DEVELOPMENT OF LARVAL SMOOTH FLOUNDER, *LIOPSETTA PUTNAMI*, WITH A REDESCRIPTION OF DEVELOPMENT OF WINTER FLOUNDER, *PSEUDOPLEURONECTES AMERICANUS* (FAMILY PLEURONECTIDAE)[1]

WAYNE A. LAROCHE[2]

ABSTRACT

Larval development is described for the first time for *Liopsetta putnami* and redescribed for *Pseudopleuronectes americanus* (Pleuronectidae). These species cooccur as larvae in Gulf of Maine estuaries during the spring and have previously been difficult to separate, especially as small larvae, due to their similar development and the lack of adequate published descriptions. Characters which distinguish *L. putnami* from *P. americanus* larvae include: presence of darkly pigmented eyes in yolk-sac larvae; lack of internal melanophores over the notochord in larvae greater than 3.2 mm; lack of melanophores on the fins of yolk-sac, preflexion, and flexion larvae; and higher ratio of snout to anus length/standard length (averages 43.6 and 41.2% standard length for yolk-sac and preflexion larvae versus 33.3 and 37.6% standard length for yolk-sac and preflexion larval *P. americanus*).

The smooth flounder, *Liopsetta putnami* (Gill), Family Pleuronectidae, occurs in the western North Atlantic Ocean from Ungava Bay, Quebec, to Providence, R.I. It is found chiefly over muddy bottoms in estuaries and nearshore, marine waters <10 m deep (Bigelow and Schroeder 1953; Leim and Scott 1966). The winter flounder, *Pseudopleuronectes americanus* (Walbaum), Family Pleuronectidae, occurs from Battle Harbour and Windy Tickle, Labrador (lat. 55°45′ N), to Georgia. It is caught over hard bottoms to depths of ≈142 m on the offshore fishing banks and also in estuaries and nearshore, marine waters (Bigelow and Schroeder 1953; Leim and Scott 1966). From Providence, R.I., northwards, *L. putnami* and *P. americanus* cooccur in shallow coastal and estuarine waters where both are known to spawn (Bigelow and Schroeder 1953).

Previously, two large larvae and one small juvenile *L. putnami* have been illustrated and described (Laszlo 1972), while larval and juvenile *P. americanus* have been illustrated and their development briefly described in various publications (Sullivan 1915; Breder 1923; Bigelow and Welsh 1925; Bigelow and Schroeder 1953; Scotton et al. 1973; Lippson and Moran 1974; Klein-MacPhee 1978; Martin and Drewry 1978; and others). However, existing descriptions of *P. americanus* do not accurately present all characters necessary for reliable separation of small larvae when the species cooccur.

This paper describes the larval development of *L. putnami* for the first time from reared and field-collected specimens, redescribes the larval development of *P. americanus*, and compares the two.

METHODS

Two ripe female and one ripe male *L. putnami* were collected from the cooling water intake screens of the Maine Yankee Atomic Power Plant located on Montsweag Bay, Wiscasset, Maine, on 7 February 1974. Most *L. putnami* collected on that date were spent. The ripe fish were artificially spawned, and the eggs were fertilized in the field. Eggs were kept at 5° C in darkened containers of gently aerated 23‰ salinity water, conditions approximating those at the capture site. Field-collected larvae were captured in February and March and also were reared in the laboratory. Larvae were fed field-collected plankton.

Larvae of both *L. putnami* and *P. americanus* were collected and preserved in 3-5% Formalin[3] during 1972, 1973, and 1974 from the Sheepscot

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[2]Ira C. Darling Center, University of Maine, Walpole, Maine; present address: Gulf Coast Research Laboratory, P.O. Drawer AG, Ocean Springs, MS 39564.

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

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and Damariscotta River estuary systems. Larvae were collected with meter nets, ½ m buoyed and anchored nets, and a small beam trawl. The smallest *L. putnami* larvae (3.1 and 3.6 mm) were hatched from the artificially spawned eggs. The 7.1 and 7.6 mm specimens were field collected as small larvae and reared in the laboratory. All other specimens in the series were field collected and preserved. The *P. americanus* series includes only field-collected specimens.

Some specimens were lightly stained with alizarin to facilitate counting of body parts. Illustrations were prepared using a camera lucida. Measurements were taken on the right side of each specimen with an ocular micrometer mounted in a dissecting microscope. Measurements taken include:

Standard length (SL) = snout tip to notochord tip preceding development of caudal fin, then to posterior margin of hypural plate.

Total length (TL) = snout tip to tip of caudal fin membrane or fin rays.

Snout to anus length = horizontal distance from snout tip to a vertical through posterior margin of large intestine at anus.

Head length (HL) = snout tip to posterior margin of otic capsule until cleithrum becomes visible (5.4 mm in *L. putnami* vs. 3.7 mm in *P. americanus*), then to the cleithrum; to the posterior margin of the operculum on postflexion larvae >7.0 mm of both species.

Snout length = snout tip to anterior margin of orbit of right eye.

Upper jaw length = snout tip to posterior margin of maxillary.

Eye diameter = greatest width of right eye.

Body depth at pectoral fin base = vertical distance across body at pectoral fin base, not including depth of dorsal fin pterygiophores.

Maximum body depth at pectoral fin base = vertical distance across body at pectoral fin base including depth of dorsal fin pterygiophores.

