

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:

Gehring, 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
for Library of Congress

Interior. Library

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

{r55e1}

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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.

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. hawaiiensis* Regan; Fowler (1931) illustrated an *E. saurus* larva; Holstvoogd (1936) discussed larval development of *E. hawaiiensis* (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. hawaiiensis*, *E. australis* Regan, *E. machinata* Forsk., and *E. lacerta* Valenciennes³—only *E. saurus* occurs on the Atlantic coast of the United States. Hildebrand (1939) found no evi-

dence 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). Bi-weekly 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."

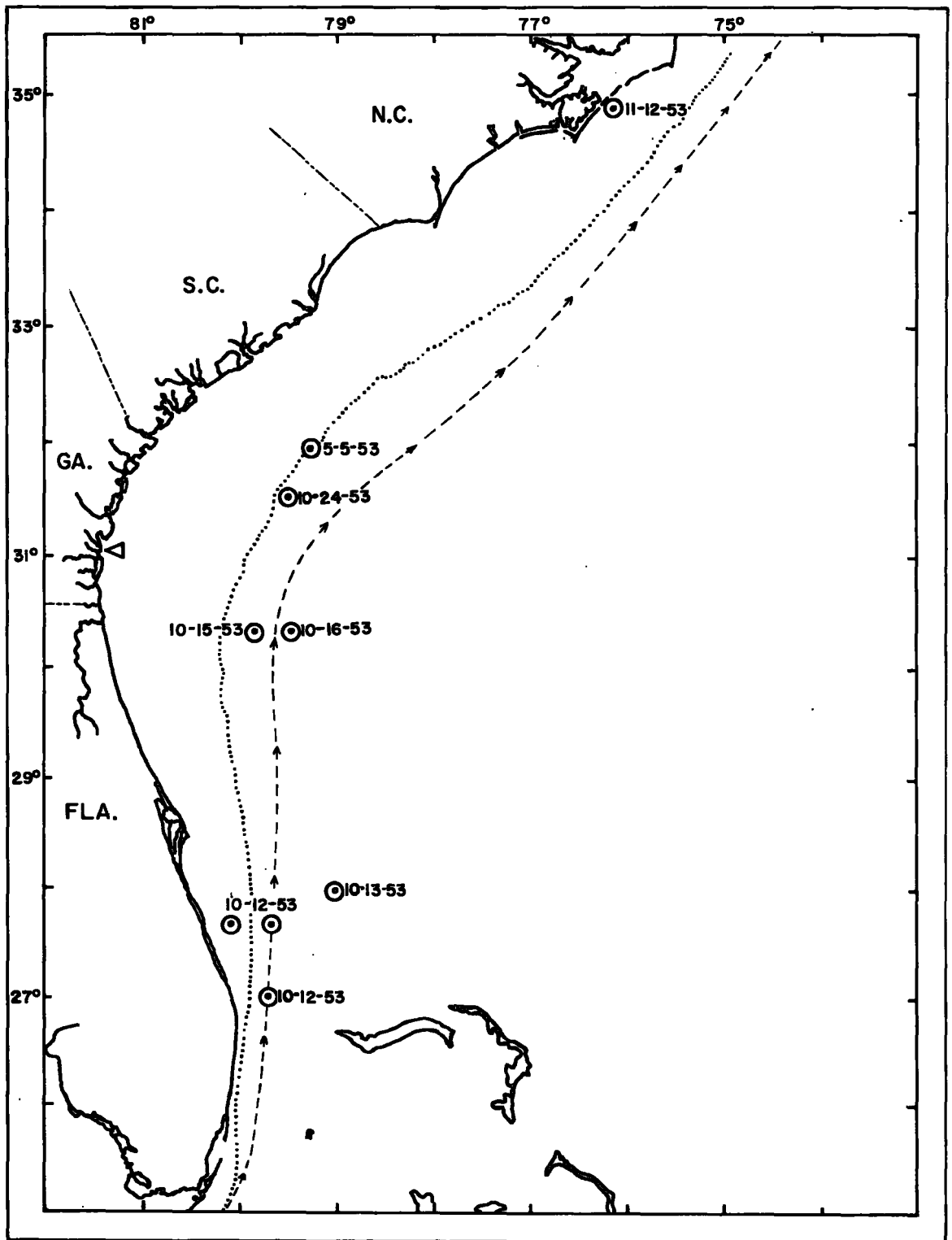


FIGURE 1.—Locations and dates of capture for leptocephali in plankton samples of *T. N. Gill* cruises off the south Atlantic coast of the United States. Location of seining station on Georgia coast is indicated by a triangle, 100-fathom curve shown as dotted line, and approximate axis of Gulf Stream 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

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					
	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	
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	-----	-----	-----	-----	12.6	13.2	15.1	15.6	17.6	17.8	19.0	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	-----	-----	-----	-----	-----	-----	16.6	16.8	19.0	19.4	21.1	26.1	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	0+19+0	0+19+0	0+19+0	0+19+0	-----	-----	-----	-----	-----	bud	bud	2	2	3	11	15	17	18	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	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	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
Number at kidney	-----	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 anus	70	70	72	71	70	65	71	72	66	72	69	67	71	71	70	70	68	59	61	59	-----	-----	-----	-----	
Teeth:	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
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:												
25.0-20.9 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 an-

terior 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

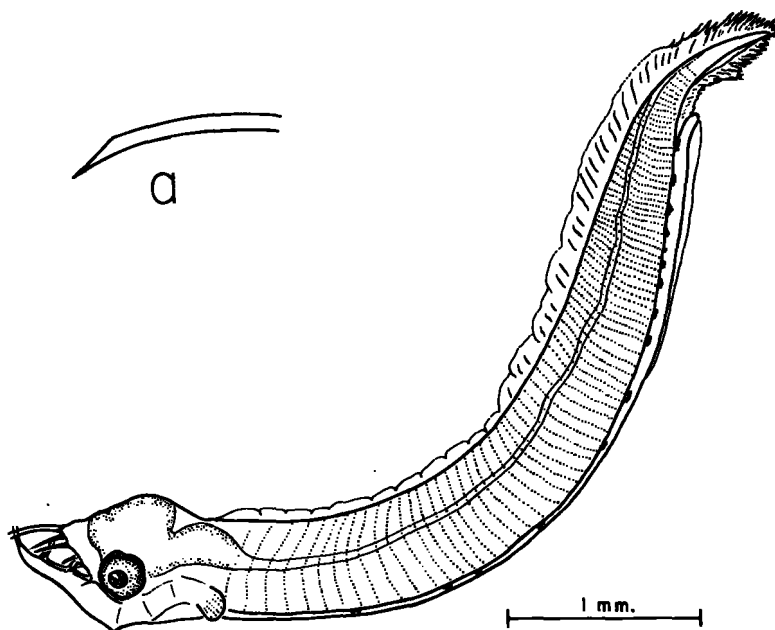


FIGURE 2.—Leptocephalus, 5.3 mm. standard length. (a) Side view of one of fanglike teeth in upper jaw, showing end beveled on upper surface.

