests were determined by a complete count in a section or estimated from a large sampled portion. These data are listed in Table 31.

Large concentrations of nests immediately below the obstacles readily suggest their restraining effect on the upstream migration of lampreys. The presence of few nests above the Newfield station is indicative of a nearly impassible barrier. Absence of lamprey nests in sections A and B is due to the unsuitable composition of the substrate.

Sex Ratio

The sex ratio of adult sea lampreys in the spawning run in Cayuga Inlet was first measured by

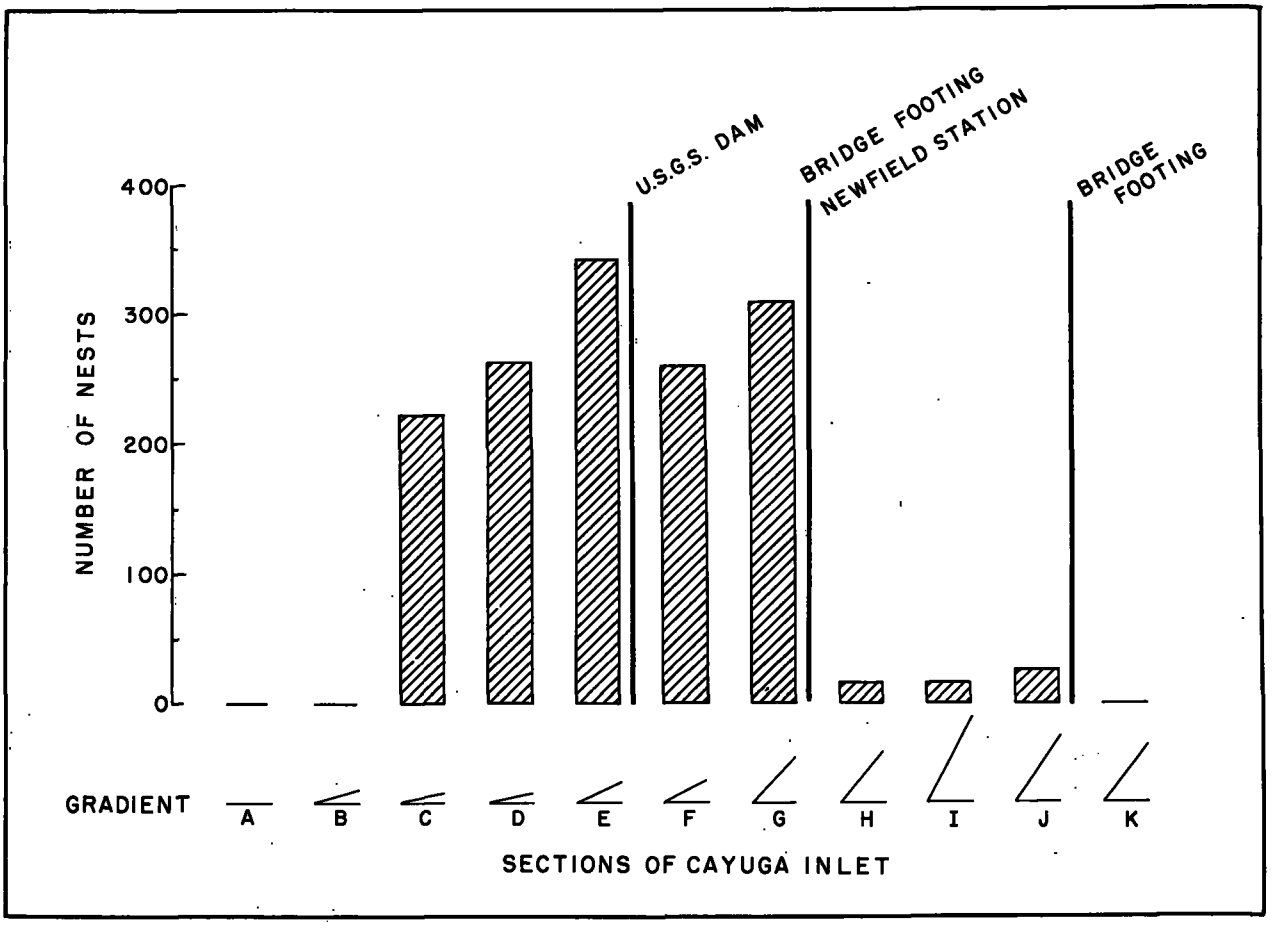

FIGURE 12.—Number of sea lamprey nests in each 1-mile section of Cayuga Inlet at the height of the 1951 spawning season. An index of stream gradient is given for each section, and obstacles to upstream movement are shown in their respective locations.

Meek (1889) in 1886. Throughout a 2-week period beginning May 21, he determined the sex of 745 lampreys, of which 480 were males and 265 were females, a ratio of 180 males per 100 females (table 24).

Surface (1899) made sex determinations for a larger sample from Cayuga Inlet during the spring of 1898. In a total of 1,686 specimens 589 were males, 551 were females, and the sex was undetermined in 546. These figures give a sex ratio of 107 males per 100 females.

Collections of 372 adult lampreys on their spawning migration in Cayuga Inlet, made in this study between May 5 and June 12, 1950, gave a sex ratio of 157 males per 100 females (table 25). Similar collections in 1951 gave a sex ratio of 155 males per 100 females (1,820 specimens, table 25). Finally, comparable collections made in 1952 had 116 males per 100 females (1,306 specimens, table 25).

TABLE 24.—*Sex ratio of 745 sea lampreys in the spawning migration in Cayuga Inlet, 1886*

[Data from Meek, 1889]

Date	Number of males	Number of females	Sex ratio (males:females)
May 21	156	69	226:100
May 25	132	110	120:100
Later (?)	106	37	286:100
Later (?)	86	49	175:100
Total	480	265	180:100

TABLE 25.—*Sex ratio of sea lampreys in the spawning migration in Cayuga Inlet during 1950, 1951, and 1952*

Date	Number of males	Number of females	Sex ratio (males:females)
1950			
May 5–7	135	88	154:100
May 15–17	34	24	142:100
May 24–30	26	14	186:100
June 8–12	32	19	169:100
Total	227	145	157:100
1951			
Apr. 22–28	120	57	210:100
Apr. 29–May 11	490	314	156:100
May 6–12	158	92	172:100
May 13–19	336	247	131:100
Total	1,107	713	155:100
1952			
May 7–10	450	348	117:100
May 20	19	18	106:100
May 26	220	166	132:100
June 3	13	36	36:100
Total	702	604	116:100

As is shown in tables 24 and 25, samples containing a small number of specimens yield apparently inconsistent estimates of the sex ratio. Some of these values are undependable because of the small sample. Others can be attributed to differential activity and availability of the sexes and to fluctuations in the actual sex ratio. Apparently, discrepant values should not be rejected arbitrarily, however, because, as suggested below, they may represent true fluctuations of the population that are not well understood.

Surface reported (1899) that males predominate among early migrants, and females among late migrants. This general trend was found in Cayuga Inlet during the present study. For instance, in 1951, the year in which the samples were largest, the ratio changed from 210 males per 100 females in late April to 131 males per 100 females in mid-May.

In addition to the general trend of a changing sex ratio, there was a secondary rise in the abundance of males that led to two "cycles" similar to the main trend. These secondary pulses occurred each year for which sex ratio data are available (last column in tables 24 and 25). Whether this secondary rise was created by segments of the population delayed in fruitless searches in or for other tributaries, is not known.

Annual differences in the sex ratio are related to the abundance of lampreys (table 26). Male specimens were relatively more abundant in years when lampreys were plentiful, approximately 3 males to 2 females. In years when lampreys were few, the sex ratio was nearly 50–50. These annual changes are large and well defined.

Other sea lamprey populations likewise exhibit a changeable sex ratio. In Lake Huron the relative abundance of male sea lampreys increased steadily from 165 to 258 males per 100 females during the years 1947–51 (Applegate, Smith, McLain, and Patterson, 1952). Over this same period the numbers of sea lampreys were increasing.

TABLE 26.—*Sex ratio and estimates of the number of sea lampreys in the spawning migrations in Cayuga Inlet*

Year	Estimated number of sea lampreys	Sex ratio (males:females)
1886 [1]		180:100
1898 [2]	1,686	107:100
1950	10,000–15,000	157:100
1951	9,390	155:100
1952	4,435	116:100

[1] Meek (1889).
[2] Surface (1899).

Size of Upstream Migrants

Early arrival of the larger sea lampreys in the spawning migration was observed by Surface (1899) in Cayuga Inlet and by Applegate (1950) for Lake Huron stocks. During 1950, 1951, and 1952 the early upstream-migrants in Cayuga Inlet were again found to be both longer and heavier than late migrants (tables 27, 28). Comparison of average lengths of early with late migrants reveals that the former averaged 0.2 to 0.7 inch longer. In weight, the early migrants averaged 0.2 and 0.6 ounce heavier in 1950 and 1952, respectively, but in 1951 their weight averaged 0.4 ounce less than that of late migrants. Although the sex ratio of upstream-migrants changed during the season, this change had no effect on the size of early and late migrants as the sexes had the same mean size.

TABLE 27.—*Mean lengths of adult sea lampreys taken early and late in the spawning migration in Cayuga Inlet*

Date	Number of specimens	Length (inches)		
		Mean	Minimum	Maximum
1950				
May 5	111	15.2	11.5	19.8
May 15	45	15.0	12.0	18.7
1951				
Apr. 28	124	15.3	12.4	19.7
May 14	162	15.0	11.4	20.3
1952				
May 7–9	516	16.2	12.0	21.3
May 21	423	15.5	11.5	20.8

TABLE 28.—*Mean weights of adult sea lampreys taken early and late in the spawning migration in Cayuga Inlet*

Date	Number of specimens	Weight (ounces)		
		Mean	Minimum	Maximum
1950				
May 5–7	203	5.1	2.2	11.3
May 15	32	4.9	2.5	7.6
1951				
Apr. 28	124	4.3	1.8	8.3
May 15	138	4.7	2.0	9.5
1952				
May 7–9	506	5.2	1.9	12.1
May 21	419	4.6	1.8	10.7

Body Color

Recently transformed sea lampreys are bluish-black [6] dorsally and laterally and silvery-white ventrally. With increasing age the epidermis becomes dark olive. The body is mottled by black pigment in the dermal layer, especially on the dorsal surface; the ventral surface is nonpigmented. At the height of the spawning season the dark-olive epidermal layer changes to a medal-bronze on the majority of individuals, although there is much variation. A few lampreys, often the largest and most mature, develop a xanthine-orange coloration. Others, often the smallest and least mature, remain bluish-black or dark-olive.

Pigmentation on the dorsal fin is sparse and rather indistinct in comparison with that on the trunk. A band of skin along the base of both dorsal fins is pigmented much the same as the trunk. An indistinct band, approximately one-fourth the fin height, on the margin of the dorsal fins is nonpigmented. The caudal fin bears dark pigmentation on its posterior portion which diminishes anteriorly. A ridgelike continuation of the ventral portion of the caudal fin forward to the urogenital opening is nonpigmented.

In 1951 a study was made of the correlations between color and size, sex, and time during the spawning period. To facilitate the recording and calculation, five color categories were established and given index numbers as follows: (1) xanthine orange; (2) raw sienna; (3) medal bronze; (4) dark olive; and (5) bluish-black. This series is listed here in reverse order of color changes that occur as sexual maturity is approached. Numbers of specimens were: 183 males and 110 females captured on the spawning run in Cayuga Inlet during the period April 26–30, 1951; 152 males and 144 females taken during the period May 13–16, 1951.

The linear regressions of color on length (fig. 13) illustrates the tendency for large lampreys to be lighter and more colorful than small ones. Males were lighter and a more golden color than females of similar size. Early migrants were approximately one color category lighter than late migrants. A measure of closeness of the relation between color and total length is provided by the correlation coefficient. Correlation coefficients for the April collections, as shown in the tabulation, indicate considerable variation. Correlation coefficients for the May collections are rather high, indicating relatively little variation; however, only the females in the May collections have a significantly high value (indicated by asterisk).

Individual records of 20 specimens whose color was recorded when they were captured on their upstream migration and tagged, and again recorded after spawning was completed, were used as an

[6] Color standards employed in this description are those given by Ridgway (1912).

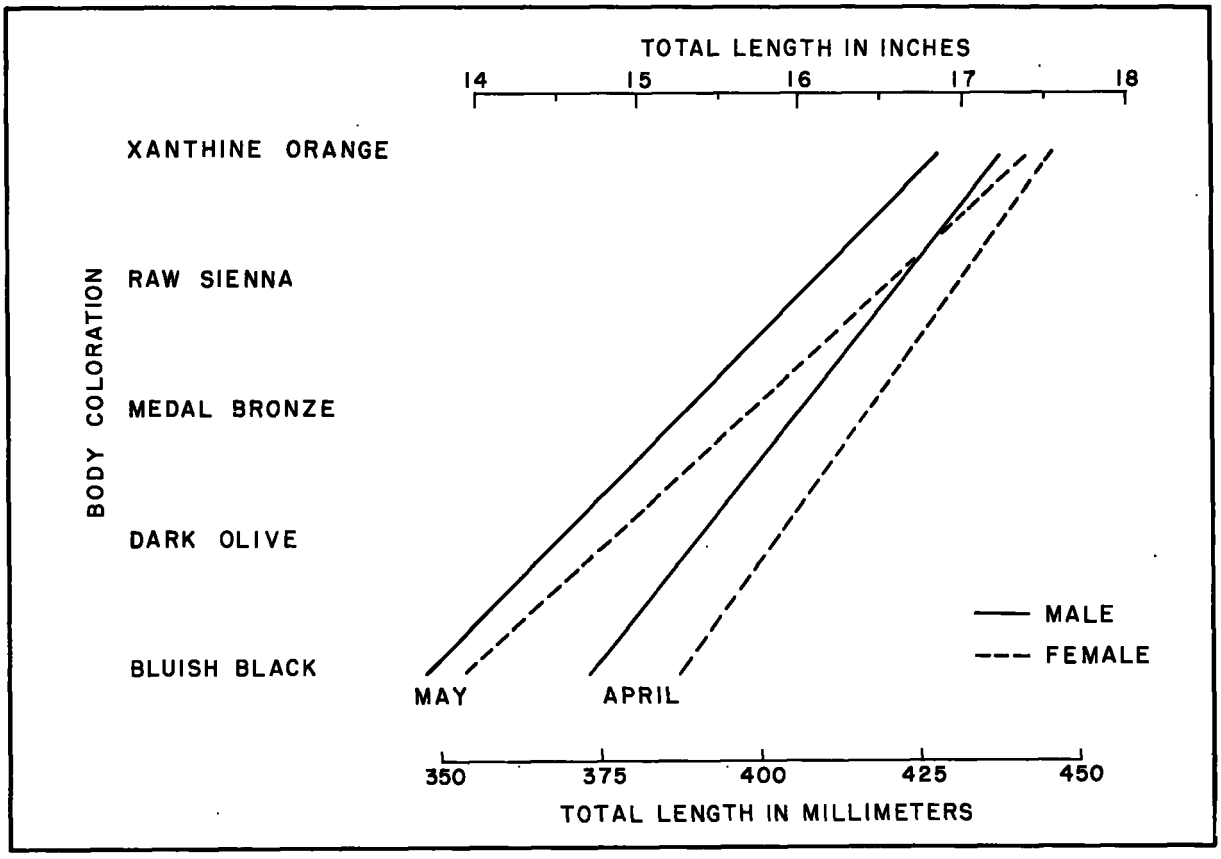

FIGURE 13.—Regression of body coloration on total length of mature sea lampreys during April and May April collections represent early migrants; May collections represent late migrants.

Date collected and sex	Correlation coefficient	Probability level
April		
Male	0.6568	0.21
Female	.5722	.28
May		
Male	.8428	.08
Female	.8901	*.04

indication of color transition that occurs during the spawning period. All migrants acquired a lighter color of from one-half to two color categories. The late migrants which were generally darker made the greatest change.

SPAWNING HABITS

The spawning habits of the Cayuga Lake sea lamprey have been reported by Gage (1893) and Surface (1899). Coventry (1922) and Applegate (1950) have reported on the spawning habits of sea lamprey populations in the Great Lakes. In view of the considerable available data on this subject, only a brief summary will be presented here of observations made in Cayuga Inlet during the present investigation.

Sea lampreys that arrive in the spawning tributary in mid-April spend 4 to 5 weeks in the stream before they begin nest construction. Those that do not arrive until mid-May spend less than a day in the spawning tributary before nesting. Practically all of the prespawning period is occupied in moving upstream to suitable nesting sites. Late arrivals utilize the low reaches of the stream, and therefore spend little time in upstream travel (p. 582).

Nest Building

Water temperature seems to have a strong influence on the time of spawning. In Cayuga Inlet, nest building usually starts toward the latter part of May, when the evening water temperatures approach 65° F. During the first few evenings of nest building, the lampreys' movements are slow and, if the water cools enough during the evening, nest excavation may last for only a few hours. These abortive attempts at nest construction

usually result in small pockets that are later abandoned, though they may be enlarged by other lampreys at a later date.

Sea lampreys utilize only certain portions of the stream for spawning. The principal physical characters that affect the suitability of an area as a nesting site are the type of substrate and water velocity. For successful spawning the lamprey requires a substrate of stones small enough to be moved and some fine sand to help sink and cover the eggs. Also, a rather swift flow of water seems to be required. The nests are commonly located at the downstream end of a pool, where the rate of flow is at least 2 feet per second. In Cayuga Inlet, the center of the stream presents more attractive nesting sites than do areas along the bank.

The lamprey nest is a shallow, irregular, bowl-shaped pocket excavated in the streambed. For nest construction the lamprey attaches its suctorial mouth to a stone to be moved; if necessary the stone is loosened from the bottom by a few violent jerks. It is then carried to the edge of the nest and dropped. Most stones are placed in a crescent-shaped pile at the downstream edge, but a few are carried to the upstream edge. Gravel usually less than 1 inch in diameter remains to make the nest floor. Most of the silt particles are stirred up by the writhing bodies and carried out of the nest by the current during the excavation. Rocks comprising the streambed of Cayuga Inlet are predominantly shales. In table 29 are listed a number of nest measurements and the size of stones lining the nest floor. The stone diameters of the rubble represent only the larger flat surfaces.

The nests are usually oval with the long axis parallel with the water current. Nest size varies greatly but most are approximately 1 to 1½ feet in diameter, and 3 to 5 inches deep. Nearly all nests are located in water one-half to 2 feet deep.

Customarily, males begin the nest construction and are later joined by a female who assists with the work. Males habitually start several nests which they abandon. Usually they proceed upstream as the nests are constructed and deserted.

Occasionally several males or several females are together in one nest. These communal nests are large, often 2 to 3 feet in diameter. Lack of suitable nesting area does not appear to be the cause of communal nesting. The fact that they are more commonly found toward the latter part of the nesting season suggests that the arrangement may be a timesaving device of late spawners.

TABLE 29.—*Measurements (inches) and materials in the floor of sea lamprey nests as observed in section E of Cayuga Inlet on May 30, 1951*

Depth in center	Dimensions of nest		Depth to downstream summit	Bottom type in floor of nest [1]
	Length	Width		
11.5	18	11	8.5	P, M.
11	10	8	8.5	P, M.
11.5	10	7	7.0	M, P, E.
13.5	13	14	9.0	M, P, E, R.
12.5	10	10	7.5	M, P, E.
12	19	15	7.0	M, P, E.
10	12	8	8.0	M, P.
9.5	13	9	7.5	M, P, E.
10.5	13	10	7.5	E, M, P.
12	14	17	8.0	M, E, P, R.
11	16	15	6.0	E, M, P, R.
9.5	12	9	5.5	M, P, R.
8.5	11	5	4.0	M, S, P.
8.5	11	9	4.0	P, M, E.
16	21	12	11.0	M, P.
16.5	22	11	11.0	M, R, P.
13	13	12	8.5	E, R, P.
12	19	13	5.5	R, M, E.
13	10	9	9.0	E, M, R.
15	18	16	8.5	M, P, R.
15.5	13	9	10.0	R, M, P.
17	29	19	10.0	R, E, M.

[1] Size of material in the floor of each nest was recorded in order of dominance: P pea gravel, 3/16 to 3/8 inch in diameter; M marble gravel, ½ to 1 inch in diameter; E egg gravel, 1¼ to 2½ inches in diameter; R rubble; S sand.

Time of Construction and Location of Nests

The first nesting activity of the 1951 season was observed on the night of May 21 in section *E* of Cayuga Inlet. Four male sea lampreys were seen on nests in the earliest stage of construction. Large-scale nest building started on May 25. By May 30 a majority of the nests had been constructed, and spawning reached a peak May 30–June 1. After June 1, nest building dropped off rapidly and consisted mostly of enlarging previously existing nests. No spawning or nest building was observed after June 10.

During the 1951 spawning period, May 21 to June 7, counts were made of the number of nests in each of eleven 1-mile sections (fig. 10) of Cayuga Inlet. All sections were examined at least twice, and the most heavily populated areas as many as six times. Some nest counts include an examination of the entire section; most counts however, were based on samples of one-quarter to three-quarters of a section. To provide a measure of nest-building and spawning activity, nests were classified as occupied or unoccupied (table 30). Any nest in which one or more lampreys were found was considered occupied. On May 21, all nests were occupied. The percentage of occupied nests decreased irregularly to about 50 percent on May 24–25 and approximately 20 percent by the

end of the month. On June 6 and 7 the percentage of occupied nests had decreased to 12.

In sections *C* through *G* where the spawning population was high, superimposition of one nest on another and the indefinite boundaries between adjoining nests prevented accurate determination of the total number of nests. In areas where spawners were less numerous, nest building and spawning were orderly. In such areas no superimposition or consolidation of nests was observed and usually but one pair of lampreys was seen in one nest.

TABLE 30.—*Occupancy of sea lamprey nests in Cayuga Inlet, between May 21 and June 7, 1951*

[No observations on May 28 or June 2-5]

Date	Number of nests		Percentage of nests	
	Occupied	Unoccupied	Occupied	Unoccupied
May 21	4	0	100	0
May 22	3	2	60	40
May 23	4	10	29	71
May 24	6	6	50	50
May 25	110	129	46	54
May 26	88	170	34	66
May 27	34	48	41	59
May 29	33	131	20	80
May 30	91	160	36	64
May 31	49	339	13	87
June 1	52	187	22	78
June 6	28	225	11	89
June 7	31	213	13	87

The number of nests per section of stream as of May 30–June 1 is considered a reliable index to the total number (table 31 and fig. 12). This period was chosen because it was the last date when accurate nest counts could be made. The figures given are believed to be only slightly lower than the actual total numbers.

The greatest density of nests, one per 15 feet of stream, was found in section *E*, the area immediately downstream from the U.S. Geological Survey dam. The first nest-building activities were in this section. Section *G*, the area just below Newfield station, ranked second in nesting density with one nest per 17 feet of stream. Sections *D*, *F*, and *C* followed in decreasing order. Densities were extremely low in sections *H*, *I*, *J*, and *K*, all located upstream from the Newfield station. These sections may be considered as of little importance for lamprey spawning when low or moderate water levels, similar to those of 1951, prevail (see fig. 9 for water volumes).

Some nests were not used for spawning, whereas others were utilized by several pairs. An investigation into the number of nests actually utilized

TABLE 31.—*Number and density of sea lamprey nests in each 1-mile section of Cayuga Inlet, May 30–June 1, 1951*

[See fig. 10 for locations of sections]

Section	Number of nests	Feet of stream per nest	Section	Number of nests	Feet of stream per nest
A	0		G	311	17
B	0		H	19	278
C	223	24	I	19	278
D	264	20	J	27	189
E	343	15	K	1	5,280
F	261	20			

was made June 9 and 12, 1951, when 137 nests were examined for eggs. A shallow rectangular funnel, its mouth 18 inches square, made of brass screen, 60 meshes per inch, was placed downstream from each nest. A few large stones were placed alongside and slightly behind each nest to guide the water current into the funnel. When the funnel was in position the sand and gravel in the nest pocket was scooped up with a shovel, lifted to the water's surface, then slowly poured back into the nest to free the lamprey eggs. This process was repeated until some eggs were obtained or until all material in and around the nest had been thoroughly sifted. Lamprey eggs and occasionally sucker eggs from the nest site drifted downstream into the screen. The results revealed 59 (43 percent) nests with sea lamprey eggs, and 78 (57 percent) nests without. Five nests contained an estimated 10,000 eggs or more. Only a few hundred were recovered from most nests which contained eggs.

Spawning

Gage (1893 and 1928) and Surface (1899) have previously reported on the spawning of the Cayuga Lake sea lamprey. A recent and more detailed description was given by Applegate (1950) of spawning in the Ocqueoc River, a tributary of Lake Huron. Since Applegate's description agrees well with observations made in Cayuga Inlet, comments are limited here to an explanation of figure 14. (*A*) The female, on the left, is securely anchored by her oral disc to a stone at the upstream edge of the nest; the male is brushing his oral disc along the dorsolateral portion of the female from the region of the first dorsal fin forward to the head; (*B*) the male, above and to the right, has just adhered to the top of the female's head and has bent the posterior portion of his body to the left in preparation to hold the female; (*C*) the

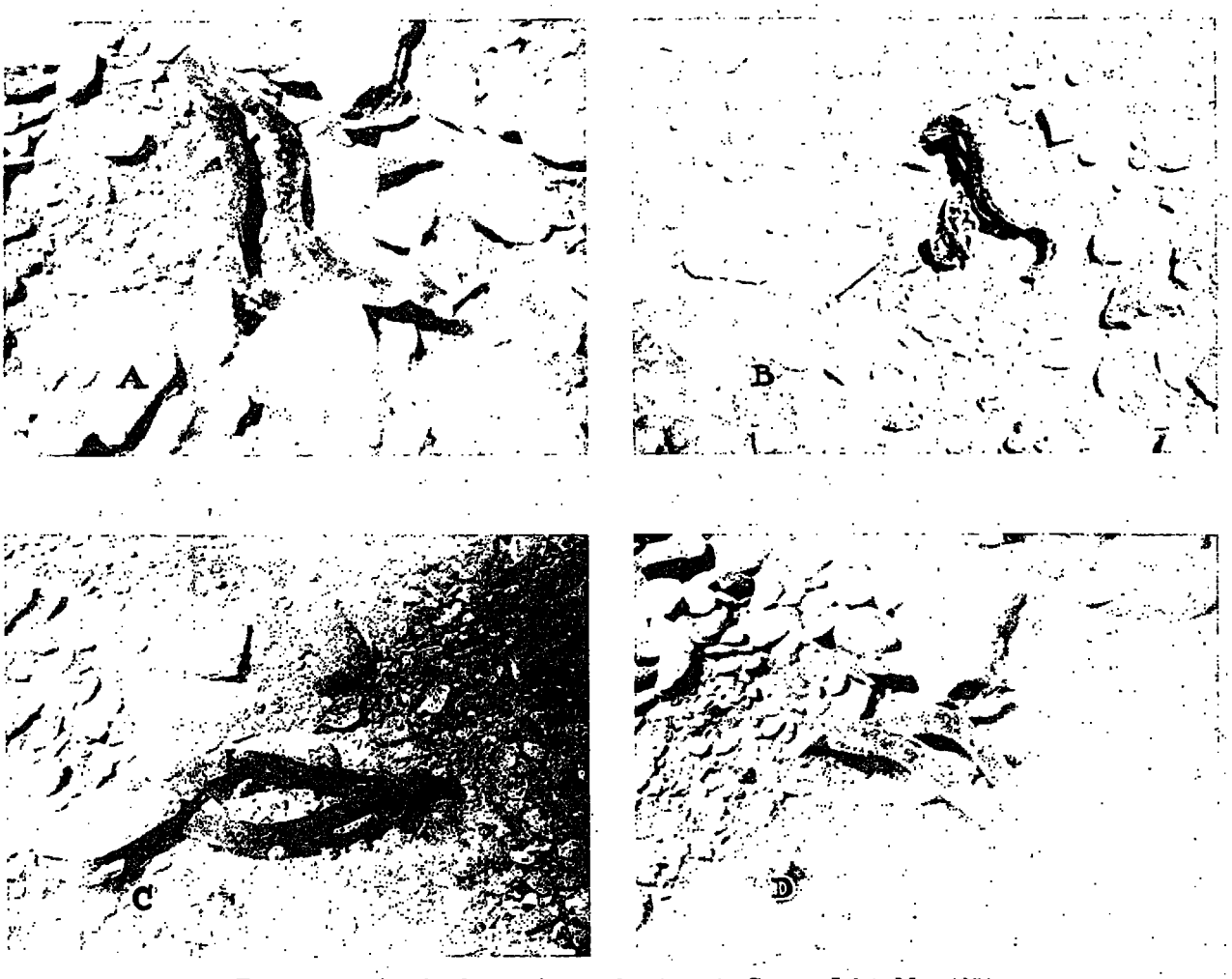

FIGURE 14.—A pair of spawning sea lampreys in Cayuga Inlet, May 1951.

male, above, has completely encircled the female by spiraling the posterior portion of his trunk about her (note the thin opaque covering of the male's eye; he is blind); (*D*) in the final stage, the male, above and to the right, and the female rapidly vibrate their bodies as both eggs and sperm are emitted from their closely approximated vents (fine particles of sand stirred from the floor of the nest by the vibrating lampreys adhere to the sticky surface of the eggs and aid considerably in retaining them in the nest).

Actual copulation lasts only a few seconds, but is repeated at intervals of one minute to one-half hour depending on water temperature, time within the spawning season, and other factors. Spawning by a pair of sea lampreys commonly lasts about 1½ to 2 days.

Fecundity

Surface (1899) placed the production of eggs by Cayuga Lake sea lampreys at an average of 27,500 (range of 25,000 to 30,000), and Gage (1928) gave the fecundity of three specimens as 63,000, 65,000, and 108,270 eggs. Applegate (1950) determined a mean of 61,500 eggs (corresponding mean length of 17.4 inches) and a range of 24,021 to 107,138 in sea lampreys from Lake Huron tributaries. Vladykov's (1951) estimates of 72,870 eggs for sea lampreys from Lake Michigan and 55,913 for Lake Huron specimens agree well with Applegate's findings.

The gravimetric method has been found to be the most desirable means for calculating the number of eggs in a sea lamprey ovary. Detailed studies by Applegate (1950) on the ovary of the

sea lamprey from Lake Huron tributaries, revealed no appreciable size differences of ova from the anterior, middle, and posterior portions. In accordance with the results of Applegate's studies, the method used in calculating the number of eggs contained in Cayuga Lake specimens was as follows: total body length and weight of the specimen were measured; the ovary was dissected from the body, weighed, and preserved in 5-percent formalin; at a later date, the ovary was removed from the preservative, drained, and blotted dry as possible; the entire ovary was weighed to the nearest 0.01 gram; a small portion (1.00–1.55 grams) from the midsection of the ovary was removed and weighed to the nearest 0.01 gram; the total number of eggs in the sample was counted and the number of eggs in the entire ovary was computed.

Determinations of fecundity were made for 29 sea lampreys collected in Cayuga Inlet on April 30, 1951. The size of each specimen and the number of eggs each contained are listed in table 32. These lampreys averaged 15.6 inches in length; minimum and maximum lengths, 11.7 and 20.1 inches; total body weight averaged 5.1 ounces; and weight extremes were 1.8 and 11.7 ounces. None of the lampreys had deposited any eggs prior to capture, since spawning did not take place until 1 month after they were collected. The regression of number of eggs on the total length of lamprey is presented in figure 15. The regression line was fitted mathematically. Extreme egg counts among the specimens were 14,000 and 85,000.

Average length of female lampreys in the 1951 spawning migration in Cayuga Inlet was 15.2 inches. A female of this size produces approximately 43,000 eggs.

It is obvious from figure 15 that great variation in egg number occurred even among lampreys of the same length. The major source of this variation was diversity in ovary size. Large females tended to have a proportionately larger ovary and fewer eggs per unit weight of ovary.

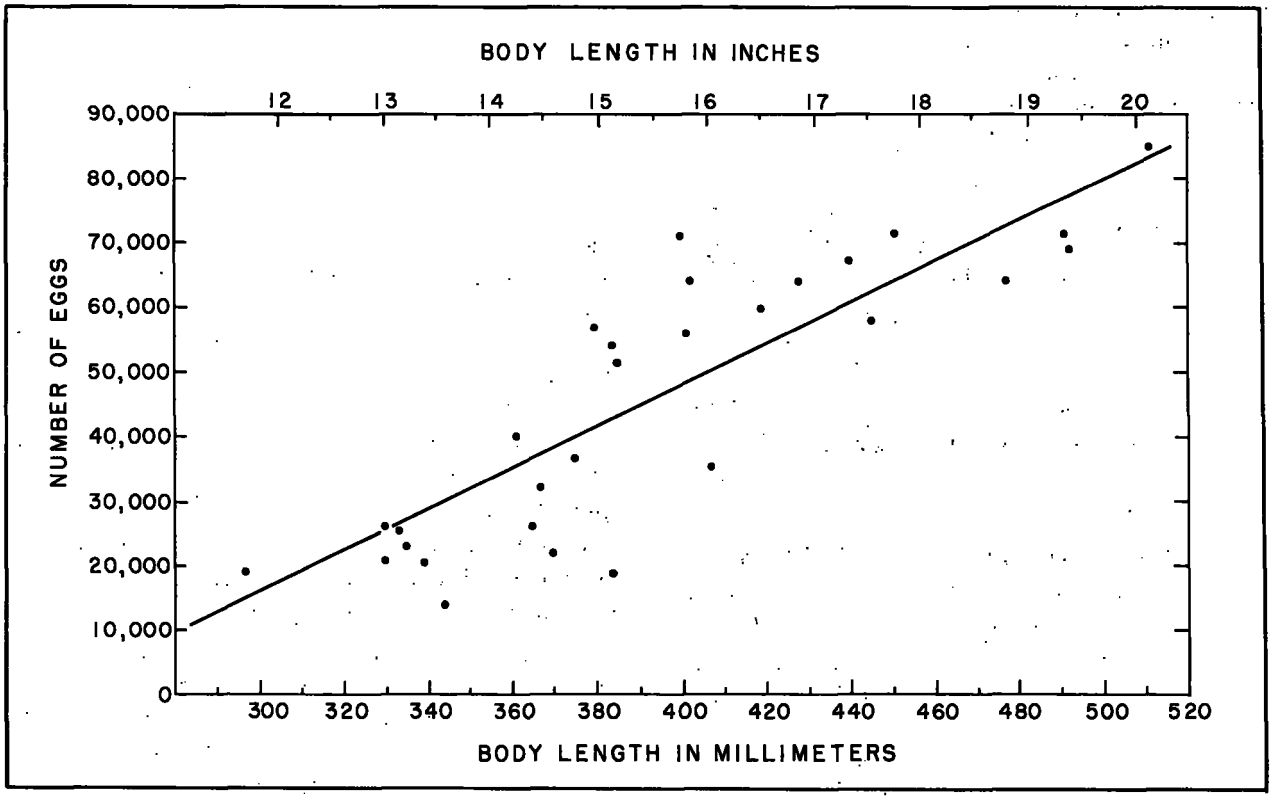

FIGURE 15.—Regression of the number of eggs per female sea lamprey on total length.

TABLE 32.—*Number of eggs in relation to body size and ovary weight of sea lampreys collected in Cayuga Inlet on Apr. 30, 1951*

Length (inches)	Weight (ounces)	Weight of ovary (ounces)	Number of eggs		
			Total	Per ounce of body weight	Per ounce of ovary weight
11.7	1.8	0.21	19,107	10,615	90,985
13.0	2.3	.29	20,821	9,053	71,796
13.0	2.6	.28	26,214	10,082	93,621
13.1	2.4	.30	25,636	10,681	85,453
13.2	2.4	.30	23,089	9,619	76,963
13.3	3.3	.29	20,606	6,244	71,055
13.5	2.6	.17	13,974	5,373	82,200
14.2	3.6	.67	40,139	11,149	59,909
14.4	3.7	.34	26,140	7,064	76,882
14.5	4.2	.49	32,195	7,664	65,704
14.6	4.1	.37	21,692	5,290	58,627
14.8	3.5	.47	36,689	10,482	78,061
15.0	5.0	.92	57,234	11,445	62,211
15.1	3.8	.31	18,747	4,932	60,474
15.1	6.2	.92	54,128	8,730	58,833
15.2	4.4	.67	48,797	11,090	72,830
15.7	5.6	.87	71,324	12,735	81,982
15.8	4.9	.61	55,851	11,398	91,559
15.8	5.4	.74	64,608	11,963	87,308
16.0	4.7	.52	35,429	7,538	68,132
16.5	5.2	.60	59,844	11,507	99,740
16.8	6.2	1.12	63,905	10,307	57,058
17.5	7.9	1.28	58,279	7,377	45,530
17.7	8.3	1.24	71,597	8,626	57,739
18.0	7.6	.97	66,850	8,796	68,946
18.8	8.5	1.07	63,974	7,526	59,788
19.3	8.5	1.13	71,427	8,403	63,210
19.3	10.0	1.41	68,861	6,886	48,838
20.1	11.7	1.56	85,162	7,405	54,591

Ovary development and growth takes place at a rapid rate during the 2 weeks immediately prior to spawning. A comparison was made of the ovary weights from a series of 22 lampreys collected in Cayuga Inlet on May 15, 1951, with 29 collected on April 30, 1951.

Date of capture	Mean total length	Mean body weight	Mean ovary weight	Ovary as percentage of body weight
	Inches	*Ounces*	*Ounces*	
Apr. 30	15.6	5.1	0.69	13.5
May 15	15.5	4.9	.86	17.6

In the April 30 collection the ovary comprised 13.5 percent of total body weight, whereas in the May 15 collection the ovary made up 17.6 percent of total body weight.

