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DEVELOPMENT OF THE LINED SOLE, ACHIRUS LINEATUS, DESCRIBED FROM LABORATORY-REARED AND TAMPA BAY SPECIMENS

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Marine Research Laboratory
Florida Department of Natural Resources
Division of Marine Resources
St. Petersburg, Florida

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DEVELOPMENT OF THE LINED SOLE, ACHIRUS LINEATUS, DESCRIBED FROM LABORATORY-REARED AND TAMPA BAY SPECIMENS

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ABSTRACT

Morphological development of the lined sole, *Achirus lineatus*, is described from specimens reared in the laboratory at Miami, Florida, and from plankton collected in Tampa Bay. The pelagic eggs were spherical, averaged 0.74 mm diameter, and had multiple oil globules. Growth of laboratory-reared larvae to 27 days after hatching is described. Larvae grew an average of 0.26 mm per day. Of the initial stock of 300 fertilized eggs, 33 juveniles survived for 30 days after hatching, a survival rate of 0.11. Behavior of larvae in the rearing tank is described. Metamorphosis began in laboratory-reared larvae at 10 days after hatching, when they averaged 3.2 mm SL (standard length). Tampa Bay larvae began to metamorphose at 3.0 mm SL. Metamorphosis was essentially completed at 5.0 mm SL. The sequence of initiation of fin development was: pectorals, dorsal, anal, caudal, and pelvics. Pectoral fins developed on both sides of larvae but disappeared on the left side after metamorphosis. A dorsal tentacle, posterior to the head, developed on larvae, grew to about 50% SL when larvae began to metamorphose, and then gradually disappeared as larvae completed metamorphosis. Four major rows of spinous scales developed on

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the sides of larvae before they began to metamorphose. Three prominent spinous bony ridges were present on each side of the head, one of which (the right frontal ridge) became the interorbital ridge when the left eye migrated across the dorsal midline. Eye migration was characterized by the left eye moving across the midline under a "hook" formed by the dorsal fin. Body proportions changed during growth and metamorphosis; head length increased and preanal length decreased relative to standard length. The only pigment on embryos and newly hatched larvae was scattered white chromatophores. Distinctive patterns of dark brown, stellate melanophores developed on older larvae. An interbranchial foramen developed in larvae at about 3.0 mm SL. The presence of the foramen and dorsal tentacle serve to separate *A. lineatus* larvae from the otherwise similar *Trinectes maculatus*. Larvae of *A. lineatus* from Tampa Bay usually were more developed at a given length than were laboratory-reared larvae of the same length, and body proportions differed significantly between the two groups. Juveniles from Tampa Bay, Biscayne Bay, and the rearing experiment also differed with respect to certain meristic and morphometric comparisons. Probable reasons for the differences are discussed.

ACKNOWLEDGMENTS

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INTRODUCTION

Eggs and larvae of the lined sole, *Achirus lineatus* (Linnaeus), have not been described, even though the species is one of the most common flatfishes found along the southeastern coast of the United States. The species occurs along the Atlantic coast from Florida to Uruguay, and is widespread along the coast in the Gulf of Mexico (Briggs, 1958). We studied development and metamorphosis of the species, from a series of laboratory-reared specimens and from specimens in plankton catches. Laboratory-reared larvae originated from fertilized pelagic eggs collected in Biscayne Bay, near Miami on the east coast of Florida. Plankton collections were from

Tampa Bay, on the west coast of Florida. The two groups were compared to determine if development differed. We hypothesized that some differences might occur, due either to the rearing tank environment or to differences in the gene complements of the two populations.

Descriptions of development of soles (Soleidae) are uncommon in the literature. A review of studies on development of many European soles has been included in the work of Padoa (1956). Kyle (1913, 1921) described larvae and development of a number of European flatfishes, including some soles. Many aspects of flatfish larval development were discussed by Norman (1934). *Trinectes maculatus* is the only American sole for which larval development has been described (Hildebrand and Cable, 1938). In addition to the description of development of *A. lineatus* given in this report, Futch and Houde (in manuscript) have studied the osteology of the species, including that of the larval stages.

METHODS AND MATERIALS

Meristics and Morphometrics

All counts and measurements were made with a binocular dissecting microscope and ocular micrometer. Counts of dorsal and anal fin rays sometimes were counts of pterygiophores, which developed prior to the associated rays. Counts of pectoral and pelvic fin rays were made on both sides of larvae. Measurements were made on the left side of larvae in which the left eye had not passed the dorsal midline during metamorphosis. Larvae that had developed to the stage where both eyes were on the right side were measured on that side. We measured the following:

Total Length (TL): Tip of snout to tip of caudal fin.

Standard Length (SL): Tip of snout to tip of notochord in young larvae. Tip of snout to posterior margin of hypural plate in older larvae.

Preanal Length: Tip of snout to anus.

Head Length: Tip of snout to posterior edge of operculum.

Body Depth: Measured at anus, including width of dorsal fin.

Dorsal Tentacle Length: Base of dorsal fin at the insertion of tentacle to tip.

Eye Diameter: Horizontal distance between margins of fleshy orbit of right eye.

Developmental Description

Premetamorphosing and metamorphosing stages can be recognized in developing *A. lineatus* larvae. We described morphometric and meristic characters as they developed within each of the two stages rather than describing the entire larva at each length class. This method gives continuity to the record of changes in the development of particular characters.

Premetamorphosing and metamorphosing larvae were distinguished by determining whether the left eye had begun to migrate toward the dorsal midline. This distinction was made by measuring the distance from the insertion of the pectoral fin to the posterior margin of the orbit. In premetamorphosing larvae no difference in this measurement could be detected when left and right sides were compared, but in metamorphosing larvae the distance on the left side exceeded that on the right.

Development was described from both laboratory-reared and Tampa Bay larvae. Illustrations were made of laboratory-reared specimens only. Because age data were lacking for Tampa Bay larvae, characters in the two groups were compared by examining their development at comparable standard lengths. When possible, rates of development for some characters were compared by regression or covariance analyses.

Laboratory-reared Larvae

Eggs were collected on 28 July 1969 at Bear Cut, Biscayne Bay, in a 0.5 m plankton net suspended at the surface. Collections were made between 10:00 and 15:00 (EST), when average surface temperature was 30.8° C and salinity was 32.25 o/oo. Three hundred eggs were placed in a 75-liter aquarium for rearing. Two liters of a dense *Chlorella* bloom were added to provide a good bloom in the rearing tank on subsequent days. *Chlorella* has been demonstrated to promote growth and increase survival of fish larvae, probably by removing harmful nitrogen metabolites. Temperature ranged from 26.0 to 29.0° C (mean 27.1° C) and salinities increased from 32.8 to 35.8 o/oo (mean 34.4 o/oo) during the first 20 days of rearing. Larvae fed on zooplankton collected in a 35 μ mesh plankton net. Only plankton less than 150 μ body width was offered for the first 6 days after hatching.

Subsequently, larger food was added, including plankton and, commencing on the 16th day after hatching, brine shrimp *(Artemia salina)* nauplii. Further details of our techniques for rearing larval fish were described by Houde and Palko (1970).

Three to five specimens from the rearing experiment were preserved each day in 5% buffered formalin to obtain a series for study. Four embryos and 62 larvae were used to describe development during the 27-day period after hatching. Specimens were accessioned into the Tropical Atlantic Biological Laboratory (TABL) Museum Fish Collection.

Tampa Bay Larvae

Larvae were collected from Tampa Bay between January 1962 and June 1963 in 0.3 m plankton nets of 667 μ mesh or 0.5 m nets of 175 μ mesh. Station descriptions were given by Eldred *et al.* (1965) and Eldred (1966). Specimens were preserved in 3 to 5% buffered formalin. A total of 224 larvae, 1.6 to 5.0 mm TL, were collected, and 95 undamaged specimens were examined. Tampa Bay larvae were accessioned into the Florida Department of Natural Resources Ichthyological Collection (FSBC).

Juveniles

Juvenile specimens from Tampa Bay, Biscayne Bay, and from the rearing experiment were examined for morphometric and meristic differences. Of 49 specimens, 22 (10.2 to 61.0 mm SL) were from Tampa Bay; 15 (19.2 to 50.7 mm SL) were from Biscayne Bay; and 12 normally metamorphosed (31.4 to 52.2 mm SL) were from the rearing experiment.

LARVAL DEVELOPMENT

Growth

Laboratory-reared larvae grew in length throughout the premetamorphosing and metamorphosing stages (Figure 1). Changes in growth rate did not occur during metamorphosis. Larvae averaged 1.59 mm SL (1.68 mm TL) at 6 hr after hatching and 8.60 mm SL (10.60 mm TL) at 27 days, when metamorphosis was essentially complete. Growth in length was expressed by the equation $\text{Log } Y = 0.2365 + 0.0261X$, where Y is standard length and

X is days after hatching (coefficient of determination, $r^2 = .951$). Growth rate increased slowly throughout the larval period. Mean daily growth increment for the 27 days was 0.26 mm. Thirty-one juveniles reared beyond 27 days averaged 14.0 mm SL at 70 days and 26.2 mm SL at 125 days. Twenty specimens averaged 37.5 mm SL at 200 days. Juveniles grew approximately 0.18 mm per day, a somewhat slower rate than that of larvae.

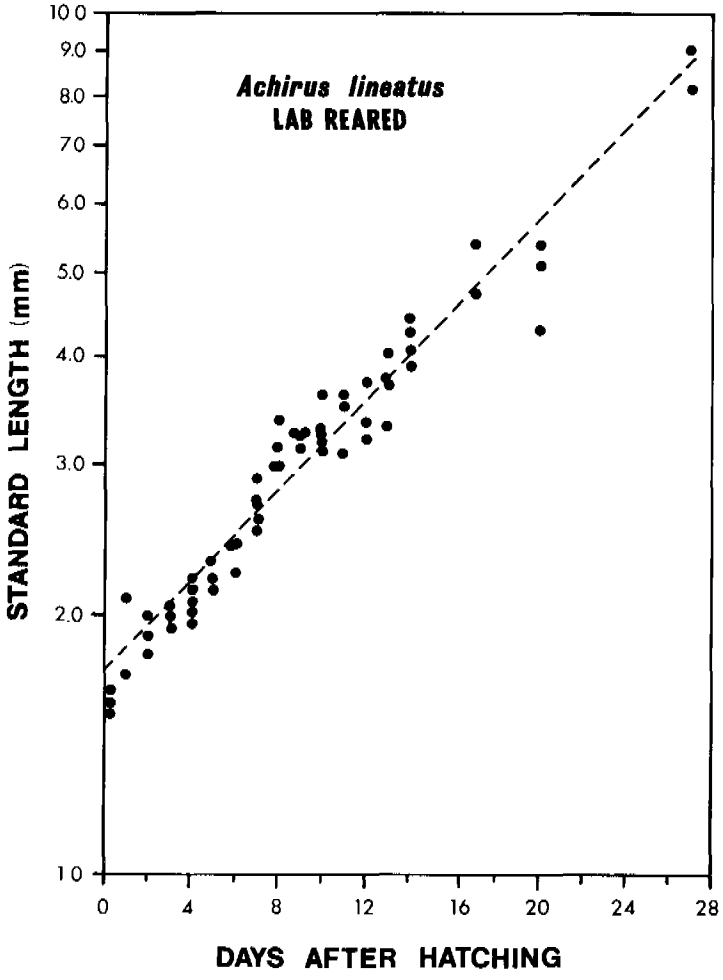

Figure 1. Growth of laboratory-reared *Achirus lineatus*.

Mortality

A total of 33 juveniles survived until 30 days. Survival rate was 0.11 based on the 300 embryos placed in the rearing tank. Most mortality occurred in the first 15 days, but no catastrophic losses such as might be associated with a "critical period" (Marr, 1956) were observed. Included in the total mortality were 62 specimens preserved for study. If that deliberate source of mortality and natural mortality are considered independent, the 30 day survival rate would have been 0.14. Only two juveniles died of natural causes from 30 to 200 days.