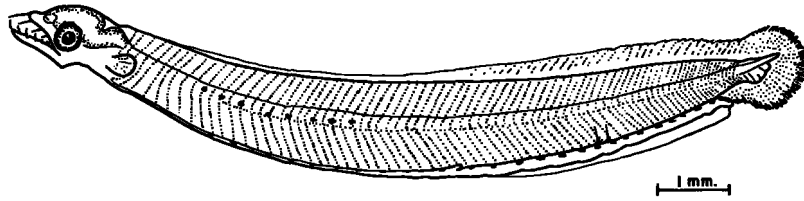


FIGURE 3.—Leptocephalus, 11.2 mm. standard length.

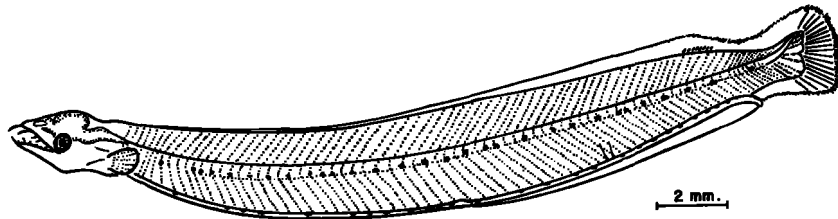


FIGURE 4.—Leptocephalus, 15.2 mm. standard length.

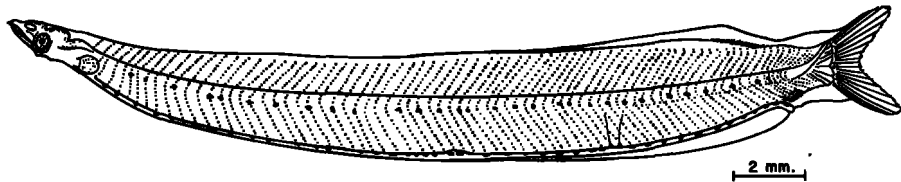


FIGURE 5.—Leptocephalus, 22.4 mm. standard length.

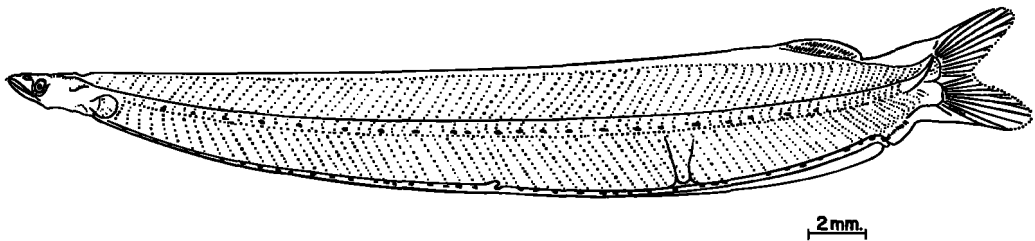


FIGURE 6.—Leptocephalus, 31.3 mm. standard length.

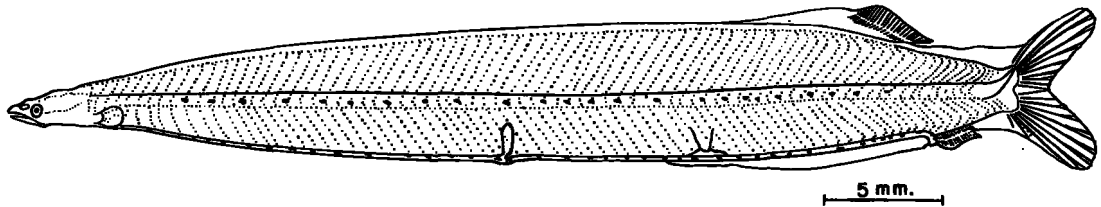


FIGURE 7.—Early metamorphic larva (or leptocephalus), 43.3 mm. standard length.

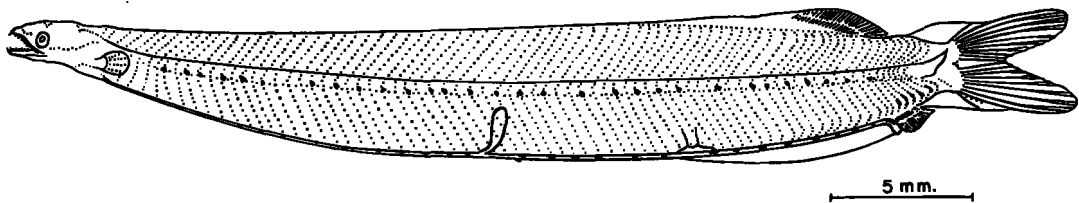


FIGURE 8.—Early metamorphic larva, 34.0 mm. standard length.

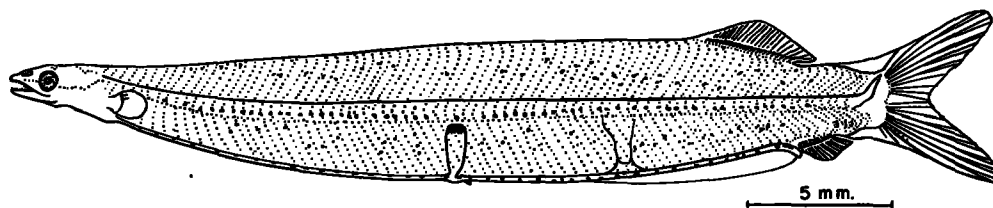


FIGURE 9.—Early metamorphic larva, 30.9 mm. standard length.

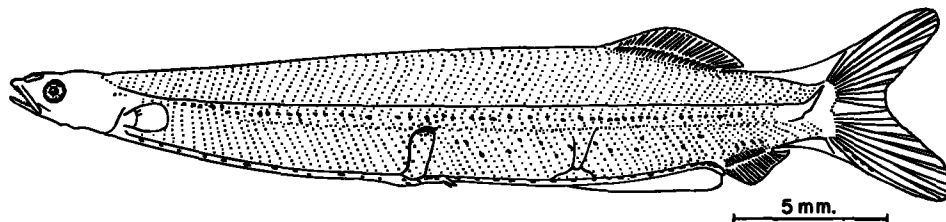


FIGURE 10.—Early metamorphic larva, 26.8 mm. standard length.

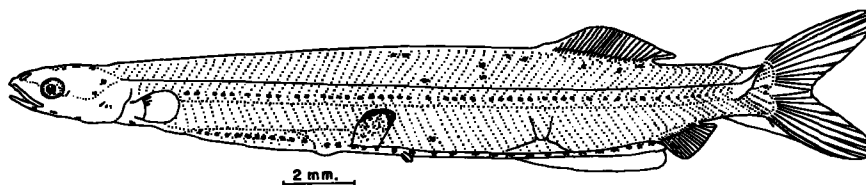


FIGURE 11.—Mid-metamorphic larva, 21.5 mm.

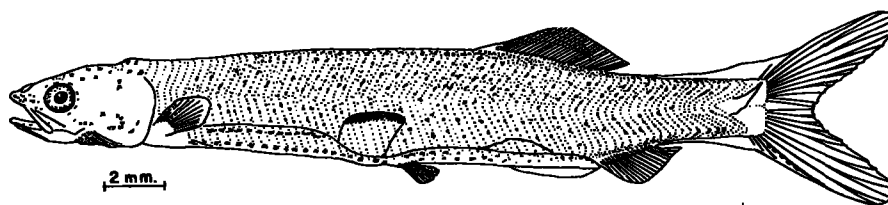


FIGURE 12.—Mid-metamorphic larva, 24.7 mm.