Postspawning Habits and Morphological Changes

Evidence gathered by Surface (1899), Gage (1928), Shetter (1949), and Applegate (1950) indicates that sea lampreys die soon after spawning. This evidence is based on anatomical degeneration of digestive and excretory organs, absence of immature ova in the ovary, sloughing of the epidermis, frequent blindness, field observations of dead and dying specimens, and field experiments in which spent lampreys were held in cages in their natural habitat. However, doubts concerning the fate of spent sea lampreys still existed.

Additional evidence which substantiates the contention that sea lampreys die after spawning was obtained during the spring and summer of 1951. The lamprey weir installed in Cayuga Inlet caught all postspawning, downstream-migrant lampreys. The total catch amounted to only 238 specimens, 2.5 percent of the estimated 9,390 that entered the stream for spawning. Eighty to ninety percent of the 238 specimens were dead, and the remaining 10 to 20 percent that were still alive were in such a debilitated physical state that none of them were likely to survive more than a few days.

After spawning has been completed, the lamprey is in such an exhausted and emaciated condition that it is unable to hold its position in the spawning grounds. Attempts to swim upstream or across the stream result in their being carried downstream by the water current. Excursions along many miles of spawning area of Cayuga Inlet revealed surprisingly few dead lampreys. Thousands of lampreys were known to be present in the stream and hundreds were observed building nests and spawning, but fewer than 100 dead lampreys were found lodged against branches, rocks, and other natural obstacles. Nighttime as well as daytime inspection trips indicated that very few sea lampreys were removed by scavengers and predators. The great discrepancy in numbers was explained when digging in the silt-laden bottoms of deep pools revealed large numbers of dead lampreys.

Most of the spent lampreys taken in the weir had spawned in the 1-mile area immediately adjacent to and upstream from the weir, section *C*. Of the 20 tagged specimens observed spawning and subsequently caught in the weir, 15 had spawned in section *C*, 3 in section *D*, and 2 in section *E* (fig. 10). None of the hundreds of tagged specimens observed spawning farther upstream were among those later captured at the weir. It thus appears that spent lampreys are rarely carried downstream more than 3 miles, and usually not more than 1 mile, before becoming entangled in debris or buried in the stream bottom.

Measurements of intestinal diameters provide an index of the progressive atrophy. Six speci-

mens captured in August had a mean intestinal diameter of 0.67 inch. In 55 spent lampreys captured in June the mean intestinal diameter was 0.06 inch. Since the intestine had no noticeable taper, this measurement was taken at approximately the midregion. These values indicate a shrinkage of nearly 94 percent in the diameter of the sea lamprey's intestine prior to and during the spawning period.

Loss of Body Weight and Length

Length measurements and weights of 27 male and 37 female sea lampreys that were tagged on their upstream migration and recaptured after spawning, provided information on the absolute and percentage loss in weight and length (table 33).

Loss in weight during the spawning season amounted to 8.5 percent for males and 34.1 percent for females. There is little evidence of correlation between prespawning weight and subsequent percentage loss of weight.

Greater weight of sex products discharged by females at spawning accounts for part, but by no means all, of the sex difference in total loss of weight (table 34). In prespawning samples the testis made up 2.9 percent of the total weight of males and the ovary 17.5 percent of the total weight of females. The gonads did not disappear entirely, however, at spawning. An estimated 26 percent of the testis and 1 percent of the ovaries were present in the postspawning lampreys; consequently, the maximum estimated losses through discharge of sex products were 2.1 (2.9×0.74) percent for males and 17.3 (17.5×0.99) percent for females. Additional weight losses are accordingly 6.4 (8.5−2.1) percent for males and 16.8 (34.1−17.3) percent for females. The loss of weight in females, in addition to that attributable to discharge of sex products, is between 2 and 3 times that of males.

TABLE 33.—*Losses in length and weight of mature sea lampreys during the spawning season*

Item and sex	Prespawning value			Decrease			Percentage of decrease		
	Average	Minimum	Maximum	Average	Minimum	Maximum	Average	Minimum	Maximum
Length (inches):									
Males	14.9	12.6	18.0	1.7	0.8	2.6	10.9	5.9	16.8
Females	15.6	13.1	18.6	2.8	1.8	3.9	17.9	12.5	23.6
Weight (ounces):									
Males	3.30	2.26	6.35	.33	.04	1.06	8.5	.9	19.3
Females	4.52	2.29	7.80	1.54	.49	2.72	34.1	16.7	48.5

TABLE 34.—*Mean percentage composition of total weight made up by gonads and percentage losses in weight due to deposition of reproductive products and from other causes*

[Figures in parentheses are the number of specimens upon which the mean values are based]

Sex	Percentage				
	Body weight made-up by gonad		Loss in weight during spawning	Gonad remaining after spawning	Unaccountable loss in weight
	Apr. 19	May 15	May 30–June 8	May 30–June 8	May 15–June 8
Male	1.5 (10)	2.9 (10)	8.5 (27)	26 (10)	6.4
Female	12.8 (26)	17.5 (41)	34.1 (37)	1 (16)	16.8

Loss in length was 11 percent in males and 17.9 percent in females. In absolute measures this shrinkage amounted to a loss of several inches in total length. The sex difference in percentage loss of length was smaller than in percentage loss in weight. The percentage loss in length tended to be greater among the longer than among the shorter males, but in females no correlation between length and relative decrease in length was detectable.

EGG DEVELOPMENT AND HABITS OF AMMOCOETES

Egg Development

Freshly deposited sea lamprey eggs are light tan or cream color, nearly spherical, and have an average diameter of approximately 1 millimeter. This small size permits them to fall into the interstices of the gravel in the nest bottom where they are covered and protected during incubation.

An experiment in artificial propagation was conducted at the Cornell Experimental Fish Hatchery. One large partially spent female and several ripe male sea lampreys were used. Milt from one male lamprey was expelled into a basin which contained approximately one teaspoonful of water. Then the eggs, an estimated 15,000, were discharged into the basin, and milt from another male was added. The eggs were stirred with a feather for 1 minute. Next 1 cupful of water was added and the contents stirred for 10 minutes. The liquid was then decanted and replaced by 1 quart of water. After the eggs were stirred rather slowly for one-half hour they were placed in a Downing hatching jar. The water volume passing through the jar was adjusted to keep the eggs in

motion without danger of flushing them from the jar.

One-third of the eggs hatched on June 17 (13 days), and the remainder the following day (14 days). Daily morning water temperatures during this period averaged 60.7° F. (extremes of 57° and 65° F.). The source of water used in hatching these eggs was Cascadilla Creek, in which water temperatures are similar to those of Cayuga Inlet.

At hatching, the anterior portion of the trunk emerges from the chorion. The posterior portion may remain within the egg case for as long as 1 day after the anterior end emerges. The yolk sac, which is located ventrally on the posterior half or two-thirds of the body, is expanded only slightly at its anterior portion, but ends in a globular mass posteriorly. This enlargement of the yolk sac tends to hold the posterior end of the ammocoete's body within the shell.

Habits of Ammocoetes

The first 2 days after hatching, the ammocoetes remained rather inactive. At this time they were 4 mm. long, still opaque, and of cream or light tan color. The caudal portion of the trunk, which was made up largely of yolk sac at this stage, was curved ventrally and anteriorly to give them a hooked appearance. This hook shape disappeared the third day after hatching, when the ammocoetes had absorbed most of the yolk. They very soon became somewhat translucent with a light suffusion of brown pigment dorsally and dorsolaterally.

After the yolk had been absorbed the ammocoetes became active and burrowed rapidly into the soft bottom. Partially buried specimens exhibited a negative phototropism. Newly hatched ammocoetes remain in the nest for several days, but later emerge in search of other niches. In Michigan, Applegate (1950) found that newly hatched ammocoetes left the nest between 18 and 22 days after fertilization. In Cayuga Inlet, the newly hatched ammocoetes were located along the stream margins, buried in the fine sand-silt sediment. Possibly they were present in the deeper waters also, but they may have been overlooked because of the difficulty in seeing such small creatures in deep water.

Larger ammocoetes occupy various habitats, but most commonly are found in sand and silt deposits into which they can easily burrow. Portions of the stream with medium to strong water currents and suitable sediments appear to be most satisfactory. Ammocoetes and transforming lampreys do not emerge from their burrows unless disturbed or unless radical changes occur in water conditions.

Observations on ammocoetes held in aquariums revealed their method of burrowing. They penetrate the bottom sediments by thrusting the head downward perpendicular to the bottom and making very rapid undulatory motions. As soon as the snout and head enter the bottom they draw the body downward by constant undulation of the head and snout in an S-shaped pattern. After the trunk is approximately two-thirds buried, the swimming motions of the posterior end cease, but the undulations of the anterior end continue to pull the body into the sediment. The ammocoetes begin to turn in a horizontal direction after approximately half the body is buried. They then gradually move toward the surface of the sediment until a second opening to the water has been made. This maneuver forms a U- or crescent-shaped burrow. The sediment fills in the burrow behind the posterior end of the ammocoete. All the water which provides food and oxygen passes through the remaining entrance.

Mucus secreted by the ammocoete lines the burrow and holds the particles of the bottom material in place. This lining prevents the entrance to the burrow from collapsing when the ammocoete retracts within it. The burrow is believed to be a stable excavation within which the ammocoete lives until driven from it, or until it is destroyed by floods or other forces. Once the ammocoete leaves the burrow it constructs a new one immediately. The length of the burrow is usually less than twice the occupant's length and commonly only 1½ times its length. When mildly disturbed, the ammocoete moves backward, away from the mouth of the burrow. When severely disturbed it leaves the burrow and swims rapidly away to enter the bottom sediment at another location.

Details of the respiration and feeding processes are not thoroughly known. Expansion and contraction of the branchial chamber, together with action of the velum, pump a continuous stream of water into the ammocoete's oral chamber and out the gill openings. The oral papillae spread branchlike across the entrance to the oral hood. These papillae constitute an excellent strainer to

prevent large undesirable matter from entering, and a coating of mucus adds to its effectiveness. Water passes through the branchlike sieve into the gill chambers, and after leaving the gill pouches continues to move backward along the ammocoete's body and gradually filters upward through the sediment.

Food and Feeding

Creaser and Hann (1928) reported micro-organisms, primarily algae, in the digestive tracts of ammocoetes. The most common kinds of algae were diatoms and desmids. Sand grains were found in all ammocoetes examined. Although the number of protozoans was small, the authors believed that they probably furnished a generous portion of the diet, but were more quickly digested than the hard diatoms and desmids. Analysis of the water and bottom deposits from the habitat in which the larvae were living indicated that lamprey larvae obtained their food from the water and not from the sediments in which they burrowed.

Results of analyses for a few ammocoetes from Cayuga Inlet correspond closely with the observations made by Creaser and Hann. The only important difference was that Cayuga Inlet specimens contained a relatively large amount of periphyton. Crystals of sand were common, although as a rule the particles were very fine (0.125–0.062 mm.), only a fraction the size of sand grains predominant in the area.

Of importance in feeding is the endosytle, a mucus-secreting gland, located in the floor of the pharynx. According to Newth (1930), dorsoventral ridges lead out of the endostyle to form a hollow cone of mucus threads to which the food particles adhere as the water passes through. The mucus thread, with its adherent particles, is slowly drawn caudally into the alimentary tract. The accumulated mat of foreign particles is periodically thrown off the oral papillae by a reversal of the water current. Thus it appears that the only selection of "food" by ammocoetes is on the basis of particle size.

Duration of Larval Life

Past estimates of the duration of larval life of the sea lamprey have been based on different sizes of ammocoetes taken at any one time and, in more critical studies, on the identification of age groups determined from modes in length-frequency distributions. Use of the Petersen method is so well established that detailed comments on it need not be given here. Ordinarily the youngest age groups can be identified easily and accurately. Interpretations become less dependable in older groups in which extensive overlap of the distribution of adjacent age groups tends more and more to obscure the modes.

Schultz (1930) explored three statistical methods for evaluating the significance of modes as indicators of age groups in the length-frequency distribution of several thousand ammocoetes of *Lampetra planeri*. Results of this work are summarized by his statement: "A statistical analysis of the data shows the minor modes are not significant and do not represent year classes. They are rather accidental modes owing to sampling." Other workers, however, among them Okkelberg (1921 and 1922) and Hardisty (1951), have employed this method with apparently satisfactory results. The lack of a better method compelled its use in the present inquiry.

Earlier investigators of the sea lamprey in Cayuga Lake gave no quantitative data upon which their estimates of length of larval life were based. Surface (1899) stated that the ammocoete stage lasted at least 3 or possibly 4 years. Gage (1928), who based his opinion on observations of ammocoetes captured throughout the year, believed that the duration of larval life "could not be less than 4 years."

The most detailed study of the duration of larval life of the sea lamprey was that carried out by Applegate (1950) in Michigan. Length-frequency distributions of extensive collections made during August, October, and May led him to conclude that the length of larval life, including the period when transformation is occurring, was 4 years. He also stated that a rest period of 1 year, the last year of larval life, was possible.

The present study of the duration of larval life of Cayuga Lake sea lampreys was based on ammocoetes taken from a 1-mile stretch, section *C*, of Cayuga Inlet (fig. 10) located approximately 2 miles upstream from Cayuga Lake. Water depth in this section approached a maximum of 5 feet in the deepest pools; however, most of the area was considerably shallower, so that ammocoete collections were made with reasonable efficiency. Collections were made during July 1950 and 1951 by digging, seining, and with the aid of an electric

shocker. Collections in August 1951 were made entirely by use of the electric shocker. Small ammocoetes (young of the year and yearlings) were not readily collected by this method. However, since young and yearlings form distinct groups in the length-frequency distribution, relatively few specimens were necessary to establish their modal lengths.

Total length, from the anterior tip of the oral hood to the posterior margin of the caudal fin, was measured to the nearest mm. Weight was recorded to the nearest 0.01 gram. All measurements were made on fresh specimens anesthetized in a 1- to 3-percent solution of urethane.

Characteristics described by Vladykov (1950) made it possible to distinguish sea lamprey ammocoetes from larvae of the American brook lamprey, *Lampetra lamottei*, the only species of lamprey other than the sea lamprey that occurs in Cayuga Inlet. If any misidentifications of species took place, they were among the young of the year and yearlings.

In the discussion of the data on the length-frequency distribution of Cayuga Lake ammocoetes (table 35), attention is given first to measurements made on specimens collected in July (cols. 3, 4, 5, table 35; fig. 16) since in these collections only members of age groups 0 and I were taken in sufficient numbers to establish their modal lengths. Distinct modes at lengths of 0.47 and 1.46 inches represent age group 0 (approximately 1 month old) and age group I, respectively. Less definite modes at lengths of 2.64, 3.54 (estimated from minor peaks at lengths of 3.23 and 3.82 inches), 4.21, 5, 5.59, and 6.10 inches are presumed to represent the average lengths of age groups II through VII. It is recognized that some of these modes are based on a few specimens and could be due to chance variation alone. Specimens in the stage of transformation were not present in the July collections since metamorphosis does not begin until August, or at least it is not externally detectable until then.

Comparison of length frequencies of sea lamprey ammocoetes collected in July and in August 1951 indicates definitely that young-of-the-year (age group 0) ammocoetes were not represented in the August collection; furthermore, few if any 1-year-olds (age group I) were taken in August. This judgment, based primarily on comparisons with

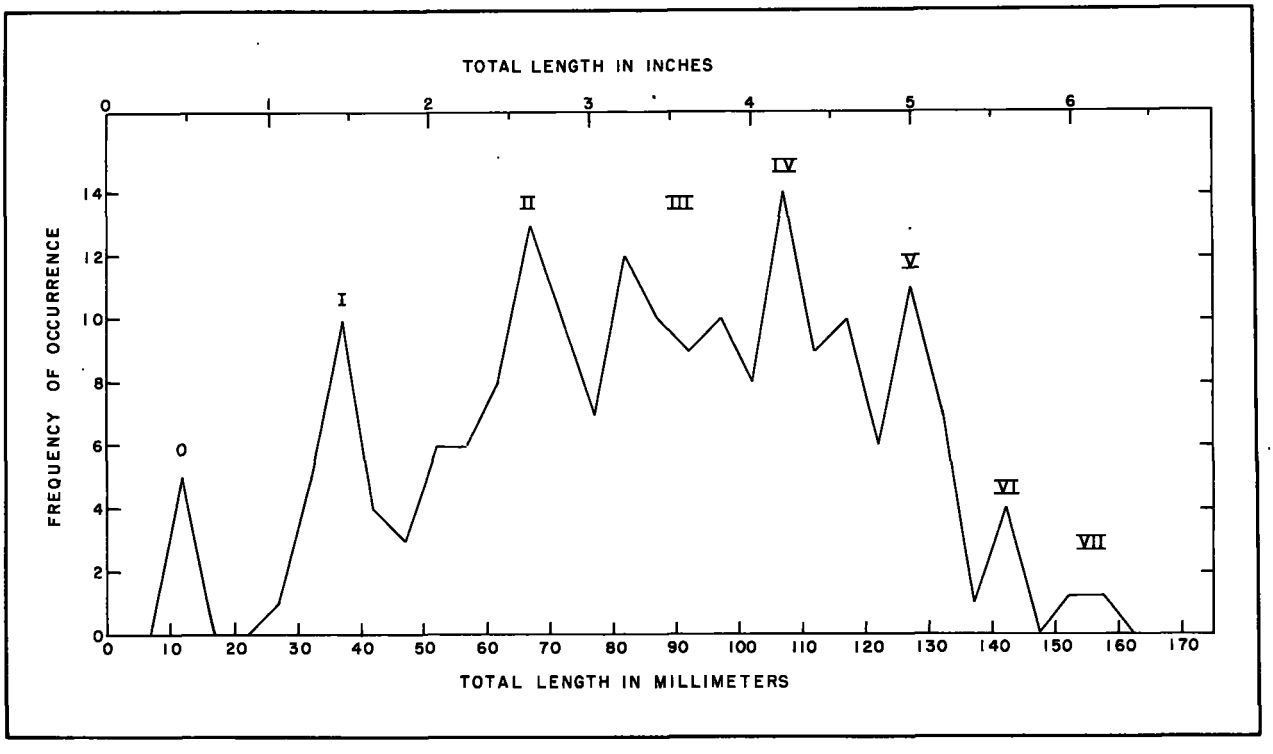

FIGURE 16.—Length-frequency distribution of sea lamprey ammocoetes taken from Cayuga Inlet during July.

TABLE 35.—*Length-frequency distribution of ammocoetes and transforming sea lampreys collected in Cayuga Inlet during July and August*

[The lengths are grouped by 5-mm. intervals]

Length class (millimeters)	Midpoint of length class (inches)	Length-frequency distribution of ammocoetes					Transforming specimens, August 1951
		July			August 1951	Total July and August	
		1950	1951	Total			
<5	0.08						
5–9	.27						
10–14	.47	5		5		5	
15–19	.67						
20–24	.87						
25–29	1.06	1		1		1	
30–34	1.26	5		5		5	
35–39	1.46	10		10		10	
40–44	1.65	4		4	2	6	
45–49	1.85	3		3	2	5	
50–54	2.05	3	3	6	6	12	
55–59	2.24	5	1	6	5	11	
60–64	2.44	8		8	5	13	
65–69	2.64	12	1	13	4	17	
70–74	2.83	10		10		10	
75–79	3.03	6	1	7	3	10	
80–84	3.23	11	1	12	10	22	
85–89	3.43	7	3	10	1	11	
90–94	3.62	9		9	6	15	
95–99	3.82	7	3	10	8	18	
100–104	4.02	6	2	8	10	18	
105–109	4.21	10	4	14	13	27	
110–114	4.41	2	7	9	15	24	
115–119	4.61	5	5	10	10	20	1
120–124	4.80	3	3	6	23	29	1
125–129	5.00	3	8	11	21	32	3
130–134	5.20	1	6	7	14	21	5
135–139	5.39		1	1	7	8	12
140–144	5.59	1	3	4	7	11	11
145–149	5.79				6	6	7
150–154	5.98		1	1	2	3	5
155–159	6.18		1	1	1	2	2
160–164	6.38						3

July collections from Cayuga Inlet, is also supported by data presented by Applegate (1950), who demonstrated that in Michigan the 0 group had a mean length of 0.63 inch and age group I had a length of 1.77 inches. It seems reasonable to assume, therefore, that the mode at 2.24 inches in figure 17 represents age-group II. It follows then, that modes at lengths of 3.23, 4.21 (corrected from the asymmetrical mode at 4.41) 4.80, and 5.51 inches represent age groups III through VI. Transforming ammocoetes (VII group) form a mode at approximately 5.51 inches.

Grouping of the July and August catches of ammocoetes and transforming sea lampreys resulted in a somewhat smoother length-frequency distribution (cols. 7, 8, table 35; fig. 18). Distinct modes at 0.47, 1.46, 2.36 (corrected from minor modes at 2.05 and 2.64), 3.23, 4.21, 5, and 5.59 inches represent age groups 0 through VI. The transforming lampreys form a nearly normal distribution with a modal length of 5.39 inches (age group VII).

Weights as well as lengths are available for ammocoetes and transforming sea lampreys collected from Cayuga Inlet during August 1951 (table 36; fig. 19). Six definite modes are present

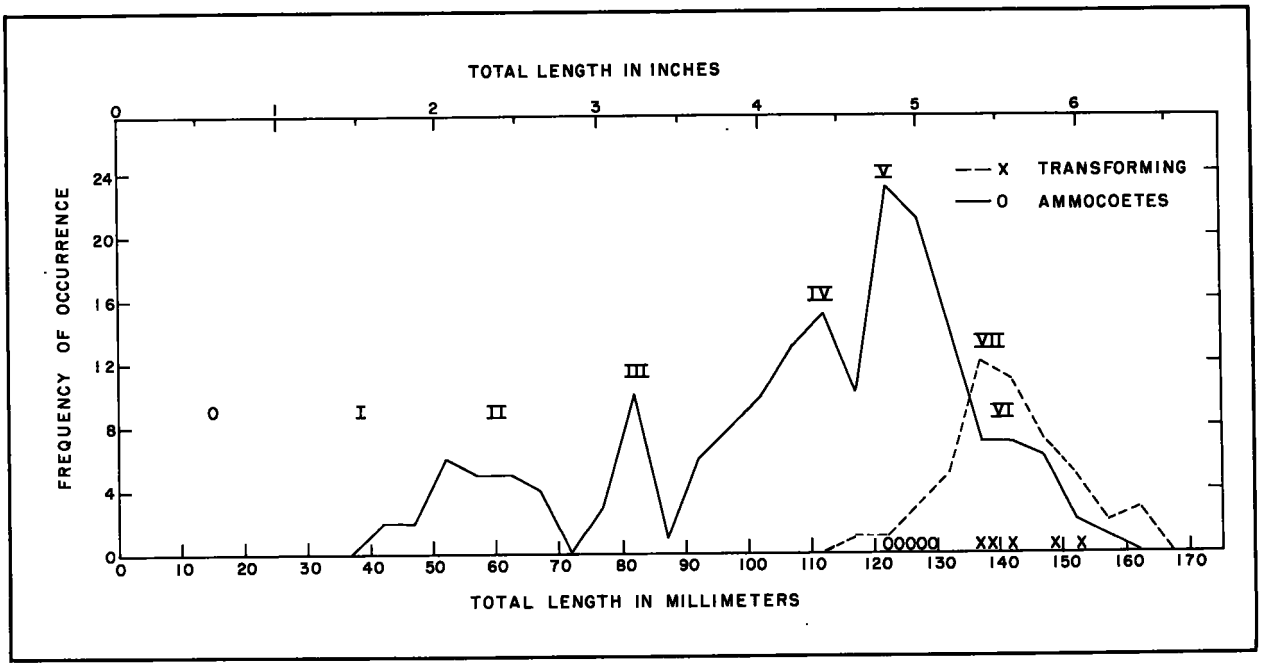

FIGURE 17.—Length-frequency distribution of sea lamprey ammocoetes and transforming specimens taken from Cayuga Inlet during August.

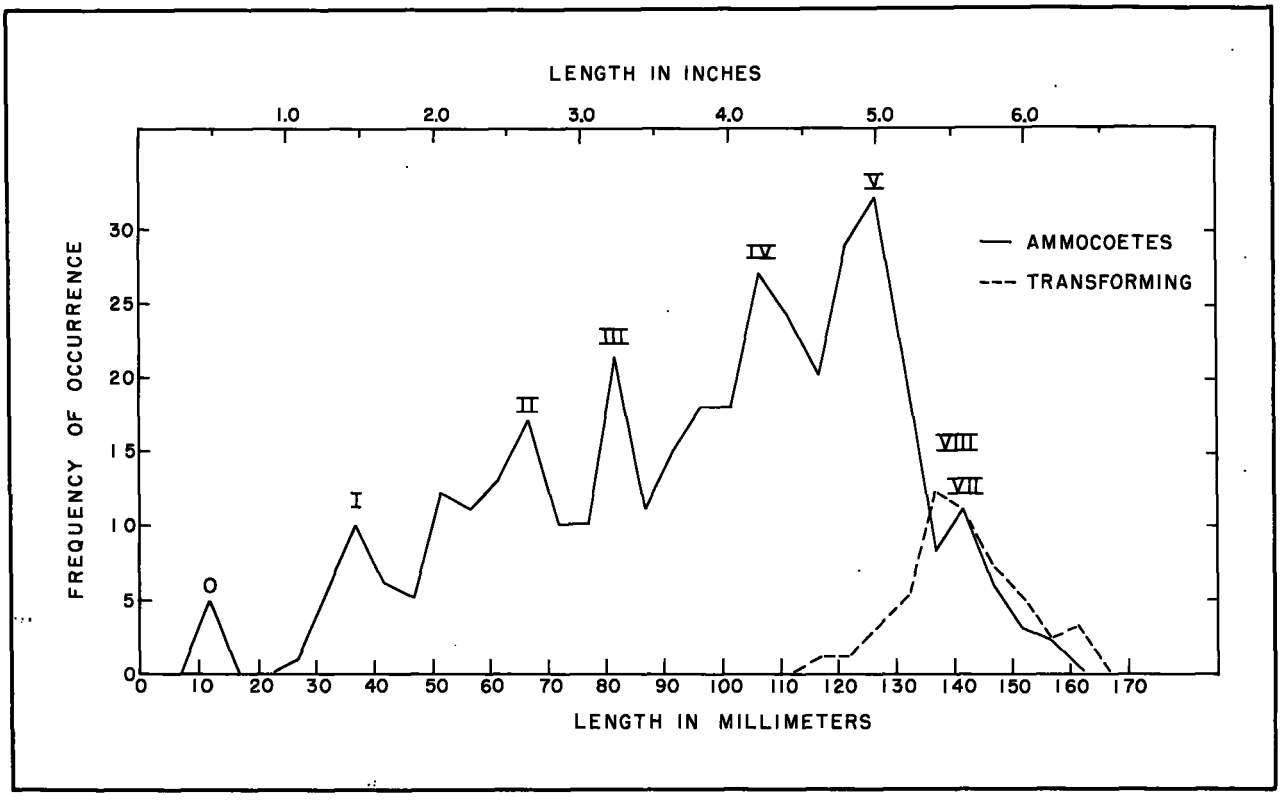

FIGURE 18.—Length-frequency distribution of sea lamprey ammocoetes (solid line) and transforming specimens (broken line) taken from Cayuga Inlet during July and August.

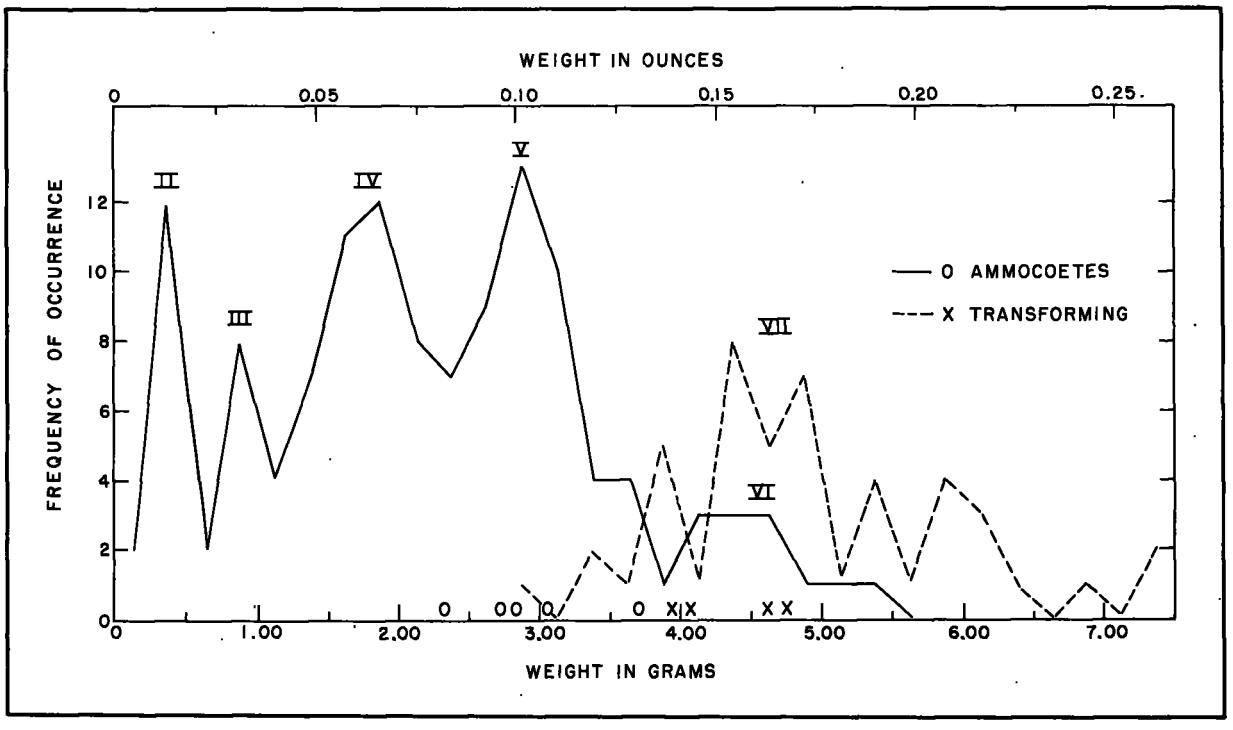

FIGURE 19.—Weight-frequency distribution of sea lamprey ammocoetes and transforming specimens taken from Cayuga Inlet, August 1951.

in the weight-frequency graph, the largest of which is composed of the transforming ammocoetes (believed to be only one age group). Since age groups 0 and I were established to be lacking in the August collections, a justified assignment of ages to the modes on the weight-frequency graph is as follows: 0.013 ounce, age group II; 0.031 ounce, age group III; 0.066 ounce, age group IV; 0.101 ounce, age group V; 0.154 ounce, age group VI; 0.172 ounce, age group VII (the transforming ammocoetes).

TABLE 36.—*Weight-frequency distribution of ammocoetes and transforming sea lampreys collected in Cayuga Inlet during August*

[Weights are grouped by 0.25-gram intervals]

Weight class (grams)	Midpoint of weight class (tenths of ounces)	Frequency	
		Ammocoetes	Transforming sea lampreys
<0.25	0.04	2	
0.25–0.49	.13	12	
0.50–0.74	.22	2	
0.75–0.99	.31	8	
1.00–1.24	.40	4	
1.25–1.49	.48	7	
1.50–1.74	.57	11	
1.75–1.99	.66	12	
2.00–2.24	.75	8	
2.25–2.49	.84	7	
2.50–1.74	.92	9	
2.75–2.99	1.01	13	1
3.00–3.24	1.10	10	
3.25–3.49	1.19	4	2
3.50–3.74	1.28	4	1
3.75–3.99	1.36	2	5
4.00–4.24	1.45	3	1
4.25–4.49	1.54	3	8
4.50–4.74	1.63	3	5
4.75–4.99	1.72	1	7
5.00–5.24	1.81	1	1
5.25–5.49	1.89	1	4
5.50–5.74	1.98		1
5.75–5.99	2.07		4
6.00–6.24	2.16		3
6.25–6.49	2.25		1
6.50–6.74	2.33		
6.75–6.99	2.42		1
7.00–7.24	2.51		
7.25–7.49	2.60		2

The distinctiveness of the modes in the weight-frequency distribution (fig. 19) is striking. Even more significant is the agreement between estimates of age made independently from length and weight distributions. From the data on the length-weight relation of ammocoetes (table 37; fig. 20) it is seen that modal lengths and modal weights agree; it may be concluded that the same general groups of ammocoetes were identified by the two methods. Although analyses of the length and weight frequencies led to the same results, the weight-frequency method seems to be the better because of greater precision in defining age groups.

TABLE 37.—*Length-weight relationship of ammocoetes and transforming sea lampreys from Cayuga Inlet*

AMMOCOETES

Length (inches)	Weight (ounces)	Length (inches)	Weight (ounces)	Length (inches)	Weight (ounces)
1.65	0.006	4.13	0.063	4.96	0.102
1.97	.009	4.13	.065	4.96	.106
2.05	.009	4.17	.056	5.00	.092
2.09	.012	4.17	.063	5.00	.098
2.13	.010	4.17	.067	5.00	.099
2.20	.011	4.17	.069	5.04	.103
2.20	.013	4.21	.060	5.04	.108
2.24	.012	4.21	.066	5.04	.127
2.32	.016	4.25	.069	5.08	.098
2.40	.015	4.29	.040	5.08	.099
2.40	.015	4.33	.067	5.08	.103
2.40	.016	4.33	.073	5.08	.106
2.40	.017	4.33	.074	5.12	.110
2.68	.018	4.37	.062	5.12	.115
2.68	.019	4.41	.060	5.16	.106
2.72	.021	4.41	.079	5.16	.107
2.95	.023	4.45	.069	5.16	.110
3.07	.028	4.45	.070	5.20	.110
3.11	.030	4.45	.078	5.20	.111
3.23	.029	4.49	.066	5.20	.115
3.23	.032	4.49	.077	5.24	.104
3.27	.032	4.49	.079	5.24	.108
3.31	.032	4.57	.078	5.27	.112
3.31	.036	4.57	.080	5.27	.117
3.31	.038	4.57	.080	5.27	.124
3.39	.031	4.57	.088	5.31	.109
3.62	.045	4.65	.079	5.43	.142
3.66	.038	4.65	.082	5.47	.132
3.66	.045	4.65	.095	5.51	.136
3.74	.045	4.72	.082	5.51	.150
3.74	.059	4.76	.082	5.55	.143
3.78	.057	4.80	.086	5.55	.147
3.86	.050	4.80	.091	5.59	.152
3.86	.057	4.84	.089	5.63	.131
3.90	.055	4.84	.090	5.71	.163
3.98	.048	4.88	.095	5.83	.158
3.98	.048	4.92	.089	5.87	.168
4.02	.050	4.92	.096	5.87	.168
4.06	.056	4.92	.099	5.94	.193
4.09	.057	4.92	.106	6.02	.162
4.09	.060	4.96	.097	6.14	.185
4.13	.063	4.96	.100		

TRANSFORMING SEA LAMPREYS

Length (inches)	Weight (ounces)	Length (inches)	Weight (ounces)	Length (inches)	Weight (ounces)
4.69	0.117	5.43	0.159	5.79	0.167
4.88	.102	5.47	.151	5.79	.173
5.00	.123	5.47	.160	5.79	.198
5.12	.133	5.51	.166	5.79	.207
5.12	.134	5.51	.173	5.83	.183
5.20	.127	5.55	.148	5.90	.207
5.20	.133	5.59	.169	5.98	.221
5.20	.155	5.59	.188	6.02	.204
5.24	.139	5.63	.173	6.06	.215
5.27	.155	5.67	.156	6.06	.243
5.35	.139	5.67	.167	6.22	.209
5.35	.151	5.67	.171	6.26	.213
5.39	.152	5.67	.172	6.34	.258
5.39	.165	5.67	.188	6.42	.258
5.39	.172	5.71	.168	6.46	.228
5.43	.154	5.75	.192		

The most questionable aspect in the interpretation of the length-frequency data on Cayuga Lake ammocoetes concerns the validity of age group VI, a group for which the mode was little apparent in the August frequencies and whose size was slightly, if at all, greater than that of transforming lampreys. Evidence that the VI group is valid was obtained from experiments with marked specimens. In this experiment a series of sea lamprey

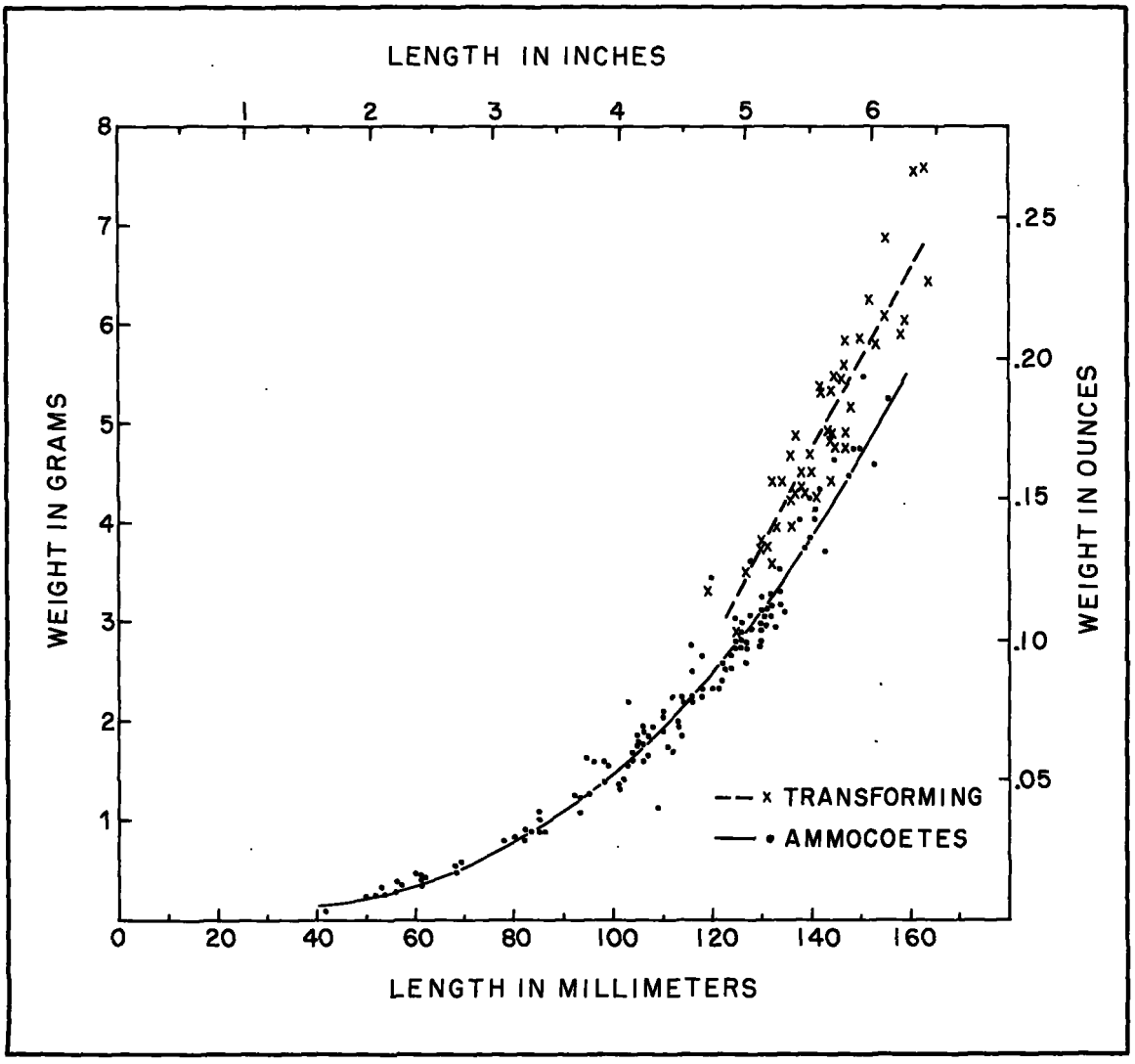

FIGURE 20.—Length-weight relationship of sea lamprey ammocoetes and transforming specimens taken from Cayuga Inlet during August. Regression formulas: for ammocoetes, $Y=1.63-0.0354\ X+0.0004\ X^2$; for transforming lampreys, $Y=5.02+0.1667\ X-0.0003\ X^2$.

ammocoetes captured in Cayuga Inlet were marked with cadmium sulfide or mercuric sulfide, as described by Wigley (1952), and installed in an outdoor hatchery raceway. The raceway bottom was covered with several inches of sand and silt, and water was supplied from Cascadilla Creek. Marked specimens with body lengths of 5.43, 5.43, 5.59, 5.91, and 6.02 inches (approximately the length of age group VI) on August 24, 1951, began transforming in August 1952. Furthermore, marked specimens 4.80, 4.80, 4.92, 4.92, and 5.12 inches long (about the length of age group V) on August 6, 1951, kept in the same raceway with the previous group, did not transform in 1952. These specimens are plotted in the length- and weight-frequencies of figures 17 and 19. This information and the modes indicated in all length- and weight-frequency distributions not only give convincing evidence that the recognition of age group VI is valid, but lends support to the validation of recognizing other modes in the length- and weight-frequency distributions.