Behavior

Newly hatched larvae were almost neutrally buoyant and drifted in the rearing tank. They did not attempt to swim until 2 days after hatching, when the fan-shaped pectoral fins developed. The large pectoral fins were the principal means of locomotion for premetamorphosing larvae. The larvae were not active swimmers compared to most perciform and clupeiform larvae we have reared. Larvae began to feed at about 40 hr when eyes were pigmented and their yolk absorbed (1.9 mm SL). A larva fed by approaching a potential food organism until its snout nearly touched it; in the next few seconds, the larva either darted at the organism or swam away in search of other food. No study was made of food items, but the first plankton organisms offered as food were less than 100 μ body width and were mostly copepod nauplii. Several cleared and stained metamorphosing larvae had copepods in their digestive tracts.

Larval behavior changed just before metamorphosis. At 6 days (2.5 mm SL), larvae began to swim for short periods near the bottom of the tank with the body axis tipped toward the left side. At 8 days (2.8 mm SL) some larvae would rest on the tank bottom for several minutes, and then return to the mid-region of the tank to feed on plankton. By the 10th day (3.15 mm SL), larvae spent nearly half of the time on the tank bottom. We could not determine whether larvae were resting on their left or right side because of the dense *Chlorella* bloom and sediments on the tank bottom. After the 12th day (3.6 mm SL), larvae spent most of each day on the bottom. However, even at 17 days (4.8 mm SL), some larvae briefly left the bottom to feed on plankton. Juveniles, 10 to 15 mm SL, occasionally spent from a few minutes

to more than an hour in the surface film feeding on plankton. Juveniles of this size also were observed clinging to the tank sides, darting out to feed on large plankton organisms.

Embryos

Laboratory-reared embryos were in late stages of development when collected (Figure 12). Four preserved eggs were spherical, ranging in diameter from 0.71 to 0.76 mm (mean 0.74 mm). The egg membrane was thin, colorless, and unsculptured. From 13 to 19 clear, slightly yellow oil globules (0.02 to 0.09 mm diameter) were scattered throughout the transparent, colorless yolk. Small white, granular chromatophores were abundant over the entire embryo and were sparsely scattered on the yolk, giving the eggs an opaque, white appearance to the naked eye. These chromatophores faded rapidly after preservation and were not illustrated in Figure 12. No other pigment was present. Eggs began to hatch at about 12 hr after collection and all were hatched at 16 hr. Because most pelagic eggs hatch within 24 to 30 hr after fertilization during the summer months in Biscayne Bay, the embryos were presumably about 12 hr old when collected.

Size at Metamorphosis

The left eye began to migrate toward the dorsal midline on laboratory-reared larvae of about 3.2 mm SL, and on Tampa Bay larvae of about 3.0 mm SL. At these lengths, the distance from the insertion of the pectoral fin to the posterior margin of the orbit began to differ between the left and right sides of larvae (Figures 2 and 3). In laboratory-reared larvae, the length at which metamorphosis began corresponded to the 10th or 11th day after hatching (Figure 1). Laboratory-reared larvae less than 3.2 mm SL and Tampa Bay larvae less than 3.0 mm SL were designated as premetamorphosing, while larger ones were considered to be metamorphosing. Other criteria (discussed later) confirmed these lengths as being diagnostic in distinguishing the two developmental stages.

Myomeres

Myomere counts on laboratory-reared larvae ranged from 25 to 27 in premetamorphosing larvae and from 26 to 27 in metamorphosing larvae. Myomeres could not be distinguished on larvae longer than 5.1 mm SL because of body thickness and dense pigmentation. The number of preanal myomeres gradually decreased

from 10 or 11 in premetamorphosing larvae to from 8 to 10 in metamorphosing larvae (Table 1). A corresponding increase in postanal myomeres was observed as larvae began to metamorphose. The numbers ranged from 14 to 17 in premetamorphosing larvae,

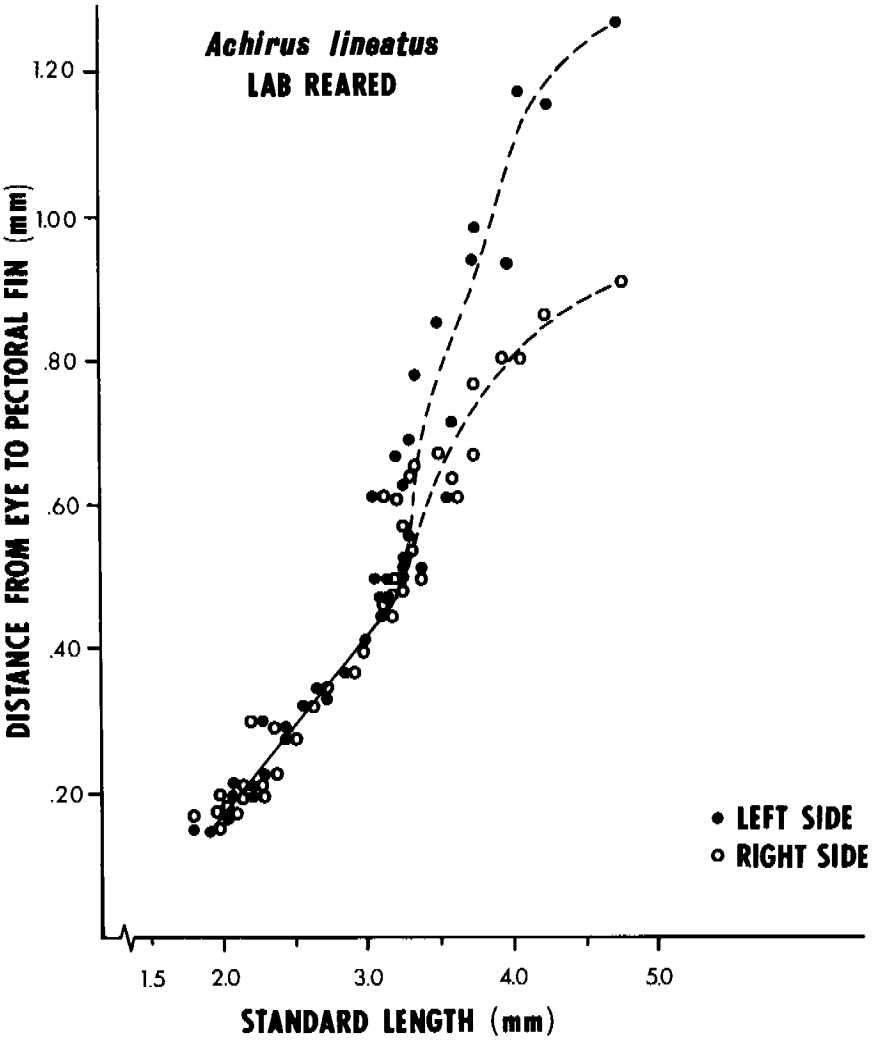

Figure 2. Size at beginning of metamorphosis for laboratory-reared *A. lineatus*. Metamorphosis begins where the distance from insertion of pectoral fin to posterior margin of the orbit diverges between the left and right sides of larvae.

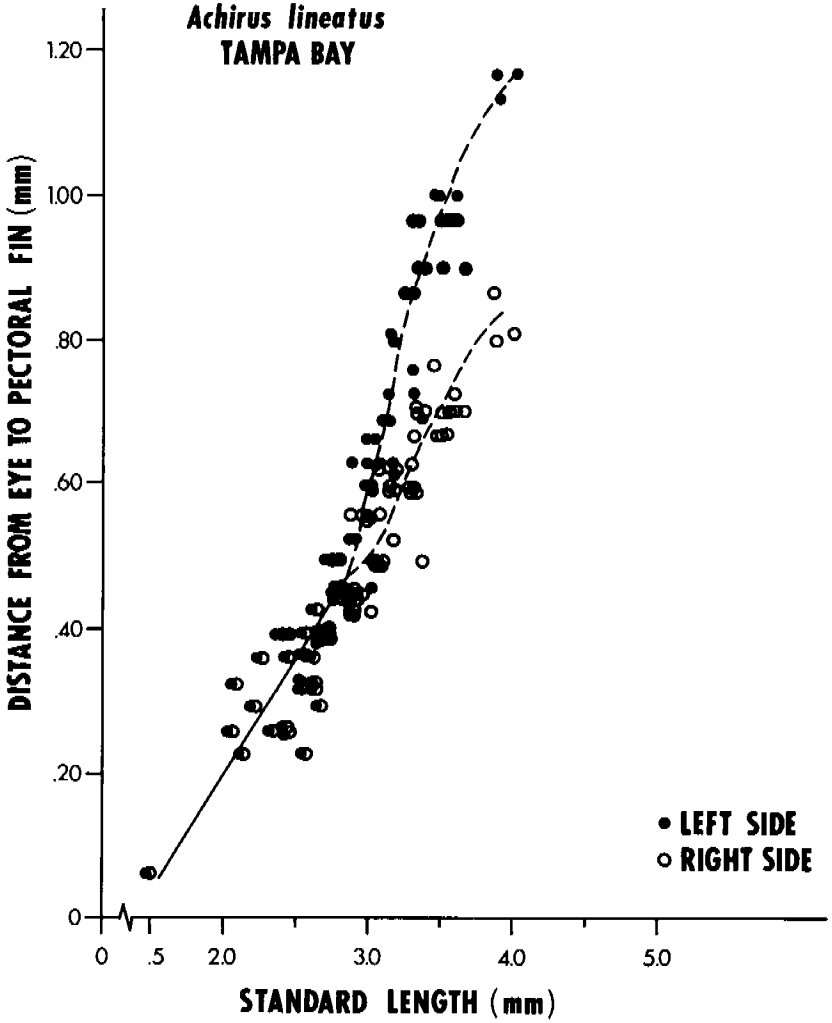

Figure 3. Size at beginning of metamorphosis for Tampa Bay *A. lineatus*. Metamorphosis begins where the distance from insertion of pectoral fin to posterior margin of the orbit diverges between the left and right sides of larvae.

but from 16 to 19 in metamorphosing larvae. The change in numbers of preanal and postanal myomeres during growth resulted from the change in proportion of certain body parts during metamorphosis, particularly shortening of the gut at this stage.

TABLE 1.—FREQUENCY OF OCCURRENCE OF PREANAL AND POSTANAL MYOMERES FOR PREMETAMORPHOSING (< 3.2 mm SL) AND METAMORPHOSING (> 3.2 mm SL) LARVAE OF *ACHIRUS LINEATUS* REARED IN THE LABORATORY.

Larval Stage	Number of Preanal myomeres					Number of Postanal myomeres					
	8	9	10	11	12	14	15	16	17	18	19
Premetamorphosing	0	0	10	22	1	1	3	21	8	0	0
Metamorphosing	4	7	11	0	0	0	0	1	11	5	5

Fins

Newly hatched larvae (Figure 13) had a well developed finfold but no paired or median fins. At 24 hr, larval pectoral fins had developed (Figure 14), and remained prominent throughout the premetamorphosing stage (Figures 15 to 20), being used as swimming organs. No rays were present in the pectoral fins of premetamorphosing larvae. Pectoral fins of metamorphosing larvae gradually became reduced (Figures 21 to 25), but remained on both sides of specimens until metamorphosis was nearly complete. From 3 to 6 rays first appeared in both pectoral fins of metamorphosing larvae at about 4.5 mm SL. At 5.4 mm SL, the left pectoral had disappeared from one specimen but remained on a second larva of the same size. Of two metamorphosed laboratory-reared individuals, 8.2 and 9.0 mm SL, the smaller had a well developed pectoral fin with 5 rays on the blind side, but the larger had none. Two Tampa Bay specimens, 8.3 and 9.2 mm SL, had no pectoral fins on the blind side. Juveniles and adults typically have a right pectoral fin with 4 to 6 rays and no pectoral fin on the blind side.