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. hawaiiensis* "leptocephalus" (an early metamorphic larva by my definition), a point inconsistent with my findings for *E. scovrus*.

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															
20.0-24.9 mm.....						1	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.....														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.																					
25.0-29.9 mm.....														1	1	1	4		3		
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													
20.0-24.9 mm.....	1		2											
25.0-29.9 mm.....						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.....								2	2	4	1			
39.9-35.0 mm.....								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.														
25.0-29.9 mm.....										1	3	2	1	
30.0-380 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	3		
80.0–380 mm																16	9		

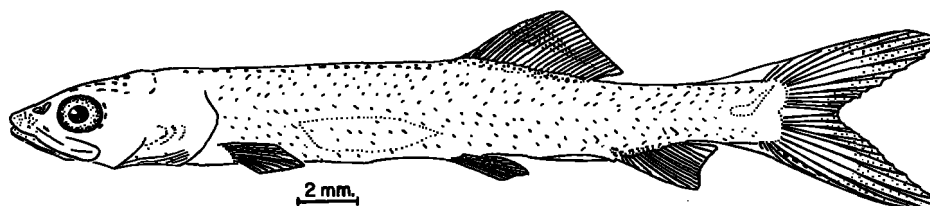


FIGURE 13.—Late metamorphic larva, 25.9 mm.

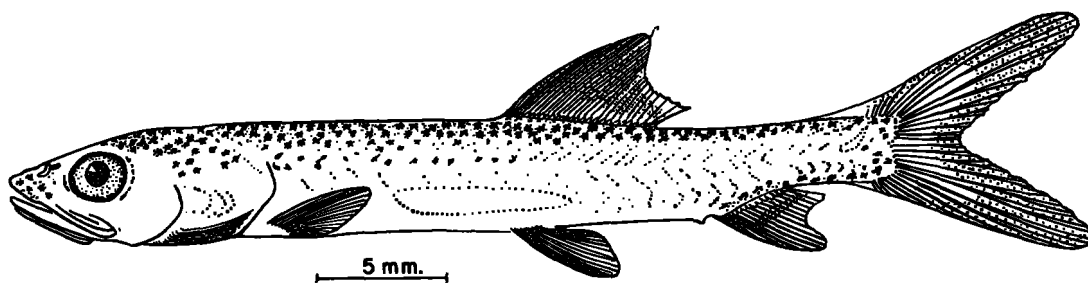


FIGURE 14.—Late metamorphic larva, 34.2 mm.

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	

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.

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—										
	9	11	11	12	13	14	15	16	17		
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		

The minute anterior secondary rays on juveniles and adults are often difficult to discern without dissection. By about 50–60 mm. the anterior-most 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. hawaiiensis*, but did not identify it. Holstvoogd (1936) discussed the development of the kidney in larval *E. hawaiiensis*, 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 upper 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		1	3				
25.0-29.9 mm	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		
60.0-69.9 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				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.

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-

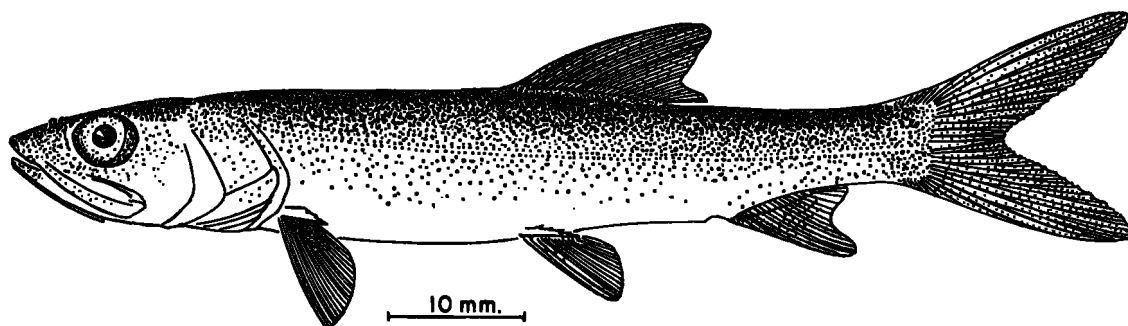


FIGURE 15.—Juvenile, 67.5 mm. standard length.

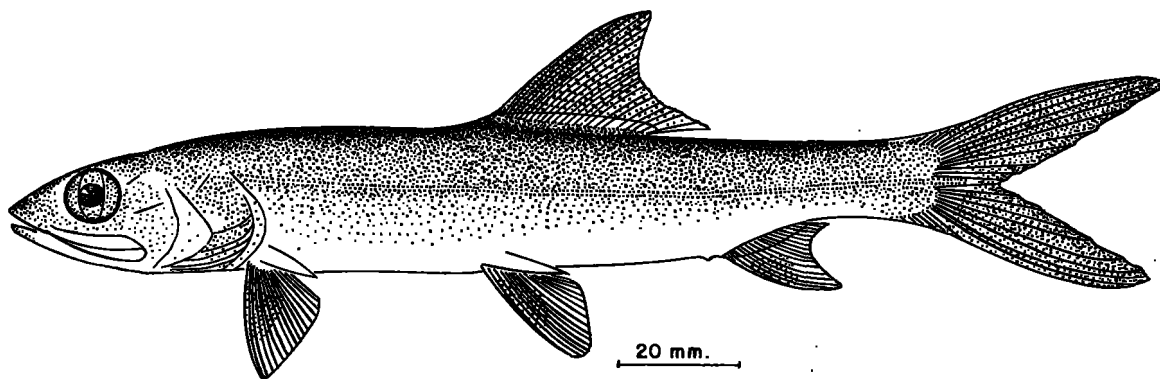


FIGURE 16.—Juvenile, 152 mm. standard length.

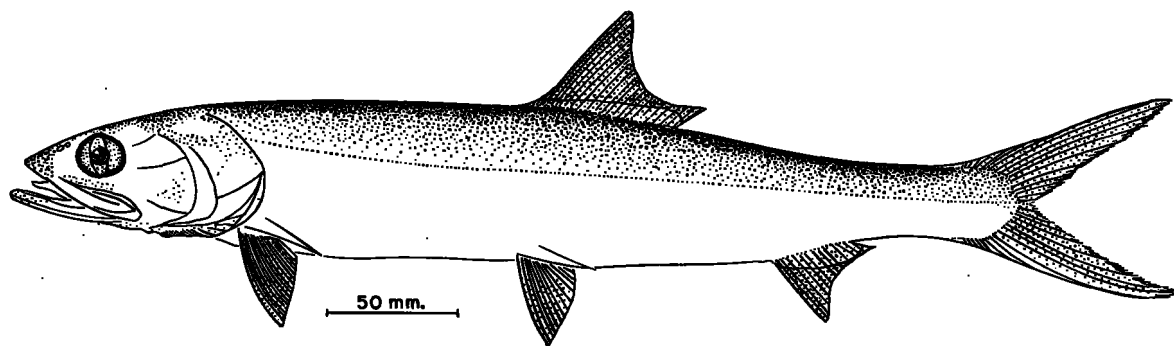


FIGURE 17.—Adult, 380 mm. standard length.