Body depth behind anus = vertical distance across body immediately posterior to anus, not including depth of dorsal fin pterygiophores.

Maximum body depth behind anus = vertical distance across body immediately posterior to anus including depth of dorsal fin pterygiophores.

Pectoral fin length = distance from base to tip of fin fold or longest fin ray.

Pectoral fin base depth = width of base of pectoral fin.

Pelvic fin length = distance from insertion of pelvic fin to tip of fin fold or longest ray.

Vertebral and fin ray counts were made on juveniles with the aid of radiographs. All length measurements are standard length unless otherwise stated.

TERMINOLOGY

Yolk-sac larva = prior to absorption of yolk material.

Preflexion larva = prior to notochord flexion.

Flexion larva = undergoing notochord flexion from time urostyle begins to slant upward until urostyle is in final upturned position and caudal fin is formed.

Postflexion larva = from alignment of urostyle in final upturned position and caudal fin formation until attainment of adult dorsal and anal fin complements.

Transforming larva = from onset of migration of left eye, development of juvenile pigment pattern, and change in behavior from pelagic swimming to benthic habit until completion of these processes and attainment of adult pelvic and pectoral fin ray complements.

IDENTIFICATION

Liopsetta putnami and *P. americanus* are the only Gulf of Maine flatfishes that commonly are found in estuaries and that spawn during late winter-early spring (Bigelow and Schroeder 1953). American plaice, *Hippoglossoides platessoides*, and Atlantic halibut, *Hippoglossus hippoglossus*, also spawn during late winter-early spring but rarely enter Gulf of Maine estuaries (Bigelow and Schroeder 1953). Larval *Hippoglossoides platessoides* were described by Bigelow and Schroeder (1953) and have three vertical bands of melanistic pigment across the postanal region. Martin and Drewry (1978) compiled and summarized descriptions of larval *Hippoglossus hippoglossus* which lack vertical bands of melanistic pigment across the postanal region and hatch at lengths >8 mm. All yolk-sac larvae collected from Montsweag Bay during March had a single vertical band of melanistic pigment across the postanal region and were <5.2 mm long.

Since *L. putnami* spawns from December through February while *P. americanus* spawns from March through May and eggs take 2 or 3 wk

to hatch (Bigelow and Schroeder 1953), larval flounders collected from Montsweag Bay in early March 1974 were tentatively identified as *L. putnami*. Yolk-sac larvae hatched from artificially spawned *L. putnami* eggs appeared identical to the field-collected larvae. Since the artificially spawned larvae were few and did not live beyond yolk absorption, larvae were collected from Montsweag Bay and reared in the laboratory to verify the identification. These larvae attained the adult dorsal and anal fin ray complement of *L. putnami* during the postflexion stage, verifying the identification. In April 1974, small yolk-sac flounder larvae matching descriptions of *P. americanus* (Martin and Drewry 1978) appeared in plankton samples collected from Montsweag Bay. Two of these larvae were reared in the laboratory to the postflexion stage and attained the adult dorsal and anal fin ray complements of *P. americanus*.

Counts that identify *L. putnami* and *P. americanus* (34-38 and 34-40 vertebrae, 48-60 and 60-76 dorsal fin rays, and 34-41 and 44-58 anal fin rays, respectively) were compiled from Jordan and Evermann (1898), Norman (1934), Bigelow and Schroeder (1953), Leim and Scott (1966), and this study.

LABORATORY OBSERVATIONS

Fertilized *L. putnami* eggs were nonadhesive and demersal in 23‰ water. Eggs ranged in diam-