Although the present study has yielded the strongest evidence for a larval life of 7 years, as compared with 3 to 5 years propounded by previous investigators, these findings should be accepted with reservation. It should be emphasized, however, that most of the estimates of the

duration of larval life which have been made were nothing more than subjective estimates based on relatively small samples. Moreover, prior to 1950 zoologists were unable to identify ammocoetes of the several species of lampreys. In view of the methods employed in the present investigation, and the consistency of the results, the findings presented herein are believed to be reliable.

Growth of sea lamprey ammocoetes was such that the annual increment in body length decreased with age, whereas the annual increment in body weight increased with age (table 38). The yearly increase in body length during the first 2 years of life was approximately 1 inch. Then, from the second year until time of transformation at the age of 7 years, the annual increase in length declined steadily. During the seventh year of life (age group VI) the length increment was approximately one-half inch. A loss in length of nearly one-half inch took place during the initial stages of transformation.

TABLE 38.—*Growth of ammocoetes in Cayuga Inlet as estimated from length-frequencies of specimens collected during July and August*

Age group	July		August		July and August	
	Length (inches)	Increment of length	Length (inches)	Increment of length	Length (inches)	Increment of length
0	0.47				0.47	
I	1.46	0.99			1.46	0.99
II	2.64	1.18	2.24		2.36	.90
III	3.54	.90	3.23	0.99	3.23	.87
IV	4.21	.67	4.21	.98	4.21	.98
V	5.00	.79	4.80	.59	5.00	.79
VI	5.59	.59	5.51	.71	5.59	.59
VII	6.10	.51	[1] 5.51	0	[1] 5.39	(—.20)

[1] Transforming sea lampreys.

Body weight of ammocoetes increased slowly during their early years but increased progressively with age. The annual increments in weight during the third through seventh years of life were: 0.018, 0.035, 0.035, 0.053, and 0.018 ounce. Ammocoetes in age group VII weighed 0.183 ounce just prior to transformation.

Transformation and Downstream Movement

The anatomical changes that take place during the transformation from the larval to the parasitic stage have been described by Gage (1928). According to Gage, transformation starts between mid-July and early September. This statement agrees with my observations. Few sea lampreys were found in the transforming stage in early August. In late August numerous specimens were in an advanced stage of transformation but few were in the early stage. These observations suggest that gross, externally visible morphological changes are completed within a period of 1 or 2 weeks after transformation begins. In contrast, it appears that internal changes are not completed before January and probably not until March.

Progress of transformation was followed in a group of sea lampreys kept in a hatchery trough, the bottom of which was provided with sediment from a streambed. From time to time during October, November, and December five specimens were dug from the sediment and put in company with a 7-inch rainbow trout, *Salmo gairdneri*, for a 10-day period. None of the lampreys fed upon or attempted to feed upon the trout. By March 13 all transforming or transformed sea lampreys kept in the trough had emerged from the bottom sediment and were clinging to the head end of the trough. A 7.8-inch brook trout, *Salvelinus fontinalis*, placed in the trough on that day, was immediately attacked by two of the lampreys. Later examination proved they had been feeding.

Measurements and weights of marked transforming sea lampreys kept in hatchery troughs under conditions corresponding to those described in the preceding paragraph provided information on changes in length and weight during transformation. Of 14 transforming specimens installed on August 24, 1951, and reweighed and remeasured on March 13, 1952, all lost weight (table 39). The individual losses ranged from 0.011 to 0.026 ounce, an average 0.019 ounce. Length, however, increased in 13 (the length of one specimen did not change). Increases in length ranged from 0.09 to 0.51 inch and averaged (for all 14) 0.28 inch.

Transforming sea lampreys in Cayuga Inlet were commonly found in bottom sediments composed of gravel one-fourth to three-fourth inch in diameter. Smaller ammocoetes, as has been shown, usually inhabit sediments of sand and silt where the particle size is much smaller.

The capture of transforming and large-sized ammocoetes in the very headwaters of Cayuga Inlet, in the vicinity of West Danby (fig. 10, section *K*), indicates that no important downstream movement takes place during the larval period in

that portion of the stream. Since the stream is small in that area, roughly 2 to 6 feet wide and with a flow of 1 to 5 cubic feet per second, it is doubtful whether floods are severe enough to wash out the ammocoetes and force them downstream. In the middle and lower reaches of Cayuga Inlet, severe floods surely must be capable of such action, but data on actual effects of flooding are not available.

TABLE 39.—*Length and weight of transforming sea lampreys measured Aug. 24, 1951, and Mar. 13, 1952*

[The lampreys were marked individually]

Length (inches)			Weight (ounces)		
Aug. 24, 1951	Mar. 13, 1952	Difference	Aug. 24, 1951	Mar. 13, 1952	Difference
5.00	5.51	+0.51	0.123	0.112	−0.011
5.20	5.28	+.09	0.127	.105	−.022
5.28	5.51	+.24	0.155	.135	−.019
5.35	5.79	+.43	0.151	.136	−.014
5.39	5.67	+.28	0.152	.128	−.024
5.43	5.43	0	0.142	.124	−.018
5.47	5.67	+.20	0.151	.133	−.018
5.67	5.75	+.09	0.172	.146	−.026
5.79	6.02	+.24	0.167	.153	−.014
5.79	6.14	+.35	0.172	.152	−.020
5.79	6.22	+.43	0.207	.186	−.022
6.02	6.26	+.24	0.204	.183	−.020
6.10	6.42	+.31	0.215	.195	−.020
6.22	6.69	+.47	0.209	.187	−.022
Mean		+.28	Mean		−.019

Six transforming sea lampreys captured in Cayuga Inlet during August 1951 were examined for food content. None of the digestive tracts contained food; in fact, they were almost without a lumen. That newly transformed sea lampreys can endure long periods without food was indicated by the survival of two specimens in a hatchery raceway from August until the following May, a 9-month period.

PARASITIC HABITS

Sea Lamprey Parasitism on Lake Trout in Cayuga and Seneca Lakes

The direct estimation of possible harmful effects of the sea lamprey upon populations of lake trout is made difficult by the deepwater habitat of both lampreys and trout. Biologists have long recognized the sea lamprey as a dangerous predator on food and game fishes. Half a century ago Surface (1898) made the statement, "* * * we have no doubt that in this region [Finger Lakes] the lampreys destroy more fish than do all the other enemies of fish or all of the fishermen combined."

He based this statement on the frequency of lamprey scars and wounds on fish from Cayuga Lake. According to Surface, more than 90 percent of the brown bullheads, *Ictalurus* [*Ameiurus*] *nebulosus*, nearly 80 percent of the white suckers, *Catostomus commersoni*, and nearly all the lake trout, *Salvelinus* [*Cristivomer*] *namaycush*, had suffered attacks by the sea lamprey.

Three decades later, Gage (1928) calculated that approximately 3 pounds of fish blood were necessary to feed one lamprey from youth to maturity. In his aquarium studies, Gage also found that most fish of relatively large size survived the lamprey's attack; small ones succumbed.

In 1949, Webster [7] placed rainbow trout, smallmouth bass, and white suckers, all 18 inches or less in length, in aquariums with nearly full-grown sea lampreys. One attack by a large (9 to 17 inches) lamprey was usually sufficient to cause death to fish of all three species.

More ominous evidence of the sea lamprey's devastating capabilities comes from the Great Lakes. Commercial lake trout catches declined disastrously in both Lake Huron and Lake Michigan during the years of tremendous increase in the sea lamprey population (Hile, 1949; Hile, Eschmeyer, and Lunger, 1951).

Royce (1950) compared the body weights of lake trout from Seneca Lake in which the species had suffered varying degrees of lamprey parasitism. He found no statistical differences in weight related to lamprey parasitism. The lake trout studied by Royce were relatively large, 22 to 33 inches long.

Information for the present study on the lamprey's effect on the lake trout in Cayuga Lake was gathered during 1949–51 activities of the New York State Conservation Department, Finger Lakes investigations,[8] which included the capture of lake trout from Cayuga Lake each summer and fall. The trout were taken by means of experimental gill nets with mesh sizes that ranged from 1 to 6 inches, extension measure. Lake trout 5 to 31 inches in fork length were caught. Nets were set during the afternoon and lifted the following morning. Possibly the congregation of lake trout caught in the nets attracted the sea lamprey to them in unnatural numbers, and, of course, the lake trout were helpless to escape attack. Be-

[7] Mortality caused by lamprey eels in aquarium experiments. Unpublished research memorandum, Department of Conservation, Cornell University, January 17, 1949. 4 pages.

[8] Data from the Finger Lakes investigations are published with permission from Dr. D. A. Webster.

cause of the relatively short time the nets were fishing, it is believed that the data are not unduly biased by attacks on trout in the nets.

A total of 1,372 lake trout were examined for lamprey scars and wounds. All were measured, but to minimize injury from handling during warm weather, only about 700 were weighed. Fork length [9] was measured to the nearest 0.1 inch and weight was measured on a Chatillon spring balance to the nearest ounce.

In this discussion, a wound is any place of lamprey attachment where the skin has been perforated and has not healed. Hemorrhaged blood vessels and inflamed tissues produce a red appearance. A scar is a wound that has healed. The lacerated tissues have coalesced and the red coloration has disappeared. The condition of marks was rarely such as to make the classification (scar or wound) questionable. That initial healing may take place within a few days was indicated by observations on brook trout held in hatchery troughs.

Loss of body weight resulting from sea lamprey attacks

Before analysis to detect and measure possible effects of sea lamprey attacks on the weight of lake trout could be undertaken, it was necessary to determine whether or not the length-weight relation differed between the sexes or from year to year. For this purpose 19 unscarred males and 19 unscarred females were selected at random from each of the collections made in 1949, 1950, and 1951. The analysis of covariance (after transformation of lengths and weights to logarithms to assure approximately linear regression) disclosed no significant differences among the several groups. Data for the sexes and the different years of capture could accordingly be combined in all further analyses.

Relation between body weight and number of scars and wounds.—Death is not inevitable to all lake trout that are attacked by a sea lamprey. The numerous trout that possess scars or wounds resulting from sea lamprey attacks offer proof. However, trout which have survived an attack may or may not have suffered a setback in growth. From the loss of blood alone it seemed likely that losses in body weight would result. Furthermore, it was reasoned that any immediate weight loss would be directly correlated with the number of lamprey wounds, and a permanent weight loss would be directly correlated with the number of lamprey scars.

Royce (1950) demonstrated that thinness was not correlated with the number of lamprey attacks on relatively large lake trout. The possibility remained, however, that small lake trout might suffer adverse effects from lamprey attacks; consequently the present study was restricted to lake trout ranging from 9 to 22 inches in length.

Lake trout whose lengths were within the size range just mentioned were divided into three major classes based on the number of scars borne by each trout. Each class was subdivided into three classes based on the number of wounds borne by each trout (table 40). The major classes were as follows: Trout without lamprey scars; trout with one lamprey scar; and trout with two or more lamprey scars. Subclasses were: trout without lamprey wounds; trout with one lamprey wound; and trout with two or more lamprey wounds. Fifteen lake trout were taken at random from each category to provide a total of 135 specimens for the analysis.

TABLE 40.—*Mean adjusted weights and rank order of weight classes of 9 groups of lake trout*

Class		Adjusted weight (ounces)	Total rank order	Wound rank order	Scar class adjusted weight (ounces)	Scar class rank order
Number of scars	Number of wounds					
0	0	27.1	1	1		
	1	25.6	4	2		
	2+	23.7	8	3	25.4	1 or 2
1	0	26.0	3	1		
	1	25.2	5	2		
	2+	25.1	6	3	25.4	1 or 2
2+	0	26.8	2	1		
	1	25.1	7	2		
	2+	23.7	9	3	25.1	3

The hypothesis that there was no difference in weight among the scar classes or among the wound subclasses was tested by an analysis of covariance. The analysis for scars produced an F value that was not significant, thus indicating that the null hypothesis should be accepted (table 40). The adjusted weights of the scar classes indicate that lake trout with the highest incidence of lamprey scars are the thinnest, but, as is shown by the scar-class rank order, the trend is not consistent.

[9] The conversion formula for transforming fork length to total length is: $T=1.082\ F+0.045$, where T equals total length and F equals fork length. Initial study on the recovery and relative survival of fingerling and yearling lake trout stocked in Cayuga Lake, by William G. Bentley, M.S. thesis, Cornell University, June 1950.

According to these data, sea lamprey attacks, indicated by scars, do not produce a significant permanent change of weight.

The analysis for wounds produced an F value that is highly significant (F=6.74 where $F_{.01}$= 4.78). Reference to the wound rank column in table 40 reveals exactly the order that would be expected on an a priori basis; i.e., the lake trout with the greatest number of wounds weigh the least. It is concluded from these data that lake trout which survive a sea lamprey attack suffer a significant temporary loss in weight.

Relation between the size of lake trout and the effect of sea lamprey attacks.—To learn the effect of sea lamprey attacks on trout of different sizes, and at the same time to verify the previous conclusion that lake trout with more lamprey wounds are thinner than those with fewer wounds, another analysis of covariance was carried out. Trout in three length classes and three wound-incidence classes were tested for thinness. To obtain sufficient range in size, lake trout between 10 and 25.9 inches in length were utilized. The lake trout were divided into the major classes according to their length, and each class was subdivided according to the number of lamprey wounds on each trout (table 41). The length classes were: 10 to 15.9 inches; 16 to 20.9 inches; and, 21 to 25.9 inches. The subclasses were: trout without lamprey wounds, trout with one lamprey wound, and trout with two or more lamprey wounds. Twenty-three trout were taken at random from each of the nine categories, giving a total of 207 lake trout in this analysis.

Results of the covariance analysis reveal a highly significant difference in weight among the wound classes (F=19.62 where $F_{.01}$=4.71). Reference to the adjusted-body-weight column and the wound-rank column in table 41 discloses that lake trout with the greatest number of sea lamprey wounds are the thinnest. This finding supports the conclusion reached in the previous analysis.

That small lake trout suffer more severe weight losses than do large trout is indicated by the highly significant F value (F=51.27 where $F_{0.01}$= 3.41) in the test for interaction of lamprey wounds on lake trout body length. Furthermore, when the nonwounded subclass in each length class is omitted from the calculation of mean adjusted weights, the smallest trout (10 to 15.9 inches) are much lighter than the larger trout. The two larger length classes (16 to 20.9 inches, and 21 to 25.9 inches) have the same mean weight.

TABLE 41.—*Mean adjusted weights and rank order of length classes and wound classes of lake trout*

Class		Adjusted weight (ounces)	Total rank order	Wound rank order	Length class adjusted weight (ounces)	Length class rank order [1]
Length (inches)	Number of wounds					
10.0–15.9	0	37.5	3	1		
	1	35.2	6	2		
	2+	31.4	9	3	33.3	3
16.0–20.9	0	39.1	1	1		
	1	36.6	5	2		
	2+	35.2	7	3	35.9	1 or 2
21.0–25.9	0	36.7	4	2		
	1	37.8	2	1		
	2+	34.0	8	3	35.9	1 or 2

[1] The nonwounded groups in each length class omitted.

The length-weight relation of three categories of lake trout, grouped according to the incidence of sea lamprey wounds sustained by each trout, is shown in figure 21. Regression formula for each group is given in the caption.

Length of trout and incidence of sea lamprey attacks

The number of sea lamprey attacks sustained by lake trout was directly correlated with the size of the trout. On the average, the largest trout possessed the greatest number of both lamprey scars and lamprey wounds. Since the perforation of the trout's body by the lamprey leaves a permanent mark, it was to be expected that the largest trout, which are the oldest and consequently have been subjected to predation by lampreys for the longest period, would bear the greatest number of lamprey scars. The incidence of lamprey wounds would be expected to be the same for trout of all sizes unless a differential mortality removed certain size groups or unless the lampreys selected certain size groups as hosts.

Unfortunately, it is nearly impossible to ascertain the actual relation between size of hosts and incidence of sea lamprey parasitism, due to the fact that some hosts succumb as a result of lamprey attacks. With the information available it has been possible to present only the incidence of lamprey attacks upon those lake trout which survived and were subsequently captured. Thus the mortality of lake trout resulting from lamprey attacks has an important bearing upon the data presented here. It must be kept in mind also that the size of lamprey in comparison to the host's size is of fundamental significance.

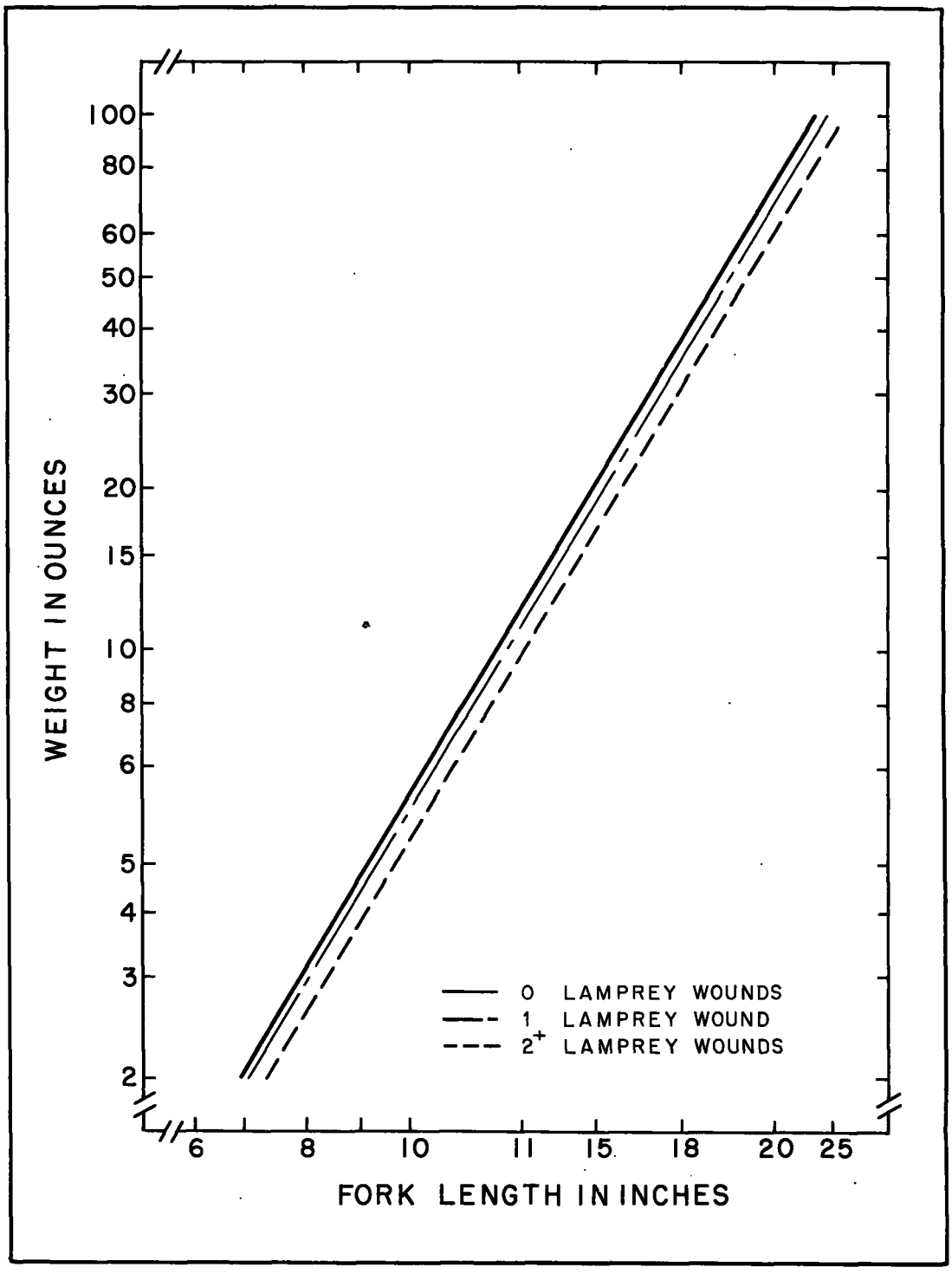

FIGURE 21.—Length-weight relation of 132 lake trout from Cayuga Lake, separated into 3 groups according to the number of sea lamprey wounds sustained by each trout. Regression formulas: unwounded trout (solid line), log $W=1.5557+3.169 \log L$; trout with one lamprey wound (broken line), log $W=1.5765+3.1057 \log L$; trout with two or more lamprey wounds (dashed line), log $W=1.5325+3.1432 \log L$.

498325 O—59——4

The number of sea lamprey marks (both scars and wounds) increased progressively with body length (tables 42, 43, and 44). Trout between 5 and 9 inches long rarely had suffered lamprey attacks. Trout from 9 to 16 inches in length showed a gradually increasing rate of attack. At a length of approximately 16 inches the apparent rate of attack increased rapidly and reached its peak of roughly 11 marks per trout for the largest specimens, which were approximately 30 inches long.

It may be asked whether sea lampreys prefer large lake trout as their host, or whether they feed

TABLE 42.—*Incidence of sea lamprey attacks on lake trout from Cayuga Lake, 1949*

Length class (inches)	Average length	Number of lake trout	Wounds		Scars		Marks [1]	
			Percentage of trout with wounds	Average number per trout	Percentage of trout with scars	Average number per trout	Percentage of trout with marks	Average number per trout
5.0–5.9	5.9	1	0	0	0	0	0	0
6.0–6.9	6.5	4	0	0	0	0	0	0
7.0–7.9		0						
8.0–8.9	8.4	7	14.3	0.14	14.3	0.14	28.6	0.29
9.0–9.9	9.4	8	25.0	.33	12.5	.11	25.0	.50
10.0–10.9	10.5	17	35.3	.82	17.6	.35	35.3	1.18
11.0–11.9	11.5	10	50.0	.60	20.0	.20	60.0	.80
12.0–12.9	12.5	12	58.3	1.17	33.3	.50	66.7	1.67
13.0–13.9	13.4	11	27.3	.36	9.1	.09	27.3	.45
14.0–14.9	14.5	8	37.5	.50	37.5	.37	50.0	.88
15.0–15.9	15.5	5	60.0	.80	20.0	.40	60.0	1.20
16.0–16.9	16.5	5	60.0	1.00	60.0	1.00	80.0	2.20
17.0–17.9	17.3	10	50.0	1.00	50.0	1.10	60.0	2.10
18.0–18.9	18.4	7	71.5	1.43	71.5	2.29	71.4	3.71
19.0–19.9	19.5	13	46.2	.46	92.3	2.00	92.0	2.46
20.0–20.9	20.4	23	65.3	1.43	95.7	1.91	100.0	3.35
21.0–21.9	21.4	27	59.2	1.52	96.4	2.89	96.3	4.41
22.0–22.9	22.5	46	63.1	1.09	95.7	3.22	100.0	4.30
23.0–23.9	23.4	67	59.7	1.27	100.0	3.73	100.0	5.00
24.0–24.9	24.5	43	72.1	2.21	95.3	5.02	97.7	7.23
25.0–25.9	25.4	50	66.0	1.51	100.0	5.12	100.0	6.50
26.0–26.9	26.4	44	75.0	2.00	100.0	3.76	100.0	5.89
27.0–27.9	27.3	34	70.7	2.44	100.0	3.59	100.0	6.03
28.0–28.9	28.4	11	54.5	1.55	100.0	6.45	100.0	8.00
29.0–29.9	29.3	3	100.0	3.00	100.0	7.33	100.0	10.33
30.0–30.9		0						
31.0–31.9	31.1	1	100.0	3.00	100.0	7.00	100.0	10.00

[1] Scars and wounds combined.

TABLE 43.—*Incidence of sea lamprey attacks on lake trout from Cayuga Lake, 1950*

Length class (inches)	Average length	Number of lake trout	Wounds		Scars		Marks [1]	
			Percentage of trout with wounds	Average number per trout	Percentage of trout with scars	Average number per trout	Percentage of trout with marks	Average number per trout
5.0–5.9	5.6	3	0	0	0	0	0	0
6.0–6.9	6.3	8	0	0	0	0	0	0
7.0–7.9	7.5	5	0	0	0	0	0	0
8.0–8.9	8.6	19	5.3	0.05	0	0	5.0	0.05
9.0–9.9	9.5	12	0	0	0	0	0	0
10.0–10.9	10.6	20	0	0	5.0	0.05	5.0	.05
11.0–11.9	11.4	27	11.1	.15	14.8	.22	14.8	.37
12.0–12.9	12.4	26	15.4	.20	3.8	.04	15.4	.23
13.0–13.9	13.4	27	25.9	.48	7.4	.07	33.3	.56
14.0–14.9	14.4	25	24.0	.32	12.0	.12	24.0	.44
15.0–15.9	15.5	19	57.9	.84	21.0	.37	68.4	1.21
16.0–16.9	16.4	18	33.3	.44	27.8	.72	50.0	1.17
17.0–17.9	17.4	13	38.5	.54	23.1	.23	61.5	.77
18.0–18.9	18.4	7	71.5	1.14	71.5	1.00	85.7	2.14
19.0–19.9	19.4	17	82.3	1.30	70.7	1.94	88.2	3.24
20.0–20.9	20.5	16	56.2	.56	87.4	2.32	93.8	2.88
21.0–21.9	21.5	20	55.0	.70	95.0	2.45	100.0	3.15
22.0–22.9	22.5	45	75.0	1.15	97.8	3.29	97.8	4.44
23.0–23.9	23.5	57	68.4	1.21	100.0	3.86	100.0	5.07
24.0–24.9	24.3	45	55.5	1.07	100.0	4.18	100.0	5.24
25.0–25.9	25.4	41	67.5	1.32	100.0	3.87	100.0	6.41
26.0–26.9	26.3	37	64.9	1.49	97.3	5.57	100.0	7.05
27.0–27.9	27.3	12	75.0	1.58	100.0	6.92	100.0	8.50
28.0–28.9	28.4	7	42.8	.71	100.0	7.58	100.0	8.29
29.0–29.9	29.0	2	100.0	2.50	100.0	8.50	100.0	11.00
30.0–30.9	30.1	1	100.0	1.00	100.0	14.00	100.0	15.00

[1] Scars and wounds combined.

TABLE 44.—*Incidence of sea lamprey attacks on lake trout from Cayuga Lake, 1951*

Length class (inches)	Average length	Number of lake trout	Wounds		Scars		Marks [1]	
			Percentage of trout with wounds	Average number per trout	Percentage of trout with scars	Average number per trout	Percentage of trout with marks	Average number per trout
5.0–5.9	5.5	2	0	0	0	0	0	0
6.0–6.9	6.5	2	0	0	0	0	0	0
7.0–7.9								
8.0–8.9	8.5	6	0	0	0	0	0	0
9.0–9.9	9.4	4	0	0	0	0	0	0
10.0–10.9	10.6	7	0	0	0	0	0	0
11.0–11.9	11.3	16	6.3	0.06	0	0	6.3	0.06
12.0–12.9	12.5	15	13.3	.20	6.7	0.07	20.0	.27
13.0–13.9	13.4	10	10.0	.10	30.0	.50	40.0	.60
14.0–14.9	14.5	22	13.6	.18	4.5	.05	18.2	.23
15.0–15.9	15.5	9	22.2	.22	11.1	.11	33.3	.33
16.0–16.9	16.4	12	58.3	.58	16.6	.25	58.3	.83
17.0–17.9	17.4	4	0	0	50.0	.75	50.0	.75
18.0–18.9	18.4	7	28.5	.29	57.2	.86	57.1	1.14
19.0–19.9	19.5	14	71.4	1.00	57.2	1.00	92.9	2.00
20.0–20.9	20.6	14	42.8	.50	78.5	.71	78.6	2.21
21.0–21.9	21.4	24	50.0	.67	79.3	2.00	91.7	2.67
22.0–22.9	22.5	30	30.0	.40	86.7	3.33	90.0	3.73
23.0–23.9	23.4	41	39.0	.63	100.0	3.51	100.0	4.15
24.0–24.9	24.5	52	57.7	.86	98.0	4.49	98.1	5.25
25.0–25.9	25.4	25	52.0	.72	96.0	5.20	100.0	5.92
26.0–26.9	26.2	20	50.0	1.05	100.0	5.95	100.0	7.00
27.0–27.9	27.3	8	62.5	1.63	100.0	6.38	100.0	8.00
28.0–28.9	28.3	2	50.0	1.00	100.0	10.50	100.0	11.50
29.0–29.9	29.3	1	0	0	100.0	6.00	100.0	6.00

[1] Scars and wounds combined.

at random on any trout they encounter. Since the largest trout possessed the highest incidence of lamprey attacks, the data presented in the preceding sections suggest preference for large trout. However, if lampreys do prefer large hosts, the percentage of trout bearing lamprey wounds (scars not considered) would be expected to increase progressively from the smallest trout to the largest.

The percentage of lake trout that possessed lamprey wounds was calculated separately for each of the three years 1949–51 (tables 42–44, fig. 22). The few specimens between 14 and 20 inches long cause rather wide fluctuations in the percentages of wounded trout within that range. Because small trout are known to have a considerably higher mortality than large ones, the relation between the size of trout and incidence of attacks is probably most unreliable for the small specimens. Since the inflections of the line fitted to the data in figure 22 were a critical part of this relation, especially that portion pertaining to the large trout, it was necessary to employ statistical methods rigorous enough to show the less obvious trends in this regression. A test of the orthogonal polynomial series (F test) revealed that the third degree polynomial regression was required (regression formulas are given in the caption of fig. 22).

The percentage of wounded lake trout leveled off at the greater lengths in 2 of the 3 years, 1950 and 1951; in 1949 the percentage continued to increase. If only the larger lake trout (20 inches or greater) are considered, it is apparent that very little increase in the percentage of wounded trout accompanies the increased body length. The lack of a continued increase in the incidence of lamprey wounds on the largest trout suggests that there is no selection for size of host specimens in this size range. The evidence is not conclusive, but it is definitely known that lampreys prey upon trout 8.2 inches up to the very largest. There is some indication that they do not necessarily prefer the large trout, at least not over the size range where they may reasonably be expected to survive an attack.

Annual variations in incidence of sea lamprey attacks

Incidence of sea lamprey attacks upon lake trout differed noticeably from year to year, and was directly correlated with the abundance of lampreys. Yearly differences in the incidence of lamprey wounds were especially noticeably because wounds are inflicted by only one year class of lampreys. During any one year the rate of wounding can be expected to reveal annual fluctuations more clearly than scars, which are accumulated over a period of years. For this reason

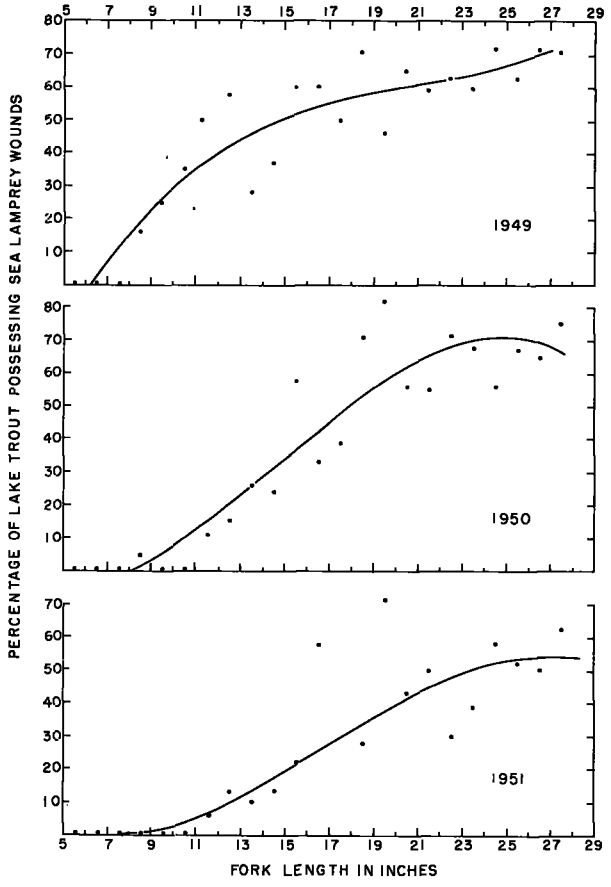

FIGURE 22.—Regressions of the percentage of lake trout possessing sea lamprey wounds on body length of lake trout for 1949, 1950, and 1951. Regression formulas: 1949, $Y=88.7628+18.8330\ X-0.8337\ X^2+0.0132\ X^3$; 1950, $Y=28.7041-11.1589\ X+1.1443\ X^2-0.0252\ X^3$; 1951, $Y=16.2757-6.3353\ X+0.6322\ X^2-0.0128\ X^3$.

further discussion is based entirely on the wounds, except to mention that annual variations in attacks on trout are evident also in the incidence of scarring.

Annual differences in the rate of lamprey parasitism show most clearly in the average number of lamprey wounds borne by lake trout. The values listed in column 5 of tables 42, 43, and 44 have been smoothed by a moving average of 3 and plotted in figure 23. It is readily apparent that the average number of wounds per trout decreased steadily during the period 1949–51. Trout of almost all sizes showed this trend.

Another measure of the intensity of lamprey parasitism is the percentage of lake trout possessing lamprey wounds (column 4 in tables 42, 43, and 44; fig. 22). The percentages of trout bearing lamprey wounds are 60, 46, and 38 for the years 1949–51. Each year the percentage of wounded trout exhibited a marked decrease; however, the yearly differences in this relation are less pronounced than are those of the number of wounds because of the high incidence of parasitism among the large trout in all years.

The most plausible explanation of the decline in sea lamprey parasitism upon lake trout from the high incidence in 1949 to the low in 1951 is that it resulted primarily from the decline in abundance of lampreys. This view is supported by the data in table 45 in which are listed the estimated numbers of sea lampreys, mean numbers of lamprey wounds per lake trout, and minimum lengths of lake trout bearing lamprey wounds for each year from 1949 through 1951.

Since the number of lampreys varied widely from one year to another, it is reasonable to assume that the ratio of lampreys to lake trout was principally dependent on the fluctuation in lamprey abundance. An estimate of the number of sea lampreys in the lake during a particular year can be determined from the number of spawning migrants. Except for a brief period in early spring, only one year class of parasitic-phase sea lampreys is present in the lake. Their abundance can be closely estimated by determining the number of migrants that enter Cayuga Inlet for spawning the following spring. Thus, the number of sea lampreys in Cayuga Lake during 1950 and 1951 was determined from the number of sea lampreys in the spawning migration in 1951 and 1952, respectively.