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

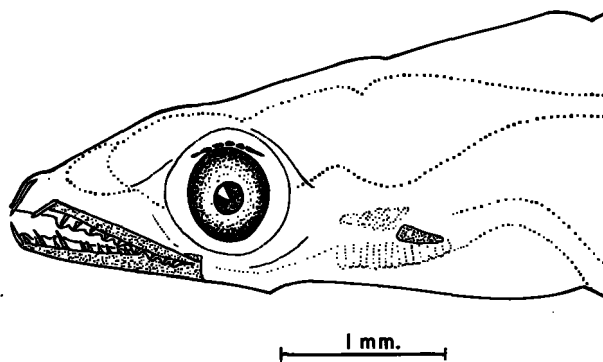


FIGURE 18.—Early metamorphic larva (or leptocephalus), 43.3 mm. standard length. Side view of head showing ossification as stippled areas (portions which stained with alizarine red).

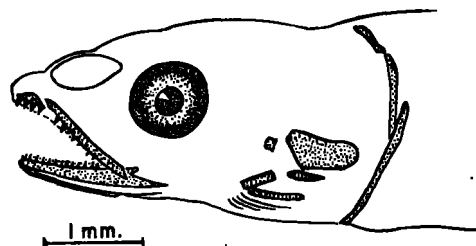


FIGURE 19.—Early metamorphic larva, 26.6 mm. standard length. Side view of head showing ossification as stippled areas.

(1936) presented the caudal osteology of juvenile or adult *E. sawrus*. 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

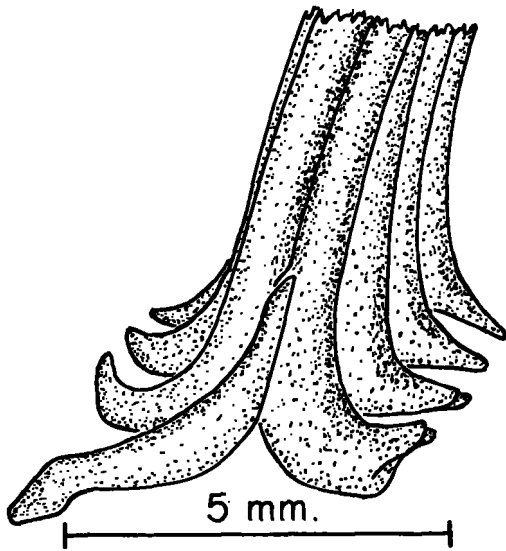


FIGURE 20.—Anterior view of the leading edge of pelvic fin of 240-mm. specimen, showing first four rays with process lying against first ray (base of process imbedded in flesh to the left of, or dorso-lateral to, the base of the first ray).

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

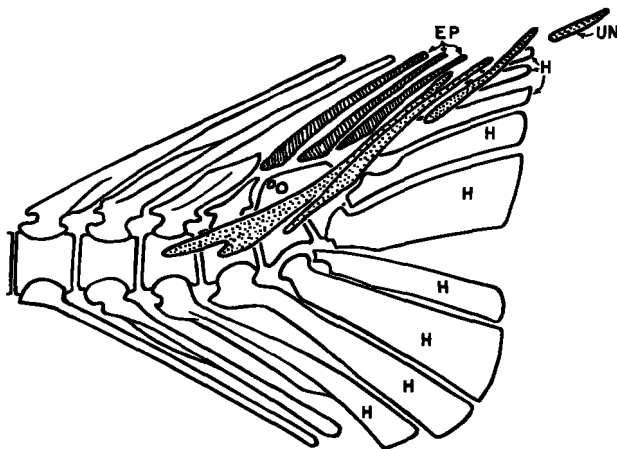


FIGURE 21.—Caudal osteology of 258-mm. *E. saurus*, (modified from Hollister, 1936, p. 261, fig. 14). The 9 hypurals are indicated by the letter H, the 4 uroneurals are stippled, and the 3 epurals are crosslined.

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.

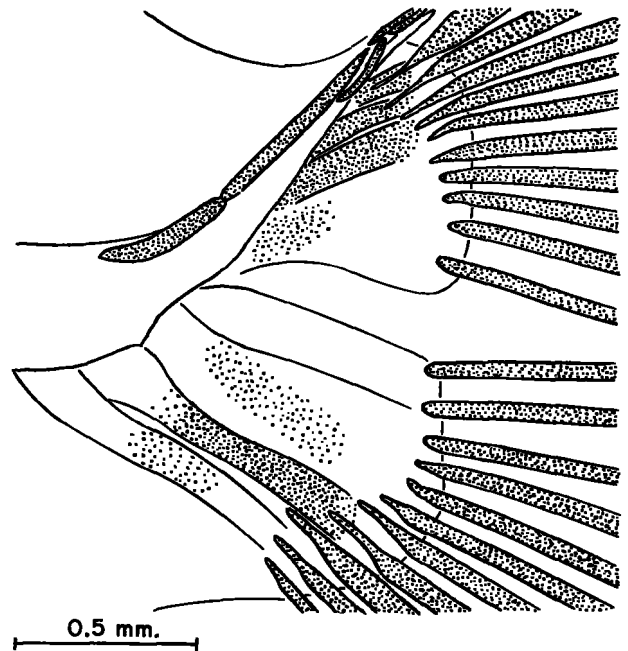


FIGURE 22.—Caudal osteology of a 31.3-mm. leptocephalus (fig. 6). Density of stippling indicates intensity of alizarine red stain.

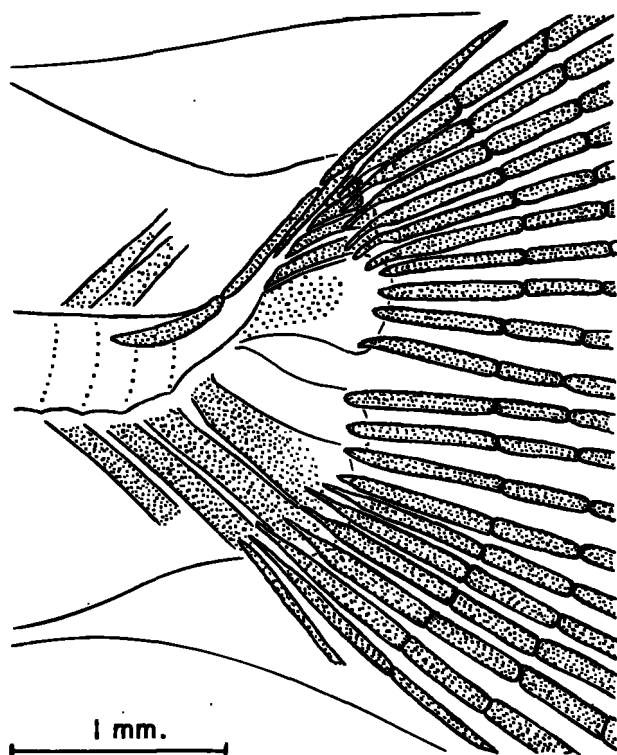


FIGURE 23.—Caudal osteology of a 30.9-mm. early metamorphic larva (fig. 9). Density of stippling indicates intensity of alizarine red stain.