Median fin elements began to develop before metamorphosis. The first structures to appear were the dorsal fin pterygiophores which were present on some laboratory-reared larvae of 2.4 mm SL (Figure 18), and some Tampa Bay larvae as small as 2.1 mm SL. Anal fin pterygiophores developed next. They were present on laboratory-reared larvae of 2.6 mm SL, but were first noted on Tampa Bay specimens of 2.1 mm SL. Dorsal and anal fin rays began to appear at 3.0 mm SL on the laboratory-reared larvae (Figure 20). Ray counts were based on pterygiophores in premetamorphosing larvae. Most dorsal and anal fin elements developed prior to metamorphosis (Figure 4). Two laboratory-reared

larvae, 8.2 and 9.0 mm SL, had nearly complete dorsal and anal fin development. The adult complement of dorsal and anal rays varies; Jordan and Evermann (1898) reported *A. lineatus* having

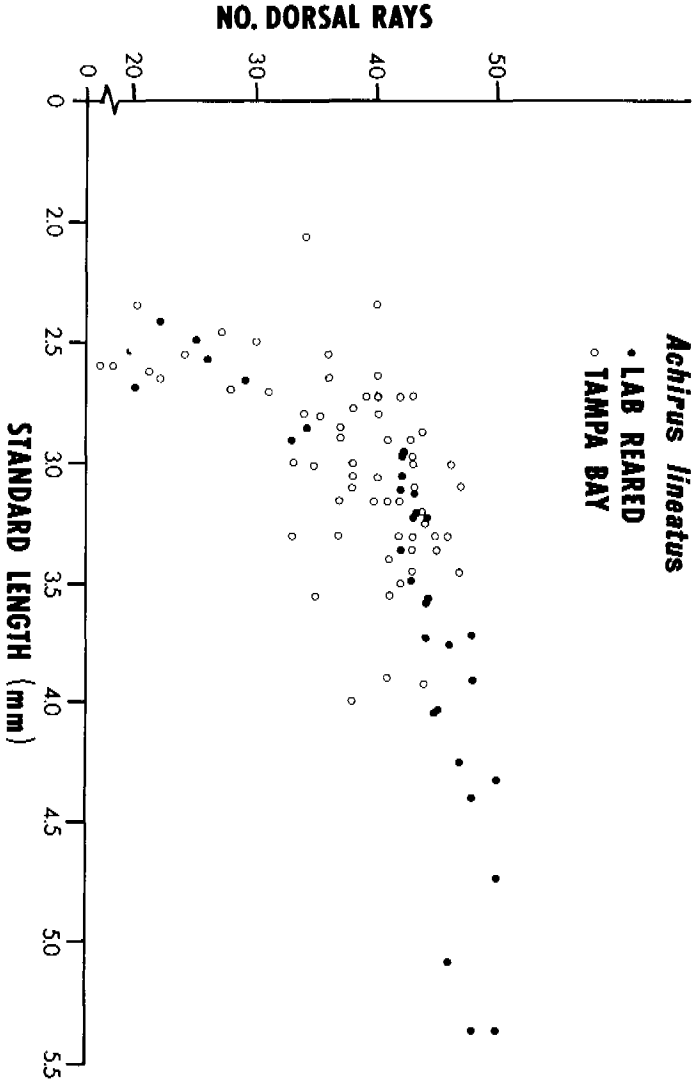

Figure 4. The number of dorsal fin rays plotted against standard length for laboratory-reared and Tampa Bay *A. lineatus* larvae.

49 to 58 dorsal rays and 38 to 44 anal rays. We found that juveniles from several Florida localities had from 47 to 54 dorsal rays and from 35 to 39 anal rays. Development of the median fins was

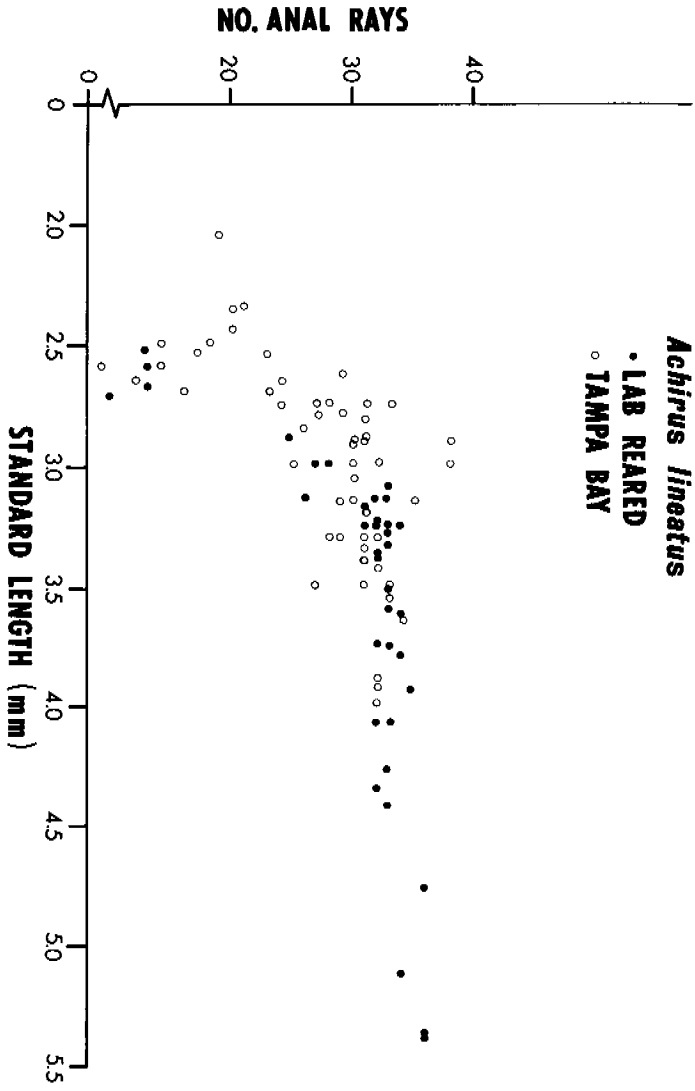

Figure 5. The number of anal fin rays plotted against standard length for laboratory-reared and Tampa Bay *A. lineatus* larvae.

completed at about 12 mm SL. The final stages of median fin development were the bifurcation of the fin rays, and the growth of a fleshy connection between the anal and pelvic fins, thus making them adnate.

Caudal fin rays developed during the latter part of the pre-metamorphosing stage and the full adult complement of 16 rays was present before metamorphosis was completed. Laboratory-reared larvae of 2.9 mm SL developed fin rays in the ventral half of the caudel finfold, at the time of notochord flexure. At 3.1 mm SL, all larvae had from 4 to 8 well developed caudal rays (Figure 20). Caudal rays were present on some Tampa Bay larvae as small as 2.4 mm SL but were not consistently present until 2.7 mm SL. Most Tampa Bay larvae had 16 caudal rays at 3.4 mm SL, but laboratory-reared larvae did not have this full complement until nearly 4.0 mm SL. Before metamorphosis, the caudal fin shape resembled that of juveniles (Figures 24 to 27). Caudal ray tips bifurcated between 9.0 mm SL and 12 mm SL.

Pelvic fins first appeared as ventral buds just anterior to the gut (Figure 19). Laboratory-reared larvae developed pelvic buds at 2.75 mm SL. Some Tampa Bay larvae of 2.4 mm SL and all larvae longer than 2.65 mm SL had pelvic buds. Pelvic fin rays developed on larvae in the metamorphosing stage. Pelvic fins had complete counts of 5 rays at 3.3 mm SL for Tampa Bay larvae and at 4.0 mm SL for laboratory-reared larvae.

Dorsal Tentacle

The lined sole is unique among described soleids in having a dorsal tentacle during the larval period. This fleshy appendage apparently develops from the anteriormost myomeres, grows dorsally into the finfold and eventually becomes a free tentacle-like structure with a slightly bulbous tip. The tentacle is supported by a fin ray. Laboratory-reared larvae developed the first trace of a tentacle at 2 days after hatching (Figure 15) when some were less than 2 mm SL. Two Tampa Bay larvae less than 1.75 mm SL had developed the bud of a tentacle. It grew rapidly (Figures 16 to 20) and was approximately 50% SL when metamorphosis began (Figures 6 and 7). Tentacle length was maximum when laboratory-reared larvae averaged 3.15 mm SL, and when Tampa Bay larvae averaged 2.95 mm SL. This difference in length was similar to that at which eye migration began in the two groups.

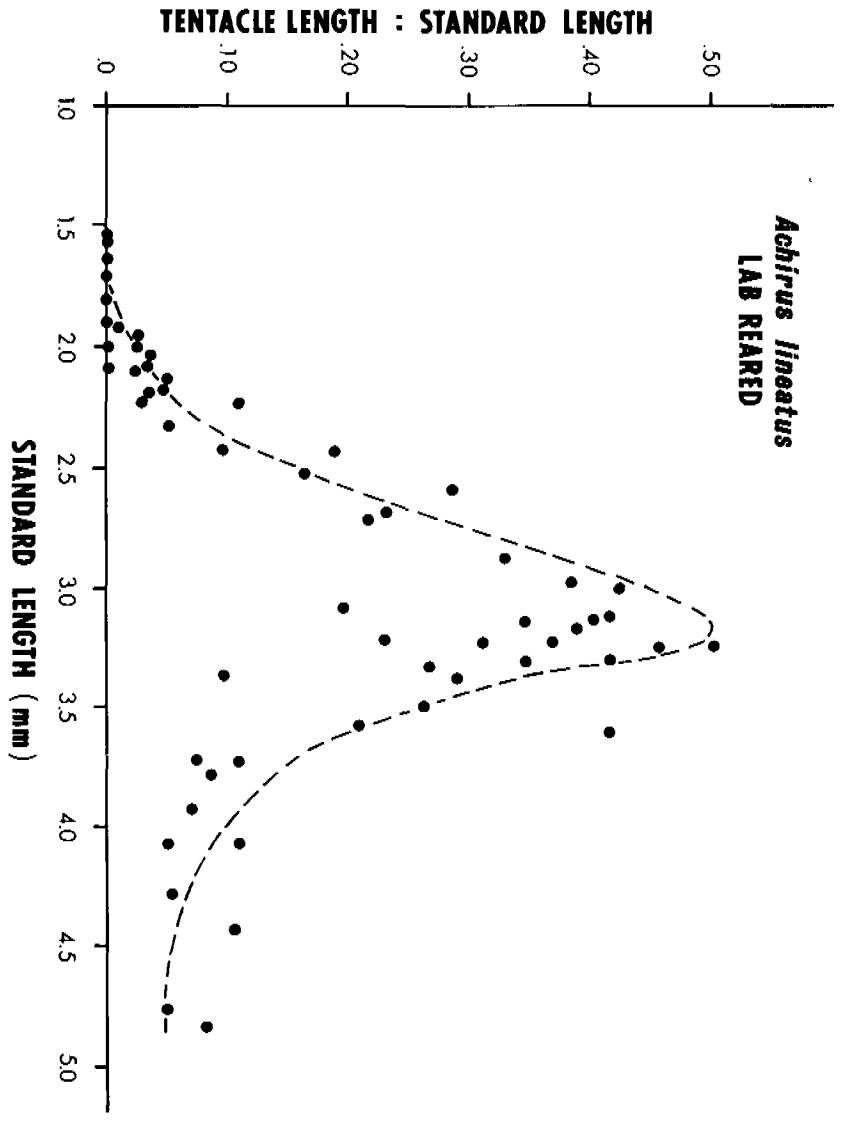

Figure 6. The ratio of dorsal tentacle length to standard length plotted against standard length for laboratory-reared *A. lineatus* larvae.