All three measures of lamprey parasitism indicate more intensive feeding in years when lampreys were most abundant, and less feeding when lampreys were fewer. As shown in table 45, the average number of lamprey wounds per trout decreased as the number of lampreys decreased. Also, the percentage of lake trout bearing sea lamprey wounds decreased as the number of lampreys decreased. The small size of the shortest trout bearing lamprey wounds when lampreys were most numerous further indicates more intensive feeding when lampreys are abundant.

Incidence of Sea Lamprey Parasitism in Various Parts of Cayuga Lake

Lake trout taken in July and August 1949–51 from five sections of Cayuga Lake differed consid-

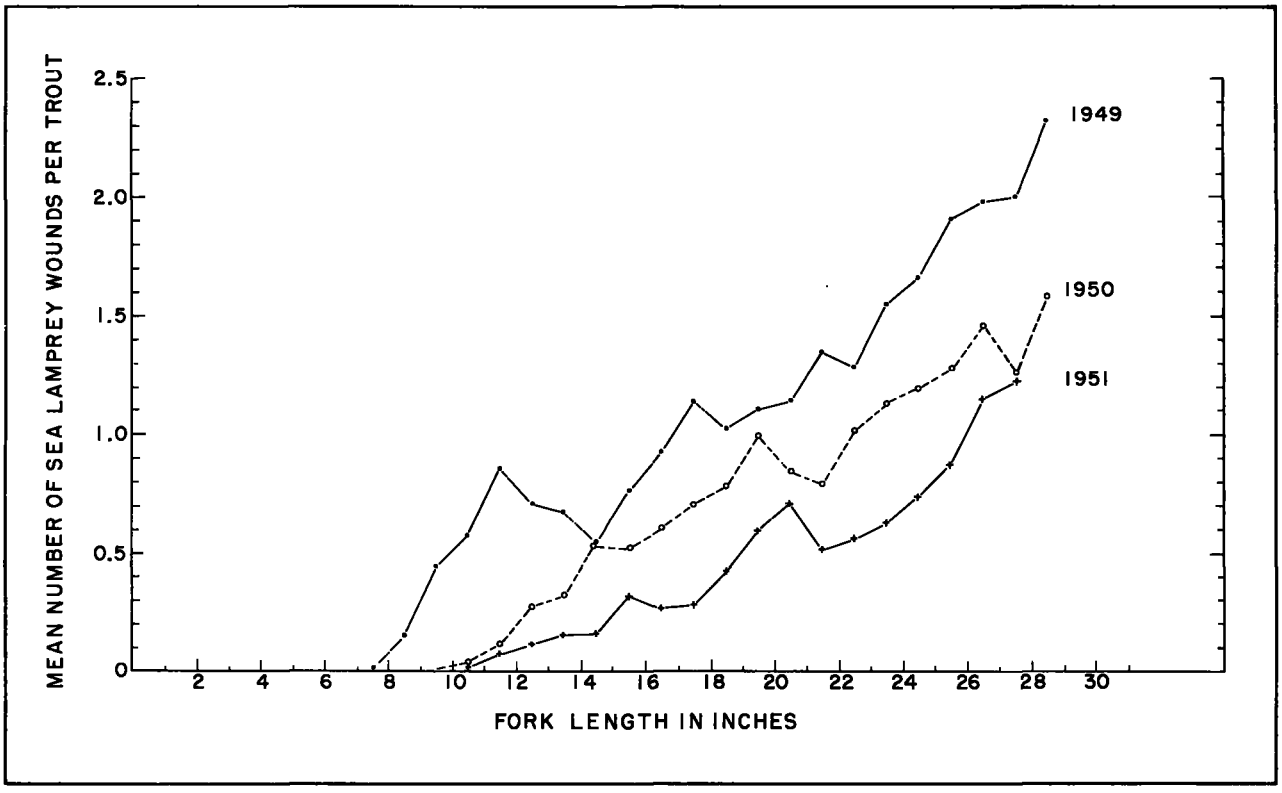

FIGURE 23.—Mean number of sea lamprey wounds on lake trout 8 to 30 inches in length during 1949, 1950, and 1951.

TABLE 45.—*Incidence of sea lamprey attacks on lake trout and sea lamprey abundance in Cayuga Lake, 1949–51*

Item	Year		
	1949	1950	1951
Number of sea lampreys	10,000–15,000	9,390	4,435
Average number of sea lamprey wounds per lake trout	1.21	0.81	0.46
Percentage of lake trout bearing sea lamprey wounds	60	46	38
Smallest lake trout bearing sea lamprey wounds (inches)	8.2	8.9	11.3

erably in both the percentage of trout wounded and in the mean number of wounds per fish. Cayuga Inlet, the only significant source of lampreys, enters the southern end of the lake, Section I (fig. 24 shows boundaries of the five sampling sections). This section extends northward 7 miles. Section II, a relatively small area off Flat Rock and Taughannock and Frontenac Points, is the major spawning ground for lake trout in Cayuga Lake. Across the lake and somewhat northward another small area, section IV, extending from Kings Ferry north to Willets, is a summer concentration area. Section III is the deep, middle portion of the lake. Section V is the northern, relatively shallow end of the lake.

Trout from section II and IV exhibited a high incidence of lamprey wounds, whereas those from sections I, III, and V showed a lower degree of parasitism (table 46). The unweighted mean numbers of lamprey wounds per trout in sections II and IV were 0.83 and 0.85, respectively. In Sections I, III, and V the mean values were 0.38, 0.44, and 0.44. The percentage of trout bearing wounds produced a similar picture. In sections II and IV the unweighted mean percentages of wounded trout were 44 and 54, respectively. Sections I, III, and V had mean percentages ranging between 26 and 38. Chi-square tests of independence indicated that differences in the incidence of parasitism among the 5 sections are significant. Section IV, the principal summer habitat of lake trout, ranked highest both in percentage of wounded fish and in number of wounds.

Seasonal trends in feeding activity of sea lampreys

Changes in feeding activity with time of year may be judged from monthly records of incidence

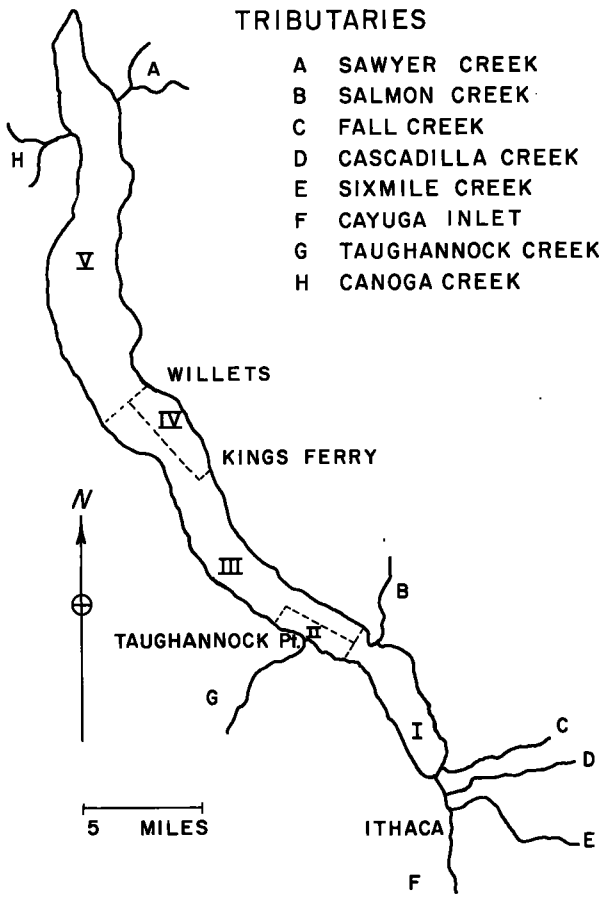

FIGURE 24.—Cayuga Lake and its major tributaries showing the five sampling sections of the lake. (Modified from Galligan, 1950; footnote 10.)

of lamprey wounds (table 47). To reduce bias arising from size differences, only large trout (between 20 and 31 inches long) were employed in the preparation of the table. As a further precaution the data are given only for lake trout from sections II and IV of Cayuga Lake to avoid bias from locality differences. Lake trout in these two areas are believed to form a single population. According to Galligan,[10] large trout gather in section IV during the summer and migrate to section II in the fall for spawning.

Feeding activity appeared to have reached a peak during August and September. A decline in feeding started in September and continued through October and November. In July the feeding activity was considerably less than maximum and was on a level with that for November.

[10] The distribution of lake trout and associated species in Cayuga Lake, by James P. Galligan, M.S. thesis, Cornell University, September 1951.

TABLE 46.—*Incidence of sea lamprey wounds on lake trout from 5 sections of Cayuga Lake*

[Boundaries of sections are shown in fig. 24]

Section of lake	Length (inches)	Number of trout	Number of trout with wounds	Percentage of trout with wounds	Mean number of wounds per trout
I	7.0–12.9	16	3	19	0.19
	13.0–19.9	7	5	71	.71
	20.0–30.9	12	3	25	.25
Total or mean		35	11	38	.38
II	7.0–12.9	17	4	24	.59
	13.0–19.9	22	12	55	.96
	20.0–30.9	19	10	53	.95
Total or mean		58	26	44	.83
III	7.0–12.9	45	6	11	.16
	13.0–19.9	54	18	33	.41
	20.0–30.9	12	8	67	.75
Total or mean		111	32	37	.44
IV	7.0–12.9	30	12	40	.67
	13.0–19.9	56	33	59	.80
	20.0–30.9	142	90	63	1.90
Total or mean		228	135	54	.85
V	7.0–12.9	11	1	9	.09
	13.0–19.9	22	4	18	.23
	20.0–30.9	2	1	50	1.00
Total or mean		35	6	26	.44

A chi-square test of independence for the 5 months gave a value corresponding to $p=0.03$. It is to be concluded that monthly variations in the percentage of wounded lake trout in the 20- to 31-inch size group are significant.

TABLE 47.—*Incidence of sea lamprey wounds on lake trout during July–November*

[All trout were 20.0 to 30.9 inches long. See fig. 24 for location of sections II and IV]

Month of capture	Section of Cayuga Lake	Number of trout	Number of wounded trout	Average number of wounds	Percentage of trout with wounds
July	IV	76	43	1.07	57
August	IV	66	47	1.12	70
September	II	177	117	1.72	66
October	II	366	218	1.25	60
November	II	55	29	1.05	53

Lake trout in the 13- to 19-inch length group resembled those of the 20- to 31-inch group in showing highest incidence of lamprey attacks during August and September.

The percentages of wounded lake trout in the 7- to 12-inch length group during July and August were 22 and 23 percent, respectively. None, however, of the small number of specimens in this size group captured during September, October, and November possessed a lamprey wound. Since the lampreys have more than doubled in length and

increased in weight more than tenfold by October, perhaps the lower incidence of predation on small trout reflects a shift in the size of host they prefer, or, an attack after September may have been fatal because of the lamprey's greater size.

Comparison of sea lamprey parasitism in Seneca and Cayuga Lakes

Lake trout in Cayuga Lake suffer a much higher incidence of sea lamprey parasitism than do lake trout in Seneca Lake. Evidence on this subject was gathered from both lakes in September and October 1950. Gill-net fishing by New York State personnel in Seneca Lake for spawning lake trout provided a total of 181 lake trout for examination. All trout were between 21.0 and 31.9 inches long. From Cayuga Lake 131 lake trout ranging in length from 21.0 to 30.9 inches were gill-netted.

The records of lamprey parasitism on these two groups of fish (table 48) reveal that the percentage of lake trout bearing sea lamprey wounds was only 18.2 for Seneca Lake specimens but was 65.7 for Cayuga Lake fish. The average number of wounds per trout was 0.28 in Seneca Lake and 1.34 in Cayuga Lake. Incidence of sea lamprey scars on lake trout was also much higher in Cayuga Lake (4.68 per fish) than in Seneca Lake (2.45 per fish). Since sea lamprey scars persist for many years, the difference in scarring rate indicates that lamprey depredations on lake trout were the higher in Cayuga Lake not only in 1950, but also during several preceding years. It may be inferred that the number of lampreys in proportion to the number of lake trout is three to five times higher in Cayuga Lake than in Seneca Lake.

TABLE 48.—*Incidence of sea lamprey parasitism on lake trout from Seneca Lake and Cayuga Lake*

[Based on trout caught in gill nets in September and October 1950. Samples include only trout between 21.0 and 31.9 inches long]

Lake	Trout with lamprey wounds		Average number of wounds	Trout with lamprey scars		Average number of scars
	Number	Percentage		Number	Percentage	
Cayuga	86	65.7	1.34	130	99.3	4.68
Seneca	33	18.2	.28	152	84.0	2.45

Location of attachment on the fish's body

Sea lampreys attach themselves most frequently to certain particular areas on their hosts' bodies. By recording the location of each lamprey scar and wound, according to the plan indicated in figure 25, the concentration of attachment in various body areas was determined. Fish for this analysis were 103 lake trout taken by gill nets in Seneca Lake on October 12 and 17, 1950. The percentage of scars was by far the highest (45 percent) in the pectoral region, section B (table 49). Next in order of scarring incidence were: prepelvic region (26 percent), section C; pelvic region (23 percent), section D; head region (5 percent), section A; and, caudal region (1 percent), section E. Only 10 scars and 2 wounds of the total number of attacks (310) were above the lateral line. Lennon (1954) reported a similar distribution of lamprey attachments on brook, brown, and rainbow trout from Lake Huron.

Wounds were distributed over the body much the same as scars. The principal difference lay in the greater incidence of wounds in the head and pectoral regions (chi-square test of independence

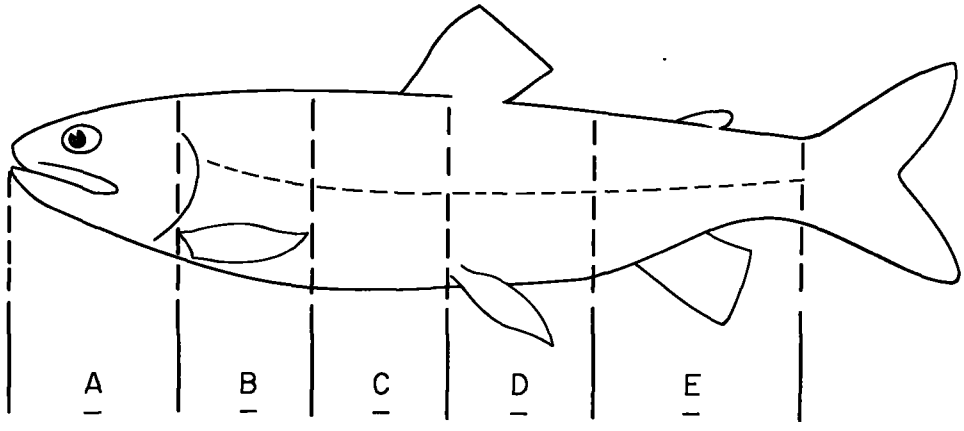

FIGURE 25.—Outline of a lake trout showing the 5 body regions for designating the location of sea lamprey attachment.

TABLE 49.—*Location of sea lamprey attachments on lake trout*

[The areas of attachment are indicated in fig. 25]

Item	Area of attachment					Total
	A	B	C	D	E	
SCARS:						
Number	13	127	71	65	2	278
Percentage	5	45	26	23	1	100
WOUNDS:						
Number	7	17	3	4	1	32
Percentage	22	53	9	13	3	100

yielded a value corresponding to $\rho=0.008$). Two explanations may be offered for this disparity. First, the superimposition of lamprey attachment over a previously existing scar would obliterate the original scar. Secondly, the mortality may be higher from wounds in the head and pectoral region than from wounds in other sections of the body.

Sea Lamprey Parasitism on the White Sucker

Information on the incidence of sea lamprey attacks on white suckers was obtained by the examination of spawning-run fish collected by means of an electric shocker from Butternut Creek, a tributary of Cayuga Inlet, on May 3, 1951, and May 6, 1952. Most of these suckers are believed to have been lake-dwelling fish that had ascended the stream to spawn. Possibly some stream-resident suckers were included.

The data on attacks on white suckers give no indication of difference between 1951 and 1952. White suckers less than 11 inches long bore no scars or wounds in either 1951 (15 fish) or 1952 (22 fish). At the greater lengths the percentage of scarred or wounded fish tended to increase with increase in size, as is brought out clearly by the following comparison of incidence of attacks in suckers 11.0–13.9 inches long and in fish 14 inches long or longer.

Fork length (inches)	1951			1952		
	Number of fish	Number with scars or wounds	Percentage	Number of fish	Number with scars or wounds	Percentage
11.0–13.9	109	21	19	76	17	22
>13.9	49	20	41	47	18	38

This trend toward a greater incidence of sea lamprey attacks among the larger white suckers is the same as that observed by Hall and Elliott (1954) in Lake Huron.

The cause for the increase in the incidence of sea lamprey attacks with increase in the size of white suckers is not known. Possibly the smaller fish are less able than larger ones to survive attack. Again, mechanical difficulties of attachment may give the smaller suckers a degree of immunity from lamprey predation.

PARASITES AND PREDATORS OF THE LAMPREY

Parasites

In the one previously published report on parasites of the sea lamprey in the Finger Lakes area, Van Cleave and Mueller (1934), who examined 12 sea lampreys from Oneida Lake, found trematode larvae. In more extensive studies, on mature sea lampreys from the Ocqueoc River and Carp Creek, tributaries of Lake Huron, Applegate (1950) and McLain (1952) reported parasitization to be rather low, generally less than 20 percent. Most common internal parasites were acanthocephalans of the genus *Echinorhynchus*, cestodes (*Triaenophorus*), and nematodes (*Cammallanus*). Externally, the leech *Pisicola milneri* was occasionally present.

The examination of 25 sexually mature sea lampreys from Cayuga Inlet during 1951 and of 53 in 1952 disclosed only one internal parasite, a small (1.5 mm.) acanthocephalan of the family Neoechinorhynchidae in the intestinal tract of a medium-sized female from the 1952 collection.

No external parasites were evident at any time during the 1950 spawning migration, but an epidemic of leeches occurred during the 1951 and 1952 migrations. The leech, *Pisicola zebra* Moore,[11] is approximately ¼-inch long and 1/16-inch wide. These leeches usually adhered in clusters to the dorsal and posterior edges of the first and second dorsal fins and the tip of the caudal fin. The leeches reached a peak of abundance on May 14, 1951, when they were present on 93 percent of the lampreys. At this time it was estimated that most of the infested lampreys carried approximately 50 to 300 leeches. The only visible damage to the lamprey was a slight erosion of the fin margins where the leeches had been attached.

[11] Identified by Dr. Marvin C. Meyer, University of Maine.

Predators

Numerous mammals and birds, a few reptiles, amphibians, and fishes were cited as predators on the sea lamprey by Surface (1899). He gave definite evidence of predation on the sea lamprey for the little green heron, the common water snake, and minnows of the genera *Rhinichthys* and *Notropis*. In Michigan, Applegate (1950) reported that walleye, northern pike, brown trout, raccoon, dogs, great blue heron, and sea gulls preyed on sea lampreys. The sea gull was the only predator of importance.

Daily excursions along Cayuga Inlet throughout the sea lamprey migratory and spawning season of 1951 and numerous visits during the 1950 and 1952 seasons, revealed amazingly little evidence of predation on spawning lampreys. Lampreys are especially vulnerable to predation while in the shallows of the tributary streams. It would be easy for almost any of the common predaceous animals to capture them. Nevertheless, the only animal actually witnessed devouring a sea lamprey was the common water snake, *Natrix sipedon*. In addition, six partially eaten lamprey carcasses were found along Cayuga Inlet during the three seasons of study. They appeared to have been killed by carnivores.

The only evidence of predation on sea lampreys in Cayuga Lake by fish was an unconfirmed report by a fisherman that he had found a sea lamprey in the stomach of a lake trout. Stomach analysis of hundreds of fish from Cayuga Lake, especially lake trout, have not produced a single instance of predation on the sea lamprey.

The only important predators on the sea lamprey in Cayuga Inlet are the small minnows that feed on the eggs. At the time of egg deposition, groups of these small fish gather just below the downstream rims of the nests. When the eggs are emitted, they quickly dart into the nest and seize as many eggs as possible before being frightened away by the spawners. Spawning lampreys never make an effort to drive these intruders from the nest, but the spawning actions seem to frighten the minnows. On June 4, 1951, the stomachs of six blacknose dace, *Rhinichthys atratulus*, contained numerous lamprey eggs.

CONTROL METHODS

Interrelationships between the sea lamprey and their host species in Cayuga Lake are only partially understood. In Lake Michigan and Lake Huron this parasite is very destructive to food and game fishes, and the sea lamprey is undoubtedly the cause of the destruction of many lake trout in Cayuga Lake. Their depredation on this fish in Cayuga Lake is compensated in part by their usefulness as an extraordinary, primitive creature for study by students in neighboring educational institutions. It is the writer's view that a program for reduction of numbers of sea lampreys in Cayuga Lake may be desirable, but that a supply should be maintained for scientific use.

Trapping operations in Cayuga Inlet have indicated the feasibility of reducing and possibly eradicating the Cayuga Lake population of sea lampreys by capturing spawning-run migrants. Also, the importance of extensive breeding and nursery areas as a factor in the abundance of the sea lamprey suggests the possibility of lowering the population level by reducing the spawning area available to them. Three methods of control appear to be practical:

1. Construction of a small barrier dam across Cayuga Inlet, 3 miles upstream from Cayuga Lake, would cut off extensive spawning areas. The initial expenditure would amount to several thousand dollars, but in the long run the dam would be more economical than traps or weirs since a barrier dam requires little or no maintenance. It blocks the migration of sea lampreys, but permits migration of game fishes. A head of 1½ to 2 feet should be effective under normal water conditions. A dam similar in design to the U.S. Geological Survey dam (fig. 11) would be suitable. A better but more expensive structure was described by Applegate and Smith (1950). An overhanging lip on the downstream side of the dam is essential.

2. An electromechanical weir and trap, similar to the one operated on the Kewaunee River, Wis. (Applegate, Smith, and Nielson 1952), should be the most efficient. The major disadvantage of this method is the expense. The device would cost several thousand dollars to purchase and install, and operational expenses would amount to several hundred dollars each spring.

3. Construction of a lamprey trap on the downstream side of the U.S. Geological Survey dam would provide an inexpensive control. This method would limit the lamprey to about 3 miles of spawning territory and bar it from 7 miles of

498325 O—59——8

spawning stream above the dam. It is estimated that about 75 percent of the entire spawning run could be captured. A trap suitable for this purpose would cost less than $50 and would require less than 50 man-hours annually for maintenance and operation.

SUMMARY

The recent invasion of the upper Great Lakes by the sea lamprey, and its depredation on the food and game fish have necessitated an investigation to discover methods of controlling this parasite. One aspect of the program was the present study of a long-established population of the landlocked sea lamprey.

Geological formation of the Great Lakes and the Finger Lakes of New York State, and the present distribution of the sea lamprey, lead to the conclusion that the lamprey entered Cayuga Lake by way of the "Champlain Sea" or the Hudson-Champlain estuary and Mohawk outlet during the latter part of the Pleistocene period.

Fieldwork was conducted from May 1950 to August 1952. Mature lampreys were captured in Cayuga Inlet by a weir, portable traps, and by hand. In all, 9,480 adult lampreys were captured. Of this number, 1,168 were tagged and 1,773 were fin-clipped and released in Cayuga Lake tributaries. Lake trout were taken by gill nets from Cayuga and Seneca Lakes. Immature, parasitic-phase lampreys were collected by removal of those adhering to lake trout taken in gill nets. Digging, seining, and electric shocking were employed for collecting larval lampreys in Cayuga Inlet.

In 1950, 1951, and 1952 the mean total lengths of adult, upstream-migrant lampreys were 15.0, 15.3, and 15.9 inches, respectively. The annual differences in length were significant, but the differences in length between males and females were not. Mean weights of upstream-migrant sea lampreys for 1950, 1951, and 1952 were 4.97, 4.34, and 4.94 ounces, respectively. In 1951, Cayuga Lake sea lampreys were approximately the same size as those taken in Carp Creek, a tributary of Lake Huron. This same year the largest landlocked sea lampreys were taken in Seneca Lake, N.Y. Mean length and weight of parasitic-phase sea lampreys captured in Cayuga Lake in September and October were 13.7 inches and 3.8 ounces. Mean length and weight of Seneca Lake sea lampreys captured during the same months were 15.5 inches and 5.3 ounces.

Transformation from the ammocoete to the adult stage began in August and terminated in March. Parasitic feeding began in March and continued approximately 14 months. During the early transformation stage the sea lamprey decreased approximately one-half inch in length. For the following 6 or 7 months, while buried in the stream bottom and in a nonfeeding phase of life, they increased approximately one-fourth inch in length and at the same time lost about 0.02 ounce in weight. After emerging from the bottom and starting their parasitic phase of life in the lake, they increased in length from 5.5 inches in March to 15.4 inches in April-May of the following year. Length-frequency distributions of specimens from both Cayuga and Seneca Lakes prove that lampreys spend only 1 full year in the lake. Essentially only one age group is present in the lake at any one time.

The length-weight relation was determined from 1,906 adult lampreys captured in Cayuga Inlet during April and May 1951.

Body proportions changed with the attainment of maturity. These proportions differed significantly between sexes at one time or another between September–October and the following June, and a majority of these proportions differed most at spawning time. Teeth, tooth-cusp, and myomere counts of Cayuga Lake specimens and Seneca Lake specimens reveal a divergence of the two populations at a racial level.

Of eight tributaries available to the lamprey for spawning, Cayuga Inlet was the only one used to any appreciable extent. The sea lampreys usually enter Cayuga Inlet during the last 2 weeks of April. Sea lampreys that arrived in the tributaries for spawning in mid-April spent 4–5 weeks in the stream before initiating nest construction. Activity of lampreys on the spawning migration was closely associated with water temperature.

Estimates of the number of lampreys in the spawning migration were: 1950, 10,000–15,000; 1951, 9,390; 1952, 4,435. Estimates were based on marking and recapture.

The rate of upstream travel was about 1 to 2 miles per day in the slow-moving portions of Cayuga Inlet. In the swifter, upstream area the rate of travel decreased to approximately one-

third to 1 mile per day. Upstream movement was slower during the early part of the migratory period than later. Low dams effectively retarded and sometimes blocked upstream migration of adult lampreys.

The numbers of males per 100 females in the spawning migrations were: 1950, 157; 1951, 155; 1952, 116. The relative abundance of males varied directly with the estimated total number of lampreys in the spawning run. Males were predominant among early migrants and females among late arrivals.

Coloration of mature lampreys during the spawning season varied with size, sex, and the time within the season.

Selection of nesting sites was affected by barriers to upstream migration, current velocities, substrate composition, and nesting densities. Some well-situated and apparently completed nests were not used for spawning, whereas others were utilized by several pairs. In a sample of 137 nests, only 43 percent contained lamprey eggs.

A female of average size produces approximately 43,000 eggs. Maximum and minimum numbers were: 85,162 for a 20.1-inch, 11.7-ounce lamprey, and 13,974 for a 13.5-inch, 2.6-ounce specimen.

The incubation period was 14 days at an average water temperature of 60.7° F.

A pronounced decrease in both length (11 percent for males; 18 percent for females) and weight (9 percent for males; 34 percent for females) took place during the spawning period.

Cayuga Lake sea lampreys die within a few days after spawning. Only 2.5 percent (238) of the estimated number of lampreys in the 1951 spawning run returned downstream to the weir during and after the spawning season. All were spent and approximately 80 or 90 percent were dead; the remainder were so debilitated that all were believed incapable of recuperating. Tagged or marked lampreys were not observed in the spawning runs in subsequent years. Although thousands of spent lampreys die in Cayuga Inlet each spring, few are seen without a thorough search of the deep pools.

A larval life of 7 years, including the period of metamorphosis, was ascertained from length- and weight-frequency distributions of ammocoetes. Mean lengths and weights in August for age groups II–VII were: II, 2.24 inches and 0.013 ounce; III, 3.23 inches and 0.031 ounce; IV, 4.21 inches and 0.066 ounce; V, 4.80 inches and 0.101 ounce; VI, 5.51 inches and 0.154 ounce; VII, 5.51 inches and 0.172 ounce. Weight-frequency distributions produced more definite modes for recognizing age groups than the more commonly employed length-frequency method.

Intensity of lamprey parasitism upon lake trout differed substantially from year to year, and was directly correlated with the abundance of lampreys. In Cayuga Lake the percentage of trout bearing lamprey wounds was 60 percent in 1949, 46 in 1950, and 38 percent in 1951. Lamprey scars, which are accumulated over the years, had a higher rate of occurrence: 82 percent in 1949, 60 in 1950, and 65 in 1951.

Lake trout in Cayuga Lake suffered a loss in weight that was directly related to the number of lamprey attacks and inversely related to the size of trout. Size of lamprey as well as of host fish is of great importance in determining damage by the sea lamprey. Also, mortality from lamprey attacks appears to be higher among small fish than among large ones. Incidence of lamprey wounds on lake trout from Cayuga Lake in July and August was greater in deepwater areas in which the trout concentrate in summer. Feeding activity of parasitic-phase lampreys reached a peak in August. Attachments of lampreys on lake trout were most numerous in the ventral half of the body, between the pectoral fin and the anus. The area immediately posterior to the pectoral fin was especially favored.

Lake trout are attacked much more frequently by sea lampreys in Cayuga Lake than in Seneca Lake. Evidence exists that the ratio of the number of lampreys to lake trout is 3 to 5 times higher in Cayuga Lake than in Seneca Lake.

White suckers from a tributary of Cayuga Inlet exhibited a 26-percent incidence of lamprey attacks in 1951, and a 29-percent incidence in 1952.

Numerous leeches, *Pisicola zebra* Moore, were attached to spawning-run lampreys in Cayuga Inlet in 1951 and 1952. An acanthocephalan was the only other parasite found in adult lampreys.

The only important predators on the sea lamprey in the Cayuga Lake basin are the minnows *Rhinichthys a. atratulus* and *Notropis c. cornutus*, which feed on lamprey eggs.

Control of the sea lamprey in Cayuga Lake could be accomplished at a moderate cost. Three control methods appear to be practical: barrier

dam, electromechanical weir and trap, and mechanical trap.

LITERATURE CITED

APPLEGATE, VERNON C.
1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. U.S. Fish and Wildlife Service, Spec. Sci. Rept.:—Fisheries, No. 55, 237 pp.

APPLEGATE, VERNON C., and BERNARD R. SMITH.
1951. Sea lamprey spawning runs in the Great Lakes, 1950. U.S. Fish and Wildlife Service, Spec. Sci. Rept.:—Fisheries, No. 61, 49 pp.

APPLEGATE, VERNON C., BERNARD R. SMITH, ALBERTON L. MCLAIN, and MATT PATTERSON.
1952. Sea lamprey spawning runs in the Great Lakes, 1951. U.S. Fish and Wildlife Service, Spec. Sci. Rept.:—Fisheries, No. 68, 37 pp.

APPLEGATE, VERNON C., BERNARD R. SMITH, and WILLIS L. NIELSEN.
1952. Use of electricity in the control of sea lampreys: electromechanical weirs and traps and electrical barriers. U.S. Fish and Wildlife Service, Sp. Sci. Rept.—Fisheries, No. 92, 52 pp.

COVENTRY, A. F.
1922. Breeding habits of the landlocked sea lamprey. Univ. Toronto Stud., Biol. Ser., No. 20. Publ. Ontario Fish. Res. Lab., No. 9, pp. 129–136.

CREASER, CHARLES W., and CLARE S. HANN.
1929. The food of larval lampreys. Pap. Mich. Acad. Sci., Arts, and Lett. Vol. 10 (1928), pp. 433–437.

GAGE, SIMON H.
1893. The lake and brook lampreys of New York, especially those of Cayuga and Seneca Lakes. In Wilder Quarter-Century Book. Ithaca, 1893, pp. 421–493.
1928. The lampreys of New York State—life history and economics. In: Biol. Survey of the Oswego River System, N.Y. Conservation Dept. Suppl. 17th Ann. Rept. (1927), pp. 158–191.

GOODE, GEORGE B.
1884. The lampreys—Petromyzontidae. In: The Fisheries and the Fishery Industries of the U.S., by George B. Goode and associates. Sect. 1, Pt. III, pp. 677–681.

HALL, A. E., Jr., and OLIVER R. ELLIOTT.
1954. Relationship of length of fish to incidence of sea lamprey scars on white suckers, *Catostomus commersoni*, in Lake Huron. Copeia, 1954, No. 1, pp. 73–74.

HARDISTY, M. W.
1951. Duration of the larval period in the brook lamprey (*Lampetra planeri*). Nature, vol. 167, pp. 38–39.

HILE, RALPH.
1949. Trends in the lake trout fishery of Lake Huron through 1946. Trans. Amer. Fish. Soc., vol. 76 (1946), pp. 121–147.

HILE, RALPH, PAUL H. ESCHMEYER, and GEORGE F. LUNGER.
1951. Decline of the lake trout fishery in Lake Michigan. Fish. Bull., U.S. Fish and Wildlife Service, vol. 52, pp. 77–95.

HUBBS, CARL L., and ALFRED PERLMUTTER.
1942. Biometric comparison of several samples, with particular reference to racial investigations. Amer. Nat., vol. 76, pp. 1–11.

HUBBS, CARL L., and T. E. B. POPE.
1937. The spread of the sea lamprey through the Great Lakes. Trans. Amer. Fish Soc., vol. 66 (1936), pp. 172–176.

HUBBS, CARL L., and MILTON B. TRAUTMAN.
1937. A revision of the lamprey genus *Ichthyomyzon*. Misc. Publ. Mus. Zool., Univ. Mich., No. 35, 109 pp.

JORDAN, DAVID S., and CHARLES H. GILBERT.
1883. Synopsis of the fishes of North America. Bull. U.S. Nat. Mus., vol. 16, 1,018 pp.

LOEB, HOWARD A., and ALBERT E. HALL, Jr.
1952. Sea lamprey spawning: Michigan streams of Lake Superior. U.S. Fish and Wildlife Service, Sp. Sci. Rept.:—Fisheries, No. 70, 68 pp.

LENNON, ROBERT E.
1954. Feeding mechanism of the sea lamprey and its effect on host fishes. Fish. Bull., U.S. Fish and Wildlife Service, vol. 56, pp. 247–293.

MACKAY, H. H., and EARL MACGILLIVRAY.
1949. Recent investigations on the sea lamprey, *Petromyzon marinus*, in Ontario. Trans. Amer. Fish. Soc., vol. 76 (1946), pp. 148–159.

MEEK, SETH E.
1889. The fishes of the Cayuga Lake basin. Ann. N.Y. Acad. Sci., vol. 4, pp. 297–316.

MCLAIN, ALBERTON L.
1952. Diseases and parasites of the sea lamprey, *Petromyzon marinus*, in the Lake Huron basin. Trans. Amer. Fish. Soc., vol. 81 (1951), pp. 94–100.

NEWTH, H. G.
1930. The feeding of ammocoetes. Nature, vol. 126, pp. 94–95.

OKKELBERG, PETER.
1921. The early history of the germ cell in the brook lamprey, *Entosphenus wilderi* (Gage), up to and including the period of sex differentiation. Jour. Morph., vol. 35, pp. 1–151.

OKKELBERG, PETER.
1922. Notes on the life-history of the brook lamprey, *Ichthyomyzon unicolor*. Occ. Pap. Mus. Zool., Univ. Mich. No. 125, 14 pp.

RADFORTH, ISOBEL.
1944. Some considerations on the distribution of fishes in Ontario. Contrib. Royal Ontario Mus. Zool., No. 25, 116 pp.

RIDGWAY, ROBERT.
1912. Color standards and color nomenclature. Published by the author, Washington, D.C., 131 pp.

ROYCE, WILLIAM F.
1950. The effect of lamprey attacks upon lake trout in Seneca Lake, New York. Trans. Amer. Fish. Soc., vol. 79 (1949), pp. 71–76.

SCHAEFER, MILNER B.
1951. Estimation of size of animal populations by marking experiments. Fish. Bull., U.S. Fish and Wildlife Service, vol. 52, pp. 191–203.

SCHULTZ, LEONARD P.

1930. The life history of *Lampetra planeri* Bloch, with a statistical analysis of the rate of growth of the larvae from western Washington. Occ. Pap. Mus. Zool., Univ. Mich. No. 221, 35 pp.

SHETTER, DAVID S.

1949. A brief history of the sea lamprey problem in Michigan waters. Trans. Amer. Fish. Soc., vol. 76 (1946), pp. 160–176.

SURFACE, H. A.

1898. The lampreys of Central New York. Bull. U.S. Fish Comm., vol. 17 (1897), pp. 209–215.

1899. Removal of lampreys from the interior waters of New York. In 4th Ann. Rept. of the Comm. of Fisheries, Game and Forests of the State of New York (1898), pp. 191–245.

TRAUTMAN, MILTON B.

1949. The invasion, present status, and life history of the sea lamprey in the waters of the Great Lakes, especially the Ohio waters of Lake Erie. Franz Theodore Stone Lab., Ohio State Univ., 7 pp. [Mimeographed].

VAN CLEAVE, HARLEY J., and JUSTUS F. MUELLER.

1934. Parasites of Oneida Lake fishes. Pt. III. A biological and ecological survey of the worm parasites. Roosevelt Wild Life Ann., vol. 3, pp. 161–334.

VLADYKOV, VADIM D.

1950. Larvae of eastern American lampreys (Petromyzonidae). Naturaliste Canad., vol. 77, pp. 73–95.

1951. Fecundity of Quebec lampreys. Canad. Fish Culture, Issue 10, pp. 1–14.

WIGLEY, ROLAND L.