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

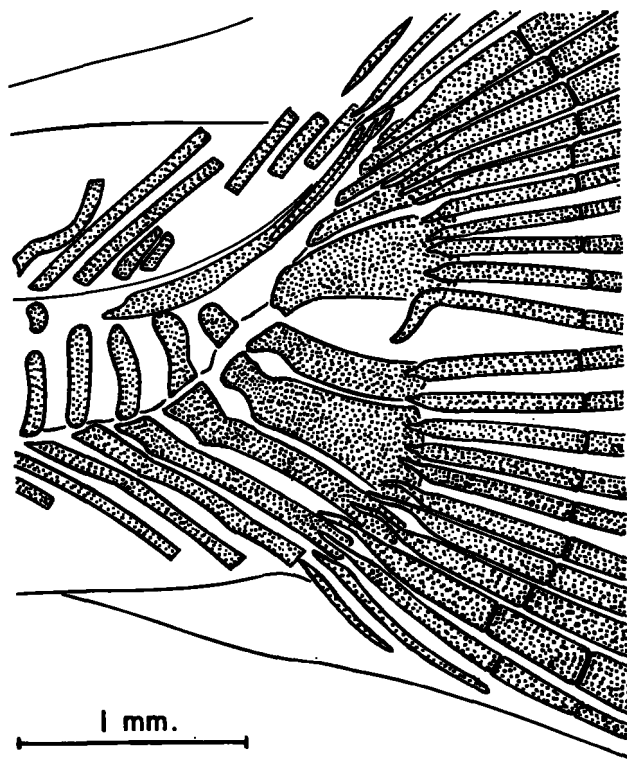


FIGURE 24.—Caudal osteology of 25.9-mm. late metamorphic larva (fig. 13). Stippling indicates alizarine red stain.

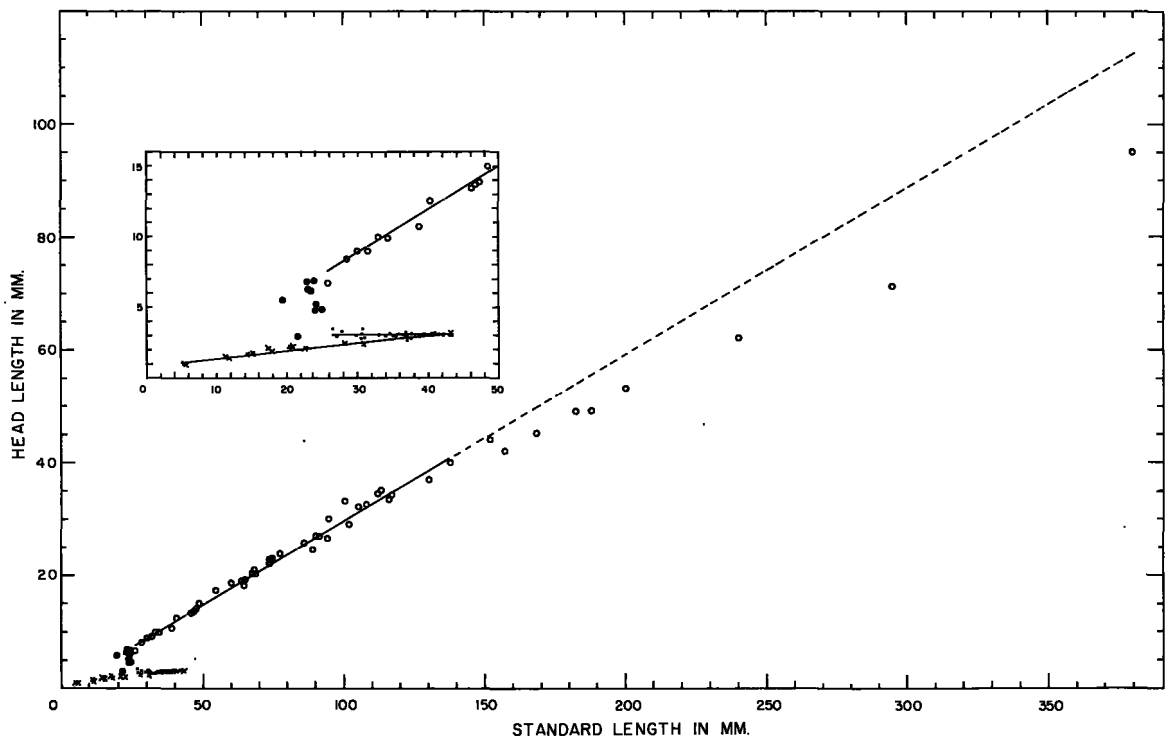


FIGURE 25.—Relation of head length to standard length. X's represent leptocephali; small dots, early metamorphic larvae; large dots, mid-metamorphic larvae; and circles, late metamorphic larvae to adults.

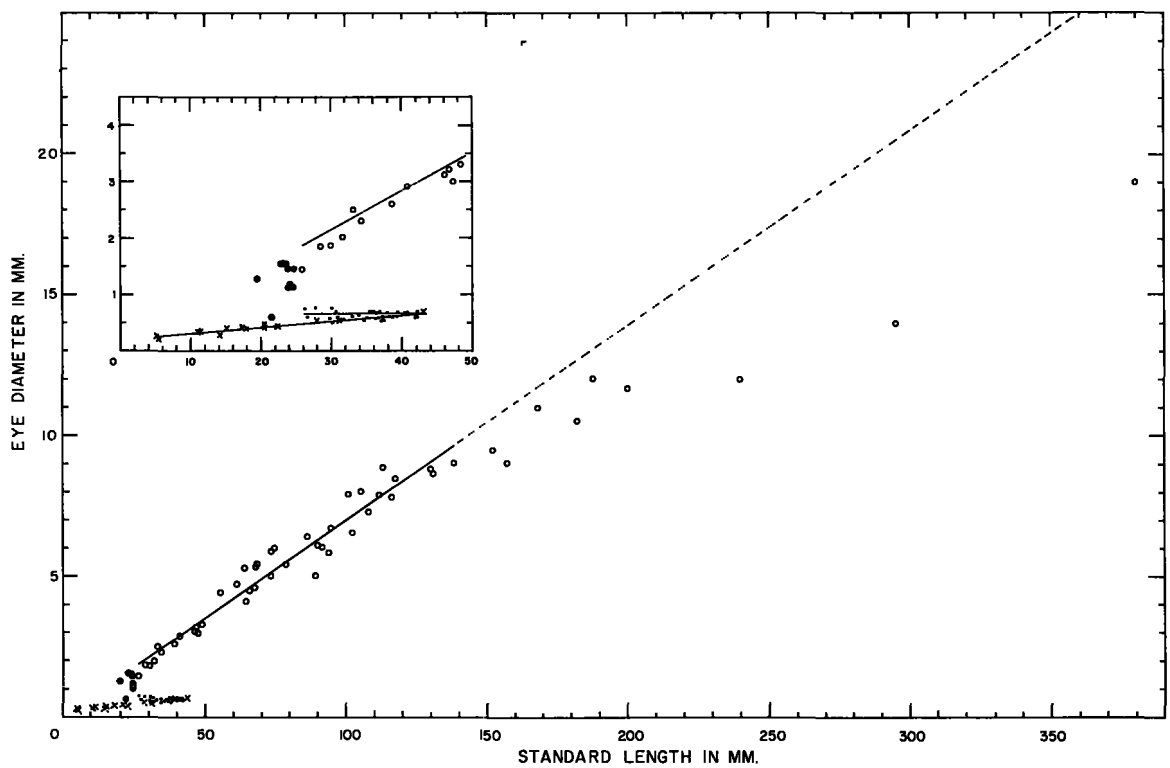


FIGURE 26.—Relation of eye diameter to standard length. X's represent leptocephali; small dots, early metamorphic larvae; large dots, mid-metamorphic larvae; and circles, late metamorphic larvae to adults.