Reduction in tentacle size was rapid during metamorphosis but basic shape remained the same, being gradually reduced to a

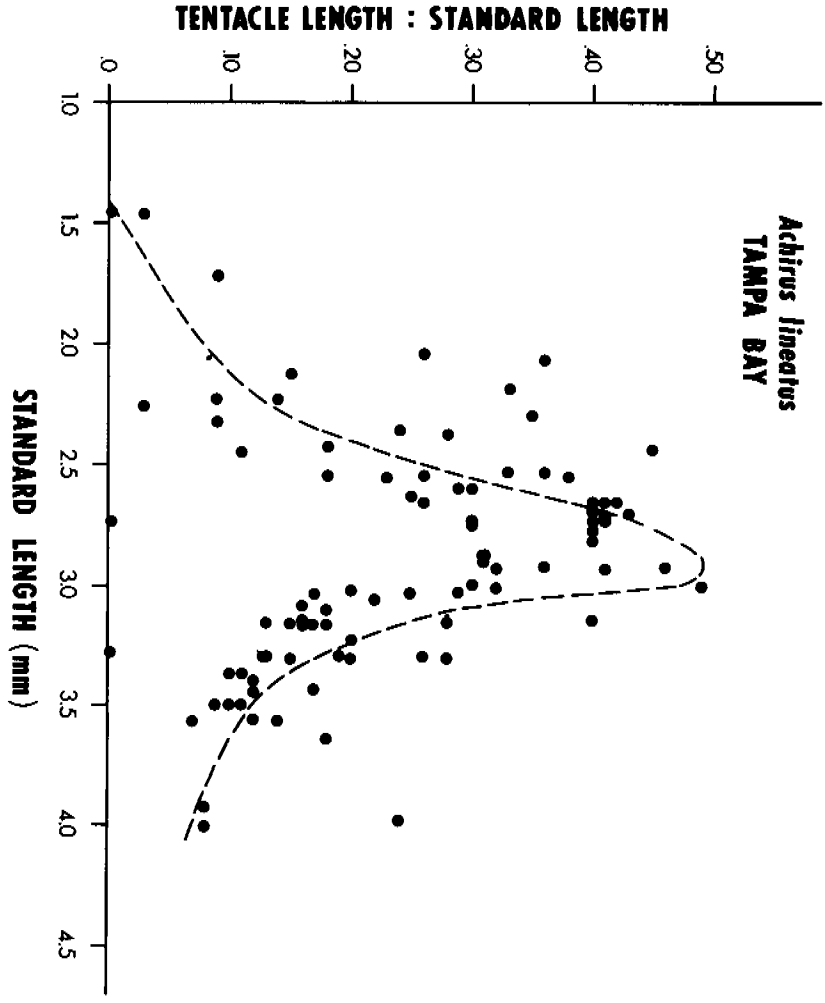

Figure 7. The ratio of dorsal tentacle length to standard length plotted against standard length for Tampa Bay *A. lineatus* larvae.

fleshy protuberance on the dorsal fin (Figures 22 to 25). A vestige remained on nearly metamorphosed larvae (Figure 26), but the tentacle had completely disappeared in laboratory-reared specimens of about 5 mm SL (Figure 27).

Regan (1916) suggested that modified fin rays, such as the

dorsal tentacle of flatfishes, might serve a sensory function, particularly as feelers used to detect food. Kyle (1913) proposed that flatfish tentacles might protect the cranium from attacks by predators. Tentacles might be used as flotation and balancing organs or to help present a deceptively large image to potential predators. We found no evidence demonstrating that laboratory-reared *A. lineatus* larvae used the tentacle in any of these capacities. We do not believe the tentacle serves as a flotation device to insure extensive larval transport because the pelagic larvae of *A. lineatus* are confined to relatively shallow water. Larvae of *Trinectes maculatus,* which are similar in most respects to *A. lineatus,* do not have a dorsal tentacle (Hildebrand and Cable, 1938), yet both species may occur in similar habitats. Larvae of *A. lineatus* and *T. maculatus* were occasionally found together in Tampa Bay collections.

Scale Development

Distinctive papilla-like structures on the sides of larvae, which absorbed and retained alizarin stain, apparently are rows of developing spinous scales. Four rows were present during most of the larval period and an indistinct fifth row developed on nearly metamorphosed larvae. In addition, some spinous scales were scattered over the gut and opercular region of metamorphosing larvae. The spines became longer as larvae developed. Bases of spinous scales had from 4 to 7 short, radiating arms. The number of spinous scales increased as larvae grew and they usually were present in equal numbers on the left and right sides.

Spinous scales began to develop on laboratory-reared larvae of 2.24 mm SL and were present on Tampa Bay larvae as small as 2.05 mm SL. The first spinous scales developed in a row immediately dorsal to the level of the notochord (Figure 18). Three additional rows developed later (Figures 19 to 25), one dorsal and two ventral to the first. The fourth, or ventral-most row, originated on the posterior gut region, ran dorsad and then caudad along the ventral body margin. The third row started posterior to the opercular region and ran caudad. The two dorsalmost rows originated on the posterior head region and ran caudad. Numbers of spinous scales varied among individuals of the same size from both Tampa Bay and the laboratory. Large, nearly metamorphosed laboratory-reared larvae, 5.0 to 5.4 mm SL, had mean row counts

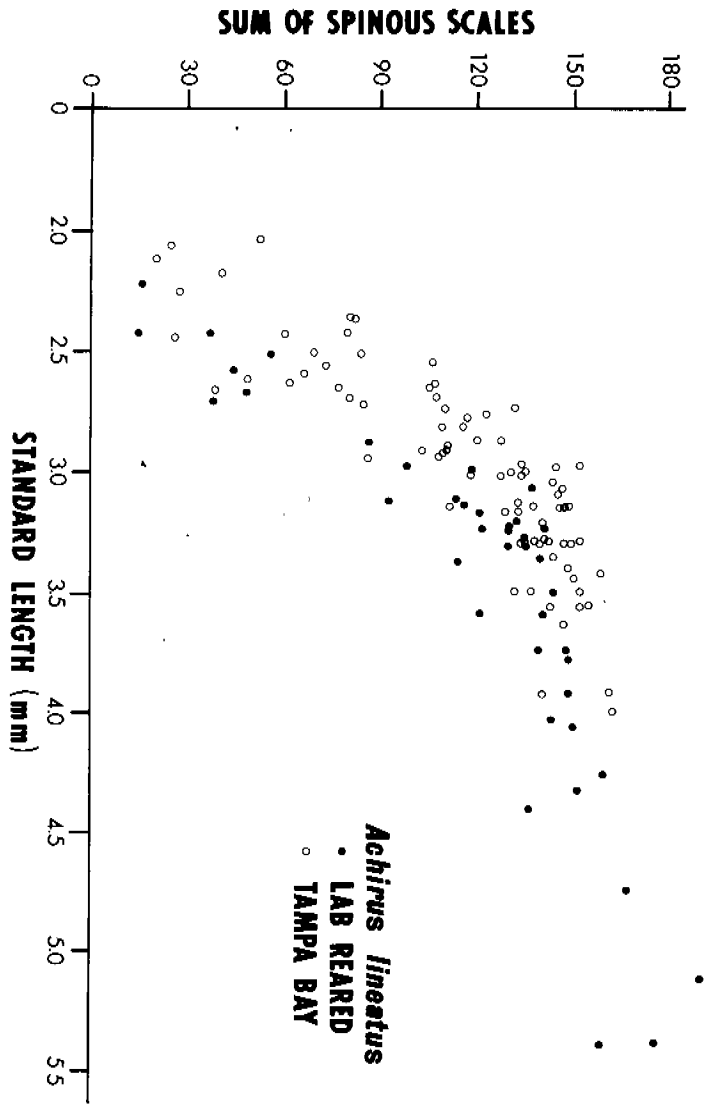

Figure 8. The relation between development of spinous scales and standard length of laboratory-reared and Tampa Bay *A. lineatus* larvae.

of 25, 25, 24, and 16, counting dorsal to ventral. The rate of increase in the total numbers of spinous scales was rapid in the

premetamorphosing phase, but they were added more slowly during metamorphosis (Figure 8). The fifth indistinct row of 3 to 5 spinous scales developed on laboratory-reared larvae of about 4.0 mm SL (Figure 26) ; it was located ventral to the others, originating just posterior to the gut region. Two large, laboratory-reared larvae, 8.2 and 9.0 mm SL, had many more spinous scales than smaller specimens. The scales were distributed over most of the body at these larger sizes and not associated with the five larval rows.

Papillae

Long finger-like papillae developed on larvae greater than 4.3 mm SL (Figure 27). Initially, 3 or 4 papillae developed on both sides in the posterior epaxial region. Papillae were numerous on two laboratory-reared specimens, 8.2 and 9.0 mm SL, in the epaxial and hypaxial regions. They were most numerous on the ocular side of the two individuals. The number of papillae apparently continues to increase on the ocular side after metamorphosis. They were very abundant on the ocular side of juveniles, but not present on the blind side. Papillae on the blind side were lost after metamorphosis.

Interbranchial Foramen

A distinguishing character of juvenile and adult *A. lineatus* is the presence of a perforate branchial septum, the interbranchial foramen (Norman, 1966). This character separates *Achirus* from *Trinectes,* which does not have a perforate branchial septum. When viewed in transmitted light, the foramen appears as a translucent area just anterior to the cleithrum in the hpyobranchial region. It developed in laboratory-reared larvae at about 3.0 mm SL and in Tampa Bay larvae at 2.9 mm SL. The presence of a foramen and dorsal tentacle in *A. lineatus* larvae separates them from larvae of *Trinectes maculatus,* which are otherwise similar.

Development of the Head

As larvae developed, many important changes took place in the shape and structure of the head region. Most involved bone structure and have been discussed by Futch and Houde (in manuscript). Some of the external changes in head structure are given in the following report.

The overall shape of the head of newly hatched larvae differed markedly from that of specimens about to begin metamorphosis. Larvae retained a prominent, crest-like hump on the head (Figure 13), throughout the premetamorphosing stage. In early stages of metamorphosis the hump became smaller (Figures 20 to 22), coincident with a steepening of the forehead which preceded the beginning of the migration of the left eye toward the dorsal midline (Figures 23 and 24).

Three prominent, spinous bony ridges were present on the head of *A. lineatus* larvae (see Futch and Houde, in manuscript), similar to those of *Trinectes maculatus* larvae illustrated by Hildebrand and Cable (1938). The first and largest of these ridges (frontal ridge) was directly over the eye, and developed on laboratory-reared larvae of 2.00 mm SL (Figure 14). At 4 days the second ridge (parietal) developed posterior to the first (Figure 16), and at 7 days the third ridge (autopterotic) appeared, also posterior to the first (Figure 19). The parietal ridge moved dorsad during development and its former position became occupied by the developing autopterotic ridge. All three ridges remained throughout metamorphosis. The frontal ridges were asymmetric; the larger on the right side eventually became the interorbital bony ridge. The three ridges contribute to the laterosensory canal system (Futch and Houde, in manuscript).

During metamorphosis the left eye moved forward and across the dorsal midline (Figures 21 to 26).to the right side. The right eye moved slightly ventrad during metamorphosis (Figures 26 and 27). As the left eye migrated, the dorsal fin and its underlying tissue began to form a "hook," under which the eye passed (Figure 25). In larvae that metamorphosed normally, this "hook" gradually grew forward and eventually down toward the snout, becoming adnate to it when eye migration was complete.

Numerous cirri and short spinelike structures began to develop on the left side of the head of 4.0 mm SL laboratory-reared larvae just after the left eye had crossed the dorsal midline. Most surrounded the mouth and presumably are used in a sensory capacity during feeding. Other bony processes developed in relation to the cephalic laterosensory system (Futch and Houde, in manuscript).

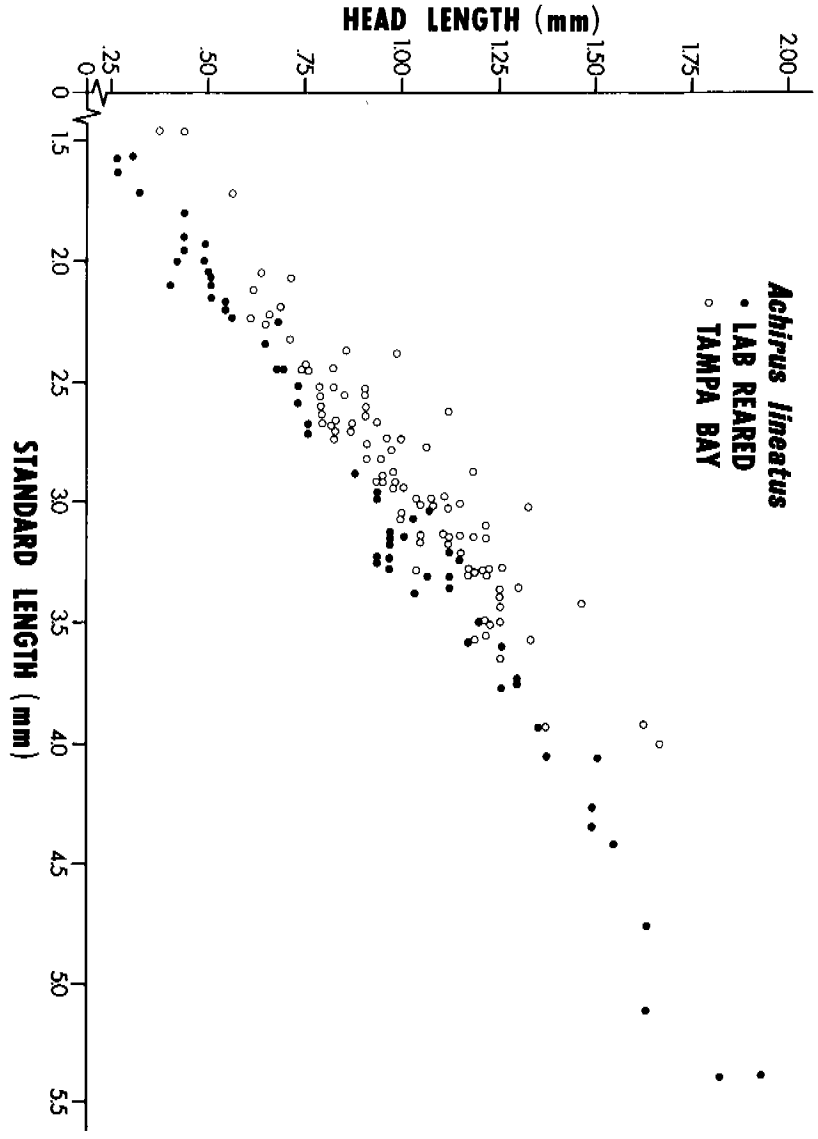

Figure 9. The relation between head length and standard length of laboratory-reared and Tampa Bay *A. lineatus* larvae.