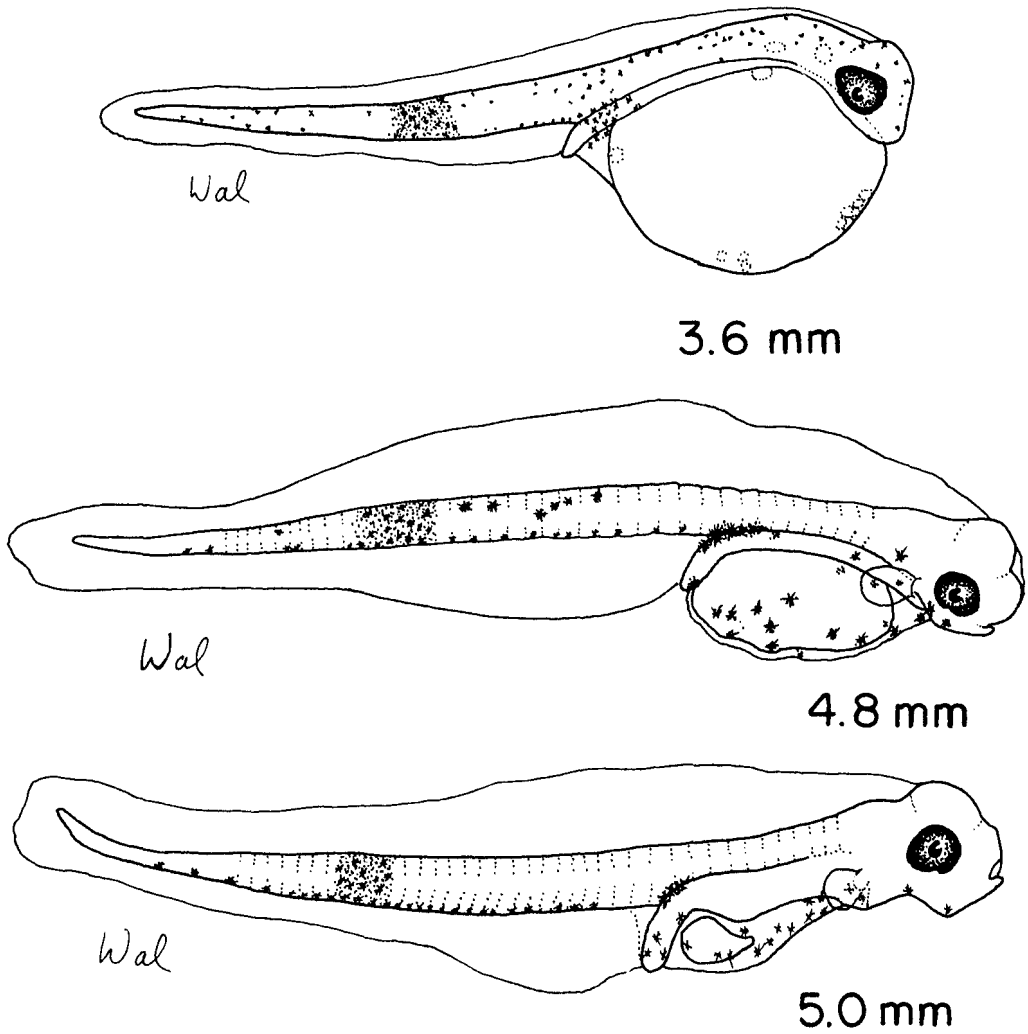

FIGURE 1.—Yolk-sac larvae of *Liopsetta putnami*.

eter from 1.1 to 1.4 mm, averaging 1.2 mm. Yolk diameter ranged from 0.9 to 1.2 mm, averaging 1.1 mm. No oil globules were obvious in newly fertilized eggs. At 5° C hatching began on the 25th day after fertilization. Newly hatched larvae were 3.1-3.6 mm long.

DISTINGUISHING FEATURES

Characters useful to distinguish larval *L. putnami* and *P. americanus* from other Gulf of Maine flatfishes are: number of myomeres, 34-38 and 38-40; hatching length, 3.1-3.6 mm and ≈2.4 mm; number of dorsal fin rays, 48-60 and 60-76; number of anal fin rays, 34-41 and 44-58; and presence of a single vertical band of melanistic pigment across the postanal region of both species.

Characters useful to distinguish yolk-sac larvae of *L. putnami* from *P. americanus* are: percentage snout to anus length/standard length, averaging 43.6% vs. 33.3%; presence of eye pigment at hatching vs. absence of eye pigment at hatching; length at hatching, 3.1-3.6 mm vs. ≈2.4 mm; and length at yolk-sac resorption, ≈5.2 mm vs. ≈3.7 mm.

Characters useful to distinguish larval *L. putnami* from *P. americanus* are: absence of internal melanophores over the notochord vs. presence of internal melanophores over the notochord; length at which gut loops, ≈5.5 mm vs. ≈4.3 mm; and absence vs. presence of anal fin pigmentation in specimens <6.3 mm.

GENERAL DEVELOPMENT
(Figures 1-8)

Reared *L. putnami* were 3.1-3.6 mm long at hatching. The smallest field-collected *L. putnami* larvae were ≈3.5 mm long. Newly hatched field-collected *P. americanus* larvae were ≈2.4 mm long. The yolk sac is resorbed by ≈5.2 and ≈3.7 mm in *L. putnami* and *P. americanus*. The gut loops by ≈5.5 mm in *L. putnami* and between 4.2 and 4.4 mm in *P. americanus*. The notochord begins to flex in *L. putnami* and *P. americanus* at ≈6.0 and ≈5.0 mm;