1952. A method of marking larval lampreys. Copeia, 1952. No. 3, pp. 203–204.

○

Blank page retained for pagination

UNITED STATES DEPARTMENT OF THE INTERIOR, Fred A. Seaton, *Secretary*

FISH AND WILDLIFE SERVICE, Arnie J. Suomela, *Commissioner*

EARLY DEVELOPMENT AND METAMORPHOSIS OF THE TEN-POUNDER *Elops saurus* Linnaeus

BY JACK W. GEHRINGER

Drawings by the author

FISHERY BULLETIN 155

From Fishery Bulletin of the Fish and Wildlife Service

VOLUME 59

PUBLISHED BY U.S. FISH AND WILDLIFE SERVICE • WASHINGTON • 1959

PRINTED AT U.S. GOVERNMENT PRINTING OFFICE, WASHINGTON

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington 25, D.C. Price 30 cents

Library of Congress catalog card for this bulletin:

Gehringer, Jack W

Early development and metamorphosis of the ten-pounder, *Elops saurus* Linnaeus. Washington, U. S. Fish and Wildlife Service, 1959.

iv, 619–647 p. illus., map, diagrs., tables. 26 cm. (U. S. Fish and Wildlife Service. Fishery bulletin 155)

"From Fishery bulletin of the Fish and Wildlife Service, volume 59."

Bibliography: p. 646–647.

1. Elops saurus. 2. Embryology—Fishes. I. Title. (Series: U. S. Fish and Wildlife Service. Fishery bulletin, v. 59, no. 155)

[SH11.A25 vol. 59, no. 155] Int 59–91

U. S. Dept. of the Interior. Library
for Library of Congress

Library of Congress catalog card for this series, Fishery Bulletin of the Fish and Wildlife Service:

U. S. ***Fish and Wildlife Service.***
Fishery bulletin. v. 1–
Washington, U. S. Govt. Print. Off., 1881–19

v. in illus., maps (part fold.) 23–28 cm.

Some vols. issued in the congressional series as Senate or House documents.
Bulletins composing v. 47– also numbered 1–
Title varies: v. 1–49, Bulletin.
Vols. 1–49 issued by Bureau of Fisheries (called Fish Commission, v. 1–23)

1. Fisheries—U. S. 2. Fish-culture—U. S. I. Title.

SH11.A25 639.206173 9–35239 rev 2*

Library of Congress [r55e½]

TABLE OF CONTENTS

	Page
Introduction	619
Methods and data	621
Definitions of terms	621
Study material	623
Measurements and meristic values	623
Development and growth	623
Myomeres	623
Fin formation	623
Teeth	630
Kidney	630
Air bladder	630
Gill rakers	630
Pseudobranchia	630
Branchiostegals	630
Gular plate	631
Scales and lateral line	631
Adipose eyelid	631
Changes in body form	631
Pigmentation	631
Osteology	633
Regressions of body parts on standard length	634
Laboratory growth experiments	641
Occurrence of larvae	644
References	646

ABSTRACT

Leptocephalid forms of the ten-pounder, *Elops saurus* Linnaeus, 5.1 to 31.3 mm. in standard length, were identified from plankton samples taken in waters off the south Atlantic coast of the United States during May, October, and November, 1953. These forms represent a larval stage heretofore undescribed. A developmental series was compiled from the plankton specimens and material obtained by seine in beach and marsh waters in Georgia, representing the following periods or stages of development: larval (leptocephalus, early metamorphic, mid-metamorphic, and late metamorphic), juvenile, and adult. The series is illustrated and described; and changes in form are discussed, in particular the shifting of the dorsal and anal fins anteriorly during metamorphosis. Several early metamorphic larvae, reared through metamorphosis in the laboratory, shrank in length from 35 mm. to about 20 mm. in 17–27 days.

It is suggested that leptocephali occupy an offshore habitat and move into beach and marsh waters when about 40–45 mm. long. The shrinking period (early metamorphic) is spent in beach and marsh waters, and ends at about 25 mm. The mid-metamorphic period (shrinking from 25 mm. down to 18–20 mm. and subsequent length increase to 25 mm.) is also spent in inshore waters. The late metamorphic period ends, and the juvenile stage begins, at about 50–60 mm., when all fins have full complements of rays, scales are present, the lateral line is formed, axillary scales are present on paired fins, and subsequent developments are principally changes in body proportions. This period is also spent in inshore waters.

The occurrence of leptocephali in offshore plankton samples indicates offshore spawning. No leptocephali have been reported from inshore waters. The length of time spent in the leptocephalid period is unknown. The presence of "shrinking" larvae in beach and marsh waters in Georgia from March to October suggests a prolonged spawning season.

EARLY DEVELOPMENT AND METAMORPHOSIS OF THE TEN-POUNDER *ELOPS SAURUS* LINNAEUS

BY JACK W. GEHRINGER, FISHERY RESEARCH BIOLOGIST

In the initial phase of the study of biological, chemical, and oceanographic conditions in the waters between Cape Hatteras and the Florida Straits, the U.S. Fish and Wildlife Service, in cooperation with the U.S. Navy Hydrographic Office, the Office of Naval Research, the Georgia Game and Fish Commission, and the Florida State Board of Conservation, collected data and samples with the MV *T. N. Gill* from January 1953 to December 1954. The second phase in the biological study involved the identification of fish and plankton organisms collected at sea. During the course of such studies, forms are at times discovered which have never been described. Understanding the life histories of fishes is prerequisite to an understanding of the interrelationships of species and to analysis of the biological potential of the waters involved. The identification of the undescribed forms often adds considerably to our knowledge of a particular species. Such was the case when leptocephali of the ten-pounder, *Elops saurus* Linnaeus, 5.1 to 31.3 mm. in standard length, were identified from plankton samples taken in offshore waters during May, October, and November, 1953 (fig. 1).

The ten-pounder, *E. saurus*, undergoes a peculiar larval development. The first post-yolk-sac larval stage is a ribbon-like leptocephalus which grows to about 40 mm., then shrinks in length to about 20 mm. while metamorphosing into the adult form. The development of the bonefish, *Albula vulpes* (Linnaeus), and the tarpon, *Tarpon atlanticus* (Valenciennes)[1] is similar. The shrinking of the leptocephalid form of *E. saurus* during metamorphosis has been known for some time, as shrinking and metamorphosing larvae are found on the beaches and in the marshes. Leptocephali prior to the period during which shrinking begins have not previously been described. It has been suggested (Hildebrand 1943) that the absence of earlier stages of the ten-pounder in inshore waters indicates offshore spawning and early growth. This is substantiated by leptocephali of *E. saurus* 5.1 to 31.3 mm. in standard length in the plankton samples taken in offshore waters along the south Atlantic coast of the United States.

In Georgia, shrinking larvae appear in seine collections from the open beach beginning in March or April. Within a few weeks, they appear in marsh collections, and are present in marsh collections through metamorphosis. Beach collections contain only occasional larvae after May, but some have been found in late October. During May of 1953 several larvae in the shrinking stage, about 30 to 40 mm. in standard length, were reared through metamorphosis in the laboratory. Other larvae, which were undergoing or had undergone metamorphosis before capture, were maintained in laboratory aquaria for varying periods of time. A developmental series (from leptocephalus to adult) was compiled from plankton samples, laboratory experiments, and seine samples collected over a period of 4 years.

This paper describes and illustrates a developmental series from a 5.3-mm. leptocephalus to a 380-mm. adult (figs. 2 to 17), changes in rates of growth of various body parts, and changes in body structures during development; and gives selected measurements and meristic values for leptocephali to adults, results of laboratory growth experiments, and seasonal distribution of larvae.

A review of important contributions to our knowledge of the larval development of the ten-pounder (*E. saurus*), the bonefish (*A. vulpes*), the tarpon (*T. atlanticus*), and some closely related Pacific forms follows:

Dr. C. H. Gilbert in 1889 first identified the leptocephalid larva of bonefish, *A. vulpes*, but it was 1905 before figures and descriptions prepared from his material were presented by Jordan, and in 1907 by Gill. Subsequently, various authors

[1] In accordance with Bailey (1951), single authority is used.

NOTE.—Approved for publication May 7, 1958. Fishery Bulletin 155.

presented descriptions or illustrations of individual specimens or a series: Meek and Hildebrand (1923), Delsman (1926), Hildebrand (1934, 1943), Hollister (1936), Whitley (1937), Gopinath (1946), and Fitch (1950).

Van Kampen (1908) first identified and described the larvae of the East Indian tarpon, *Megalops cyprinoides* (Broussonet) (translated from the German by Beebe, 1927). Other contributors were; Delsman (1926), Holstvoogd (1936), Hollister (1939), Gopinath (1946), Chidambaram and Menon (1948), Alikunhi and Rao (1951), and the Indian Council of Agricultural Research (1951). Our knowledge of the larval development of the Atlantic tarpon, *T. atlanticus*, is meager: Hildebrand (1934 and 1943), Hollister (1939), and more recently, the University of Miami Marine Laboratory (anon. 1955).

Jordan and Evermann (1896) recognized the ribbonlike form of *E. saurus* larvae, and Smith (1907) mentioned it, but larvae of this genus were not described until 1923, when Meek and Hildebrand described leptocephali of *E. affinis* Regan. Delsman (1926) illustrated a leptocephalus of *E. hawaiensis* Regan; Fowler (1931) illustrated an *E. saurus* larva; Holstvoogd (1936) discussed larval development of *E. hawaiensis* (in particular, the development of the kidney); Hildebrand (1943) treated *E. saurus;* Gopinath (1946) added notes on *E. indicus* (Swainson);[2] Alikunhi and Rao (1951) illustrated and described in detail the shrinking and metamorphosis of leptocephali of *E. saurus* from laboratory reared specimens in India; the Indian Council of Agricultural Research (1951) discussed larval development of *E. indicus;*[2] and Nair (1952) illustrated an *E. saurus* leptocephalus.

All these publications treat the shrinking and metamorphosing larvae, but contain only speculation on initial development of the leptocephalus.

Regan's 1909 revision of the fishes of the genus *Elops* is generally accepted today. Of the seven species he lists, *E. saurus*, *E. affinis*, *E. senegalensis* Regan, *E. hawaiensis*, *E. australis* Regan, *E. machnata* Forsk., and *E. lacerta* Valenciennes[3]—only *E. saurus* occurs on the Atlantic coast of the United States. Hildebrand (1939) found no evidence of *E. saurus* moving through the Panama Canal into the Pacific, or the Pacific coast species, *E. affinis*, moving through the Canal into the Atlantic. According to Regan (1909), the east and west coast species are quickly separated on number of gill rakers: *E. saurus* has 12–15 on the lower limb, and *E. affinis* has 18–20. *E. senegalensis*, found off West Africa, has 12–14 gill rakers, which overlaps the 12–15 count for *E. saurus;* but *E. saurus* has 103–118 scales in the lateral line, while *E. senegalensis* has 94–98. Hildebrand (1943) gives the following counts for several specimens he examined: *E. saurus*, 10–15 gill rakers on lower limb, 103–120 scales; *E. affinis*, 16–20 gill rakers, 104–116 scales; and *E. senegalensis*, 11–12 gill rakers, 93–100 scales.

Leptocephalid forms of *Elops* are readily separated from those of *Albula* and *Tarpon* on one or more characters, depending on the stage of development. Prior to formation of fin rays, the number of body myomeres can be used: *Elops* has about 72–82 myomeres (generally more than 75), *Albula* has about 66–72, and *Tarpon* has fewer. One specimen examined by Hildebrand (1934) had 52, and a 17.5-mm. specimen from *T. N. Gill* collections had 57. Myomeres are discernible in *E. saurus* larvae through the early and mid-metamorphic periods. Hildebrand (1943) stated that after dorsal and anal fins become sufficiently developed to permit enumeration of the rays, the species are readily separated by ray counts; *E. saurus* has 21–25 dorsal rays and 14–17 anal rays, whereas *A. vulpes* has 14–17 dorsal rays and 8–9 anal rays. His *Tarpon* larva of 20 mm. had 12 dorsal and 20 anal rays (the *Gill* specimen had 11 dorsal ray bases and 20 anal bases). *Albula* leptocephali may reach 3 or 3½ inches (about 76–88 mm.) before starting to shrink (Gill 1904); *Elops* leptocephali begin shrinking at about 40 mm. The size of *Tarpon* leptocephali before shrinking commences is not known.

I gratefully acknowledge the assistance given by various staff members of the South Atlantic Fishery Investigations during this study and in the preparation of the manuscript. Special thanks are extended to Frederick H. Berry and Hugh M. Fields for their critical reading of the manuscript. Special thanks are also due to Dr. Elbert H. Ahlstrom for critical reading of the manuscript and suggestions for presentation of data, and to Bruce

[2] *E. indicus* Swainson a synonym of *E. saurus* Linnaeus, after Misra (1947).

[3] In accordance with Bailey (1951), single authority is used.

Taft for comments and suggestions on statistical treatment of the data.

METHODS AND DATA

All measurements less than 50 mm. were made to the nearest 0.1 mm. with a micrometer eyepiece and binocular stereoscopic microscope (eye diameters less than 2.0 mm. were recorded to the second decimal); and those exceeding 50 mm. were made to the nearest half or whole millimeter with drafting dividers and a Paragon scale. Scale drawings of specimens 34.2 mm. and smaller were made with the aid of a calibrated grid reticule, and those of the 67.4-mm. and larger specimens were made from tracings of enlargements of photographic negatives.

Original measurements were used in the graphs, figures 25 to 30. The regressions of body parts on standard length were determined by the method of least squares. Unless otherwise stated, specimen lengths are standard length measurements. Hollister (1936) and Evans (1948) procedures were followed in staining specimens with alizarine red to show ossification.

Method of making plankton tows was that of Anderson, Gehringer, and Cohen (1956). Biweekly sampling with a seine in beach and marsh habitats was done at the same place, at approximately the same tide conditions, low tide on the beach and high tide in the marsh.

DEFINITIONS OF TERMS

Total length. Distance from tip of snout to most posterior projection of caudal fin.

Standard length. Distance from tip of snout to tip of urostyle (or notochord) or posterior border of hypural bones.

Head length. Distance from tip of snout to posterior fleshy margin of opercle.

Head depth. Vertical measure of head at angle of jaws.

Head width. Horizontal distance between verticals at lateral margins of eyes.

Eye diameter. Horizontal distance, width.

Body depth at pectoral. Measure of depth at insertion of pectoral fin.

Snout to dorsal. Distance from tip of snout to origin of dorsal fin.

Snout to pelvic. Distance from tip of snout to insertion of pelvic fin.

Snout to anal. Distance from tip of snout to origin of anal fin.

MERISTIC COUNTS:

Dorsal, anal, pelvic, and pectoral fin rays. Total number of rays, including rudiments.

Caudal fin rays. Listed as: dorsal secondary+principal+ventral secondary rays (including rudiments). The full complement, 10 dorsal and 9 ventral principal rays, with 8–9 dorsal and 6–8 ventral secondary rays. Principal rays are attached to the hypurals and include all branched rays plus one upper and one lower unbranched ray (one or more small secondary rays are also attached to the anteriormost hypural). In small specimens some of the principal rays which eventually branch were not branched.

Teeth. Number in each side of the upper and lower jaws.

Myomeres. Number of body myomeres (last few in caudal region are indistinct).

Gill rakers. Total number, including rudiments, on upper and lower limbs of first gill arch, on one side.

Number of the myomere at dorsal, pelvic, or anal fin origin, etc. The number of the myomere whose dorsal or ventral extremity approximates the position of part involved.

Number of scales. Lateral line scales, counted from opercular flap to posterior scale on caudal fin.

There are two periods during the larval development of the ten-pounder in which the length of the larva increases, and one in which the length decreases. First is the "leptocephalus" period of initial length increase to the size at which shrinking commences (my smallest leptocephalus is 5.1 mm. standard length and the largest is 43.3 mm.). The second period is "early metamorphic," and includes those individuals shrinking in length down to about 25 mm., the size at which marked changes in form begin. Because it was not always possible to distinguish those in the final stages of shrinking from those undergoing initial increase following shrinking, these individuals were combined in the period, "mid-metamorphic." Included are individuals undergoing the final few millimeters of length decrease, and the first few millimeters of subsequent length increase, or 25 mm. down to about 18–20 mm. and up to 25 mm. (characterized by loss of ribbonlike form, shifting of fins, and development in fins).

At about 25 mm., after length begins to increase again, the fish is still larval (without full complements of fin rays, branchiostegals, and gill rakers; scales; lateral line, etc.). From 25 mm. to about 60 mm., these characters are forming, and the period is called "late metamorphic." At about 60 mm. the fish is a miniature adult, and is called "juvenile."

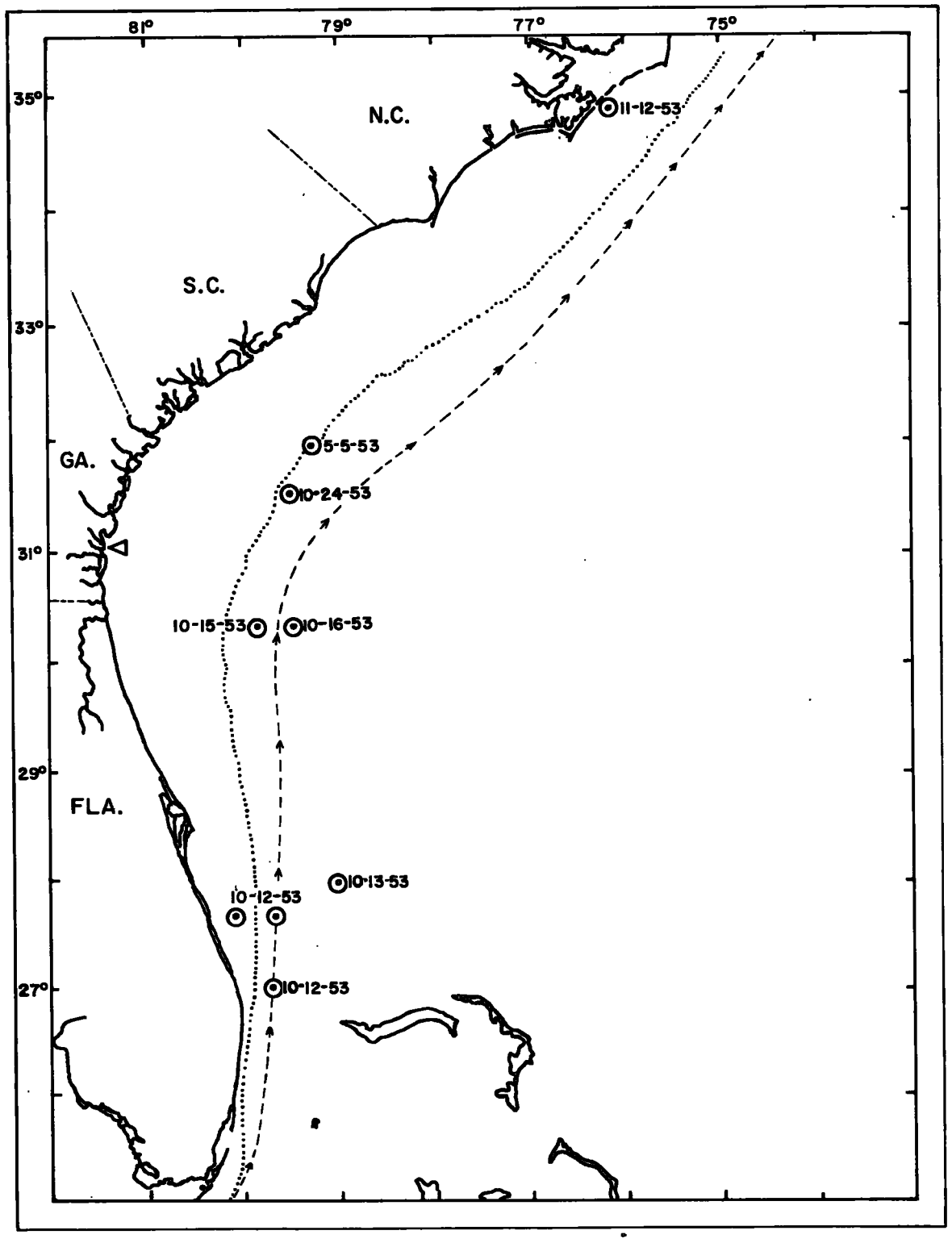

FIGURE 1.—Locations and dates of capture for leptocephali in plankton samples of *T. N. Gill* cruises off the south Atlantic coast of the United States. Location of seining station on Georgia coast is indicated by a triangle, 100-fathom curve shown as dotted line, and approximate axis of Gulf Stream indicated by dashes.

STUDY MATERIAL

The dates and locations of capture (fig. 1), and numbers and size ranges for all leptocephali from plankton collections follow:

May 5, 1953, 31°57′ N., 79°18′ W. (1 specimen, 28.0 mm.); Oct. 12, 1953, 26°58′ N., 79°40′ W. (2 specimens, 11.2 and 11.7 mm.); Oct. 12, 1953, 27°40′ N., 80°04′ W. (4 specimens, 15.2 to 22.4 mm.); Oct. 12, 1953, 27°37′ N., 79°40′ W. (1 specimen, 5.1 mm.); Oct. 13, 1953, 28°00′ N., 79°00′ W. (1 specimen, 20.5 mm.); Oct. 15, 1953, 30°19′ N., 79°50′ W. (1 specimen, 17.3 mm.); Oct. 16, 1953, 30°20′ N., 79°26′ W. (1 specimen, 5.3 mm.); Oct. 24, 1953, 31°34′ N., 79°28′ W. (1 specimen, 14.3 mm.); Nov. 12, 1953, 34°53′ N., 76°10′ W. (1 specimen, 31.3 mm.)

Table 14 presents the dates and locations of capture for metamorphic larvae, juveniles, and adult. Beach seining was done on St. Simons Island, Ga.; and marsh seining was done at Sapelo Marsh, McIntosh County, Ga. (an estuarine area behind the barrier islands), and estuarine marshes near Brunswick, Glynn County, Ga.

MEASUREMENTS AND MERISTIC VALUES

Table 1 gives selected measurements and meristic values for all of the leptocephali (14) from plankton collections; and the 11 early metamorphic larvae, juvenile, and adult which are figured and described. Table 10 gives selected measurements for all specimens, and includes those from which regression lines were derived.

DEVELOPMENT AND GROWTH

The development and growth of body parts is traced from the leptocephalus to the juvenile or adult for each part separately, rather than in a simultaneous treatment of all parts for each period.

MYOMERES

The smallest leptocephalus I have ascribed to *E. saurus* is 5.3 mm. standard length (fig. 2). It has about 78 myomeres (the last few in the caudal region are indistinct), which precludes its being either *Tarpon* or *Albula*, both of which have fewer than 72. Except for the monotypic genus *Cyema*, of the family Cyemidae, I have been unable to find reference to eel leptocephali having fewer than 100 myomeres. *Cyema atrum* Günther has 73 myomeres, and the larva ascribed to this genus, *Leptocephalus cyematis atri*, has 75–77 myomeres (Fish 1927). According to Berg (1947), *Cyema* is "widely distributed, deepwater," and has 75–79 vertebrae. Bertin (1937, p. 5) gives a myomere count of 74 (41 are preanal) for a damaged 11.2-mm. specimen of *Cyema*. He figures a 20-mm. *Cyema* leptocephalus which has 74 myomeres, 40 of which are preanal, and a body which is much deeper than the head. My 5.3-mm. leptocephalus has 70 preanal myomeres, and the head is deeper than the body. These differences rule out the genus *Cyema*. There remains the possibility that some fish other than these has an undescribed leptocephalid development to which the specimen may be ascribed.

Table 2 shows the number of myomeres for specimens of different sizes and stages of development. During the leptocephalus, and early and mid-metamorphic periods the body is translucent and thin, so that with transmitted light, the myomeres are visible. However, the myomeres in the caudal region are not always distinct, and the range shown (72–82) might reflect indefinite counts. During the first part of the late metamorphic period the body becomes opaque, and myomeres are indistinct. About 83 percent of the specimens on which counts were made had 78–81 myomeres.

FIN FORMATION

Dorsal and anal.—The rudimentary anterior rays in the dorsal and anal fins of some soft-rayed fishes are disregarded by some authors when ray counts are given, possibly because they are variable in number or difficult to discern without dissection. Instead of the total number of rays, their counts include only the branched rays plus one unbranched ray. In larvae I examined, in which rays were forming or branching, all were discernible without dissection. On some specimens exceeding 50 mm. in standard length it was necessary to scrape away tissue covering the small anterior dorsal and anal rays before they could be seen, but on others all rays were discernible without dissection. My counts include the small rudimentary rays.

On the smallest leptocephalus, 5.3 mm. (fig. 2), a median finfold begins immediately back of the head, continues posteriorly, around the tip of the urostyle, and forward ventrally to the anus. It is swollen or bullate throughout most of its length, and the margin is frayed or ruffled. A median

499662 O—59——2

TABLE 1.—*Selected measurements and meristic values for leptocephali; and the metamorphic larvae; juveniles and adult figured*

Measurements and counts	Leptocephali													Early metamorphic larvae				Mid-metamorphic larvae		Late metamorphic larvae to adult				
Standard length, mm	5.1	5.3	11.2	11.7	14.3	15.2	17.3	17.9	20.5	20.6	22.4	28.0	31.3	43.3	34.0	30.9	26.6	21.5	24.7	25.9	34.2	67.5	152	380
Total length, mm	5.1	5.3	11.5	12.1	14.6	15.9	18.5	18.7	22.3	------	24.0	30.2	34.2	46.7	38.4	34.5	30.3	24.4	29.0	31.1	41.4	82.5	190	450
Head length, mm	1.1	1.0	1.5	1.4	1.7	1.8	2.1	1.9	2.2	2.2	2.1	2.5	2.4	3.2	3.0	3.2	3.5	3.0	4.8	6.8	10.0	20.4	44.0	95
Head width, mm	0.6	0.6	0.8	0.8	1.1	1.0	1.1	1.2	1.0	1.5	1.2	1.3	1.6	1.9	1.9	2.1	2.1	1.7	2.4	2.7	4.0	6.0	15.5	35
Head depth, mm	0.6	0.6	0.8	0.7	0.8	0.9	0.8	0.9	1.1	0.8	0.8	1.0	0.9	1.4	1.5	1.6	1.7	1.6	2.5	3.1	4.6	8.5	21.0	49
Body depth at pectoral, mm	0.5	0.4	0.7	0.8	0.8	0.9	0.9	0.9	1.1	1.0	1.0	1.3	1.4	1.7	1.8	1.8	2.2	1.8	2.7	3.0	4.3	9.4	22.0	56
Eye diameter, mm	0.30	0.24	0.36	0.36	0.30	0.42	0.42	0.39	0.48	0.42	0.42	0.51	0.51	0.68	0.68	0.68	0.76	0.60	1.10	1.44	2.3	4.6	9.5	19
Snout to dorsal, mm	------	------	------	------	[1] 12.6	[1] 13.2	[1] 15.1	[1] 15.6	[1] 17.6	[1] 17.8	[1] 19.0	[1] 23.4	26.4	36.1	27.9	24.1	19.4	15.6	15.8	15.0	18.8	35.4	79.0	195
Snout to pelvic, mm	------	------	------	------	------	------	------	------	------	------	------	------	------	------	18.1	16.0	14.4	11.2	12.9	14.5	19.0	36.5	78.0	193
Snout to anal, mm	------	------	------	------	------	------	[1] 16.6	[1] 16.8	[1] 19.0	[1] 19.4	[1] 21.1	[1] 26.1	[1] 29.3	40.1	31.4	27.8	22.8	18.4	19.5	20.3	26.9	50.5	117	295
Meristic counts:																								
Dorsal rays	------	------	------	------	------	[2] 8–9	[2] 14	[2] 11	[2] 16	[2] 15	[2] 20	[2] 22	16	22	22	22	24	22	25	25	28	28	27	27
Anal rays	------	------	------	------	------	------	[2] 6	?	[2] 8	[2] 6	[2] 8	[2] 11	[2] 12	14	13	14	14	14	16	17	19	19	17	17
Pelvic rays	------	------	------	------	------	------	------	------	------	------	------	------	------	------	bud	bud	bud	bud	7	13	14	14	15	14
Pectoral rays	bud	bud	bud	bud	bud	bud	bud	bud	bud	bud	bud	bud	bud	bud	bud	2	2	3	11	15	17	18	17	17
Caudal rays	------	------	------	------	------	0+19+0	0+19+0	0+19+0	0+19+0	------	0+19+1	0+19+1	1+19+2	1+19+2	1+19+1	1+19+2	1+19+2	1+19+2	2+19+3	3+19+4	6+19+6	9+19+7	8+19+6	8+19+7
Gill rakers:																								
Upper limb	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	6	6	6	6	7
Lower limb	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	7	11	12	15	12	13
Branchiostegals: (left-right)	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	5–5	17–16	25–24	30–28	32–31	33–30	31–28
Myomeres:																								
Total number	80	78	81	80	78	74	80	80	74	81	77	75	80	82	78	80	79	72	81	80	------	------	------	------
Number at dorsal	------	------	------	------	64	61	64	65	60	64	62	59	64	62	62	61	56	49	47	38	------	------	------	------
Number at anal	------	------	------	------	------	------	73	------	68	73	70	68	72	72	71	71	69	60	62	61	------	------	------	------
Number at pelvic	------	------	------	------	------	------	------	------	------	------	------	------	------	------	36	37	37	32	36	35	------	------	------	------
Number at air bladder	------	28	35–36	35	35	32	35	36	34	35	34	33	35–36	34–35	35	36	34	28–30	29–37	18–31	------	------	------	------
Number at kidney	------	------	51–52	49–52	49–51	47–48	50–52	50–53	48–50	50–53	49–52	48–49	51–53	48–50	50–52	51–54	50–53	44–48	48–54	------	------	------	------	------
Number at anus	70	70	72	71	70	65	71	72	66	72	69	67	71	71	70	70	68	59	61	59	------	------	------	------
Teeth: [3]																								
Upper jaw (one side)	2–0	2–2	2–4	2–4	2–2	2–4	2–5	2–5	2–4	2–6	2–6	2–7	2–?	11	9	10	20	14	24	------	------	------	------	------
Lower jaw (one side)	4–0	4–0	4–2	4–3	4–6	4–6	4–7	4–7	4–6	4–8	4–8	4–8	4–?	13	14	12	24	12	20	------	------	------	------	------
Scales in lateral line	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	112	110	115

[1] Snout to dorsal or anal ray bases, no rays formed.
[2] Ray bases, no rays formed.
[3] Numbers refer to: large fanglike teeth—smaller teeth.

TABLE 2.—*Variation in number of body myomeres in individuals of different stages of development (specimens grouped by size)*

Standard length	Number of individuals with myomeres numbering—										
	72	73	74	75	76	77	78	79	80	81	82
Leptocephali:											
5.0–9.9 mm							1		1		
10.0–14.9 mm							1		1		
15.0–19.9 mm			1						2		
20.0–24.9 mm			1			1				1	
25.0–29.9 mm				1							
30.0–34.9 mm											1
35.0–39.9 mm											
40.0–44.9 mm											
Early metamorphic larvae:											
44.9–40.0 mm							1	2	3		1
39.9–35.0 mm							2	4	7	2	
34.9–30.0 mm		2					1	3		1	
29 9–25.0 mm									2		1
Mid-metamorphic larvae:											
24.9–15.0 and 15.0–24.9 mm	1							1	6	1	
Late metamorphic larvae:											
25.0–29.9 mm									1	1	
30.0–34.9 mm									2		
Total	1	2	2	1	0	1	6	10	25	6	3

preanal finfold extends from the anus anteriorly to a point about one-third the distance to the head, and has a smooth and regular margin. By about 11 mm. (fig. 3) the dorsal portion of the finfold is much reduced anteriorly, and its margin is more uniform. The caudal portion is rounded, and the margin invaginates dorsally and ventrally anterior to the urostyle. By about 15 mm. (fig. 4) dorsal ray bases are discernible, and by about 17 mm. (table 1) anal ray bases are present. Dorsal rays are discernible at about 31 mm. (fig. 6), and anal rays at 43.3 mm. (fig. 7), the largest leptocephalus examined.

The dorsal and anal finfolds diminish during the leptocephalus period to the extent that the fins are separated from it on the largest leptocephalus. During the early metamorphic period (figs. 7 to 10), the finfold is reduced to a small amount at the caudal peduncle. The preanal finfold diminishes more slowly, persisting through the mid-metamorphic period (figs. 11 and 12), and disappearing early in the late metamorphic period (25–30 mm.).

At the end of the leptocephalus period (about 40–45 mm.) metamorphosis begins, and the larval form starts to shrink in length. During the early metamorphic period (down to a size of about 25 mm.), dorsal and anal rays remain fairly constant in number, ranging 21 to 24 for the dorsal and 12 to 15 for the anal (figs. 7 to 10). The last ray of both the dorsal and anal fin is branched at its base at the size the leptocephalus begins to shrink (40–45 mm.). During mid-metamorphosis (25 mm. down to about 18–20 mm. and subsequent length increase to about 25 mm.) dorsal rays range

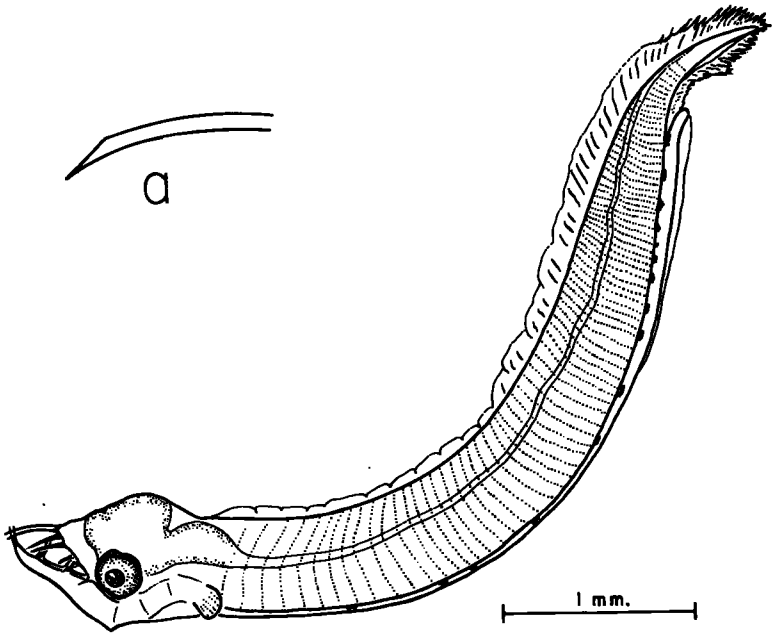

FIGURE 2.—Leptocephalus, 5.3 mm. standard length. (a) Side view of one of fanglike teeth in upper jaw, showing end beveled on upper surface.

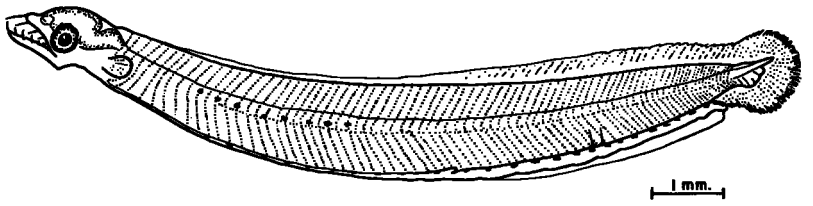

FIGURE 3.—Leptocephalus, 11.2 mm. standard length.

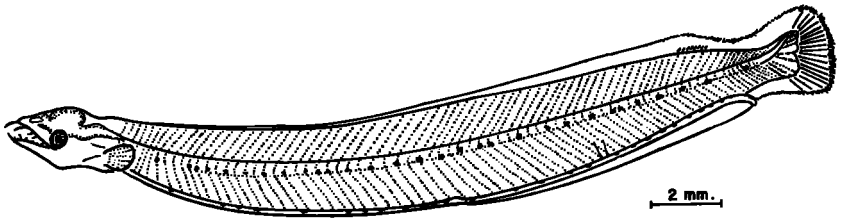

FIGURE 4.—Leptocephalus, 15.2 mm. standard length.

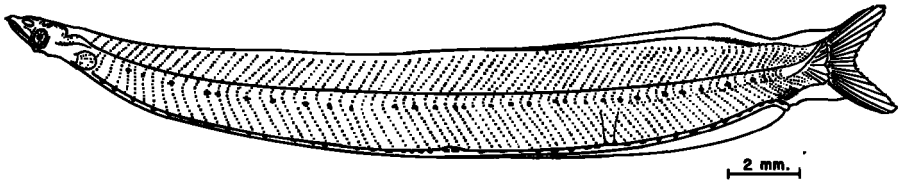

FIGURE 5.—Leptocephalus, 22.4 mm. standard length.

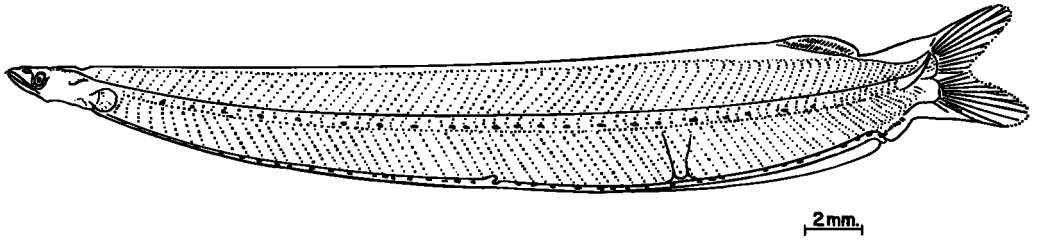

FIGURE 6.—Leptocephalus, 31.3 mm. standard length.