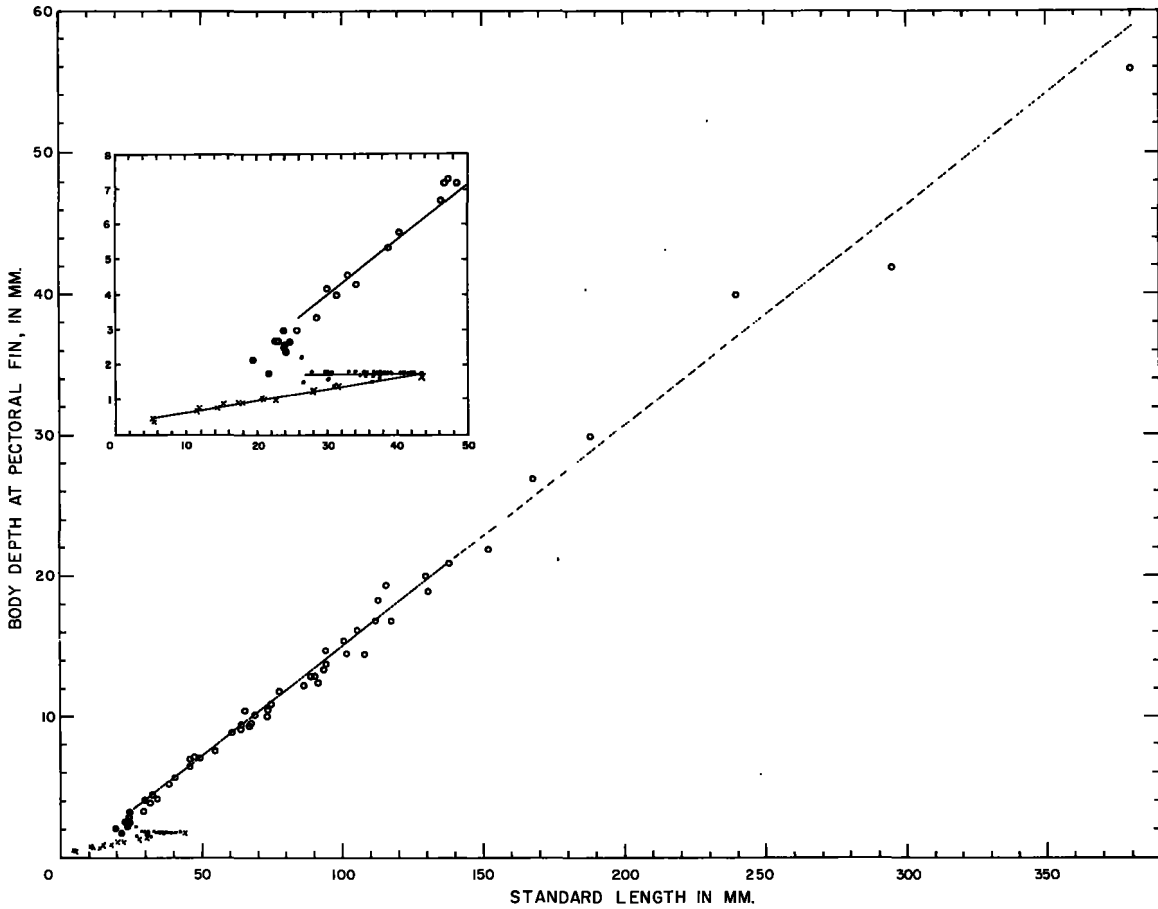


FIGURE 27.—Relation of body depth at pectoral fin to standard length. X's represent leptocephali; small dots, early metamorphic larvae; large dots, mid-metamorphic larvae; and circles, late metamorphic larvae to adults.

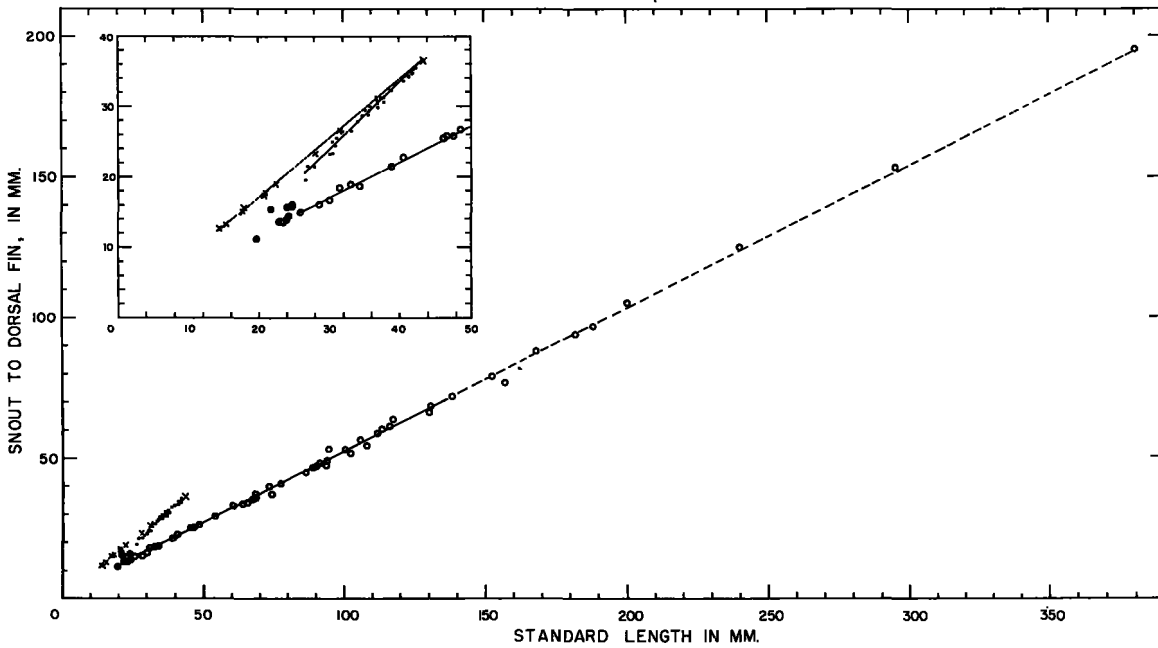


FIGURE 28.—Relation of distance snout-to-dorsal fin to standard length. X's represent leptocephali; small dots, early metamorphic larvae; large dots, mid-metamorphic larvae; and circles, late metamorphic larvae to adults.