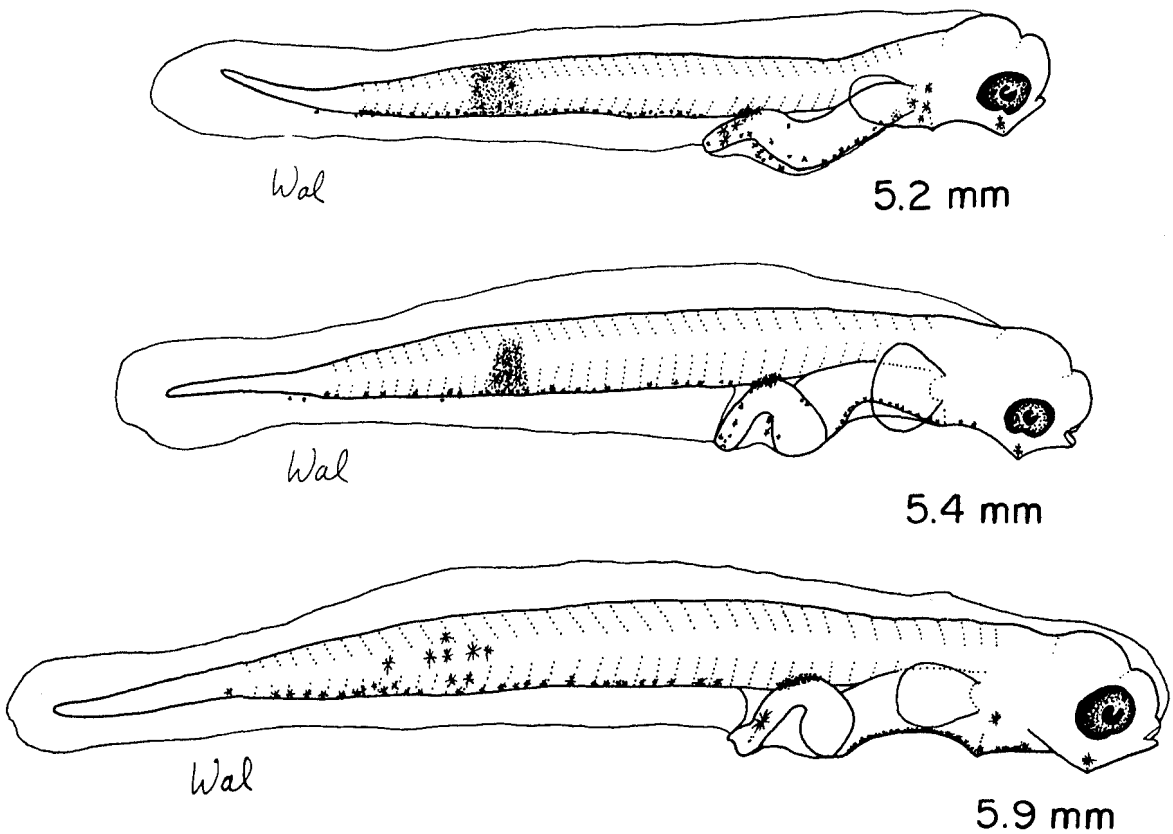

FIGURE 2.—Preflexion larvae of *Liopsetta putnami*.

flexion is completed by ≈7.1 and ≈6.6 mm; and the free tip of the notochord disappears by 7.6 and 7.3 mm. Transition from pelagic to benthic habit occurs at ≈7.3 mm in *L. putnami*. The largest pelagic field-collected *L. putnami* larva was 7.3 mm, and the largest specimen, 7.6 mm, had assumed the benthic habit in the laboratory. Transition from pelagic to benthic habit usually occurs between 6.0 and 7.0 mm in *P. americanus*. The smallest benthic-collected *P. americanus* was 5.7 mm, and the largest pelagic-collected larva was 7.4 mm long. Formation of pectoral and pelvic fin rays is completed between 8.5 and 13.0 mm (Laszlo 1972) in *L. putnami* and by ≈13 mm in *P. americanus*, marking the end of the transformation and beginning of the juvenile period.

MORPHOLOGY
(Tables 1-3)

Various body parts were measured on 40 *L. putnami* (3.1-7.6 mm) and 64 *P. americanus* (2.4-7.3 mm) larvae to examine developmental morphology. Body proportions are summarized and compared in Table 3.

The most important morphological character for separating *L. putnami* from *P. americanus*, particularly during the yolk-sac and preflexion