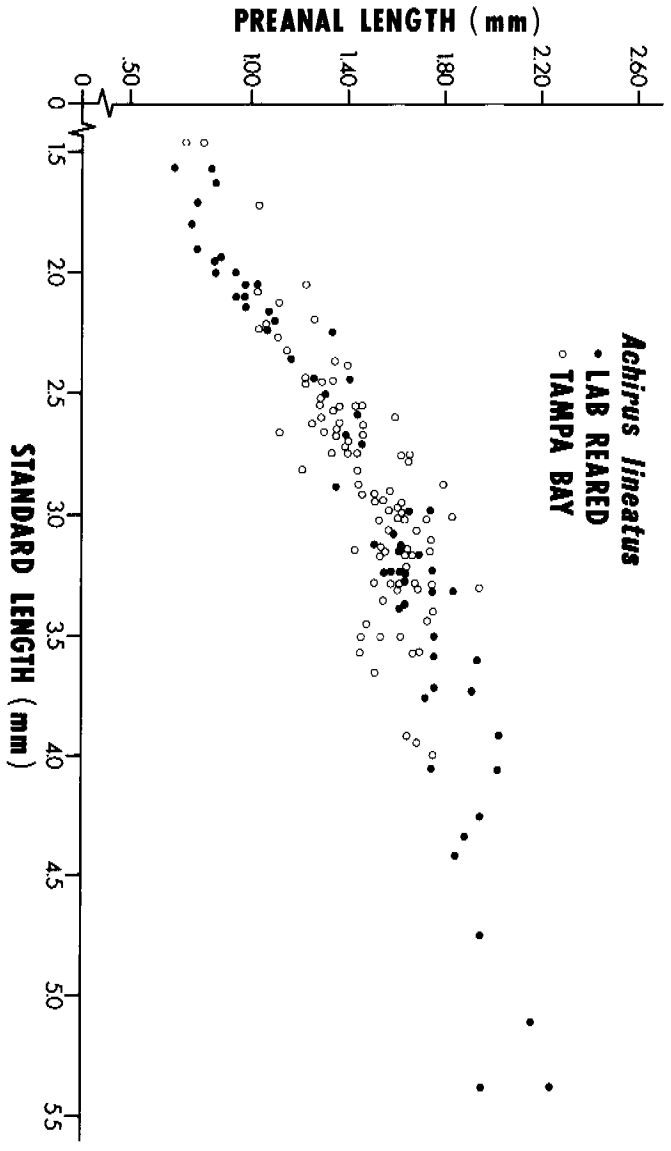

Figure 10. The relation between preanal length and standard length of laboratory-reared and Tampa Bay *A. lineatus* larvae.

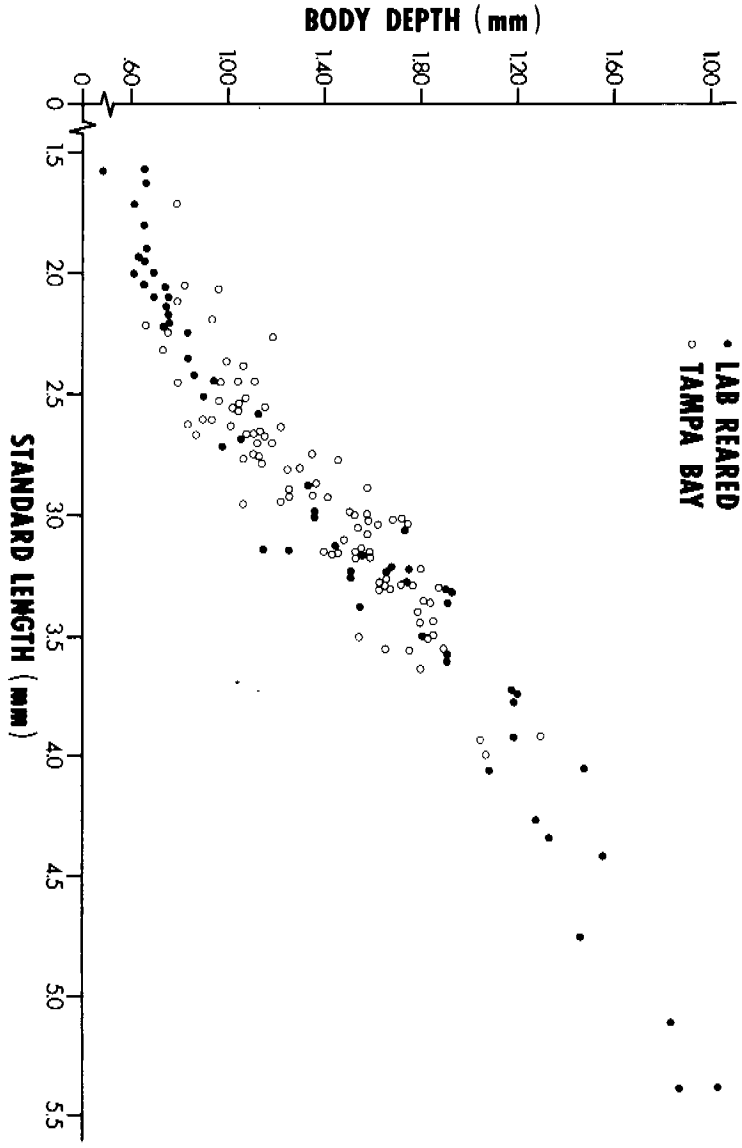

Figure 11. The relation between body depth and standard length of laboratory-reared and Tampa Bay *A. lineatus* larvae.

Head length of larvae relative to standard length increased from about 20% at hatching to nearly 40% when metamorphosis was almost complete. Head lengths were greater for Tampa Bay larvae of a given standard length than for laboratory-reared larvae (Figure 9), of the same length. Eye diameter was proportional to standard length, averaging 7.5% for larvae larger than 2.5 mm SL.

Preanal Length

Preanal length of laboratory-reared and Tampa Bay larvae decreased in proportion to standard length during the premetamorphosing and metamorphosing stages (Figure 10). The decrease corresponded to the decrease in numbers of preanal myomeres observed during development (Table 1). The gut region became relatively shorter during metamorphosis.

Body Depth

Body depth increased at about the same rate for laboratory-reared larvae and Tampa Bay larvae of comparable size (Figure 11). At 4.0 mm SL, larvae resembled juveniles in general body shape.

Pigmentation

Larval pigmentation consisted of dark brown, stellate melanophores which became increasingly abundant on the head, body, and fins during growth. Typical black melanophores were absent. Considerable variation in melanophore size and distribution was observed on larvae of the same size. Pigment was concentrated in tiny specks on some, but dispersed on others. Individual differences probably reflected an ability of larvae to adjust pigmentation to their surroundings.

Embryos and larvae up to 2 days old had no melanophores. Tiny granular white chromatophores were distributed on the body, yolk, and in the finfold of newly hatched larvae. Much of this white pigment had disappeared between 4 and 5 days after hatching, but some was retained in the finfold, on the lower jaw, and at the base of the caudal fin. White pigment was lost when larvae were preserved.

The eye became darkly pigmented at 2 days (Figure 15). Brown pigment first developed on the body at 4 days, when laboratory-reared larvae averaged 2.1 mm SL. Pigment was distributed in a thin line dorsal to the gut region and as a few melanophores at the base of the dorsal tentacle (Figure 16). Most premetamorphosing larvae subsequently added pigment in the following sequence: mid-body in epaxial region, extending into finfold (Figure 17); ventral margin of postanal myomeres; crest on head and on lower jaw; gut region (Figure 18); dorsal margin of postanal myomeres. At 7 days, larvae of 2.8 mm SL were pigmented over much of the body, and a characteristic pigment pattern had developed on the dorsal tentacle and in the dorsal and anal finfolds (Figure 19).

Melanophores became more numerous and widely distributed in metamorphosing larvae. The dorsal tentacle typically was pigmented near its tip, at mid-length, and at its base (Figures 22 and 23). Two areas of pigment were distinctive in the dorsal fin, one near mid-body, and the other about ⅔ the distance from snout to end of caudal fin. Two areas of pigmentation also developed in the anal fin, one near its anterior end, and the other posterior to the first (Figures 20 to 24). A heavy band of dark pigment formed at the base of the caudal fin (Figures 24 to 27). Each of these areas had a few white chromatophores. Pigment patterns in median and caudal fins persisted until metamorphosis was nearly completed. Two laboratory-reared larvae of 8.2 and 9.0 mm SL were equally pigmented on both sides, but a 9.2 mm SL Tampa Bay specimen was more heavily pigmented on the ocular side.

Swimbladder

Larvae had a well developed swimbladder, which persisted until metamorphosis was nearly completed. This structure, first observed at 4 days in laboratory-reared larvae of 2.1 mm SL (Figure 16), was somewhat displaced to the left side. The swimbladder of dextral flatfish larvae is usually displaced to the right (Kyle, 1921). At 4.0 mm SL, the swimbladder became reduced and only one of two 5.4 mm SL larvae retained it. Swimbladders were absent in juveniles (12 to 50 mm SL) from Biscayne and Tampa Bays.

TABLE 2. MERISTICS AND MORPHOMETRICS OF *ACHIRUS LINEATUS* LARVAE REARED IN THE LABORATORY AND COLLECTED IN TAMPA BAY
(Data presented for each 0.25 mm length-class)