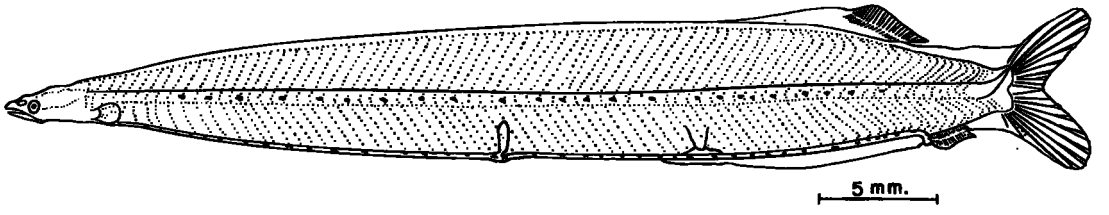

FIGURE 7.—Early metamorphic larva (or leptocephalus), 43.3 mm. standard length.

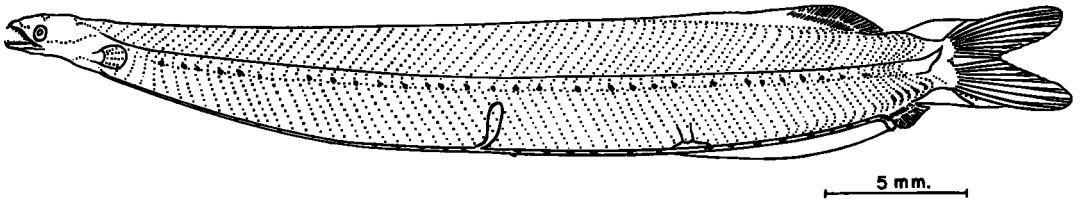

FIGURE 8.—Early metamorphic larva, 34.0 mm. standard length.

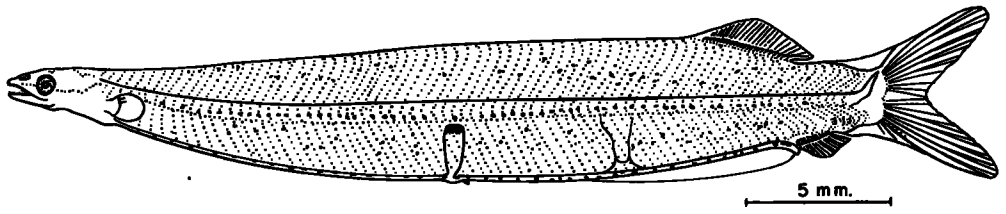

FIGURE 9.—Early metamorphic larva, 30.9 mm. standard length.

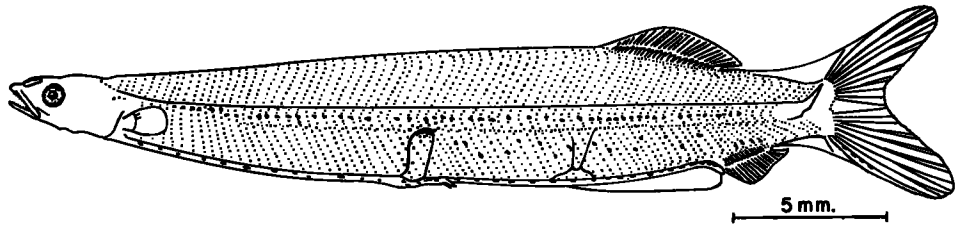

FIGURE 10.—Early metamorphic larva, 26.6 mm. standard length.

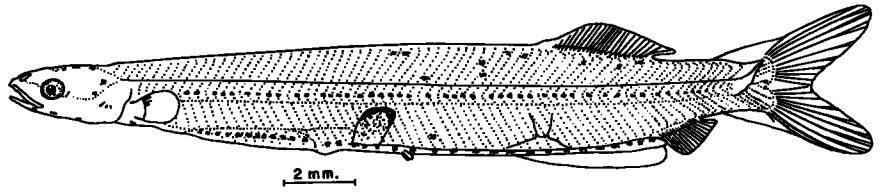

FIGURE 11.—Mid-metamorphic larva, 21.5 mm.

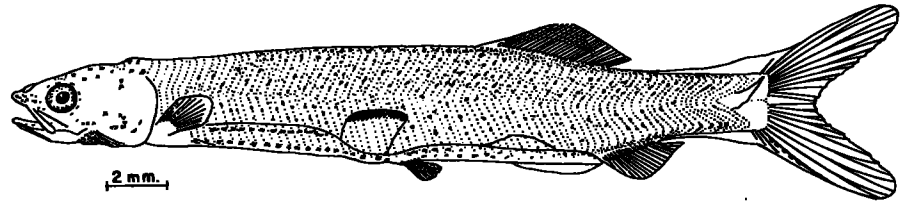

FIGURE 12.—Mid-metamorphic larva, 24.7 mm.

in number from 22 to 26, and the anal rays range from 14 to 18. From the late metamorphic period to the adult (25 mm. and larger), there are 25–29 dorsal rays and 16–19 anal rays (tables 3 and 4).

Branching of the dorsal and anal fin rays commences during the late metamorphic period, and by 35 mm. about 17 dorsal rays and 12 anal rays are branched. The last dorsal ray is branched at its base and the anterior branch is divided again. My 380-mm. adult had 17 of the 27 dorsal rays and 12 of the 17 anal rays branched. Delsman (1926) shows all dorsal (±20) and anal (±14) rays branched in his illustration of a 37-mm. *E. hawaiensis* "leptocephalus" (an early metamorphic larva by my definition), a point inconsistent with my findings for *E. saurus*.

Smith (1907) gave 20–21 as the dorsal-fin ray complement and 13 for the anal fin. Regan (1909) gave 23–26 as the range for the dorsal fin (18–20 branched), and 15–16 for the anal fin (11–12 branched). Hildebrand (1943) gave 21–25 for the dorsal fin and 14–17 for the anal. Holbrook (1860) listed 24 dorsal and 17 anal rays. Meek and Hildebrand (1923) gave 22–25 for the dorsal fin and 15–17 for the anal. It is likely that some of the small anterior rays of these fins were not included in the ranges listed.

Pectoral fin.—The pectoral fin on the 5.3-mm. leptocephalus (fig. 2) is a rounded bud. The first rays to form appear in the dorsal portion of the fin bud at about 30 mm. in the early metamorphic period (fig. 9). During the mid-metamorphic

TABLE 3.—*Number of dorsal fin rays on individuals of different stages of development (specimens grouped by size)*

Standard length	Number of individuals with dorsal rays numbering—																				
	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Leptocephali:																					
5.0–9.9 mm																					
10.0–14.9 mm																					
15.0–19.9 mm	[1] 1		[1] 1			[1] 1															
20.0–24.9 mm							[1] 1	[1] 1				[1] 1									
25.0–29.9 mm														[1] 1							
30.0–34.9 mm								1													
35.0–39.9 mm																					
40.0–44.9 mm														1							
Early metamorphic larvae:																					
44.9–40.0 mm														3	4						
39.9–35.0 mm													2	7	5	1					
34.9–30.0 mm													1	3	1	2					
29.9–25.0 mm														1	1	1					
Mid-metamorphic larvae: 24.9–15.0 mm. and 15.0–24.9 mm.														1	1	1	4	3			
Late metamorphic larvae to adult:																					
25.0–29.9 mm																	1	1			
30.0–380 mm																	4	14	21	6	3

[1] Ray bases, no rays have formed.

TABLE 4.—*Number of anal fin rays on individuals of different stages of development (specimens grouped by size)*

Standard length	Number of individuals with anal rays numbering—													
	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Leptocephali:														
5.0–9.9 mm														
10.0–14.9 mm														
15.0–19.9 mm	[1] 1													
20.0–24.9 mm	[1] 1		[1] 2											
25.0–29.9 mm						[1] 1								
30.0–34.9 mm							[1] 1							
35.0–39.9 mm														
40.0–44.9 mm									1					
Early metamorphic larvae:														
44.9–40.0 mm								2	4	1				
39.9–35.0 mm							2	5	9	1				
34.9–30.0 mm								4	2	1				
29.9–25.0 mm									3					
Mid-metamorphic larvae: 24.9–15.0 and 15.0–24.9 mm									3	1	3	2	1	
Late metamorphic larvae to adult: 25.0–380 mm											3	24	20	5

[1] Ray bases, no rays have formed.

period the number increases, and by about 30–35 mm. in the late metamorphic period the number is within the range for adults, 16–19 (figs. 11 to 14). For specimens exceeding 80 mm. in standard length, the range was 17–18. Holbrook (1860) listed 18 pectoral rays.

Pelvic fin.—The pelvic fin buds were first evident on a 34.0-mm. early metamorphic larva (fig. 8) at about the 36th myomere and just posterior to the air bladder. Rays develop during the mid-metamorphic period. Five rays were visible (after staining with alizarine red) on a 21.5-mm. specimen (fig. 11). By about 35 mm. in the late metamorphic period the full complement is present, 14–15 (table 6). Holbrook (1860) listed 15 pelvic rays.

Caudal fin.—At 5.3 mm. (fig. 2), the leptocephalus has no caudal fin. The urostyle begins to tip up slightly by about 10 mm., and four hypurals are visible (fig. 3). By about 15 mm. 8 or 9 hypurals and 19 caudal rays are discernible, and the posterior margin of the fin is somewhat truncate (fig. 4). By about 20 mm. the fin is forked, and one secondary ray is present (fig. 5). The largest leptocephalus (43.3 mm.) has 19 principal and 1 dorsal secondary and 2 ventral secondary rays, with 6 principal rays branched in each lobe (fig. 7). During the early metamorphic period (43.3 mm. down to about 25 mm.), the complement remains constant at 1+19+2 (dorsal secondary, principal, and ventral secondary rays) (figs. 7 to 10). Through the mid-metamorphic period (25 mm. down to about 18–20 mm. and up to about 25 mm.) the number of rays increases to 3+19+3, and the complement of branched rays is complete (9 in the dorsal lobe and 8 in the ventral lobe).

TABLE 5.—*Number of pectoral fin rays on individuals of different stages of development (specimens grouped by size)*

Standard length	Number of individuals with pectoral rays numbering—																	
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Early metamorphic larvae:																		
44.9–40.0 mm																		
39.9–35.0 mm																		
34.9–30.0 mm	1																	
29.9–25.0 mm	1																	
Mid-metamorphic larvae: 24.9–15.0 and 15.0–24.9 mm		1							1	2	1	1	1			1		
Late metamorphic larvae to adult:																		
25.0–29.9 mm														1		1		
30.0–34.9 mm																4		
35.0–39.9 mm																1		
40.0–49.9 mm															1	3	1	
50.0–59.9 mm																		1
60.0–69.9 mm																4	4	
70.0–79.9 mm															1	3		
80.0–380 mm																16	9	

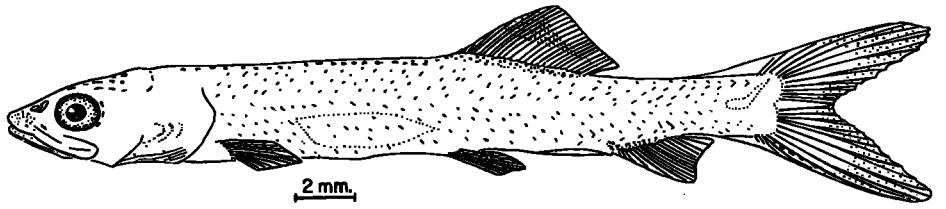

FIGURE 13.—Late metamorphic larva, 25.9 mm.

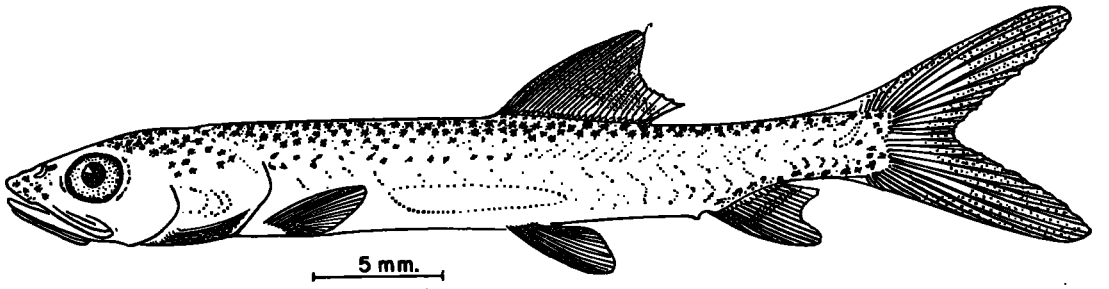

FIGURE 14.—Late metamorphic larva, 34.2 mm.

TABLE 6.—*Number of pelvic fin rays on mid-metamorphic larvae to adults (specimens grouped by size)*

Standard length	Number of individuals with pelvic rays numbering—										
	6	7	8	9	10	11	12	13	14	15	16
20.0–24.9 mm	1	1	1				2				
25.0–29.9 mm								2			
30.0–34.9 mm							1		2		1
35.0–380 mm									35	9	

TABLE 7.—*Number of secondary caudal fin rays on late metamorphic larvae to adults (specimens grouped by size and ratio of rays in ventral and dorsal lobes)*

Rays and length	Number of individuals with secondary caudal rays numbering—								
Number of rays: Total	9	11	11	12	13	14	15	16	17
Ventral lobe	5	6	5	6	6	6	7	7	8
Dorsal lobe	4	5	6	6	7	8	8	9	9
Standard length:									
30.0–39.9 mm	1	1	1	1	1				
40.0–49.9 mm					1		1	3	
50.0–380 mm						3	7	28	3

By about 50 mm. in the late metamorphic period, the full complement of caudal rays is present, 8 or 9+19+7 or 8. Table 7 presents data on the number of secondary caudal rays for late metamorphic larvae, juveniles, and adult, and shows that 9+19+7 was the most frequently occurring complement.

The minute anterior secondary rays on juveniles and adults are often difficult to discern without dissection. By about 50–60 mm. the anteriormost dorsal and ventral secondary ray is usually completely covered by an elongate, concave, bony

scale. Holbrook (1860) gave 28 as the caudal ray complement, which obviously does not include all secondary rays.

TEETH

The 5.3-mm. leptocephalus (fig. 2) has four teeth in a single row on each side in each jaw. The anterior two in the upper jaw are the largest, and are fanglike, uniform in diameter throughout their length, and beveled at their tips. The two remaining teeth in the upper jaw and those in the lower jaw are gently tapered, with sharp tips. By about 10 mm. there are 6 teeth in each side of each jaw, the anterior 4 in each jaw larger than the others. The number increases as the leptocephalus grows, and at the size the larva begins to shrink (about 40–45 mm.) there are about 10–11 teeth in the upper jaw and 12–14 in the lower (the fanglike teeth are difficult to distinguish from the others at about this size). During the early metamorphic period the number increases. During the mid-metamorphic period it becomes difficult to make an accurate count because of the varying number of developing and partially exposed teeth. At the end of the mid-metamorphic period the maxillary teeth are in bands on the ventrolateral, ventral, and ventromedial surfaces, irregularly set vomerine teeth are present, and there are 3 palatine teeth in a row on each side of the mouth. By about 35 mm. (fig. 14) teeth are present on the tongue. Juvenile and adult fish have pterygoid teeth as well, and teeth are numerous in the jaws and in the mouth.

KIDNEY

On an 11.2-mm. leptocephalus (fig. 3) two large blood vessels extend from the digestive tract into the body at the 51st and 52d myomeres. By about 20 mm. (fig. 5) it is evident that the blood vessels enter a mass of tissue along the dorsal wall of the digestive tract. Delsman (1926) showed this tissue in his illustration of a 37-mm. *E. hawaiensis*, but did not identify it. Holstvoogd (1936) discussed the development of the kidney in larval *E. hawaiensis*, defining this tissue as mesonephros and the two large blood vessels as branches of the third mesenteric artery. During the early metamorphic period the kidney enlarges, and extends from about the 48th to the 54th myomeres by the end of the mid-metamorphic period (figs. 7 to 12). The body becomes opaque at about this stage, and no further observations were made on the kidney.

AIR BLADDER

The rudimentary air bladder is visible as a slight bulge in the dorsal wall of the digestive tract at about the 35–36th myomeres on an 11.2-mm. leptocephalus (fig. 3). On the largest leptocephalus (43.3 mm.) it is a long, cylindrical, blind sac arising from the digestive tract at the 34th myomere, directed dorsally into the body. During the early metamorphic period it expands and lengthens, and by about 30 mm. it extends to the vertebral column, with its dorsal surface flattened against the column (fig. 9). During the mid-metamorphic period the air bladder becomes broader and longer, and on a 25.9-mm. late metamorphic larva it is elongate and occupies a considerable portion of the body cavity (fig. 13). By about 35 mm. in the late metamorphic period (fig. 14) it is long and thin, as in the juvenile and adult.

GILL RAKERS

Gill rakers are first visible on mid-metamorphic larvae, 20–25 mm. Tables 8 and 9 give the number of gill rakers on the first arch of mid- and late metamorphic larvae, juveniles, and adult. The counts include rudiments. The ranges for specimens exceeding 30 mm. are 5–7 for the upper limb and 11–15 for the lower. For juveniles exceeding 70 mm. and adults the ranges are 5–7 for the upper limb and 12–15 for the lower. Hildebrand (1943) gave 5–8 for the uper limb and 10–15 for the lower; Regan (1909) gave 12–15 for the lower limb; and Meek and Hildebrand (1923) gave 11–14 for the lower limb.

PSEUDOBRANCHIA

Large pseudobranchia are present on mid-metamorphic larvae.

BRANCHIOSTEGALS

Branchiostegals were first visible on mid-metamorphic larvae, 5 on each side in a 21.5-mm. specimen (fig. 11). During the late metamorphic period the number increases, and by about 35 mm. there are approximately 30 on each side, with usually more on the left side than on the right. Holbrook (1860) stated that there is always one more branchiostegal on the left side than on the

right. I found the counts for the two sides to differ by as many as 3, with a range of 27–33 for one side for juveniles and adult. Berg (1947) gave the range for *Elops* as 27–35, and Regan (1909) gave 28–36.

GULAR PLATE

The gular plate (a long, flat, narrow bone between the rami of the mandibles), which distinguishes the tarpon and ten-pounder from the bonefish, develops during the mid-metamorphic period.

TABLE 8.—*Variation in number of gill rakers on upper and lower limbs of first arch of mid-metamorphic larvae to adults*

Standard length	Number of individuals with gill rakers on first arch numbering—									
	Upper limb				Lower limb					
	4	5	6	7	10	11	12	13	14	15
20.0–24.9 mm		4			1	3				
25.0–29.9 mm	1		1			1				
30.0–34.9 mm		3	2			3	1			
35.0–39.9 mm			1			1				
40.0–49.9 mm		1	1	3		1		3	1	
50.0–59.9 mm		1						1		
60.0–69.0 mm		3	5			1		3	1	3
70.0–380 mm		4	11	16			2	16	12	1

TABLE 9.—*Variation in number of gill rakers on first arch of mid-metamorphic larvae to adults*

Number of individuals with upper limb gill rakers numbering—	Number of individuals with lower limb gill rakers numbering—					
	10	11	12	13	14	15
4					1	
5	1	6		4	4	1
6		3	3	5	6	3
7				15	4	

SCALES AND LATERAL LINE

Cycloid scales and the lateral line are first present at about 50 mm. in the late metamorphic period. The lateral line and scales extend onto the caudal fin, and the number of scales along the lateral line ranges 105–115. The head is unscaled in *Elops*. Hildebrand (1943) gave the range of scales as 103–120, with scales appearing at about 50 mm., and scalation complete by about 60–65 mm. Sheaths of scales at the bases of the dorsal and anal fins are developed by about 60 mm. Several long, and irregularly shaped axillary scales at the insertions of the pectoral and pelvic fins are present at about 50 mm.

499662 O—59——3

ADIPOSE EYELID

The adipose eyelid is present by about 50 mm. in the late metamorphic period, covering very little of the anterior and posterior margins of the eye (fig. 15). During the juvenile period the eyelid extends farther over the eye, and on the adult (380 mm.) all of the eye is covered except a vertical slit the width of the pupil (fig. 17).

CHANGES IN BODY FORM

The body of the leptocephalus at 5.3 mm. (fig. 2) is ribbonlike; long, thin, and deep (deepest about midway between the head and the anus), and tapers gently to a rodlike urostyle (or tip of notochord). The head is broader and slightly deeper than the body. By about 10 mm. (fig. 3) the body is deeper than the head, and the head is triangular in dorsal aspect. By about 20 mm. the caudal fin is forked, and the body is still ribbonlike in appearance. At the end of the leptocephalus period (fig. 7) the head is relatively smaller than at any other size or stage of development; the body is long, thin, and deep; and fins are not yet prominent. During the early metamorphic period the body shortens and thickens slightly while the head remains a constant length. During the mid-metamorphic period the ribbonlike appearance is lost as the body thickens, and the head loses its triangular shape. Also during the mid-metamorphic period the anal and dorsal fins shift anteriorly (this change in position is discussed under "Regressions of body parts on standard length"). By the end of the late metamorphic period the body form is generally that of the adult; long, round, and tapered at the head and caudal, with the fins large and well developed (fig. 15).

PIGMENTATION

The 5.3-mm. leptocephalus (fig. 2) is translucent except for a silver eye with a black pupil and a few melanophores scattered along the dorsal aspect of the digestive tract. During the leptocephalus period the melanophores along the digestive tract increase, and some develop between the body myomeres, along the mid-lateral line of the body, on the caudal fin, and between the myomeres at the anal ray bases (figs. 2 to 7). The largest lepto-

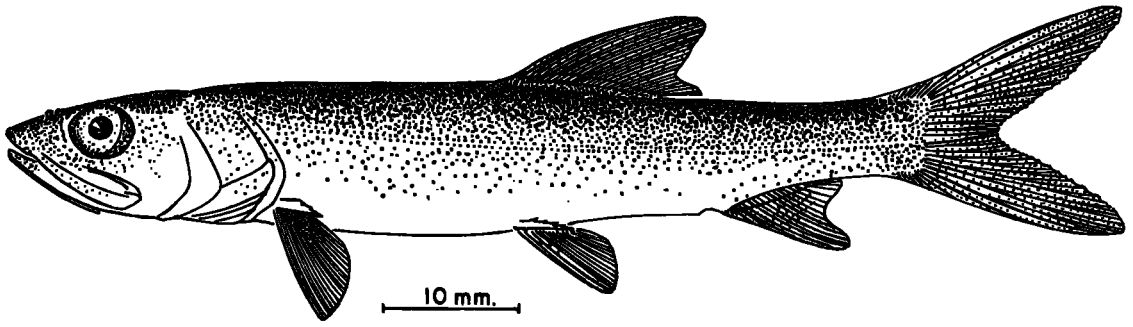

FIGURE 15.—Juvenile, 67.5 mm. standard length.

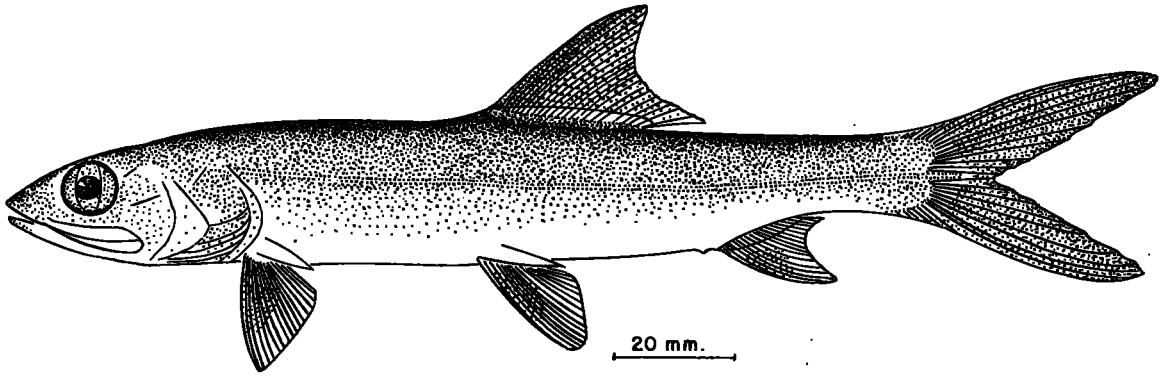

FIGURE 16.—Juvenile, 152 mm. standard length.

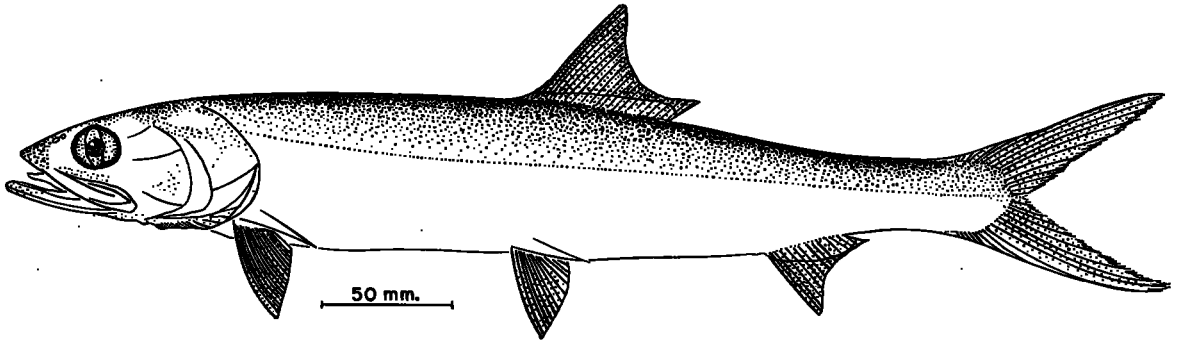

FIGURE 17.—Adult, 380 mm. standard length.

cephalus, 43.3 mm. (fig. 7), has pigment on the dorsal surface of the eye.

During the early metamorphic period, the melanophores increase in number and size, and the dorsal surface of the air bladder becomes densely pigmented (fig. 10).

During the mid-metamorphic period melanophores appear on the head, those on the body increase in number, and the dorsal and caudal fins develop a distinct pattern of pigmentation (figs. 11 and 12).

By about 35 mm. (fig. 14) during the late metamorphic period the pattern on the dorsal surface of the head and body becomes denser, the pigment on the dorsal and caudal fins extends, and some is present on the anal fin. By the end of the late metamorphic period (50–60 mm.) the dorsal pattern is a dense greenish-black, grading to silver below. The pattern on the fins is a uniform pepper-spot appearance on the dorsal and caudal fins, with a few scattered spots on the pectoral and pelvic fins, and a small group on the anal fin.

Pigmentation of the 380-mm. adult immediately after death had dorsal surfaces of head and body greenish-black overlaid with silver scales, with the sides shading to silvery below. The dorsal fin, dusky, grading to greenish-black on the anterior edge. The pectoral and pelvic fins, dusky on the anterior portions. The anal, hyaline with a few greenish spots. The caudal fin, dusky to greenish-black, with the ventral lobe darker than the upper (the lowest principal rays are nonpigmented). The eye, greenish-gold and silver with a black pupil.

OSTEOLOGY

Several leptocephali and early, mid-, and late metamorphic larvae were stained with alizarine red, using methods described by Hollister (1936) and Evans (1948), to study in particular the development in the caudal fin.

The fin rays begin to ossify in the following order: caudal, dorsal, and anal rays in the leptocephalus period; pectoral rays in the early metamorphic period; and pelvic rays in the mid-metamorphic period. The maxillary and mandible ossify in the leptocephalus period (fig. 18), premaxillary in the early metamorphic period (fig. 19), and branchiostegals begin to ossify in the mid-metamorphic period (fig. 11). No attempt was made to trace the development of ossification of the various other bones of the head.

Immediately anterior to and lying against the basal portion of the first pectoral and pelvic ray is a short, slender process which resembles the spinous ray on the paired fins of spiny-rayed fishes (fig. 20). However, its single, flattened base is embedded in the flesh dorsolateral to the insertion of the fins. The ridge on the forward edge of the first ray is replaced by this process (which lies in a depression on the ridge) near the base of the ray. I find no mention of this structure in the literature.

Caudal development.—The caudal osteology was given special attention when it became apparent that the degree of ossification might be of use in separating leptocephali and early metamorphic larvae of similar size and general appearance. Figures 22 to 24 illustrate the degree of ossification for specimens of similar size but in different stages of development. The density of stippling in the illustrations is to approximate the intensity of the stain. Regan (1910) and Hollister

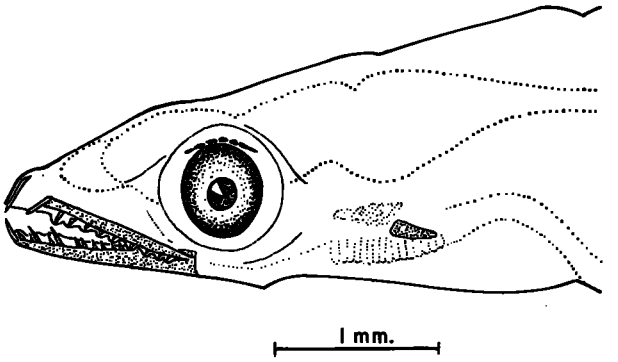

FIGURE 18.—Early metamorphic larva (or leptocephalus), 43.3 mm. standard length. Side view of head showing ossification as stippled areas (portions which stained with alizarine red).

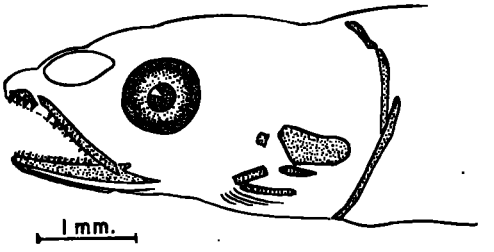

FIGURE 19.—Early metamorphic larva, 26.6 mm. standard length. Side view of head showing ossification as stippled areas.

(1936) presented the caudal osteology of juvenile or adult *E. saurus*. Figure 21, after Hollister (1936), is of the caudal osteology of a 258-mm. specimen. Nomenclature of caudal bones follows Hollister (1936).

Figure 22 shows the caudal fin of the 31.3-mm. leptocephalus (fig. 6). Seven hypurals and several uroneurals are partially ossified. There are 1 dorsal and 2 ventral secondary rays ossified in addition to the 19 principal rays. The ventralmost principal ray appears to originate between the two lowermost (anterior) hypurals.

The complement of rays is the same for the 30.9-mm. early metamorphic larva shown in figure 9. However, the illustration of its caudal fin (fig. 23) shows the 5 upper hypurals, 3 of the 4 lower hypurals, 1 haemal process, and 2 neural processes as partially ossified. There is no change in the uroneurals.

Figure 24 shows the caudal fin of the 25.9-mm. late metamorphic larva (fig. 13). Although this specimen is smaller than the other 2 larvae, the

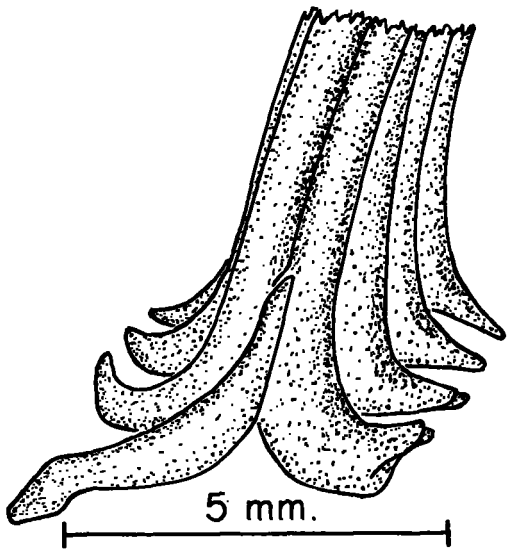

FIGURE 20.—Anterior view of the leading edge of pelvic fin of 240-mm. specimen, showing first four rays with process lying against first ray (base of process imbedded in flesh to the left of, or dorso-lateral to, the base of the first ray).

ossification is so far advanced it is considered of similar size for this comparison. All 9 hypurals, the uroneurals, the 3 epurals, and neural and haemal processes have ossified; and some of the centra are partially ossified. The lowermost principal ray is attached to the anteriormost hypural, as is the next ventral ray, a secondary. A 34.2-mm. late metamorphic larva (fig. 14) showed partial ossification in all 85 vertebrae, development progressing anteriorly.

The degree of ossification will separate leptocephali from early metamorphic larvae for sizes smaller than about 35 mm. Individual variation in development in larvae exceeding 35 mm. rules out this character for separating the larger larvae.

REGRESSIONS OF BODY PARTS ON STANDARD LENGTH

Several measurements were selected to show changes in form of various body parts and shifting of the dorsal and anal fins anteriorly.

The unique development of *E. saurus* precludes depicting the regression of a part on the standard length with a continuous line through all periods of development. The size at which the leptocephalus period ends varies with the individual specimen, as does the size at which shrinking ceases. I have no observations on living specimens passing from the leptocephalus period to the early metamorphic period, and few observations on living specimens in the mid-metamorphic period. I was unable to determine the average size at which shrinking begins and the size at which it ceases.

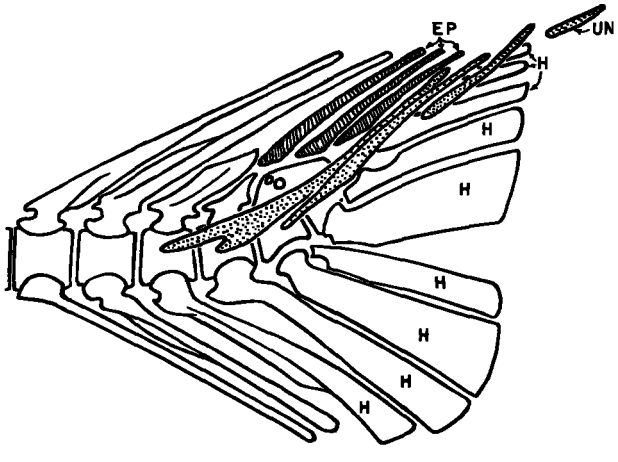

FIGURE 21.—Caudal osteology of 258-mm. *E. saurus*, (modified from Hollister, 1936, p. 261, fig. 14). The 9 hypurals are indicated by the letter H, the 4 uroneurals are stippled, and the 3 epurals are crosslined.

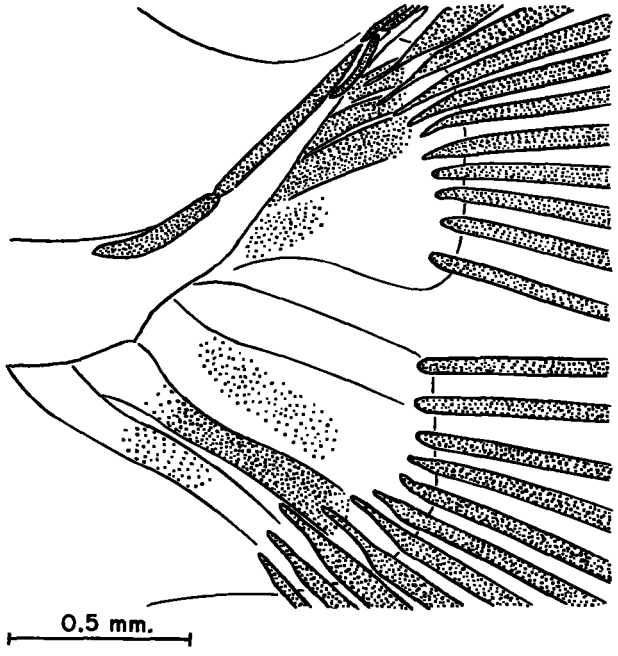

FIGURE 22.—Caudal osteology of a 31.3-mm. leptocephalus (fig. 6). Density of stippling indicates intensity of alizarine red stain.

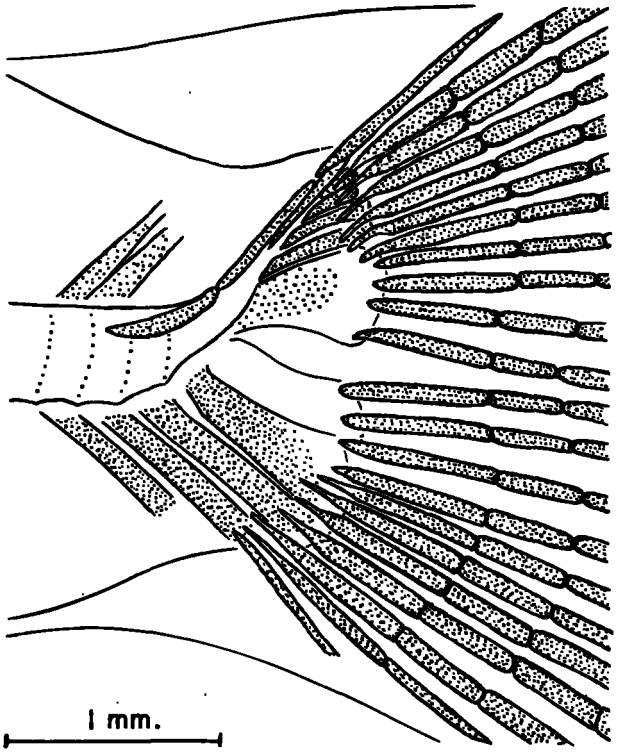

FIGURE 23.—Caudal osetology of a 30.9-mm. early metamorphic larva (fig. 9). Density of stippling indicates intensity of alizarine red stain.

Original, individual measurements (table 10) plotted on the graphs showing relations of various body parts to standard length (figs. 25 to 30) were used in the calculation of the regression lines (determined by the method of least squares). Table 11 presents the statistics describing the regressions of the body parts on standard length. Arithmetical plots of individual variates indicated that in most instances the formula for a rectilinear regression, $Y=a+bX$, adequately describes the relationships.