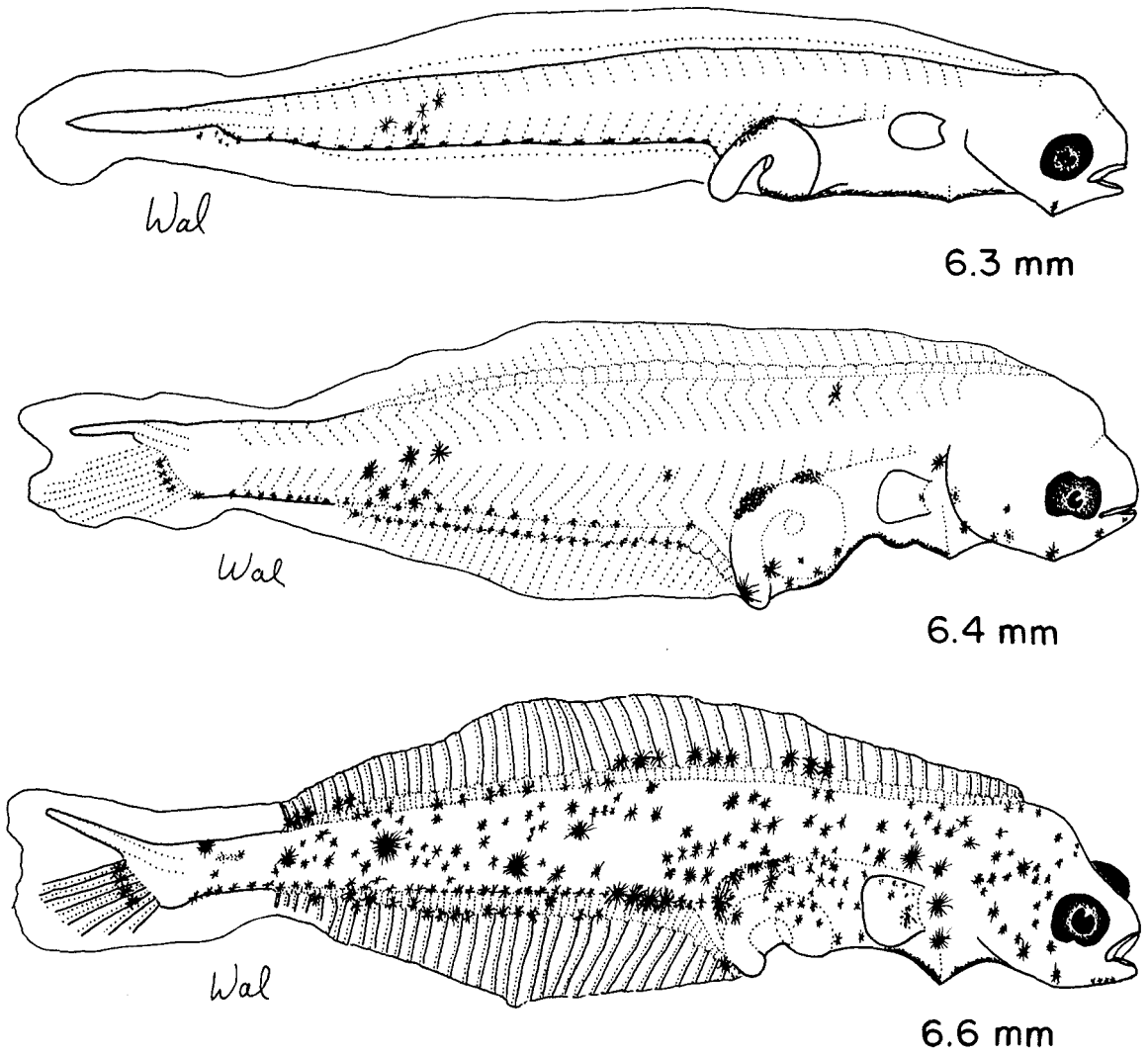

FIGURE 3.—Flexion larvae of *Liopsetta putnami*.

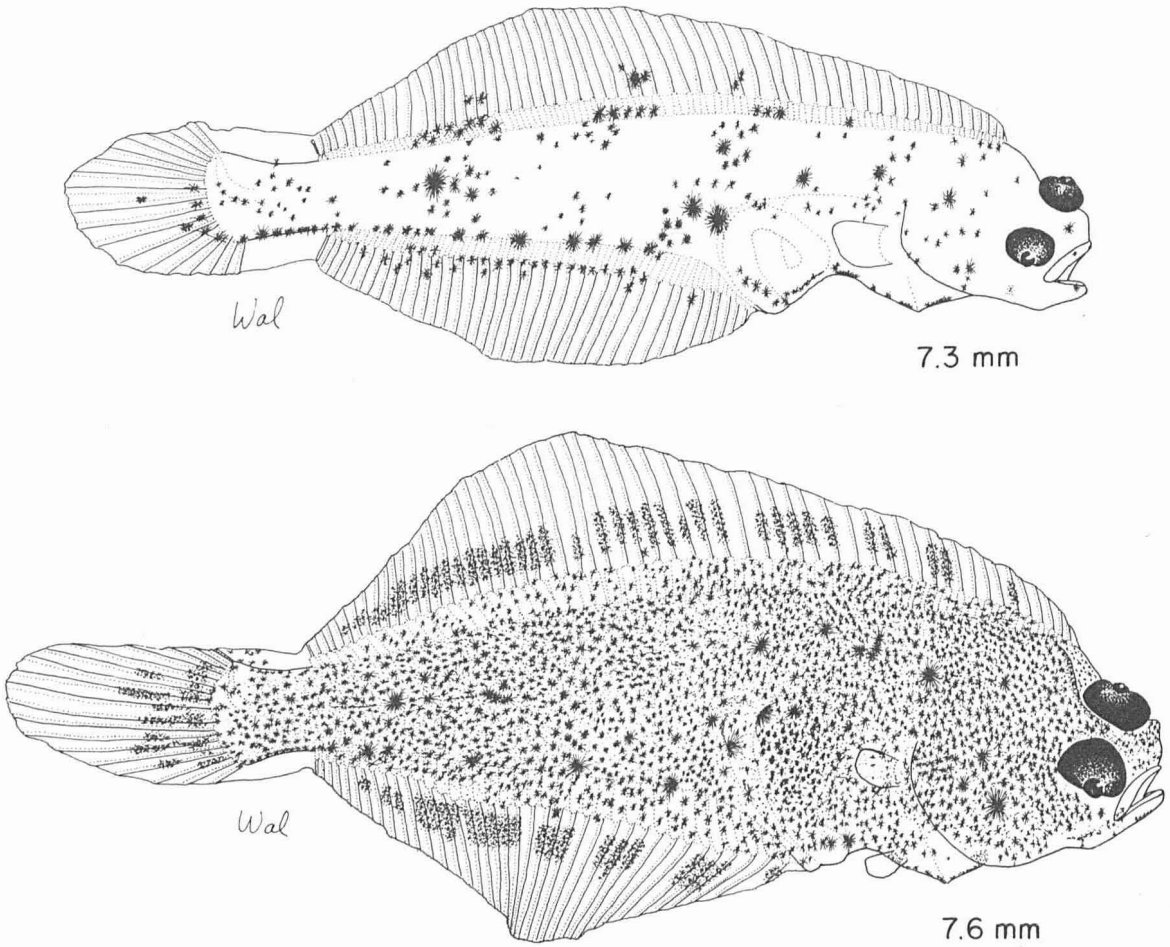

FIGURE 4.—Postflexion and transforming larvae (7.1 and 7.6 mm) of *Liopsetta putnami*.

stages, is snout to anus length/standard length. In *L. putnami* it averages 43.6 and 41.2% for yolk-sac and preflexion larvae while in *P. americanus* it averages 33.3 and 37.6% for yolk-sac and preflexion larvae.