A. Laboratory-Reared Larvae

Length (SL mm)	Number of Specimens	Mean SL		Dorsal Rays	Anal Rays	Caudal Rays	Spinous Scales Left Side	Spinous Scales Right Side	Preanal Length (mm)	Head Length (mm)	Body Depth (mm)	Eye Diam. (mm)	Dorsal Tentacle (mm)
<1.5	0		$\bar{x}$										
			Range										
1.51-1.75	4	1.62	$\bar{x}$	0	0	0	0	0	.78	.29	.60	.12	0
			Range	–	–	–	–	–	.68-.85	.27-.32	.49-.66	.09-.15	–
1.76-2.00	6	1.93	$\bar{x}$	0	0	0	0	0	.84	.45	.65	.16	.020
			Range	–	–	–	–	–	.76-.93	.42-.49	.61-.69	.15-.17	0.00-0.049
2.01-2.25	9	2.14	$\bar{x}$	0	0	0	1.00	0.67	1.05	.53	.74	.18	.086
			Range	–	–	–	0-.9	0-6	.93-1.34	.39-.69	.66-.83	.15-.22	.00-.24
2.26-2.50	3	2.40	$\bar{x}$	7.33	0	0	7.67	9.33	1.28	.67	.88	.22	.27
			Range	0-22	–	–	0-17	0-20	1.17-1.41	.64-.69	.83-.95	.20-.24	.12-.46
2.51-2.75	4	2.62	$\bar{x}$	25.00	12.25	0	23.50	23.25	1.40	.75	1.02	.24	.59
			Range	20-29	10-13	–	19-28	19-28	1.30-1.46	.73-.76	.90-1.12	.24	.41-.73
2.76-3.00	3	2.95	$\bar{x}$	39.33	26.67	5.00	50.67	50.00	1.58	.91	1.36	.25	1.12
			Range	34-42	25-28	4-6	45-62	41-56	1.35-1.73	.86-.94	1.33-1.37	.25	0.94-1.26
3.01-3.25	10	3.18	$\bar{x}$	42.40	31.70	9.10	62.20	61.10	1.62	1.01	1.52	.28	1.16
			Range	38-44	26-34	3-14	44-71	49-70	1.51-1.76	.94-1.15	1.15-1.76	.25-.29	.61-1.62
3.26-3.50	6	3.35	$\bar{x}$	43.20	32.67	10.83	65.16	67.33	1.71	1.09	1.81	.26	.94
			Range	42-45	32-33	7-13	57-68	57-76	1.62-1.84	.97-1.21	1.55-1.91	.23-.29	.32-1.37
3.51-3.75	4	3.66	$\bar{x}$	45.00	33.00	13.00	70.25	69.25	1.84	1.26	2.05	.28	.73
			Range	44-48	32-34	12-14	65-74	66.73	1.77-1.93	1.17-1.30	1.91-2.20	.28-.29	.28-1.50
3.76-4.00	2	3.85	$\bar{x}$	47.00	34.50	15.50	75.00	75.00	1.88	1.31	2.19	.28	.30
			Range	46-48	34-35	15-16	73-77	75	1.72-2.03	1.26-1.35	2.19	.28	.28-.32
4.01-4.25	2	4.06	$\bar{x}$	45.00	32.50	14.00	72.00	74.50	1.88	1.44	2.28	.30	.33
			Range	45	32-33	13-15	70-74	74-75	1.75-2.02	1.37-1.51	2.09-2.48	.29-.32	.22-.44
4.26-4.50	3	4.34	$\bar{x}$	48.33	32.67	15.67	73.67	75.00	1.93	1.51	2.39	.32	.35
			Range	47-50	32-33	15-16	68-81	68-78	1.89-1.96	1.49-1.55	2.28-2.56	.32	.23-.46
4.51-4.75	0												
4.76-5.00	1	4.76	$\bar{x}$	50	36	14	81	86	1.96	1.63	2.47	0.32	.23
5.01-5.25	1	5.11	$\bar{x}$	46	34	16	91	98	2.17	1.63	2.84	0.37	0
5.26-5.50	2	5.39	$\bar{x}$	49.00	36	16	87	84.50	2.10	1.88	2.95	.38	0
			Range	48-50	36	16	81-93	77-92	1.96-2.24	1.82-1.94	2.87-3.03	.36-.39	0

B. Tampa Bay Larvae

Length (SL mm) Range	Number of Specimens	Mean SL		Dorsal Rays	Anal Rays	Caudal Rays	Spinous Scales Left Side	Spinous Scales Right Side	Preanal Length (mm)	Head Length (mm)	Body Depth (mm)	Eye Diam. (mm)	Dorsal Tentacle (mm)
<1.5	2	1.46	$\bar{x}$	0	0	0	0	0	.76	.40	.55	.16	.02
			Range	–	–	–	–	–	.73-.80	.37-.44	.54-.56	.12-.19	0-.05
1.51-1.75	1	1.72	$\bar{x}$	0	0	0	0	0	1.04	.57	.79	.21	.17
1.76-2.00	0												
2.01-2.25	6	2.14	$\bar{x}$	5.66	3.16	0	11.83	11.66	1.13	.65	.82	.21	.47
			Range	0-34	0-19	–	0-26	0-27	1.04-1.26	.61-.72	.66-.97	.19-.23	.19-.75
2.26-2.50	8	2.38	$\bar{x}$	10.87	7.62	1.37	27.00	23.85	1.26	.78	.98	.22	.55
			Range	0-40	0-21	0-3	0-45	0-39	1.11-1.40	.65-.99	.72-1.19	.20-.24	.09-1.12
2.51-2.75	22	2.63	$\bar{x}$	24.44	15.94	2.88	41.52	42.94	1.38	.87	1.07	.24	.89
			Range	0-43	0-33	0-9	20-64	18-69	1.12-1.62	.79-1.12	.83-1.36	.21-.28	.46-1.15
2.76-3.00	15	2.89	$\bar{x}$	38.61	29.76	8.07	58.93	59.40	1.55	1.00	1.35	.25	1.05
			Range	33-44	26-38	5-13	41-76	44-76	1.21-1.80	.90-1.19	1.08-1.58	.22-.31	.72-1.48
3.01-3.25	17	3.10	$\bar{x}$	41.12	31.62	11.17	68.17	67.64	1.63	1.12	1.57	.27	.66
			Range	35-47	25-38	6-16	56-76	59-74	1.44-1.75	1.00-1.33	1.40-1.80	.25-.31	.43-1.26
3.26-3.50	16	3.36	$\bar{x}$	42.35	29.56	13.56	71.75	72.50	1.63	1.23	1.74	.27	.48
			Range	37-47	27-37	9-16	64-80	66-87	1.47-1.96	1.04-1.47	1.54-1.88	.25-.30	.31-.94
3.51-3.75	4	3.58	$\bar{x}$	37.00	32.50	15.75	73.00	76.00	1.58	1.25	1.77	.27	.43
			Range	35-41	30-34	15-16	70-77	73-80	1.44-1.69	1.19-1.33	1.65-1.90	.25-.29	.25-.68
3.76-4.00	3	3.95	$\bar{x}$	41.00	32	16	78.66	75.33	1.70	1.54	2.14	.29	.21
			Range	38-44	32	16	71-85	70-80	1.65-1.76	1.36-1.66	2.06-2.30	.28-.31	0-.32

COMPARISON OF LABORATORY-REARED AND TAMPA BAY LARVAE

Differences were observed in morphometric and meristic characters of laboratory-reared and Tampa Bay larvae. Although the sequence of development was the same for each group, those from Tampa Bay usually were more developed at any given length than were those reared in the laboratory (Table 2). Fin rays and spinous scales were more numerous, and most proportional measurements differed within length classes. The differences became less pronounced on larger larvae nearing completion of metamorphosis. Metamorphosis apparently began at a shorter length for Tampa Bay larvae (Figures 2 and 3); development of the dorsal tentacle and subsequent reduction also occurred at shorter lengths for Tampa Bay larvae (Figures 6 and 7).

We examined three characters by analysis of covariance to determine whether the two groups of larvae differed significantly in their development. Head length, preanal length, and body depth were regressed on standard length (Figures 9 to 11). In each case, the variances for the two groups were homogenous ($P>.05$), although Tampa Bay specimens were always more variable than laboratory-reared specimens. Head length and preanal length differed significantly between the two groups during development (Table 3). During growth, head length increased at about the same rate for Tampa Bay and laboratory-reared larvae. However, head length was greater for Tampa Bay larvae at any given standard length within the range of lengths available in our samples. Preanal length increased at a faster rate for laboratory-reared larvae but preanal lengths of Tampa Bay larvae averaged greater than those of laboratory-reared larvae of the same standard length during the premetamorphosing stage. Body depth did not develop at a significantly different rate among the two groups, although Tampa Bay larvae less than 2.5 mm SL usually were deeper bodied than laboratory-reared larvae of the same lengths (Table 2).

Differences in larvae from the two sources may have originated in three ways: Populations from Tampa Bay may be genetically distinct from those in Biscayne Bay; laboratory rearing may have produced larvae that developed atypically; and the

TABLE 3. REGRESSIONS OF HEAD LENGTH, PREANAL LENGTH, AND BODY DEPTH (Y) ON STANDARD LENGTH (X) FOR LABORATORY-REARED AND TAMPA BAY *ACHIRUS LINEATUS* LARVAE.

Character	Larvae Source	Regression	Coefficient of determination (r^2)	Probability slopes equal	Probability adjusted means equal
Head length	Tampa Bay	$Y = -0.299 + .45\ X$	0.880	$P \cong .25$	$P < .005$
	Lab	$Y = -0.373 + .43\ X$	0.978		
Preanal length	Tampa Bay	$Y = 0.416 + 2.34 \log X$	0.706	$P < .005$	-
	Lab	$Y = 0.115 + 2.94 \log X$	0.936		
Body depth	Tampa Bay	$Y = -0.704 + .71\ X$	0.848	$P > .99$	$P > .25$
	Lab	$Y = -0.711 + .71\ X$	0.953		

long preservation time (about 8 years) for Tampa Bay larvae may have caused shrinkage and distortion of some body parts. Existing evidence leads us to believe that the second and third suggestions may have contributed to the differences. A number of laboratory-reared specimens metamorphosed abnormally (data not included), although no deformities were observed until metamorphosis was nearly completed. Tampa Bay specimens often were distorted and difficult to measure, implying that the collection and preservation process might have caused the apparent differences in rates of development between the two groups. Among Tampa Bay larvae, the greater observed morphometric and meristic variability also suggested that distortion may have been responsbile for the differences.

JUVENILES

Juveniles from Biscayne Bay, Tampa Bay, and from the laboratory rearing experiment were examined, and differences in meristic and morphometric characters were found suggesting that differences observed in larvae from the laboratory and Tampa Bay may have been real. Numbers of dorsal, anal, and caudal rays were compared (Table 4); means differed significantly (Tukey's test) among at least two of the groups in each comparison. Juveniles reared in the laboratory collected from Biscayne Bay had a significantly greater number of dorsal rays than those from Tampa Bay. Mean number of anal rays was greatest for laboratory-reared fish and least for Tampa Bay specimens. All three groups differed significantly in mean anal ray counts. Laboratory-reared specimens had fewest caudal rays; the mean differed significantly from those of both Biscayne and Tampa Bays.

Morphometric variation in juveniles from the three sources was examined by comparing head length, preanal length, and body depth. These three characters were regressed on standard length for each of the three groups of fish and the regressions were then compared by analyses of covariance. The adjusted mean head length, preanal length, and body depth were computed for each group of larvae as were their regression coefficients (Table 5). Regression coefficients were significantly different among the three groups of juveniles for each character. Adjusted means of each character also differed among the three groups. The dif-

TABLE 4.—NUMBERS OF DORSAL RAYS, ANAL RAYS, AND CAUDAL RAYS ON JUVENILE *ACHIRUS LINEATUS* FROM THE LABORATORY REARING EXPERIMENT, BISCAYNE BAY AND TAMPA BAY.

Character	Source of larvae	Number of specimens	Number of rays Range	Mean
Dorsal Rays	Lab reared	12	50-54	51.33
	Biscayne Bay	15	49-53	50.86
	Tampa Bay	20	47-52	49.70
Anal Rays	Lab reared	12	37-39	38.08
	Biscayne Bay	15	37-39	37.73
	Tampa Bay	20	35-39	37.35
Caudal Rays	Lab reared	12	14-16	15.41
	Biscayne Bay	15	16-17	16.06
	Tampa Bay	20	15-16	15.95

TABLE 5.—REGRESSION COEFFICIENTS AND ADJUSTED MEANS FOR THE REGRESSIONS OF HEAD LENGTH, PREANAL LENGTH AND BODY DEPTH AGAINST STANDARD LENGTH OF *ACHIRUS LINEATUS* JUVENILES FROM THE LABORATORY REARING EXPERIMENT, BISCAYNE BAY AND TAMPA BAY.

Character	Source of larvae	Number of specimens	Regression coefficients	Adjusted means (mm)
Head length	Lab reared	12	0.2297	8.55
	Biscayne Bay	15	0.2612	8.99
	Tampa Bay	22	0.3060	9.03
Preanal length	Lab reared	12	0.2417	6.37
	Biscayne Bay	15	0.1768	7.33
	Tampa Bay	22	0.2818	7.50
Body depth	Lab reared	12	0.6830	18.76
	Biscayne Bay	15	0.5982	18.13
	Tampa Bay	22	0.7161	19.18

ference between regression coefficients for each character was tested for significance by comparing each pair of groups (Table 6). The slopes did not differ significantly for any of the three characters when laboratory-reared and Biscayne Bay specimens

were compared. Laboratory-reared and Tampa Bay individuals had significantly different slopes for head length regressed on standard length but not for preanal length or body depth. The regression coefficients were significantly different for each case when juveniles from Biscayne and Tampa Bays were compared. Because the regression coefficients were not homogenous, adjusted means were not tested, but it seemed apparent that laboratory-reared juveniles had shorter head lengths and preanal lengths than those from either Biscayne or Tampa Bay of the same standard length (Table 5). Body depth apparently was somewhat greater for Tampa Bay specimens than for those from Biscayne Bay.