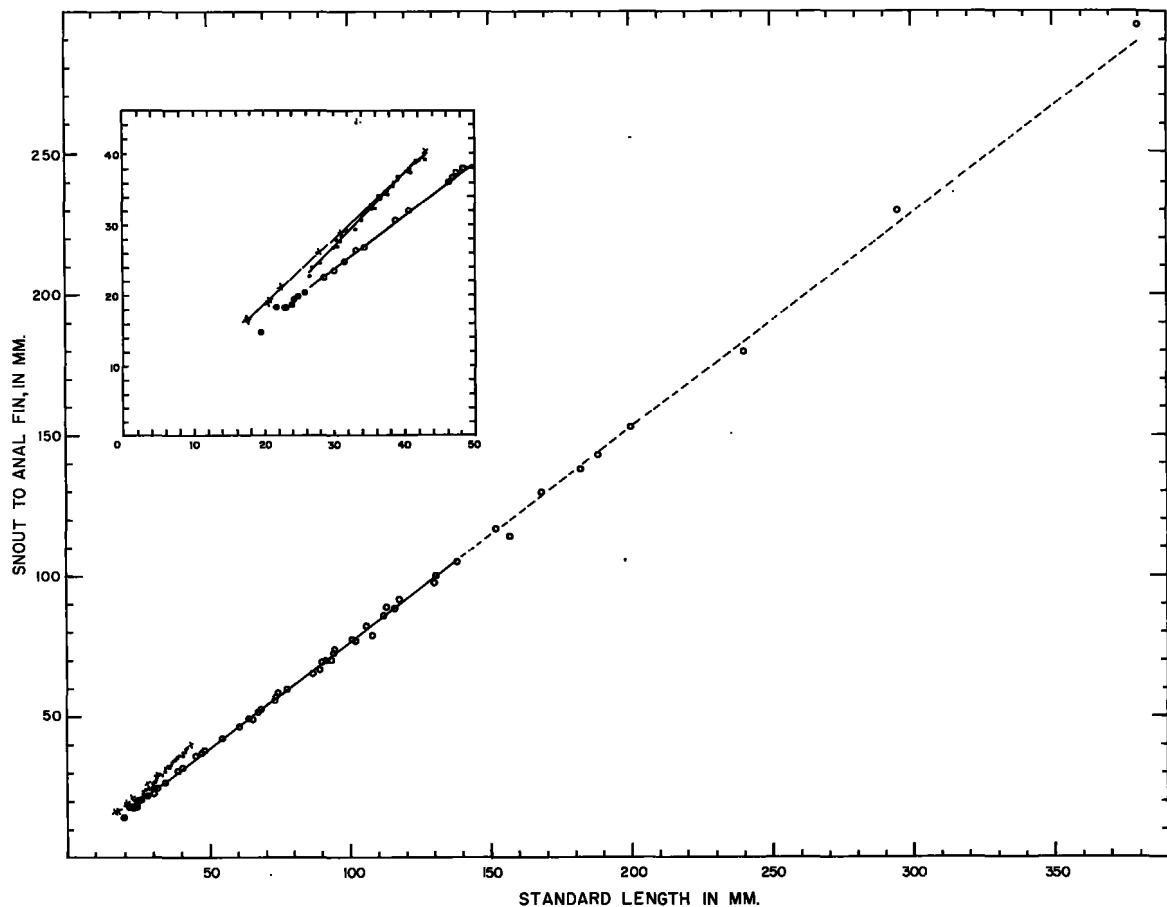


FIGURE 29.—Relation of distance snout-to-anal fin to standard length. X's represent leptocephali; small dots, early metamorphic larvae; large dots, mid-metamorphic larvae; and circles, late metamorphic larvae to adults.

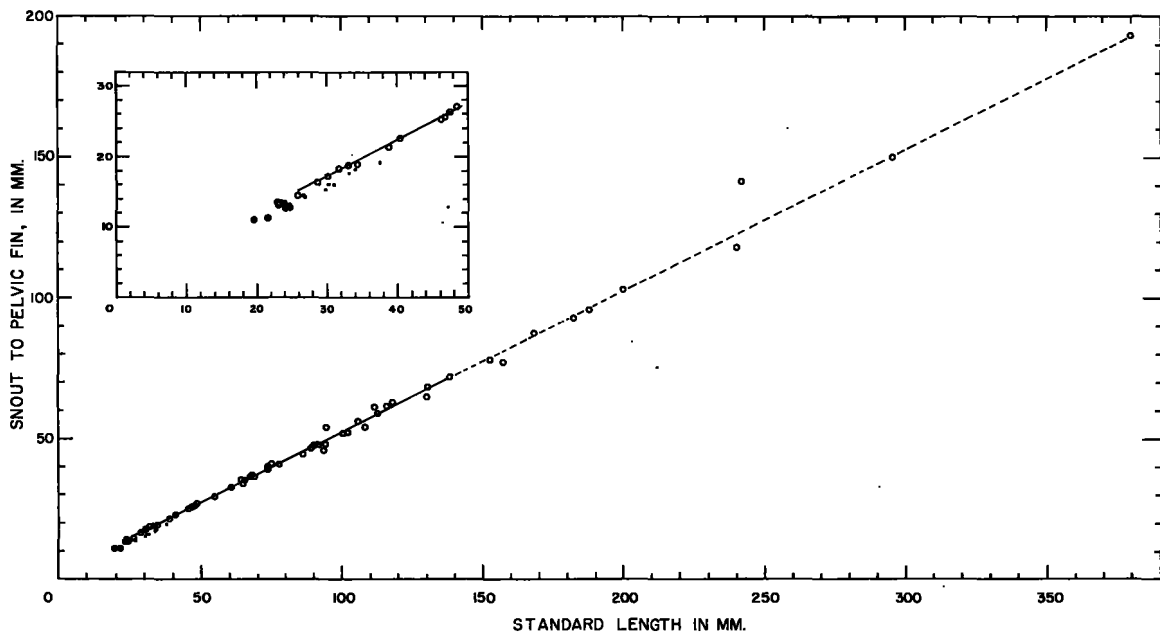


FIGURE 30.—Relation of distance snout-to-pelvic fin to standard length. Small dots represent early metamorphic larvae; large dots, mid-metamorphic larvae; and circles, late metamorphic larvae to adults.