Three regression lines were calculated for the relations of head length, eye diameter, body depth at pectoral, snout to insertion of the dorsal fin, and snout to insertion of the anal fin to standard length; one for the leptocephalus period, one for the early metamorphic period, and one for the late metamorphic and juvenile periods combined. A single line was calculated for the regression of snout to insertion of the pelvic fin on standard length (late metamorphic period into juvenile) since this fin did not develop until the early metamorphic period and I had few values for this period. The variation in the body parts during the mid-metamorphic period and the difficulty in separating the shrinking larvae from those increasing in length preclude fitting regression lines for this period.

Regression lines for the late metamorphic and juvenile periods were determined from specimens 138 mm. or less in standard length as my data beyond 138 mm. are insufficient for calculating regressions. I have extended the calculated regression lines beyond 138 mm. as broken lines to determine whether the relation suggested by smaller specimens continues beyond 138 mm. The insets in the graphs expand the scale for specimens less than 50 mm. to better show the relationship in this size range.

Head length.—During the leptocephalus period the head length increases 0.055 mm. for each millimeter increase in standard length (fig. 25, table 11). During the early metamorphic period the increase is 0.005 mm. for each millimeter decrease in standard length. During the late metamorphic

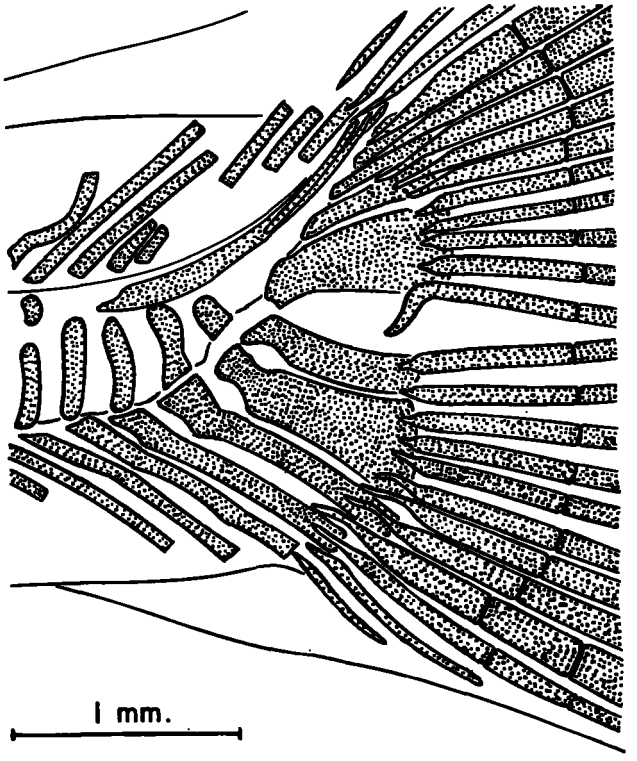

FIGURE 24.—Caudal osteology of 25.9-mm. late metamorphic larva (fig. 13). Stippling indicates alizarine red stain.

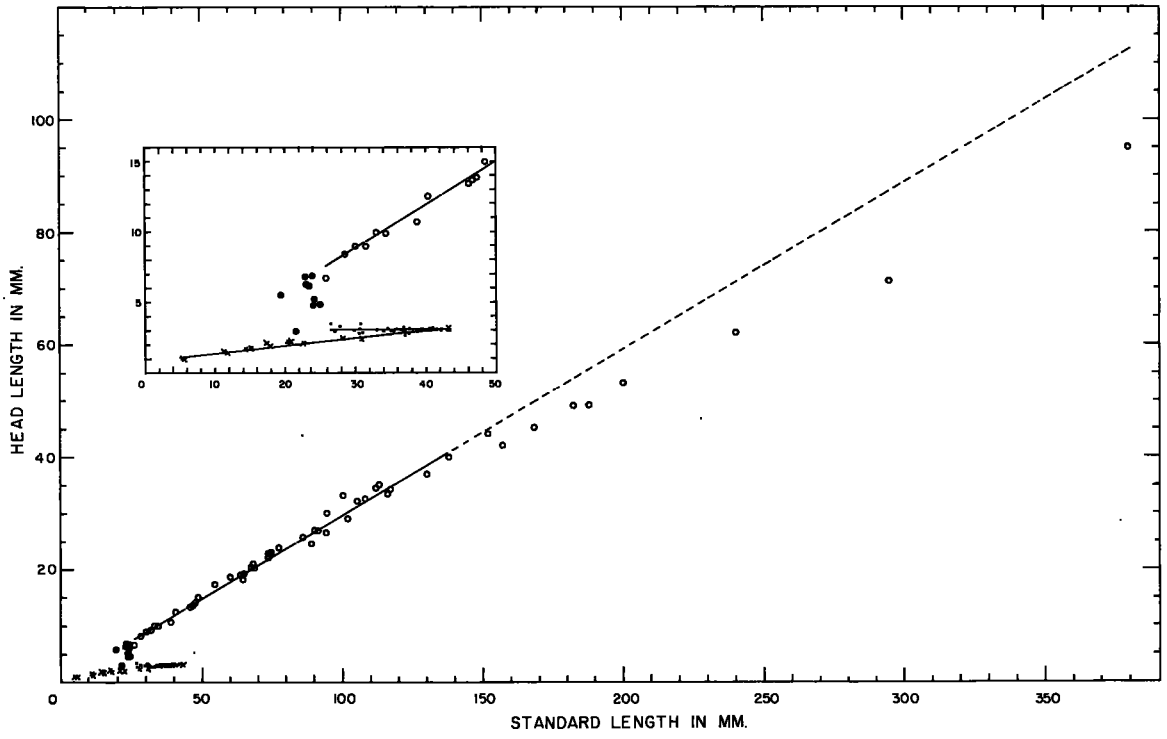

FIGURE 25.—Relation of head length to standard length. X's represent leptocephali; small dots, early metamorphic larvae; large dots, mid-metamorphic larvae; and circles, late metamorphic larvae to adults.

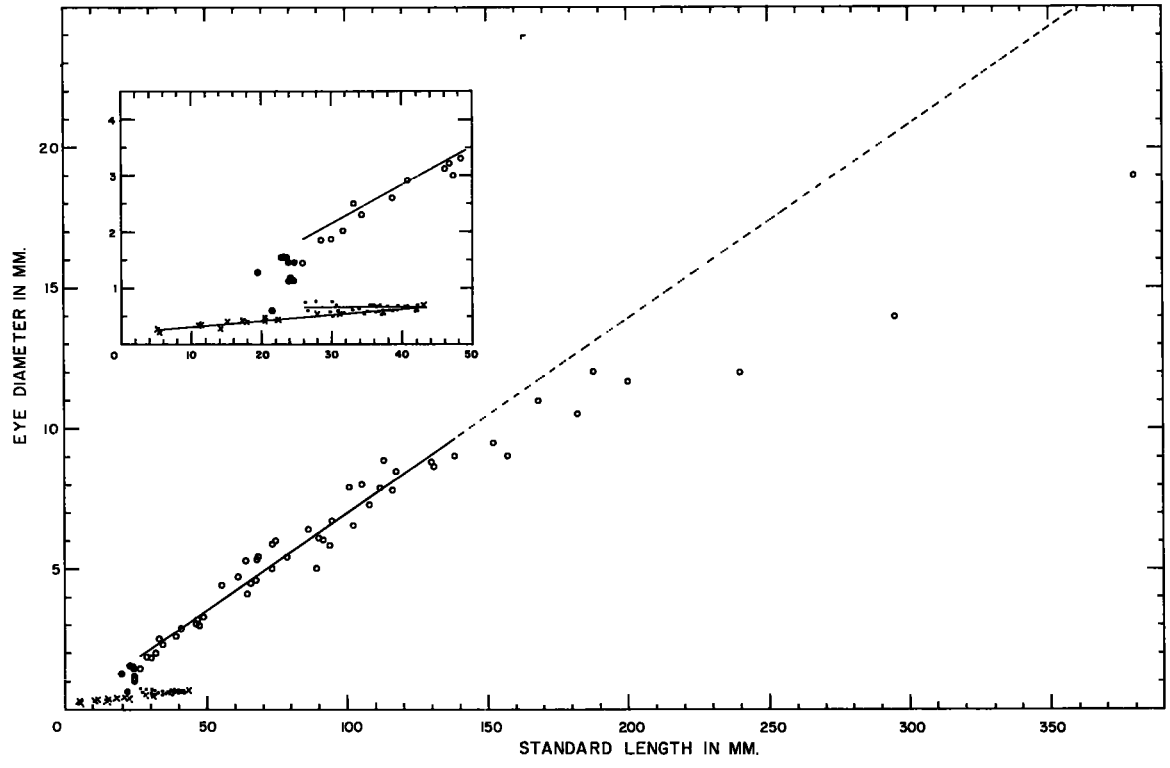

FIGURE 26.—Relation of eye diameter to standard length. X's represent leptocephali; small dots, early metamorphic larvae; large dots, mid-metamorphic larvae; and circles, late metamorphic larvae to adults.

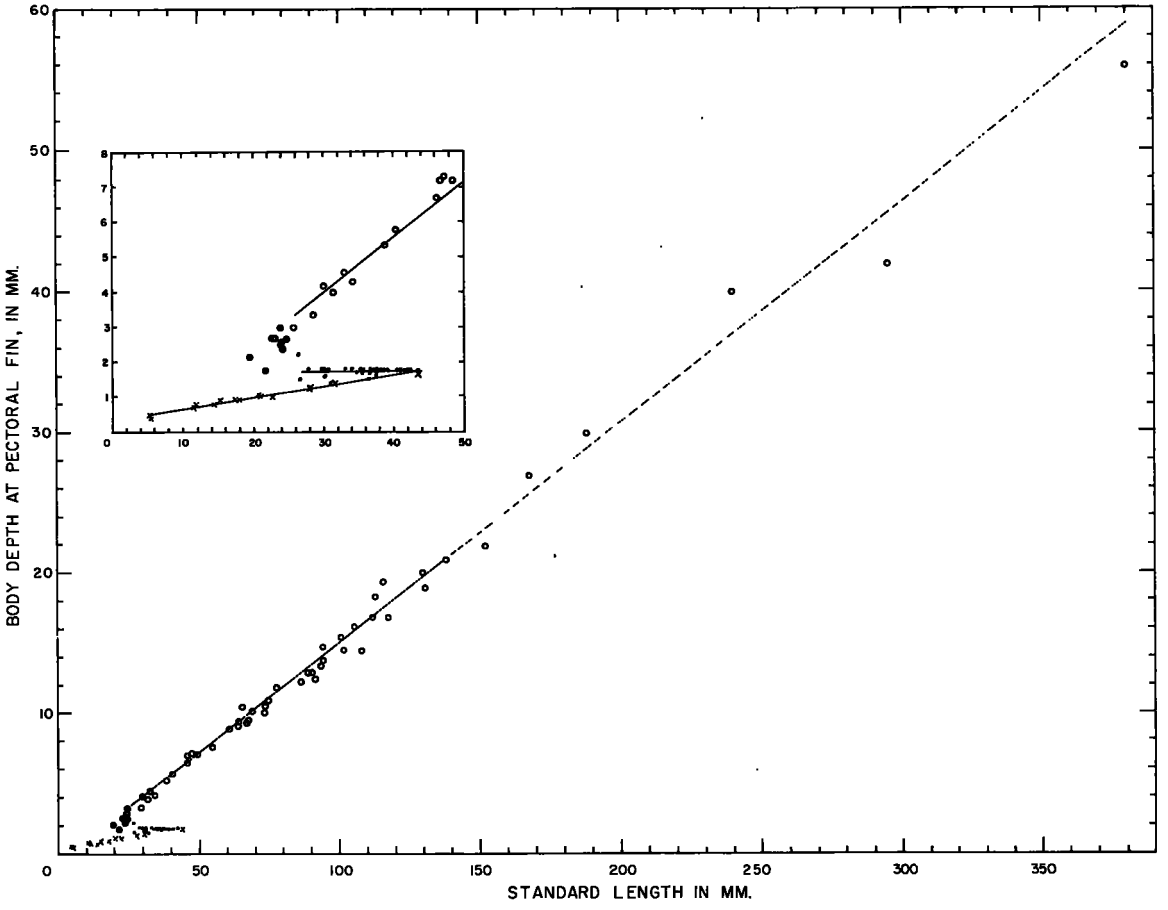

FIGURE 27.—Relation of body depth at pectoral fin to standard length. X's represent leptocephali; small dots, early metamorphic larvae; large dots, mid-metamorphic larvae; and circles, late metamorphic larvae to adults.

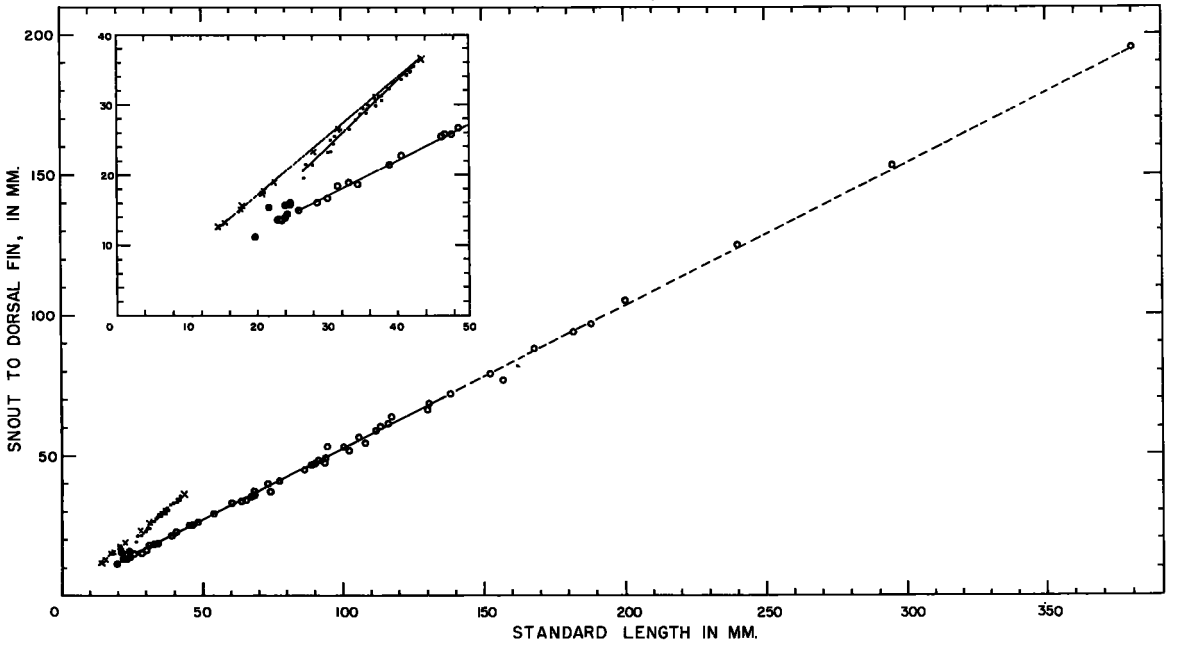

FIGURE 28.—Relation of distance snout-to-dorsal fin to standard length. X's represent leptocephali; small dots, early metamorphic larvae; large dots, mid-metamorphic larvae; and circles, late metamorphic larvae to adults.

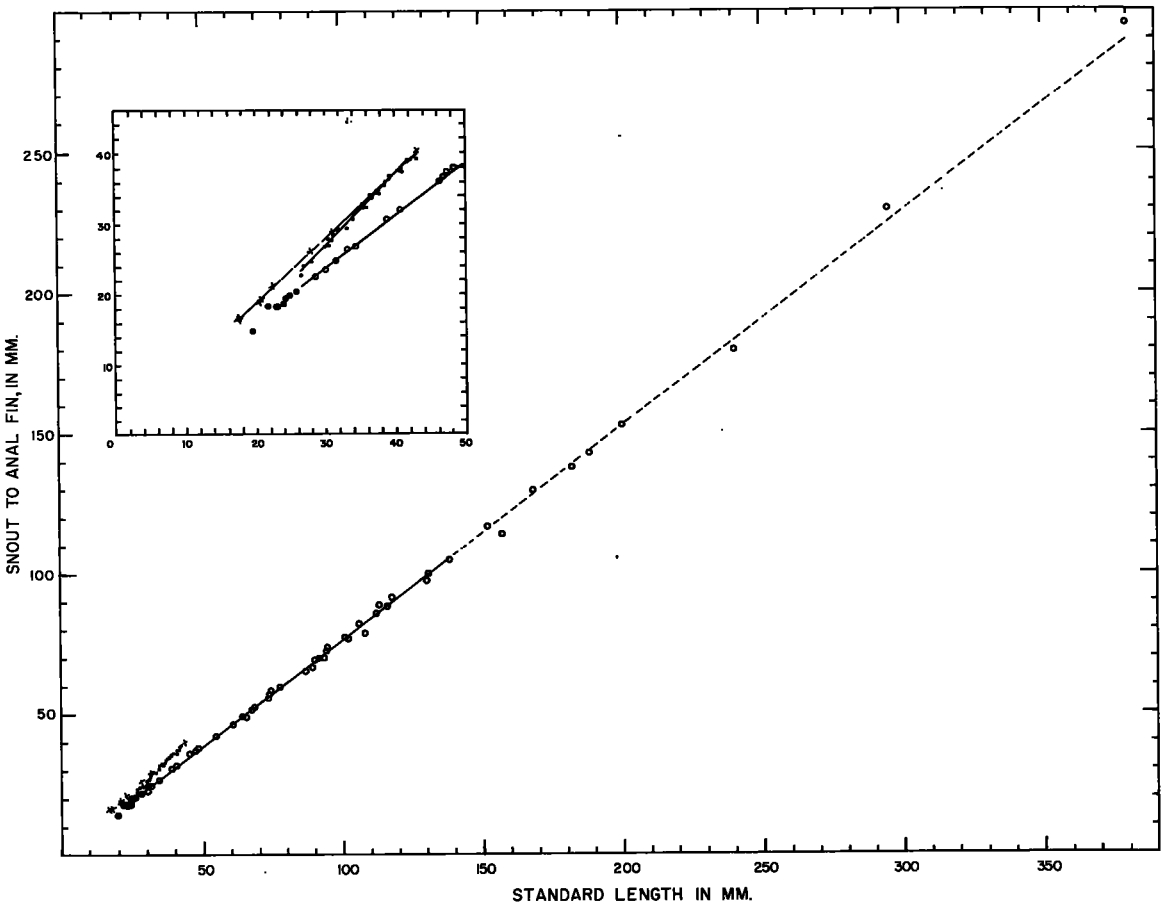

FIGURE 29.—Relation of distance snout-to-anal fin to standard length. X's represent leptocephali; small dots, early metamorphic larvae; large dots, mid-metamorphic larvae; and circles, late metamorphic larvae to adults.

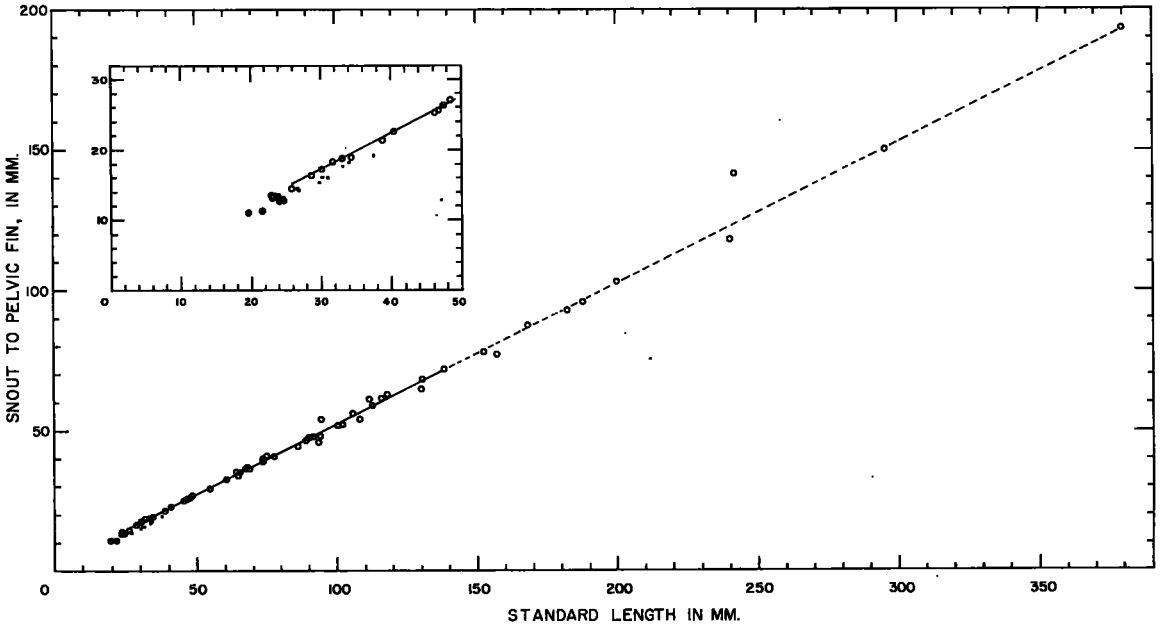

FIGURE 30.—Relation of distance snout-to-pelvic fin to standard length. Small dots represent early metamorphic larvae; large dots, mid-metamorphic larvae; and circles, late metamorphic larvae to adults.

TABLE 10.—*Measurements used in calculating regressions of body parts on standard length, arranged by specimen size and stage of development*

[Measurements in millimeters]

Standard length	Head length	Body depth at pectoral	Eye diameter	Distance from snout to—		
				Dorsal fin	Anal fin	Pelvic fin
Leptocephali:						
5.1	1.1	0.5	0.30			
5.3	1.0	.4	.24			
11.2	1.5	.7	.36			
11.7	1.4	.8	.36			
14.3	1.7	.8	.30	12.6		
15.2	1.8	.9	.42	13.2		
17.3	2.1	.9	.42	15.1	16.6	
17.9	1.9	.9	.39	15.6	16.8	
20.5	2.2	1.1	.48	17.6	19.0	
20.6	2.2	1.0	.42	17.8	19.4	
22.4	2.1	1.0	.42	19.0	21.1	
28.0	2.5	1.3	.51	23.4	26.1	
31.3	2.4	1.4	.51	26.4	29.3	
43.3 [1]	3.2	1.7	.68	36.1	40.1	
Early metamorphic larvae:						
42.1	3.0	1.8	.68	35.5	39.0	
42.0	3.0	1.8	.59	35.2	39.0	
41.8	3.1	1.8	.59	34.6	38.9	
41.0	3.2	1.8	.68	34.1	37.5	
40.8	3.1	1.8	.68	34.2	37.8	
40.6	3.1	1.8	.68	33.8	37.7	
39.3	3.0	1.8	.68	33.0	36.8	
39.3	3.1	1.8	.59	33.0	36.3	
38.7	3.0	1.8	.59	32.3	35.9	
38.4	3.0	1.8	.59	32.6	35.5	
37.7	3.1	1.8	.68	30.5	34.3	
37.6	2.8	1.7	.51	31.3	34.9	
37.5	2.7	1.6	.51	31.3	34.6	19.3
37.3	3.1	1.8	.59	31.3	34.5	
36.8	3.2	1.7	.68	29.7	33.8	
36.8	3.1	1.8	.68	30.5	34.0	
36.6	2.9	1.7	.59	31.1	34.0	
36.5	3.0	1.5	.68	31.3	34.2	
35.9	3.1	1.8	.68	30.0	32.2	
35.8	3.1	1.8	.68	29.2	32.8	
35.5	3.0	1.8	.68	28.8	32.2	
35.1	3.0	1.7	.59	29.4	32.7	
34.5	3.1	1.7	.51	28.4	32.0	
34.0	3.0	1.8	.68	27.9	30.6	19.4
34.0	3.0	1.8	.68	27.9	31.4	18.1
33.0	3.1	1.9	.60	26.4	29.5	17.7
31.8	2.6	1.4	.54	26.4	29.4	
31.0	2.9	1.4	.60	25.5	28.3	
30.9	3.2	1.8	.68	24.1	27.8	16.0
30.3	3.5	1.8	.78	23.4	27 0	16.0
30.3	2.9	1.6	.51	24.9	27.9	
29.9	3.0	1.8	.59	23.2	26.7	15.4
27.9	3.3	1.8	.76	21.5	24.7	
26.8	2.9	1.5	.60	21.5	24.0	14.3
26.0	3.5	2.2	.76	19.4	22.8	14.4
Mid-metamorphic larvae:						
24.0	4.9	2.6	1.01	15.8	18.8	12.8
21.5	3.0	1.8	.60	15.6	18.4	11.2
19.4	5.6	2.2	1.27	11.3	14.8	11.0
22.9	6.8	2.7	1.52	13.5	18.2	13.5
23.0	6.3	2.7	1.52	13.5	18.2	13.1
23.6	6.2	2.5	1.52	13.5	18.6	13.4
23.9	6.9	3.0	1.44	13.9	18.7	13.5
24.1	5.3	2.4	1.18	14.5	19.4	12.8
24.7	4.8	2.7	1.10	15.8	19.5	12.9
24.7	4.8	2.6	1.44	16.0	19.8	13.1
Late metamorphic larvae to adult:						
25.9	6.8	3.0	1.44	15.0	20.3	14.5
28.5	8.4	3.4	1.86	16.0	22.4	16.3
30.0	9.0	4.2	1.86	16.6	23.5	17.3
31.6	9.0	4.9	2.0	18.2	24.9	18.6
33.0	10.0	4.6	2.5	19.0	26.2	19.0
34.2	10.0	4.3	2.3	18.8	26.9	19.0
38.8	10.7	5.3	2.6	21.5	30.6	21.5
40.4	12.5	5.8	2.9	22.8	32.0	22.8
46.1	13.5	6.7	3.1	25.4	36.0	25.4
46.7	13.7	7.2	3.2	25.8	36.3	25.8
47.3	13.9	7.3	3.0	25.8	37.2	26.4
48.4	15.0	7.2	3.3	26.7	38.0	27.1
54.5	17.4	7.7	4.4	29.5	42.3	29.5
60.5	18.7	9.0	4.7	33.0	46.4	32.5
64.0	19.0	9.2	5.3	34.0	49.5	35.0
64.5	18.2	9.4	4.1	34.5	49.0	34.0
65.5	19.1	10.5	4.5	34.0	49.1	35.0
67.5	20.4	9.4	4.6	35.4	50.5	36.5
67.5	20.6	9.6	5.3	37.6	51.5	36.6
68.0	21.0	10.1	5.3	37.7	52.5	37.5

TABLE 10.—*Measurements used in calculating regressions of body parts on standard length, arranged by specimen size and stage of development*—Continued

[Measurements in millimeters]

Standard length	Head length	Body depth at pectoral	Eye diameter	Distance from snout to—		
				Dorsal fin	Anal fin	Pelvic fin
Late metamorphic larvae—Continued						
68.5	20.5	10.3	5.4	36.0	52.5	37.0
73.5	22.5	10.6	5.0	39.0	56.0	39.5
73.5	22.0	10.1	5.9	39.5	57.5	40.0
74.5	23.0	11.0	6.0	30.7	58.5	31.0
77.5	23.6	12.0	5.4	40.7	60.0	41.0
86.0	25.6	12.4	6.4	45.6	65.0	44.9
89.0	24.5	13.0	5.0	46.5	66.5	46.0
90.0	27.0	13.0	6.1	47.0	69.5	47.5
91.5	27.0	12.5	6.0	48.0	70.0	48.0
93.5	26.1	13.5		47.4	70.5	46.0
94.0	26.5	14.7	5.8	49.0	72.5	48.0
94.5	30.0	13.9	6.8	53.0	74.5	54.5
101	33.4	15.5	7.9	53.5	77.5	52.0
102	28.8	14.6	6.5	51.5	77.0	52.5
106	32.4	16.4	8.0	56.5	83.0	56.5
108	32.5	14.5	7.3	54.0	79.0	54.0
112	34.5	17.0	7.9	59.0	86.0	61.0
113	35.0	18.4	8.9	60.0	89.0	59.0
116	33.5	19.4	7.8	62.0	88.5	61.5
117	34.3	16.9	8.5	60.5	91.0	60.5
130	36.8	20.1	8.8	66.0	97.0	65.0
130	37.0	19.0	8.6	68.5	100	68.0
138	40.0	21.0	9.0	72.0	105	72.0
152	44.0	22.0	9.5	79.0	117	78.0
157	42.0	24.0	9.0	77.0	114	77.0
168	45.0	27.0	11.0	88.0	130	87.0
182	49.0	28.0	10.5	94.0	138	93.0
188	49.0	30.0	12.0	97.0	143	96.0
200	53.0	30.0	11.6	105	153	103
240	62.0	40.0	12.0	125	180	118
295	71.0	42.0	14.0	153	230	150
380	95.0	56.0	19.0	195	295	193

[1] Either leptocephalus or an early metamorphic larva.

period, and to a juvenile size of 138 mm., the head increases 0.294 mm. per millimeter increase in standard length. The extension of this regression line beyond 138 mm. suggests an inflection at about 120 mm., and that the rate of increase above 120 mm. is less than for smaller specimens.

Eye diameter.—During the leptocephalus period the eye diameter increases 0.015 mm. per millimeter increase in standard length (fig. 26, table 11). During the early metamorphic period the increase is 0.002 mm. per millimeter decrease in standard length. During the late metamorphic period and juvenile period to 138 mm. it increases 0.069 mm. per millimeter increase in standard length. The extension of the regression line beyond 138 mm. indicates a lower rate above 120 mm. (as was seen in regression of head length on standard length). A curve might better fit the data in the late metamorphic period to adult size range since most of the values for specimens smaller than 50 mm. and larger than 120 mm. fall below the calculated straight line.

TABLE 11.—*Statistics describing regressions of body parts on standard length for ten-pounder leptocephali to juveniles*

Independent variable x	Dependent variable y	Stage of development	Specimen size range (mm.)	$\bar{x}$	$\bar{y}$	N	b	a	Sy.x
Standard length	Head length	Leptocephali	5.1–43.3	18.86	1.94	14	0.055	0.892	0.143
Do	do	Early metamorphic larvae	43.3–26.6	35.76	3.05	36	−.005	3.221	.178
Do	do	Late metamorphic larvae to juveniles	25.9–138	75.37	22.40	43	.294	.261	1.089
Standard length	Eye diameter	Leptocephali	5.1–43.3	18.86	0.42	14	.010	.224	.035
Do	do	Early metamorphic larvae	43.3–26.6	35.76	0.64	36	−.002	.689	.072
Do	do	Late metamorphic larvae to juveniles	25.9–138	74.93	5.27	42	.069	.097	.492
Standard length	Body depth	Leptocephali	5.1–43.3	18.86	0.96	14	.033	.336	.064
Do	do	Early metamorphic larvae	43.3–26.6	35.76	1.75	36	.003	1.654	.144
Do	do	Late metamorphic larvae to juveniles	25.9–138	75.37	11.11	43	.157	−.724	.639
Standard length	Snout to dorsal fin	Leptocephali	14.3–43.3	23.08	19.68	10	.809	1.015	.133
Do	do	Early metamorphic larvae	43.3–26.6	35.76	29.42	36	.960	−4.898	.568
Do	do	Late metamorphic larvae to juveniles	25.9–138	75.37	40.07	43	.505	2.018	1.027
Standard length	Snout to anal fin	Leptocephali	17.3–43.3	25.16	23.55	8	.914	.541	.178
Do	do	Early metamorphic larvae	43.3–26.6	35.76	32.80	36	1.006	−3.161	.382
Do	do	Late metamorphic larvae to juveniles	25.9–138	75.37	57.94	43	.756	.934	1.148
Standard length	Snout to pelvic fin	Late metamorphic larvae to juveniles	25.9–138	75.37	40.13	43	.500	2.432	1.268

$\bar{x}$=mean of values of x
$\bar{y}$=mean of values of y
N=number of specimens
b=rate of increase of y
a=y-intercept of regression line
Sy.x=standard deviation from regression (standard error of estimate)

Body depth at pectoral fin.—During the leptocephalus period the body depth at pectoral increases 0.033 mm. per millimeter increase of standard length (fig. 27, table 11). During the early metamorphic period it decreases 0.003 mm. per millimeter decrease in standard length, and during the late metamorphic period and juvenile period to 138 mm. it increases 0.157 mm. per millimeter increase in standard length. The extension of the regression line beyond 138 mm. appears to fit the data for the larger sizes, suggesting the relation to be constant for the late metamorphic period to adult.

Snout to dorsal fin.—During the leptocephalus period the distance from snout to the origin of the dorsal fin increases 0.809 mm. per millimeter increase in standard length (fig. 28, table 11). During the early metamorphic period it decreases 0.960 mm. per millimeter decrease in standard length, a slightly higher rate of decrease than the rate of increase in the leptocephalus period. During the late metamorphic period and to a juvenile size of 138 mm., the rate of increase is 0.505 mm. per millimeter increase in standard length. This regression line extended beyond 138 mm. fits the plot of measurements for larger specimens, suggesting the relation to be constant for the late metamorphic period to adult. The shifting of the dorsal fin anteriorly during the early and mid-metamorphic periods is evident when we compare the distance from the snout to the dorsal fin for specimens of similar size, 28 mm. standard length for example, in various periods of development: leptocephalus, about 24 mm.; early metamorphic, about 22 mm.; and late metamorphic, about 16 mm. (values are averages determined from regression line).

Snout to anal fin.—During the leptocephalus period the distance from the snout to the origin of the anal fin increases 0.914 mm. per millimeter increase in standard length (fig. 29, table 11). During the early metamorphic period, it decreases 1.006 mm. per millimeter decrease in standard length. During the late metamorphic period and to a juvenile size of 138 mm., the increase is 0.756 mm. per millimeter increase in standard length. As in the regression of snout to dorsal fin on standard length, the extension of the regression line beyond 138 mm. appears to fit the data for larger sizes, suggesting a constant relation from the late metamorphic period to adult. Shifting of the anal fin anteriorly during the early and mid-metamorphic periods is less than the shift of the dorsal fin; for example, at 28 mm. standard length, the distances from snout to anal fin are; about 26 mm. for leptocephalus, about 25 for early metamorphic larvae, and about 22 for late metamorphic larvae (averages determined from the regression line).

Snout to pelvic fin.—The pelvic fin is first discernible during the early metamorphic period, and the plot of distances from snout to insertion of pelvic on standard length indicates there is little if any shifting of this fin during metamorphosis (fig. 30). The slightly lower values for specimens in the early metamorphic period, as compared with those for late metamorphic larvae of similar size, may indicate a slight shift posteriorly, or it

may merely reflect individual variation. I have not attempted to fit a regression line to the early metamorphic larvae because of the narrow size range involved. For late metamorphic larvae and juveniles to a size of about 138 mm., the distance from snout to insertion of pelvic fin increases 0.500 mm. per millimeter increase in standard length (fig. 30, table 11). Extension of the regression line beyond 138 mm. suggests the relation is constant from the late metamorphic period to adult.

LABORATORY GROWTH EXPERIMENTS

Three early metamorphic (shrinking) larvae were reared through metamorphosis, and several late metamorphic larvae were reared to juveniles. Water from the location of capture of the fish was used, and an inch of washed builder's sand was placed in 4-gallon aquaria. The water was aerated but never changed, and uneaten food and excrement were siphoned off regularly. The water level in the aquaria was maintained by adding distilled water as necessary. Water salinity was checked periodically, and water temperatures were checked daily (more frequently during periods of extreme heat). Occasionally a bacterial growth (which smelled of hydrogen sulfide) covered the sand, and it was necessary to move the water and fish from one aquarium to another. In such cases the water was strained through No. 20 silk bolting cloth.

Feeding habits.—Specimens were fed once daily from the beginning of the experiments on April 10 to August 25, and two feedings were made daily from August 25 to conclusion of the experiments on October 1 (fig. 31). Early metamorphic larvae readily ate brine shrimp (*Artemia* sp.), often in such quantities that the digestive tract in vicinity of the air bladder would be distended. No special care was exercised to exclude unhatched shrimp eggs when feeding shrimp to the larvae, and these were often eaten (but apparently not digested).

Late metamorphic larvae readily took pieces of shrimp (*Penaeus* sp.), small, live killifish (*Fundulus* sp.), and mosquito fish (*Gambusia* sp.), and

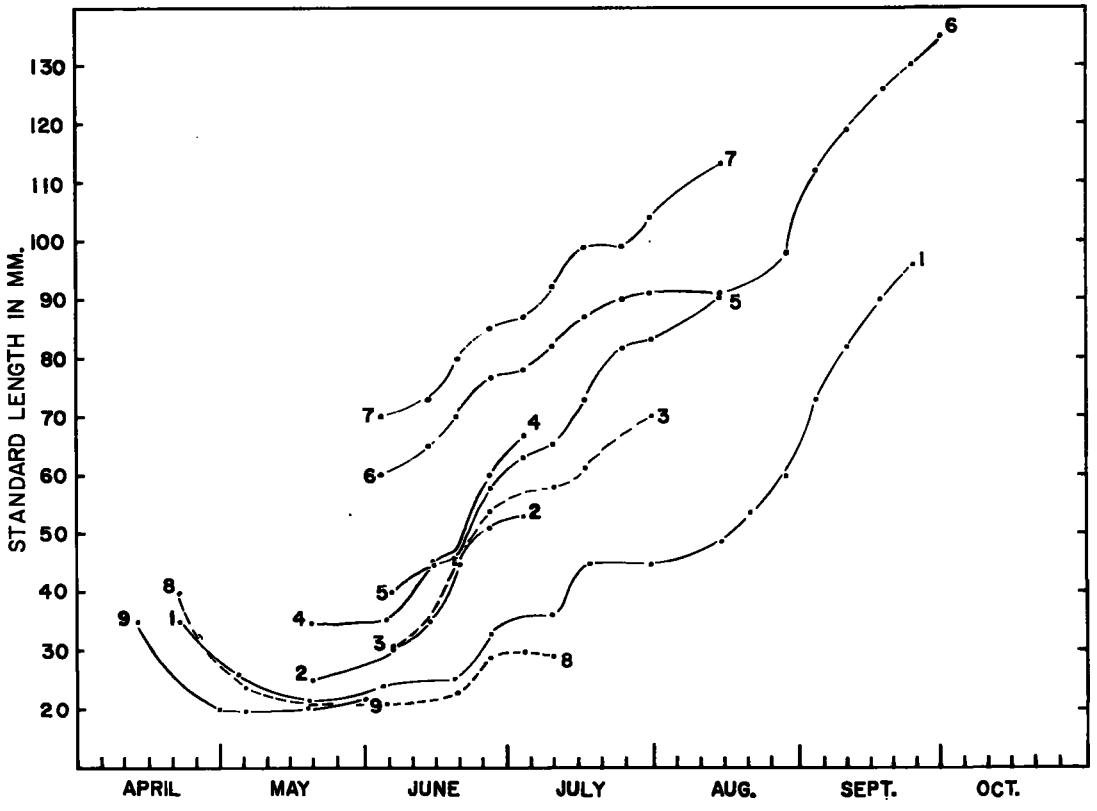

FIGURE 31.—Growth of laboratory-reared specimens. Standard length measurements for individual specimens are connected to indicate individual growth rates. Numbers associated with growth lines refer to specimen numbers in table 12.