TABLE 6.—COMPARISON OF REGRESSION COEFFICIENTS FROM ANALYSES OF COVARIANCE FOR HEAD LENGTH, PREANAL LENGTH AND BODY DEPTH REGRESSED ON STANDARD LENGTH OF *ACHIRUS LINEATUS* JUVENILES.

Character	Comparison	Probability regression coefficients do not differ
Head length	Lab reared x Biscayne Bay	$P \cong .20$
	Lab reared x Tampa Bay	$P < .001$ **
	Biscayne Bay x Tampa Bay	$P \cong .005$ **
Preanal length	Lab reared x Biscayne Bay	$P > .15$
	Lab reared x Tampa Bay	$P > .30$
	Biscayne Bay x Tampa Bay	$P < .001$ **
Body Depth	Lab reared x Biscayne Bay	$P > .20$
	Lab reared x Tampa Bay	$P > .50$
	Biscayne Bay x Tampa Bay	$P < .005$ **

Specimens were from a laboratory rearing experiment, Biscayne Bay, and Tampa Bay. Probabilities were derived from calculated values of "Student's t."

A. lineatus is a species that varies greatly over its range (Jordan and Evermann, 1898). The three groups of juveniles we examined differed in several respects, even though laboratory-reared and Biscayne Bay specimens shared a common gene pool. Adult lined soles from Biscayne Bay spawned the eggs for our rearing experiment, yet the laboratory-reared juveniles differed in many respects from those collected in the Bay. We believe that much of the variability observed in this species may be environ-

mentally induced. Many individuals metamorphosed abnormally in the rearing experiment, probably because of tank confinement. Some of the observed differences between laboratory-reared and Tampa Bay larvae (Tables 2 and 3) probably resulted from the environmental conditions under which the two groups developed.

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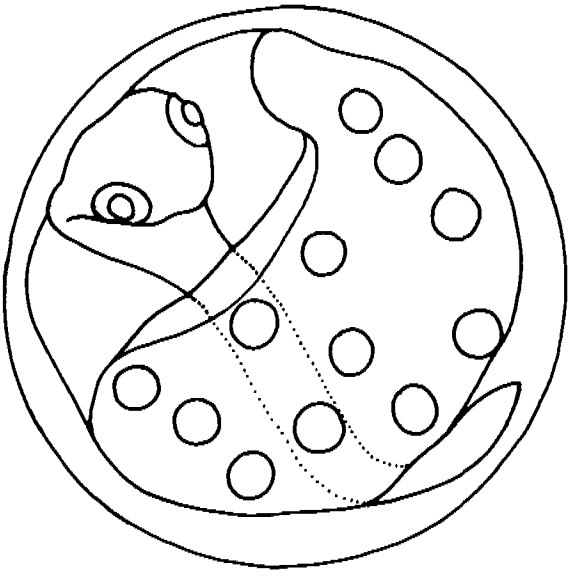

Figure 12. Embryo of *Achirus lineatus* at time of collection, an estimated 12 hours after fertilization.

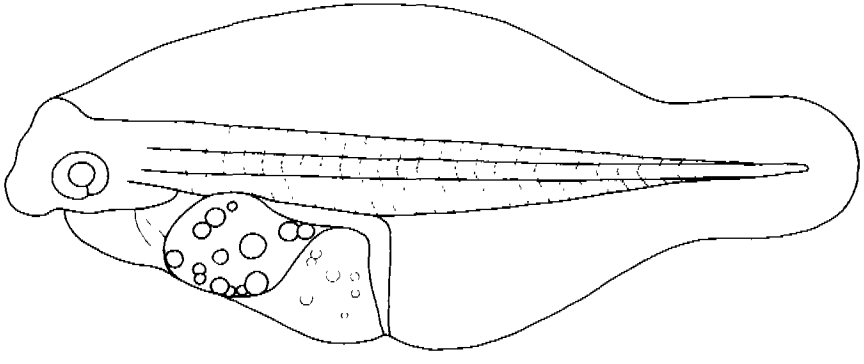

Figure 13. Newly hatched larva of *A. lineatus*. 1.6 mm SL.

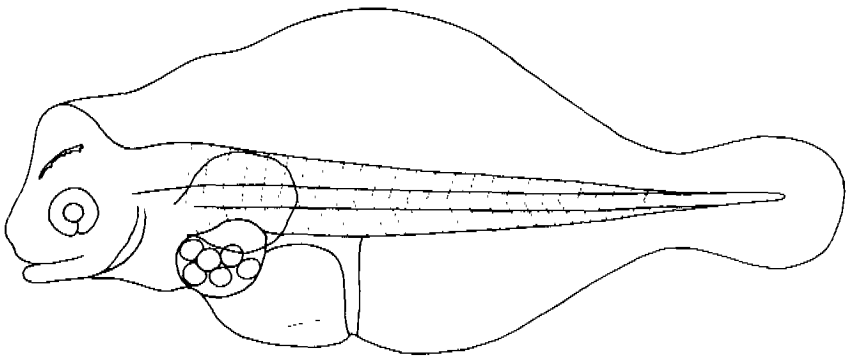

Figure 14. One day old larva of *A. lineatus*. 2.1 mm SL.

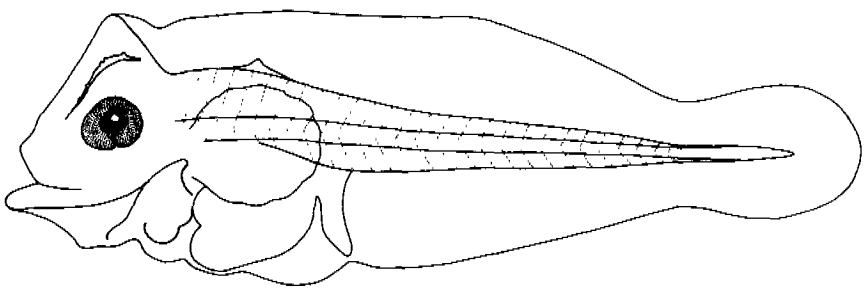

Figure 15. Two day old larva of *A. lineatus*. 2.0 mm SL.

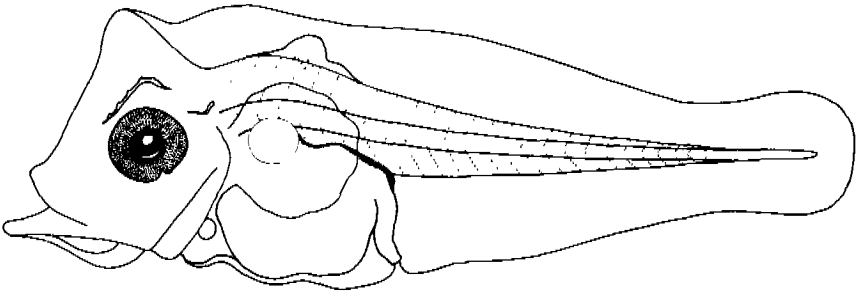

Figure 16. Four day old larva of *A. lineatus*. 2.2 mm SL.

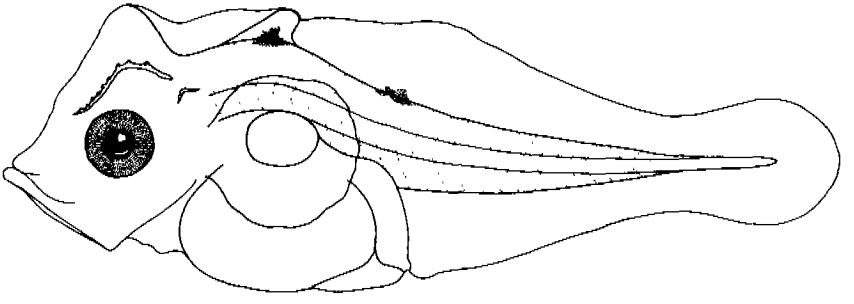

Figure 17. Five day old larva of *A. lineatus*. 2.3 mm SL.

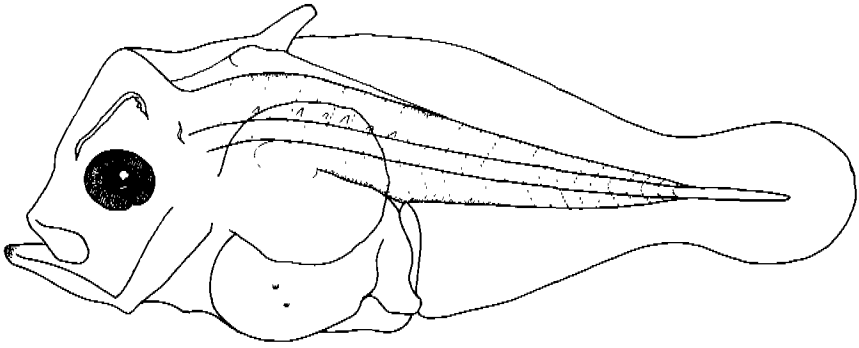

Figure 18. Six day old larva of *A. lineatus*. 2.4 mm SL.

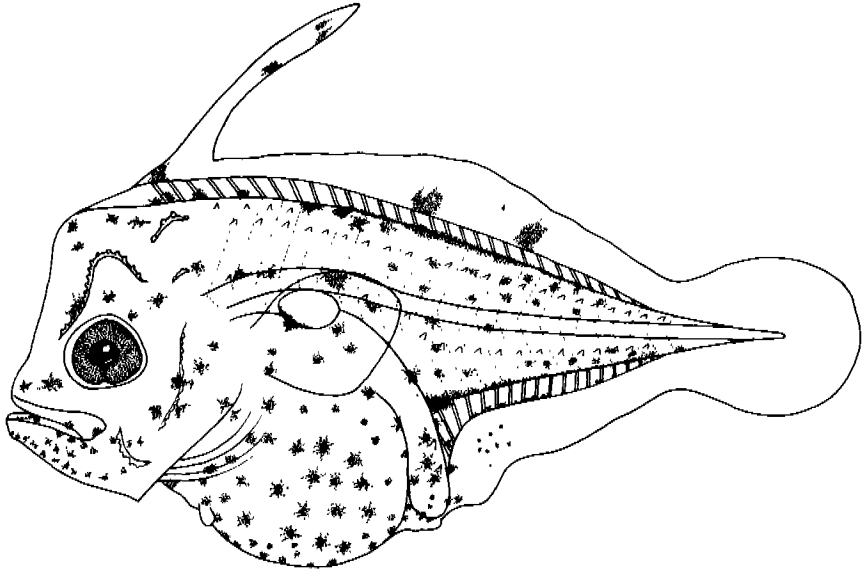

Figure 19. Seven day old larva of *A. lineatus*. 2.9 mm SL.

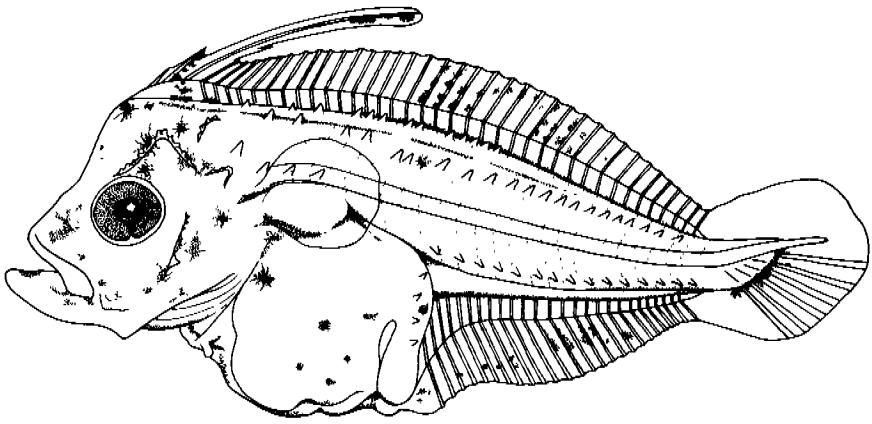

Figure 20. Nine day old larva of *A. lineatus*. 3.1 mm SL.