TABLE 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

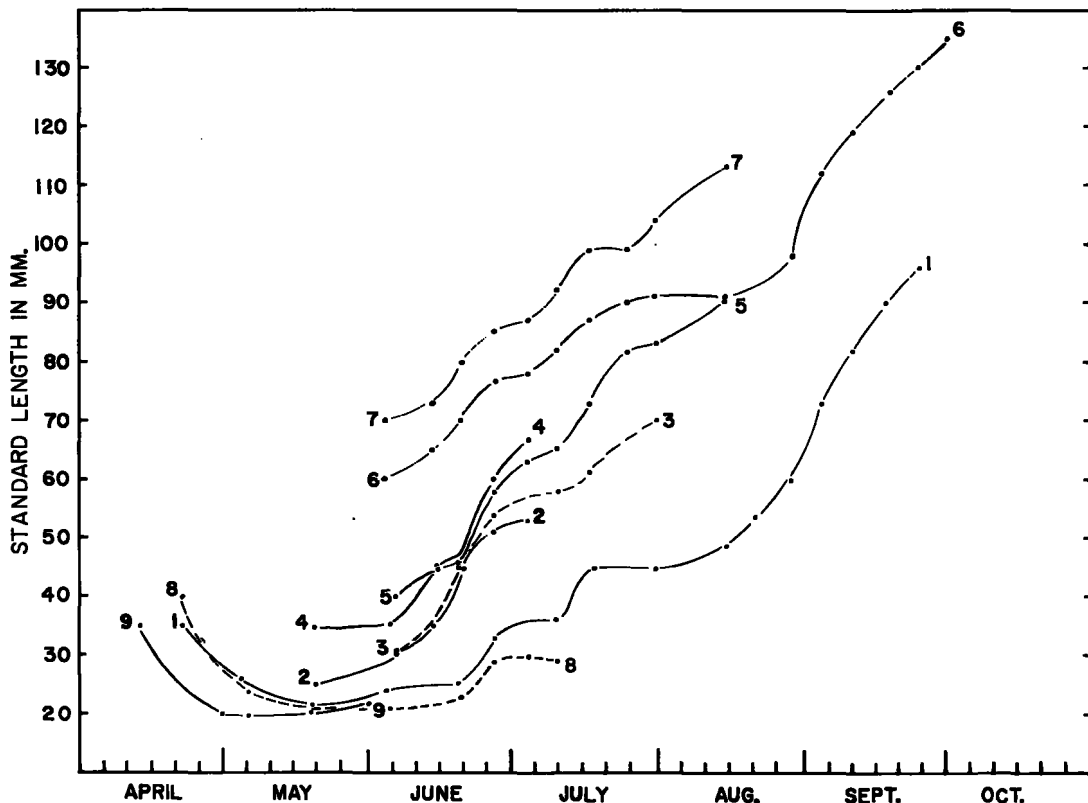


FIGURE 31.—Growth of laboratory-reared specimens. Standard length measurements for individual specimens are connected to indicate individual growth rates. Numbers associated with growth lines refer to specimen numbers in table 12.

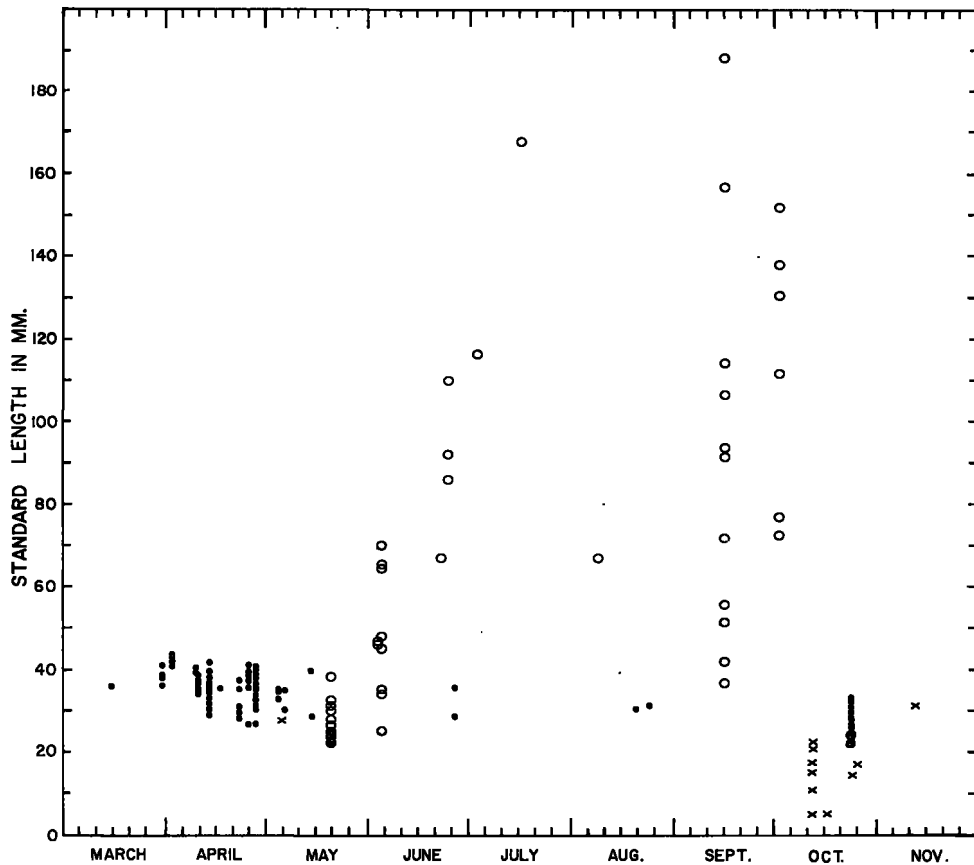


FIGURE 32.—Distribution of leptocephali (X's) from plankton samples; and early metamorphic larvae (small dots), mid-metamorphic larvae (large dots), and late metamorphic larvae and juveniles (circles) from seine samples; by size frequencies and dates of capture for the period from March 1953 to October 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 cross-ways 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	
20		25		35					
30									22
June 5	24			35		60	70		
6		30	30		40			23	
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		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			

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.

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 meta-morphic:					
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-meta-morphic:					
1	May 4-May 19	26-21	15	-5	-0.333
8	May 6-May 19	24-21	13	-3	-0.231
9	Apr. 20-Apr. 30	25-20	10	-5	-0.500
1	May 19-June 14	31-25	26	+6	+0.154
8	May 19-June 5	21-23	17	+2	+0.118
Late meta-morphic:					
1	June 14-Aug. 28	25-60	75	+35	+0.467
2	May 20-July 4	25-53	45	+28	+0.622
3	June 6-July 17	30-61	41	+31	+0.758
4	May 20-June 27	35-60	38	+25	+0.658
5	June 6-July 4	40-63	28	+23	+0.821
Juvenile:					
1	Aug. 28-Sept. 25	60-96	28	+36	+1.286
3	July 17-July 31	61-70	14	+9	+0.643
5	July 4-Aug. 15	63-91	42	+28	+0.667
6	June 4-Oct. 1	60-135	119	+75	+0.630
7	June 4-Aug. 15	70-113	72	+43	+0.597

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 experienced 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		12																
24, 1953																		
25, 1953																		
29, 1954																		
29, 1956		9																
Apr. 2, 1953	1	5																
8, 1955																		
10, 1953	11	10	13															
13, 1956	12	25	13	1														
16, 1954		1																
22, 1953		2	1	2														
25, 1955	11	4		1														
27, 1956	19	88	30	11														
May 4, 1954		13	1															
6, 1953			1		1													
9, 1955																		
14, 1956	11				11													
18, 1954																		
20, 1953					2	12	7	1										
24, 1955																		
28, 1956																		
June 3, 1954																		
4, 1953						1	1	3	3		5	1						
9, 1955																		
11, 1956																		
17, 1954																		
19, 1953																		
22, 1955											1		1	1				
26, 1956		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																		
24, 1956				1	1													
26, 1953																		
Sept. 1, 1954																		
6, 1955																		
7, 1956																		
9, 1953																		
15, 1956								1	1	2			3	2		1	1	
19, 1955																		
27, 1956																		
Oct. 2, 1955												2			1	2	1	
11, 1956																		
14, 1955																		
23, 1956																		
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."

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