FIN DEVELOPMENT

Newly hatched larvae of both *L. putnami* and *P. americanus* have an undifferentiated fin fold extending along the body midline from the head around the notochord tip to the anus. No other fins were observed on the smallest *L. putnami* larva (3.1 mm); however, the smallest *P. americanus* larva (2.4 mm) and a 3.8 mm *L. putnami* larva had undifferentiated pectoral fin folds.

Pectoral fin rays are the first to begin development in both *L. putnami* and *P. americanus*, by 5.2 and 5.3 mm. However, pectoral fin rays are the last to complete development, completed between 8.5 and 13 mm in *L. putnami* (Laszlo 1972) and by 13 mm in *P. americanus*. Pectoral fin length is greatest in both species during the preflexion and flexion periods, averaging 7.8 and 7.1% SL in *L. putnami* and 7.7 and 7.8% SL in *P. americanus*, and shortest during yolk-sac and postflexion stages, averaging 3.8 and 5.0% SL in *L. putnami* and 3.0 and 4.7% SL in *P. americanus*. Dorsal, anal, and caudal fin rays begin development in preflexion *L. putnami* and *P. americanus* at ≈5.9 and ≈5.6 mm. Adult complements of dorsal and anal fin rays and principal caudal fin rays are present by ≈8 and ≈7 mm. Fin rays within dorsal and anal fins of both species seem to form simultaneously except the two or three posteriormost rays in each fin which form last. Principal caudal fin rays form first and

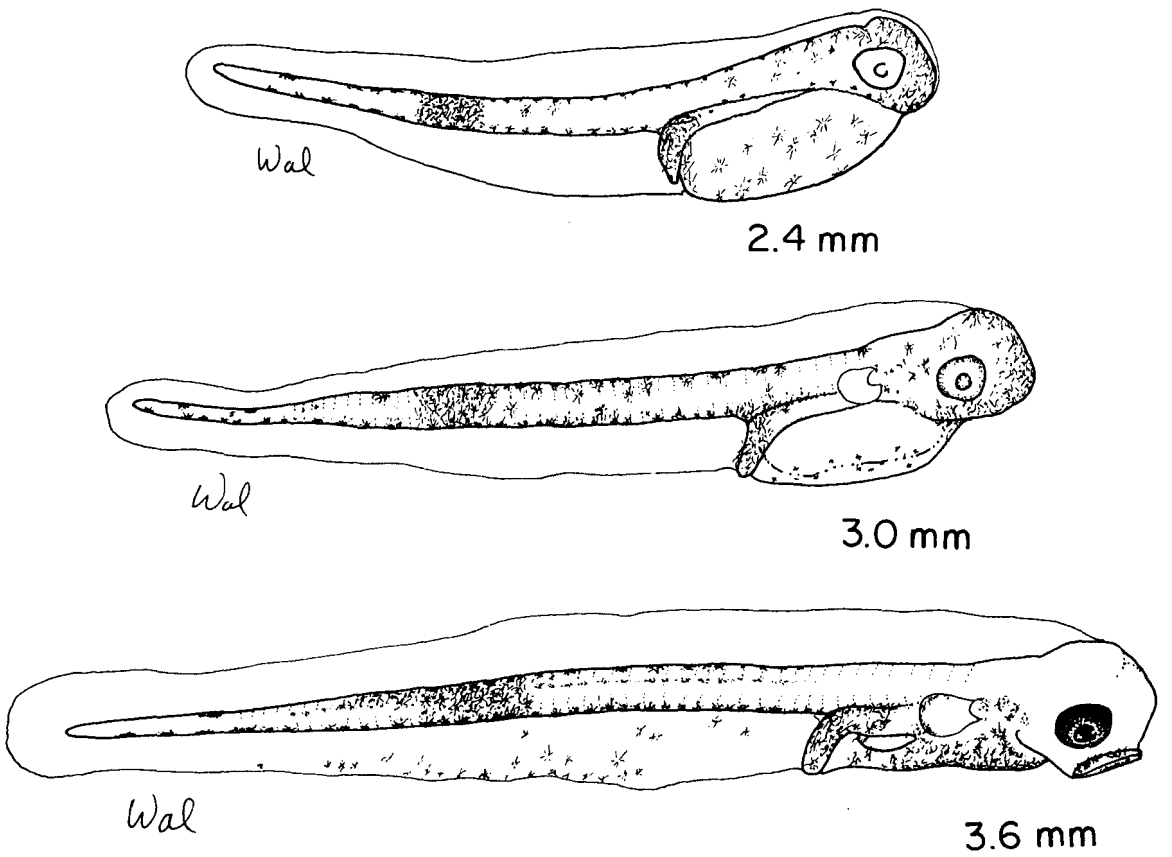

FIGURE 5.—Yolk-sac larvae of *Pseudopleuronectes americanus*.

secondary rays are gradually added anteriorly. The pelvic fin bud appears at ≈7 mm in postflexion *L. putnami* larvae. Fin rays begin to develop by 7.6 mm, and development is completed by 13 mm (Laszlo 1972). The pelvic fin bud appears at ≈6.6 mm in postflexion *P. americanus* larvae; and development is complete by 7.3 mm.