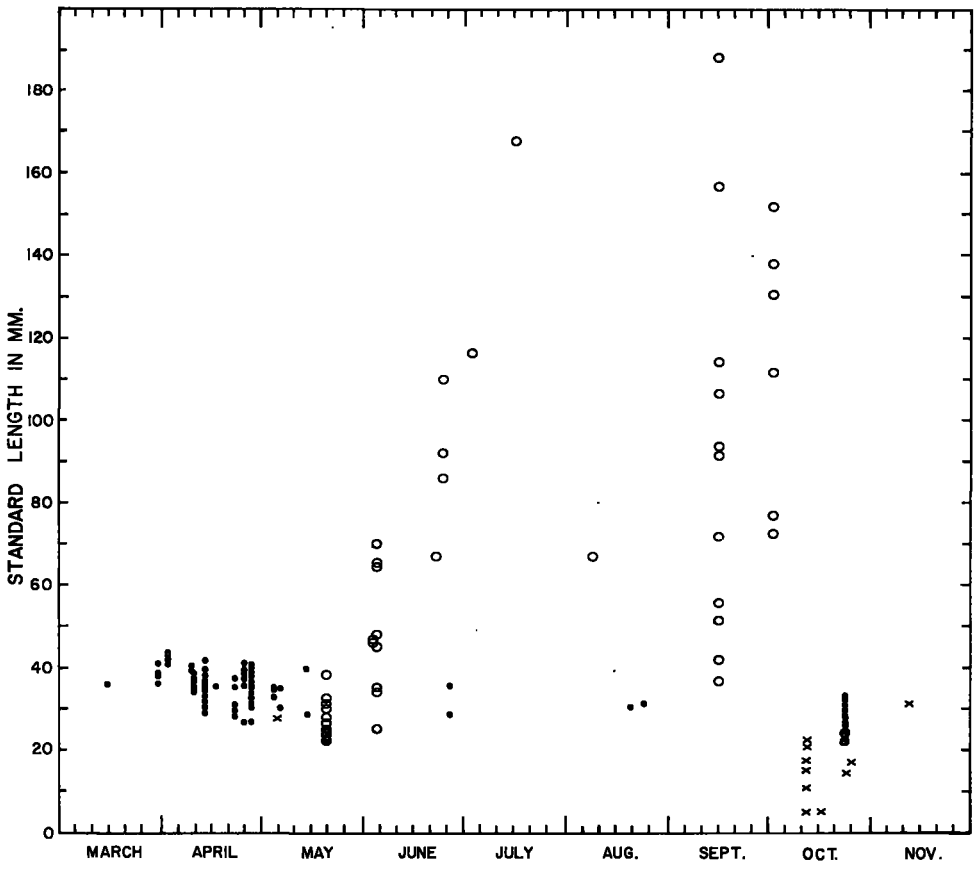

FIGURE 32.—Distribution of leptocephali (X's) from plankton samples; and early metamorphic larvae (small dots), mid-metamorphic larvae (large dots), and late metamorphic larvae and juveniles (circles) from seine samples; by size frequencies and dates of capture for the period from March 1953 to October 1956.

pieces of both fish. The live fishes were swallowed head first, the *Elops* usually swimming alongside its prey for some time before darting ahead, turning abruptly, and seizing it. A fish grabbed crossways would be released and recaptured head-on. Bits of fish lying on the bottom of the aquaria were often snatched from forceps and eaten as an attempt was made to remove them. A 35-mm. late metamorphic larva (*E. saurus*) was eaten by a 73-mm. juvenile *E. saurus* within a half hour after being placed in the aquarium with the larger fish.

Treatment of water.—On several occasions the fins of some fish were attacked by fungus or bacteria. Treatment of the water in the infected tanks with several drops of Mercurochrome usually cleared up the infection, and fins later regenerated. Other than this treatment, and removal of bacteria covered sand mentioned previously, no special attention was given the aquaria.

Measurement of specimens.—About once a week the fish were removed from their aquaria and measured with dividers and a millimeter rule. Care was exercised to minimize injury to specimens during handling. By separating specimens by date of capture and size (a few to each aquarium), it was possible to determine growth rates for individual fish.

Table 12 shows periodic measurements for individual specimens, and figure 32 is a graphic presentation of their growth. One early metamorphic larva (No. 1) was reared from 35 mm. through metamorphosis and up to a juvenile of 96 mm. standard length before death occurred. Several additional larvae lived through early and mid-metamorphosis and died. One juvenile, No. 6, lived 4 months, growing from 60 mm. to 135 mm. The mandible, and sometimes the upper jaw, of the larger specimens became blunt from pressing against the sides of the aquarium.

Metamorphosis.—Tables 12 and 13 and figure 31

TABLE 12.—*Standard length measurements for individual specimens, determined periodically during laboratory growth experiments*

Date	Standard length measurement (mm.) for specimen number—								
	1	2	3	4	5	6	7	8	9
Apr. 13									35
20									25
22	35							40	
30									20
May 4	26								
6	24							24	
19	21							21	21
20		25		35					
30									22
June 4						60	70		
5	24			35				23	
6		30	30		40				
14	25	35	35	45	45	65	73	23	
20	25	45	45	47	46	70	80	23	
26		51							
27	33		53	60	58	77	85	28	
July 4	37	53	58	67	63	78	87	30	
9				64					
10	36		58		65	82	93	29	
17	46		61		73	87	99		
25	45		67		82	90	99		
31	44		70		83	91	104		
Aug. 15	49				91	91	113		
21	54					97			
28	60					98			
Sept. 4	73					112			
11	82					120			
18	90					126			
25	96					130			
Oct. 1						135			

TABLE 13.—*Variations in rates of change in standard length during and following metamorphosis for specimens in laboratory growth experiments*

Specimen number	Period covered	Size at beginning and end of period (mm.)	Number of days	Changes in length (mm.)	Average rate of increase (or decrease) per day (mm.)
Early metamorphic:					
1	Apr. 22–May 4	35–26	12	−9	−0.750
8	Apr. 22–May 6	40–24	14	−16	−1.143
9	Apr. 13–Apr. 20	35–25	7	−10	−1.428
Mid-metamorphic:					
1	May 4–May 19	26–21	15	−5	−.333
8	May 6–May 19	24–21	13	−3	−.231
9	Apr. 20–Apr. 30	25–20	10	−5	−.500
1	May 19–June 14	21–25	26	+4	+.154
8	May 19–June 5	21–23	17	+2	+.118
Late metamorphic:					
1	June 14–Aug. 28	25–60	75	+35	+.467
2	May 20–July 4	25–53	45	+28	+.622
3	June 6–July 17	30–61	41	+31	+.756
4	May 20–June 27	35–60	38	+25	+.658
5	June 6–July 4	40–63	28	+23	+.821
Juvenile:					
1	Aug. 28–Sept. 25	60–96	28	+36	+1.286
3	July 17–July 31	61–70	14	+9	+.643
5	July 4–Aug. 15	63–91	42	+28	+.667
6	June 4–Oct. 1	60–135	119	+75	+.630
7	June 4–Aug. 15	70–113	72	+43	+.597

include data on shrinking in three early metamorphic larvae. Rates of change in standard length through the early metamorphic period, to a size of about 25 mm., ranged from −0.750 to −1.428 mm. per day, and averaged −1.061. Further shrinking to a size of about 20–21 mm. proceeded at a slower rate, −0.231 to −0.500 mm. per day, and averaged −0.342. Initial length increase following shrinking, from a size of about 20 mm. to 25 mm., was considerably slower, +0.118 and +0.154 mm. per day for the two specimens, and averaged +0.140. The slow rate during the period of initial increase following shrinking is not explained.

Alikunhi and Rao (1951, p. 103) stated concerning their experiments with *E. saurus* in Madras, India, "Events leading to the transformation of the transparent, ribbon-shaped post-larva, 35.0 mm. long, into the young adult, measuring only 23.5 to 25.0 mm. in length, have been progressing at a quick pace and were completed in the course of only 9 days." It is impossible to determine the rate of change accurately from this statement; but if the change was from 35 mm. down to 20 mm., and up to about 24 mm. in 9 days, the overall change would be 19 mm., and the rate, 2.11 mm. per day. The average rate for a similar change for my specimens was 0.474 mm. per day, or about one-fifth that for their experiment. If in the period of 9 days, their larva decreased from 35 mm. down to 24 mm., the rate would be −1.222 mm. per day, or comparable to my average rate for this period (early metamorphic), −1.061 mm. per day. The Indian Council of Agricultural Research (1951) reported the transformation completed in about 20 days for *E. saurus*, but gave no sizes.

Growth during the late metamorphic and juvenile periods.—The rates of change in standard length during the late metamorphic and juvenile periods range from +0.467 to +0.821 mm. per day, and averaged +0.626, for the late metamorphic period (from 25 mm. to 60 mm.); and +0.597 to +1.286 mm. per day, and averaged +0.694, for the juvenile period (above 60 mm.). Excluding the +1.286-mm.-per-day value for specimen No. 1, the juvenile period average was +0.628 per day, which is comparable to the +0.626 average for the late metamorphic period.

Undoubtedly the growth rates from these experiments varied from those of fish in their natural habitat, and probably were affected by water temperature, type and quantity of food, limited space in aquaria, and periodic handling during

measuring. If the 25- to 30-mm. late metamorphic larvae taken May 20 represent the same population as the 80 to 120 mm. juveniles taken on June 19 (table 14), a growth of more than 2 mm. per day is indicated, a rate of increase almost double the highest rate in my experiments, +1.286 mm. for specimen No. 1 for growth between 60 and 96 mm.

Alikunhi and Rao (1951) reported a maximum increase "following metamorphosis" of 29 mm. (35 mm. to 64 mm.) in 160 days for specimens in cement nurseries, or a rate of +0.181 mm. per day. The maximum increase they reported for growth in a laboratory aquarium during the same period was 100 mm. (35 mm. to 135 mm.), or a rate of +0.625 mm. per day. This rate is comparable to my average for growth during the late metamorphic and juvenile periods (+0.663 mm. per day, including all specimens).

The periods of little or no length increase for late metamorphic larvae and older fish in my experiments (fig. 31) are not explained, but might be attributed to type and quantity of food offered (the rate rose sharply during August when two feedings a day commenced). The rate for specimen No. 1 rose sharply after June 20 when it began to eat pieces of fish (late metamorphic period).

Tolerance to abrupt changes in salinity.—Experiments to determine the tolerance of late metamorphic larvae 25–30 mm. long to sudden changes in salinity were inconclusive. Fish captured from marsh water were placed in beach water to which varying amounts of distilled water had been added. The salinity of the marsh water was 14.8 parts per thousand, and that of the beach and combination of beach and distilled water ranged from 17.0 to 26.8 ppt. On the day of capture, the fish placed in water with a salinity exceeding 22.0 ppt. died within an hour, but on the following day other specimens tolerated a higher salinity. The shock the fish experinced during handling the day they were captured probably affected their response to the difference in salinity or other water conditions. Alikunhi and Rao (1951) reported complete success in transferring "leptocephali" from water with a salinity of about 18 ppt. to completely fresh water, by stages and by direct transfer. I transferred no larvae from saline to nonsaline water.

OCCURRENCE OF LARVAE

Figure 1 shows the locations of capture for leptocephali from waters off the south Atlantic coast of the United States in 1953. Except for the 28.0-mm. specimen taken May 5 off Charleston, S.C., all were taken during October and November. The largest leptocephalus, 31.3 mm., was taken nearest the coast, several miles off between Cape Lookout and Cape Hatteras, N.C., on November 12. I believe it was captured during its migration to the beach, and that it occupied an offshore habitat during its early development. The other leptocephali were from waters of 100 fathoms or deeper, except for several taken at a single location on the 20-fathom curve.

Table 14 and figure 32 show the seasonal occurrence of early metamorphic larvae (shrinking) by size groups in biweekly seine samples from beach and marsh habitats near Brunswick, Ga., between March 1953 and October 1956. The earliest occurrence was March 15, the latest, October 23, but most (by number and frequency of occurrence) were taken during April and early May. In April 1953 they appeared first on the beach, then in the marsh, and in May they occurred only in the marsh. In 1954, 1955, and 1956 only one metamorphic larva was taken in the marsh. All late metamorphic larvae were taken in the marsh. The greater numbers of early, mid-, and late metamorphic larvae taken during 1956 probably reflect the increased efficiency of the larger seine used during that year.

How much time elapses between hatching of the egg and appearance of early metamorphic larvae on the beach is unknown. If the early metamorphic larvae that appear on the beaches of Georgia during March, April, and May (fig. 32) are of the same population as the leptocephali taken offshore in October and November, it would indicate slow growth during the winter months of November through February, and an age of about 6–8 months when they reach the beaches. I believe the smallest leptocephali taken offshore, 5.1 and 5.3 mm., are recently hatched fish, possibly only a few days old. Larger leptocephali (10–20 mm.) taken during October possibly were spawned within a month of capture. The extent of the spawning season is not indicated, only that there is spawning during the fall. However, the

TABLE 14.—*Seasonal occurrence of early metamorphic larvae, mid-metamorphic larvae, late metamorphic larvae, and juveniles in seine collections (specimens grouped by size)*

Number of individuals captured on—	Size groups in millimeters																	
	Early metamorphic larvae				Mid-metamorphic larvae	Late metamorphic larvae to juvenile												
	44.9–40.0	39.9–35.0	34.9–30.0	29.9–25.0	24.9–15.0 and 15.0–24.9	25.0–29.9	30.0–34.9	35.0–39.9	40.0–49.9	50.0–59.9	60.0–69.9	70.0–79.9	80.0–89.9	90.0–99.9	100–119	120–139	140–169	170–199
Mar. 15, 1956		[1] 2																
24, 1953																		
25, 1953																		
29, 1954																		
29, 1956	1	9																
Apr. 2, 1953	[1] 5																	
8, 1955																		
10, 1953	[1] 1	[1] 10	[1] 3															
13, 1956	[1] 2	[1] 25	[1] 13	1														
16, 1954		[1] 1																
22, 1953		[2] 2	1	[2] 2														
25, 1955	[1] 1	[1] 4		[1] 1														
27, 1956	[1] 9	88	[1] 30	[1] 1														
May 4, 1954		[1] 3	[1] 1															
6, 1953		1	1	1														
9, 1955																		
14, 1956	[1] 1			[1] 1														
18, 1954																		
20, 1953					2	12	7	1										
24, 1955																		
28, 1956																		
June 3, 1954									2									
4, 1953						1	1	3	3		5	1						
9, 1955																		
11, 1956																		
17, 1954																		
19, 1953													1	1	1			
22, 1955											1							
26, 1956		[1] 1		[1] 1														
July 3, 1953																		
6, 1954																		
8, 1955																		
10, 1956																		
21, 1953																		
21, 1954																		
22, 1955																		
24, 1956																		
Aug. 5, 1955																		
6, 1954																		
8, 1956											1							
11, 1953																		
19, 1954																		
19, 1955			[1] 1															
24, 1956			[1] 1															
26, 1953																		
Sept. 1, 1954																		
6, 1955																		
7, 1956																		
9, 1953								[3] 1	[3] 1	[3] 2				[3] 3	[3] 2		[3] 1	[3] 1
15, 1956																		
19, 1955																		
27, 1956												[3] 2			[3] 1	[3] 2	[3] 1	
Oct. 2, 1955																		
11, 1956																		
14, 1955																		
23, 1956			[1] 25	[1] 29	[1] 3													
29, 1954																		

[1] Taken on the beach.
[2] One specimen from marsh; others from the beach.
[3] From tidal marsh, Brunswick, Ga.

occurrence of early metamorphic larvae on the Georgia beaches from late March into October indicates a prolonged spawning season.

The appearance in 1953 of late metamorphic larvae (table 14) in the seine collections at Sapelo Marsh coincided with the disappearance of early metamorphic larvae, and suggests a single population.

Hildebrand (1943) reports ripe or nearly ripe fish on October 23, and leptocephali in various stages of development at Beaufort, N.C., during most of the months of the year. Holbrook (1860, p. 183) stated for South Carolina that "The *Elops saurus* arrives on our coast about the first of June, and remains with us until October, when it disappears until another season."

REFERENCES

ALIKUNHI, K. H., and S. NAGARAJA RAO.
1951. Notes on the metamorphosis of *Elops saurus* Linn. and *Megalops cyprinoides* (Broussonet) with observations on their growth. J. Zool. Soc. India, 3 : 99–109, 2 text-figs.

ANDERSON, WILLIAM W., JACK W. GEHRINGER, and EDWARD COHEN.
1956. Physical oceanographic, biological, and chemical data, South Atlantic Coast of the United States, M/V *Theodore N. Gill* Cruise 1. U.S. Dept. Interior, Fish and Wildlife Service Spec. Sci. Rept.—Fish. No. 178, pp. 1–160.

ANON.
1955. Opening the door to discovery. Bulletin of the International Oceanographic Foundation, 1(3) : 44–47.

BAILEY, REEVE M.
1951. The authorship of names proposed in Cuvier and Valenciennes' "Histoire Naturelle des Poissons." Copeia, No. 3, pp. 249–251.

BEEBE, WILLIAM.
1928. Beneath Tropic Seas. G. P. Putnam's Sons, New York-London, the Knickerbocker Press, pp. 228–229.

BERG, LEO S.
1947. Classification of fishes both recent and fossil. English and Russian. J. W. Edwards, Ann Arbor, Mich., p. 453.

BERTIN, LEON.
1937. Les Poissons Abyssaux Du Genre *Cyema* Günther (Anatomie, Embryologie Bionomie). The Carlsberg Foundation's Oceanographical Expedition Round the World 1928–30 and Previous *Dana*-Expeditions. Dana Report No. 10, pp. 1–30, figs. 1–24.

BREDER, C. M., JR.
1939. The tiniest of tarpon now at the Aquarium. New York Zoological Society Bulletin, 42(5) : 154–155.

CHIDAMBARAM, K., and M. DEVIDAS MENOM.
1948. Notes on the development of *Megalops cyprinoides* and *Hemirhamphus georgii*. Proc. Zool. Soc. London, 117 : 756–763, figs. 1–9.

DELSMAN, H. C.
1926. Fish eggs and larvae from the Java Sea (10. on a few larvae of empang fishes). Treubia, 8(3–4) : 400–412, 17 figs.

EVANS, HOWARD E.
1948. Cleaning and staining small invertebrates, in toto, for demonstrating ossification. Turtox News, 26(2) : 42–47.

FISH, MARIE POLAND.
1927. Contributions to the embryology of the American eel (*Anguilla rostrata* Le Sueur). Zoologica, 8(5) : 289–324.

FITCH, JOHN E.
1950. Life history notes and the early development of the bonefish, *Albula vulpes* (Linnaeus). California Fish and Game, 36(1) : 3–6, 2 figs.

FOWLER, HENRY W.
1931. Fishes obtained by the Barber Asphalt Co. in Trinidad and Venezuela in 1930. Proc. Acad. Nat. Sci. Phila., 83 : 392, fig. 1.

GILL, THEODORE.
1907. The tarpon and lady-fish and their relatives. Smithsonian Misc. Coll. 48 : 31–46, figs. 1–7.

GOPINATH, K.
1946. Notes on the larval and post-larval stages of fishes found along the Trivandrum Coast. Proc. Nat. Inst. Sci., India, 12(1) : 7–21, text-figs. 1–7.

HILDEBRAND, SAMUEL F.
1934. The capture of a young tarpon, *Tarpon atlanticus*, at Beaufort, North Carolina. Copeia, No. 1, pp. 45–46.
1939. The Panama Canal as a passageway for fishes, with lists and remarks on the fishes and invertebrates observed. Zoologica, 24 (Pt. 1, No. 3) : 15–45, figs. 1–4.
1943. Notes on the affinity, anatomy, and development of *Elops saurus* Linnaeus. J. Wash. Acad. Sci., 33(3) : 90–94, figs. 1–3.

HOLBROOK, JOHN EDWARDS.
1860. Ichthyology of South Carolina. Vol. 1. John Russell, Charleston, S.C. (University Press, Cambridge) 1 : 180–185, pl. 26).

HOLLISTER, GLORIA.
1936. A fish which grows by shrinking. New York Zool. Soc. Bull., 39(3) : 104–109, 5 figs.
1936. Caudal skeleton of Bermuda shallow water fishes. I. Order Isospondyli: Elopidae, Megalopidae, Albulidae, Clupeidae, Dussumieriidae, Engraulidae. Zoologica, 21(23) : 257–290, text-figs. 1–53.
1939. Young *Megalops cyprinoides* from Batavia, Dutch East India, including a study of the caudal skeleton and a comparison with the Atlantic species, *Tarpon atlanticus*. Zoologica, 24(28) : 449–475, text-figs. 1–21.

HOLSTVOOGD, C.
1936. The development of the mesonephros in some teleosts. Proefschrift, Universiteit van Amsterdam. Meijer's Boek—en Handelsdrukkerij—Wormerveer, XVI–98 pp., 14 figs. 35 photographs.

INDIAN COUNCIL OF AGRICULTURAL RESEARCH.
1951. Madras rural piscicultural scheme—Progress Report (Period: 1st April 1950 to 31st March 1951). Indian Council of Agricultural Research, pp. 1–2.

JORDAN, DAVID STARR.
1905. A guide to the study of fishes. Henry Holt & Co., N.Y., 1 : 143–144.

JORDAN, DAVID STARR, and BARTON WARREN EVERMANN.
1896. The fishes of North and Middle America : a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Pt. I. Bulletin of the U.S. Nat. Mus. No. 47, pp. 408–412.

MEEK, SETH E., and SAMUEL F. HILDERBRAND.
1923. The marine fishes of Panama. Field Museum of Nat. Hist. Publication No. 215, Zoological Series, 15 (Pt. 1) : 173–179.

MISRA, K. S.
1947. A check-list of the fishes of India, Burma and Ceylon. II. Clupeiformes, Bathyclupeiformes, Galaxiiformes, Scopeliformes and Ateleopiformes. Rec. Ind. Mus., 45 (Pt. 4) : 382–383.

NAIR, R. VELAPPAN.
1952. Studies on some post-larval fishes of the Madras plankton. Proc. Indian Acad. Sci., 35 : 225–244, figs. 1–12.

REGAN, C. TATE.
1909. A revision of the fishes of the genus *Elops*. Ann. Mag. Nat. Hist., vol. 3, 8 ser., pp. 37–40.
1910. The caudal fin of the Elopidae and of some other teleostean fishes Ann. Mag. Nat. Hist., vol. 5, 8 ser., pp. 354–358, 2 figs.

RIDEWOOD, W. G.
1904. On the cranial osteology of the fishes of the families Elopidae and Albulidae, with remarks on the morphology of the skull in the lower Teleostean fishes generally. Proc. Zool. Soc. London, 2 : 35–81, text-figs. 8–18.

SMITH, HUGH M.
1907. The fishes of North Carolina. North Carolina Geological and Economic Survey, 2 : 114–117, figs. 36–37.

VAN KAMPEN, P. N.
1908. Die larve von *Megalops cyprinoides* Brouss. Bull. Dept. Agr. aux Indies Neerlandaises, No. 20, pp. 10–12, 1 fig.

WHITLEY, GILBERT P.
1937. Studies in ichthyology, No. 10. Australian Mus. Rec. 20 (1) : 5–7, fig. 2.

Blank page retained for pagination

INDEX TO VOLUME 59

Page

Abdominal structures of *Penaeus setiferus* 103
aculeatus, Gasterosteus, threespine stickleback 540
Age composition of yellow perch 371
Age determination by hard parts of albacore 353
Age of grayling in Grebe Lake, Wyoming 335
Albacore of North Pacific and Hawaiian waters 353–363
alalunga, Germo, tuna of the Pacific Ocean 287
Alaska, Bare and Karluk Lakes 537, 550
Albacore, Pacific Ocean:
  Central Equatorial 297
  North Pacific 289
  maturity 300
  spawning 299
Albula vulpes 619
Alosa sapidissima, shad 269
Ammocoetes, habits of 593
Angler's harvest of Grebe Lake fishes 347
Annual landings of yellowtail flounder 183
Annulus of albacore 356
Atlantic Coast, young jack crevalles 417

Bare Lake and Karluk Lake, Kodiak Island, Alaska, threespine stickleback 537
Berry, Frederick H.: YOUNG JACK CREVALLES (*Caranx* species) OFF THE SOUTHEASTERN ATLANTIC COAST OF THE UNITED STATES 417–535
Biology of the threespine stickleback 540–557
Buller, Raymond J., William F. Royce, and Ernest D. Premetz: DECLINE OF THE YELLOWTAIL FLOUNDER (*Limanda ferruginea*) OFF NEW ENGLAND 169–267

Cape Cod:
  Spawning yellowtail flounder 216
Carangid larvae:
  Comparison of *Decapterus* and *Selar* 426
Carangidae:
  food for other species 439
  nomenclature and synonomy 419
  species, diverse forms 419
Caranx crysos 442–445, 534
  C. bartholomaei 440, 472–486
  C. dentex 521, 535
  C. hippos 503–506, 534
  C. latus 488–492, 503
  C. lugubris 434
  C. ruber 471
Caranx species common occurrence 417
Caranx juveniles, larvae, and eggs 440
Caranx species compared:
  characteristics of 5 species in Atlantic 426
  distribution in Atlantic Ocean 439

Page

Caranx lugubris 535
Catch of yellowtail flounder 197
Cayuga Lake (N.Y.) sea lamprey 561
Central equatorial Pacific 289
Central North Pacific 353–363
Chesapeake Bay yellowtail flounder 217
chuss, Urophycis 229
Circulatory system, *Penaeus setiferus* 140
Commercial fishery for yellow perch 368
Connecticut River shad catches 269
Crevalles, jack, *Caranx* species 417–435

Decline of haddock on yellowtail fishing grounds 228
DECLINE OF YELLOWTAIL FLOUNDER (*Limanda ferruginea*) OFF NEW ENGLAND, by William F. Royce, Raymond J. Buller, and Ernest D. Premetz 169–267
Definition of terms, ten-pounder 621
Digestive system, *Penaeus setiferus* 150
Distribution of eggs and larvae, yellowtail flounder 217

EARLY DEVELOPMENT AND METAMORPHOSIS OF THE TEN-POUNDER, *Elops saurus* Linnaeus, by Jack W. Gehringer 619–647
Early development of ten-pounder 623
Eggs and larvae, yellowtail flounder 217
Egg development and hatching, grayling 328
Egg development of lamprey 593
Elops saurus, ten-pounder 619
El-Zarka, Salah El-Din: FLUCTUATIONS IN THE POPULATION OF YELLOW PERCH, *Perca flavescens* (Mitchill), IN SAGINAW BAY, LAKE HURON 365–415
Excretory system (*Penaeus setiferus*) 155

Faunal changes, yellowtail flounder grounds 228
Fishes of Bare Lake, Alaska:
  coho salmon 539
  king salmon 539
  dolly varden charr 539
  rainbow or steelhead trout 539
  sculpin 539
Fishes of Karluk Lake:
  chum salmon 539
  pink salmon 539
  ninespine stickleback 539
Flounder, yellowtail, New England 169
FLUCTUATIONS IN THE POPULATION OF YELLOW PERCH, *Perca flavescens* (Mitchill). IN SAGINAW BAY, LAKE HURON, by Salah El-Din El-Zarka 365–415
Food of Grebe Lake fishes 344
Gasterosteus aculeatus, 3-spine stickleback 540

Page

Gehringer, Jack W.: EARLY DEVELOPMENT AND METAMORPHOSIS OF THE TEN-POUNDER, *Elops saurus* Linnaeus 619–647
Germo alalunga, tuna:
  commercial importance 289
  frequency of spawning 300
  ovary size 300
Glyptocephalus cynoglossus, gray sole 169
Gnathothorax of *Penaeus setiferus* 47
GRAYLING OF GREBE LAKE, YELLOWSTONE NATIONAL PARK, WYOMING, by Thomas E. Kruse 307–351
Greenbank, John, and Philip R. Nelson: LIFE HISTORY OF THE THREESPINE STICKLEBACK, *Gasterosteus aculeatus*, IN KARLUK LAKE AND BARE LAKE, KODIAK ISLAND, ALASKA 537–559
Growth and development of the ten-pounder 619–647
Growth of grayling 338
  sea lamprey 562
  stickleback 544
  yellow perch 383
Grebe Lake, Wyoming:
  biological features and chemical factors 308–309
  history of fish in lake 311
  physical characters of lake 308
  population study 312

Haddock decline in New England area 228
Hard parts in age determination of albacore 354
Hawaiian Islands landings of albacore 289
Hemicaranx fasciatus 525
Hill, Donald R.: SOME USES OF STATISTICAL ANALYSIS IN CLASSIFYING RACES OF AMERICAN SHAD (*Alosa sapidissima*) 269–286
Hippoglossoides platessoides, dab or American plaice 169
History of Grebe Lake, Wyoming 311
Holarctic grayling, *Thymallus articus* 307
Hudson River shad catches 269
Hybrid trout, age and growth in Grebe Lake 341

India, capture in Madras of *Elops saurus* 643

Jack crevalles (*Caranx* species), description 441–526

Karluk Lake and Bare Lake, Alaska, 3-spine stickleback 537
Key to Western Atlantic species of *Caranx* 424
Kodiak Island, Bare Lake 537
Kruse, Thomas E.: GRAYLING OF GREBE LAKE, YELLOWSTONE NATIONAL PARK, WYOMING 307–351

Lake Huron yellow perch 365
Lamprey, sea 561–617
Landings:
  commercial catch southern New England flounder 184
  yellowtail flounder 171–172, 177, 237
Larvae of yellowtail flounder 217, 222
  horizontal distribution, New Bedford 219
  occurrence 217

Page

Length of jack crevalles 419–420
Length composition of yellowtail flounder 185
Length frequencies of yellowtail flounder 239
Length of sea lamprey upstream migrants 586
Leptocephalid forms (*Elops saurus*) 622–626
Leptocephalid, small *E. saurus* 623
Life history commercial shrimp, *Penaeus setiferus* 1–168
LIFE HISTORY OF THE SEA LAMPREY OF CAYUGA LAKE, NEW YORK, by Roland L. Wigley 561–617
Limanda ferruginea, yellowtail flounder 169–267
LIFE HISTORY OF THE THREESPINE STICKLEBACK *Gasterosteus aculeatus* Linnaeus, IN KARLUK LAKE AND BARE LAKE, KODIAK ISLAND, ALASKA, by John Greenbank and Philip R. Nelson 537–559

Maturity and spawning of albacore 287
Megalops cyprinoides 620
Metamorphosis of the ten-pounder 625–627
Migrations of yellowtail flounder 175
Migratory behavior of sea lamprey in Cayuga Lake 561, 576
MORPHOLOGY OF THE WHITE SHRIMP, *Penaeus setiferus* (Linnaeus 1758), by Joseph H. Young 1–168
Muscular system of the white shrimp 3

National Park (Wyo.) grayling in Grebe Lake 307
Nelson, Philip R., and John Greenbank: LIFE HISTORY OF THE THREESPINE STICKLEBACK, *Gasterosteus aculeatus* Linnaeus, IN KARLUK LAKE AND BARE LAKE, KODIAK ISLAND, ALASKA 537–559
Nervous system, *Penaeus setiferus* 132
New England yellowtail flounder decline 169–266
New York and New Jersey shad 269, 270
Nomenclature and synonmy of *Caranx* species 419
North Pacific albacore 287

Otsu, Tamio, and Richard N. Uchida: SEXUAL MATURITY AND SPAWNING OF ALBACORE IN THE PACIFIC OCEAN 287–305
Otsu, Tamio, and Richard N. Uchida: STUDY OF AGE DETERMINATION BY HARD PARTS OF ALBACORE FROM CENTRAL NORTH PACIFIC AND HAWAIIAN WATERS 353–363

Pacific oceanic fishery investigations on albacore 287
Parasitic habits of the sea lamprey 602
Penaeus setiferus, white shrimp 1–168
Perca flavescens (Mitchill) 365
Population of Grebe Lake:
  areas of spawning grayling 318
  egg production 327
  spawning of Grebe Lake fishes 318–326
Predators on Grebe Lake fishes 348
Predators on stickleback in Karluk and Grebe Lakes 556
Premetz, Ernest D., William F. Royce, and Raymond J. Buller:
  DECLINE OF THE YELLOWTAIL FLOUNDER (*Limanda ferruginea*) OFF NEW ENGLAND 169–267

	Page
Producing areas for yellowtail flounder	171
Protocephalon of the shrimp	3
Pseudopleuronectes americanus, blackback flounder	169
Races of shad, Statistical evidence of	274
Raja, skates	229
Rare North American game fish	307
Reproductive system of the white shrimp	155
Royce, William F., Raymond J. Buller, and Ernest D. Premetz: DECLINE OF THE YELLOWTAIL FLOUNDER (*Limanda ferruginea*) OFF NEW ENGLAND	169–267
Saginaw Bay (Mich.), yellow perch	365
sapidissima, Alosa, American shad	269–286
Scale study of grayling	334
Scale-body relation in yellow perch	200, 384
Sea lamprey (*Petromyzon marinus*)	561
size and growth	562
morphometry	569
setiferus, Penaeus	1–168
SEXUAL MATURITY AND SPAWNING OF ALBACORE IN THE PACIFIC OCEAN, by Tamio Otsu and Richard N. Uchida	287–305
Shad, American	269
Shad catches in Hudson and Connecticut Rivers	269
Shrimp, *Penaeus setiferus*	1–168
Skates, *Raja*	229
Skeletal system of white shrimp	3
SOME USES OF STATISTICAL ANALYSIS IN CLASSIFYING RACES OF AMERICAN SHAD (*Alosa sapidissima*), by Donald R. Hill	269–286
South Atlantic coast, *Elops saurus*	619
Southeastern Atlantic, jack crevalles	417, 490
Spawning investigations of albacore	287–305
Spawning of jack crevalles	440
Spawning migration of sea lamprey	576
Spawning season of yellowtail flounder	216
Statistical analysis of classifying American shad (*Alosa sapidissima*)	269–286
Stickleback, *Gasterosteus aculeatus* in Karluk Lake and Bare Lake, Kodiak Island, Alaska	537
Stickleback, ninespine	540
Stocking fish in Grebe Lake	312
STUDY OF AGE DETERMINATION BY HARD PARTS OF ALBACORE FROM CENTRAL NORTH PACIFIC AND HAWAIIAN WATERS, by Tamio Otus and Richard N. Uchida	353–363
Sucker, white, sea lamprey parasitism on	612
Tagging and returns for yellowtail flounder	176–182
Tarpon larvae	620
Tarpon Atlanticus	619
Taxonomic groups for seven *Carank* species	434
Ten-pounder early development:	
definitions of terms	621
development and growth	623
growth experiments	641
osteology	633
pigmentation	631
Thynallus arcticus, grayling	307–351
Trends in commercial fishery for yellow perch	368
Trout, hybrid, Grebe Lake (Wyo.)	319
Uchida, Richard N., and Tamio Otsu: SEXUAL MATURITY AND SPAWNING OF ALBACORE IN THE PACIFIC OCEAN	287–305
Uchida, Richard N., and Tamio Otsu: STUDY OF AGE DETERMINATION BY HARD PARTS OF ALBACORE FROM CENTRAL NORTH PACIFIC AND HAWAIIAN WATERS	353–363
Uraspis heidi	526
Vegetation in Bare Lake and Karluk Lake, Alaska	539
Vessels:	
Theodore N. Gill cruises, 1953–54, South Atlantic	417, 419, 471
Theodore N. Gill collections off Cape Hatteras and Florida Straits	619, 622
Wigley, Roland L.: LIFE HISTORY OF THE SEA LAMPREY OF CAYUGA LAKE, NEW YORK	561–617
Yellow Perch:	
growth in length	377
growth in weight	394
year-class strength	404
Yellowtail larvae taken in 1932	256
Yellowtail stocks in New England	183–184
YOUNG JACK CREVALLES (*Caranx* species) OFF THE SOUTHEASTERN ATLANTIC COAST OF THE UNITED STATES, by Frederick H. Berry	417–535
Young, Joseph H.: MORPHOLOGY OF THE WHITE SHRIMP, *Penaeus setiferus* (Linnaeus 1758)	1–168
Zoarces anguillaris, eelpout	229

U.S. GOVERNMENT PRINTING OFFICE: 1962