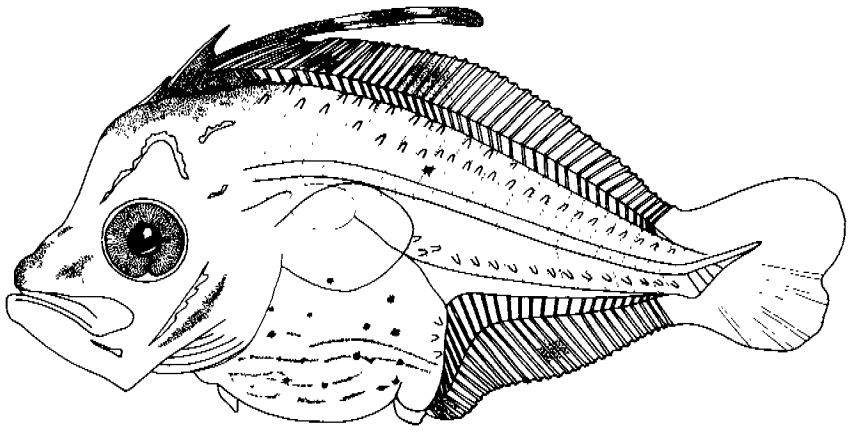

Figure 21. Eight day old larva of *A. lineatus*. 3.4 mm SL.

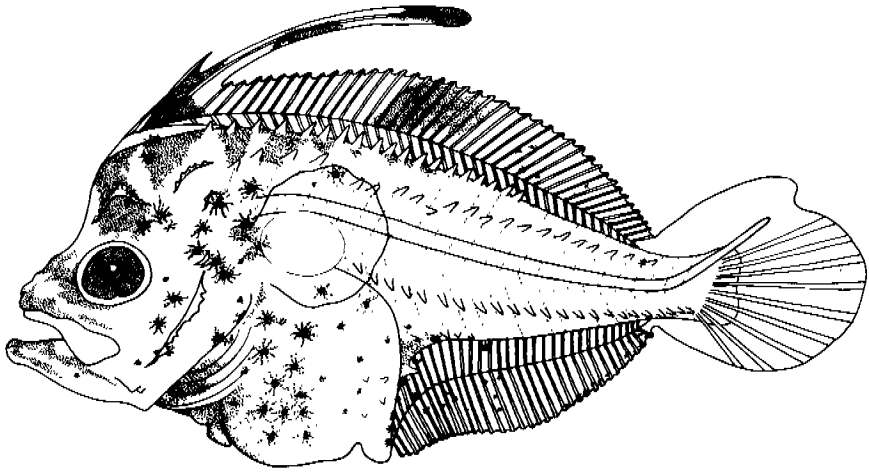

Figure 22. Ten day old larva of *A. lineatus*. 3.6 mm SL.

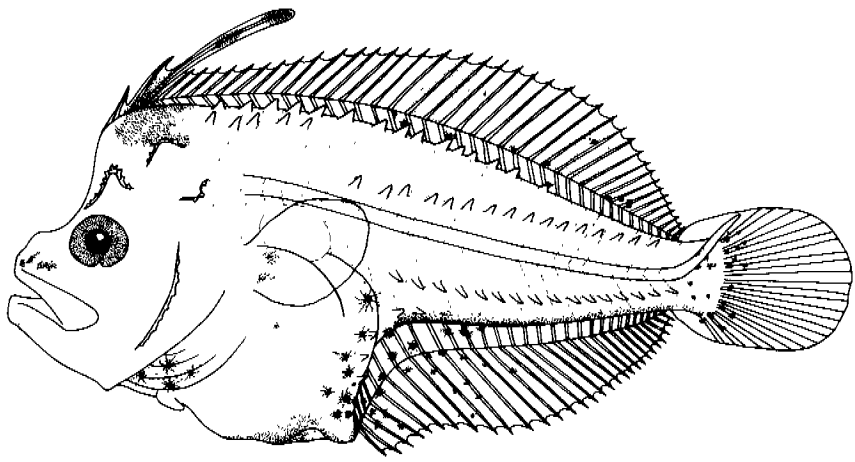

Figure 23. Eleven day old larva of *A. lineatus*. 3.6 mm SL.

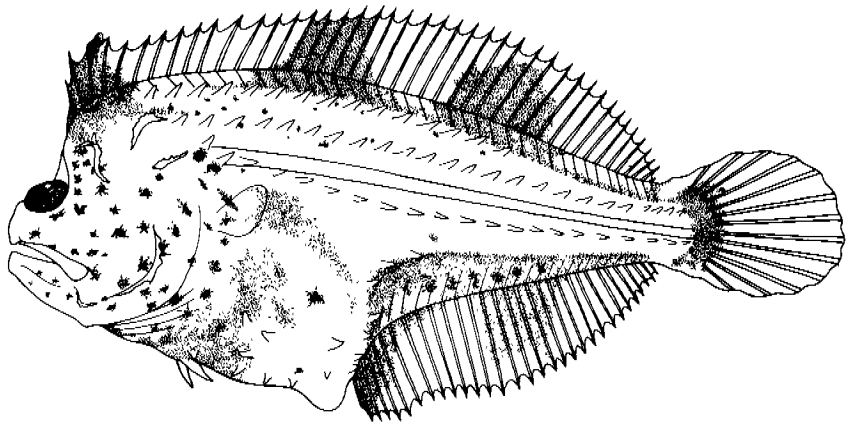

Figure 24A. Twelve day old larva of *A. lineatus*. 3.7 mm SL. Left side.

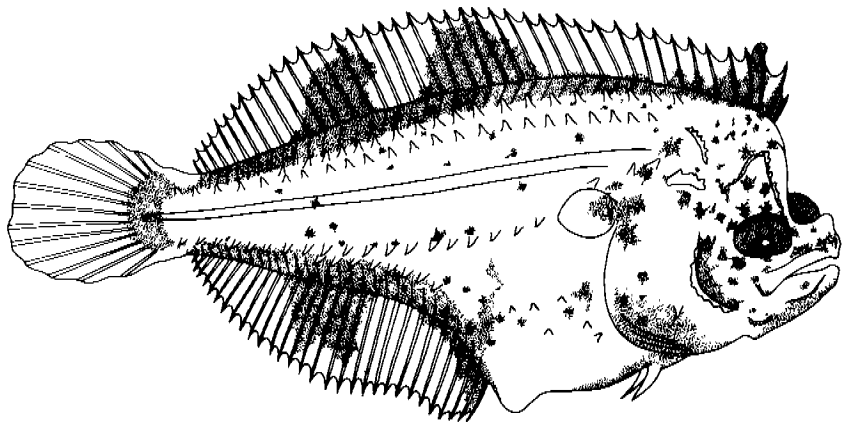

Figure 24B. Twelve day old larva of *A. lineatus*. 3.7 mm SL. Right side.

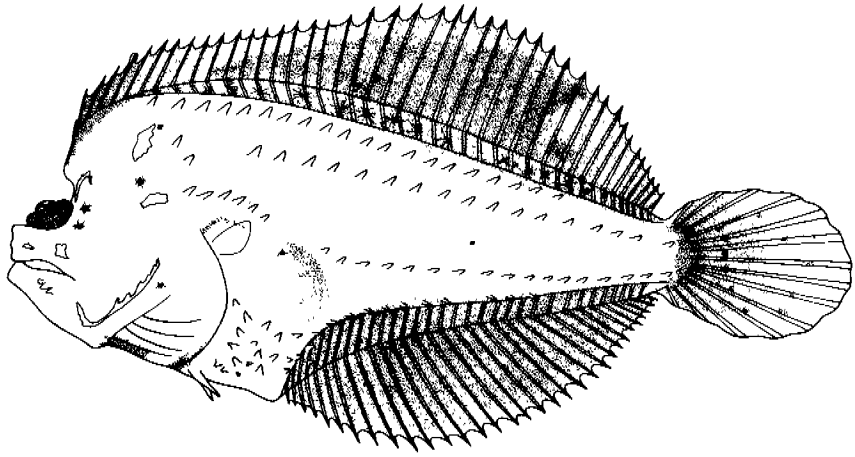

Figure 25A. Thirteen day old larva of *A. lineatus*. 4.0 mm SL. Left side.

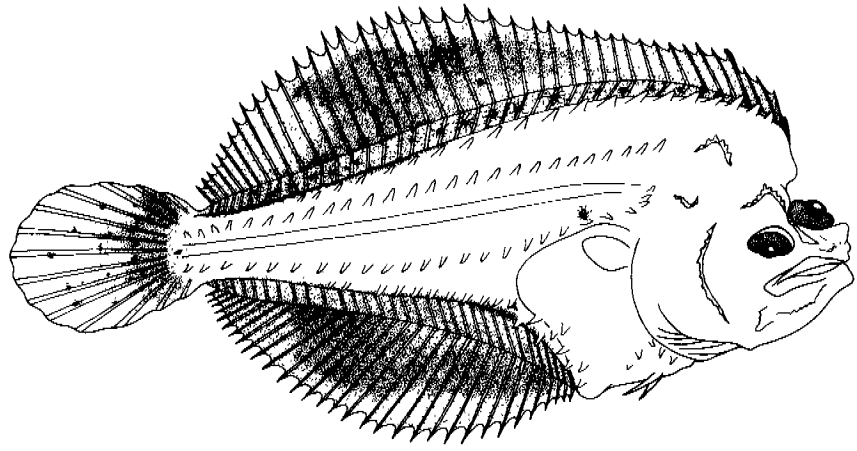

Figure 25B. Thirteen day old larva of *A. lineatus*. 4.0 mm SL. Right side.

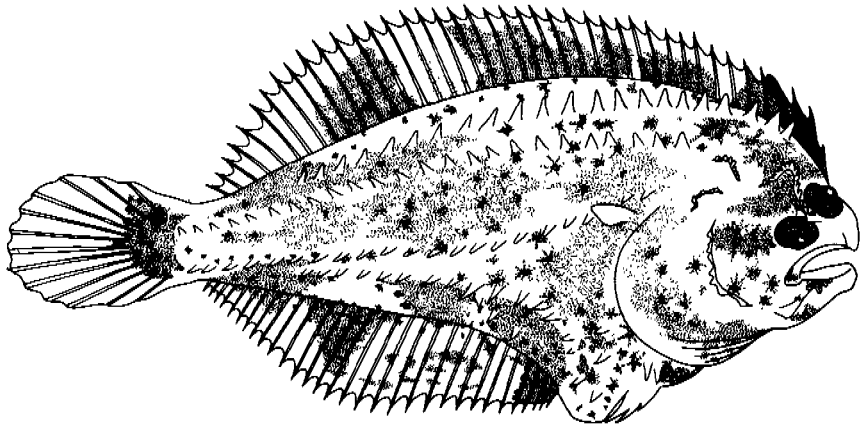

Figure 26. Fourteen day old larva of *A. lineatus*. 4.1 mm SL.

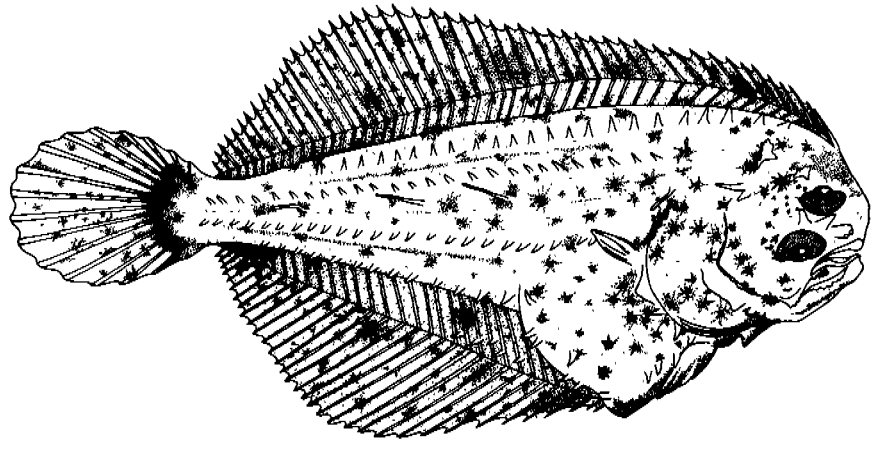

Figure 27. Seventeen day old larva of *A. lineatus*. 5.4 mm SL.