PIGMENTATION

Liopsetta putnami

The eyes of *L. putnami* are darkly pigmented at hatching. Small external melanophores are scattered over the head of the smallest larva (3.1 mm). These melanophores appear to migrate ventrolaterally, appearing on the ventral surface of the head between the isthmus and the cleithrum by ≈4.7 mm, and are aligned here on all specimens >5.4 mm long. This row often appears as a solid line of pigment due to the expanded condition of individual melanophores. A melanophore appears at the angle of the lower jaw between 4.8 and 5.4 mm, and one or two melanophores are present at this location on all specimens >5.4 mm. One or two melanophores are present at the tip of the lower jaw on most specimens >5.8 mm. A large stellate melanophore appears below the lateral midline of the head, anterior to the cleithrum at 5.2 mm. Larvae >5.4 mm often have 4-6 melanophores, internal and external, in this area. A few external melanophores appear scattered over the head, on and under the operculum, by 7.3 mm. Flexion and postflexion larvae >6.6 mm rapidly acquire the dense scattering of external melanophores characteristic of juveniles.

In the abdominal region small external melanophores scattered over the dorsolateral surfaces of the hindgut are present on the smallest larva (3.1 mm). An internal patch over the hindgut is present on all specimens in the series. The small external melanophores migrate ventrolaterally

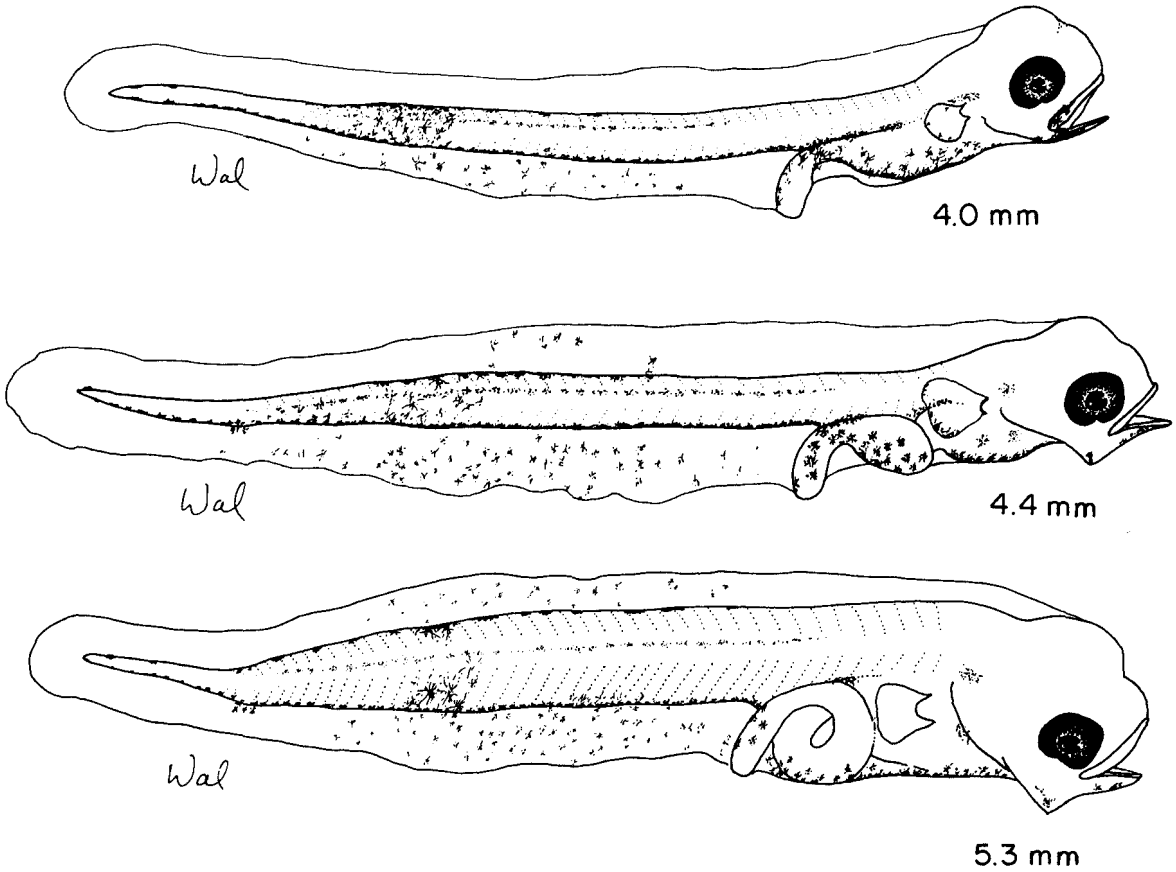

FIGURE 6.—Preflexion larvae (4.0 and 4.4 mm) and flexion larva (5.3 mm) of *Pseudopleuronectes americanus*.

becoming scattered on only the ventral surface of the body and yolk sac by 4.8 mm and form a row along the ventral midline on all specimens larger than ≈5.2 mm. This row extends from the cleithrum, where it is continuous with the row on the ventral midline of the head, to the center of the abdominal region where it becomes indistinct, merging with a group of melanophores scattered on the ventrolateral body surface between 6.6 and 7.0 mm. Specimens >7.0 mm rapidly acquire the dense scattering of external melanophores over the body surface characteristic of juveniles.

Small external melanophores are scattered over the postanal region, and a vertical band of concentrated melanophores of various sizes is present across the center of the postanal region in the smallest larva (3.1 mm). The scattered external melanophores migrate ventrolaterally and are present only on the ventrolateral surfaces by ≈4.6 mm. An irregular row of melanophores extends from the anus to the vertical pigment band along both sides of the ventral midline, and a single irregular row of melanophores along the ventral midline extends posteriorly from the pigment band on specimens 4.3-5.4 mm long. Usually one to several small melanophores appear somewhat separated from the row and located just anterior to the notochord tip. The vertical pigment band is distinct on larvae <5.4 mm, but it is usually represented by only a few large stellate melanophores on larger larvae. These melanophores become indistinguishable from other external melanophores which become scattered over the body on large larvae, >6.6 mm, indicating the initial development of the juvenile pigment pattern.

The fin folds of the smallest *L. putnami* larva are not pigmented. At ≈5.2 mm one or two melanophores move from the body onto the fin membrane just anteroventral to the notochord tip.

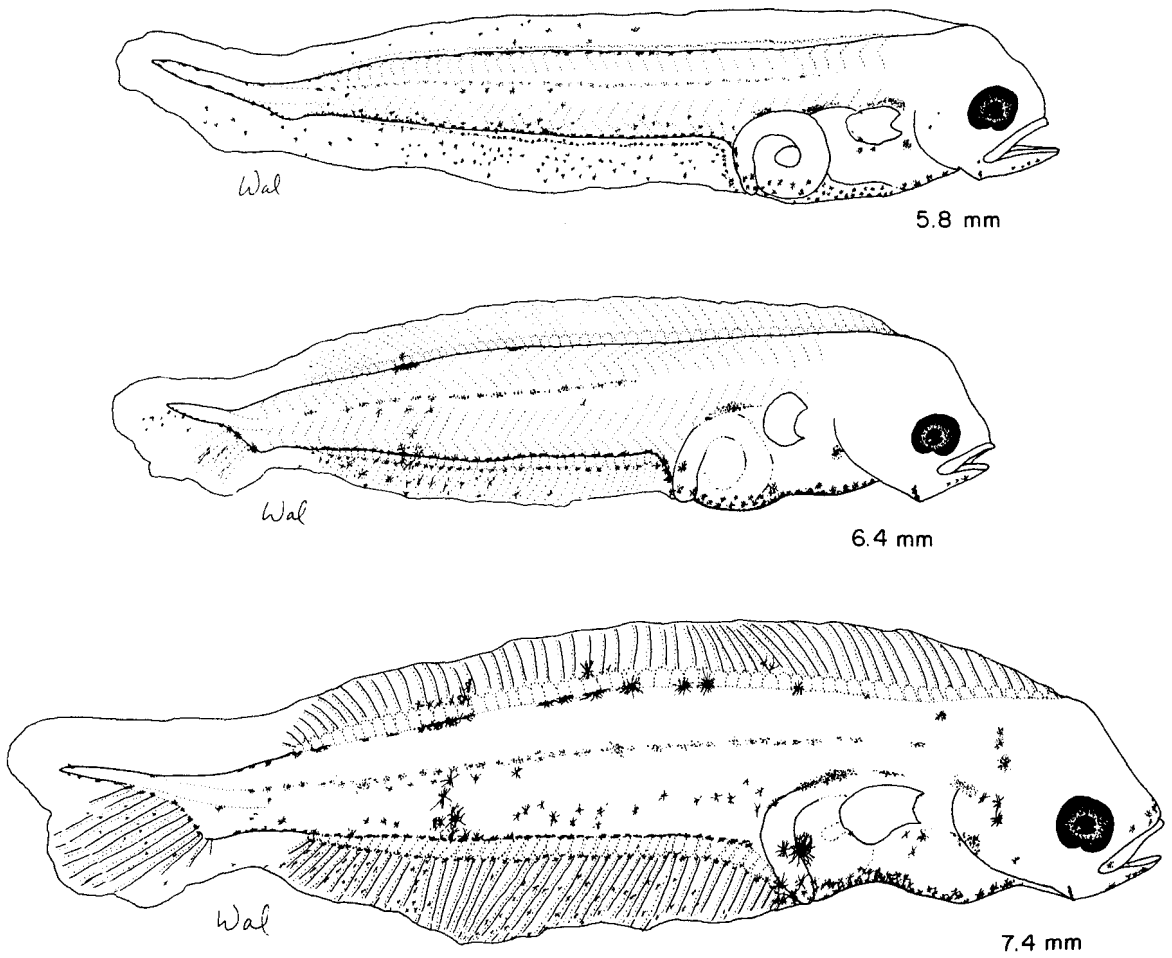

FIGURE 7.—Flexion larvae of *Pseudopleuronectes americanus*.

Several additional melanophores appear at this location by 6.3 mm and appear on the caudal fin near the base of the caudal fin rays after they form. As the pterygiophores associated with the anal fin rays begin to develop, between 6.3 and 6.4 mm, melanophores separate from the postanal ventral midline rows and appear as an irregular row along the distal margins of the pterygiophores and along the bases of the dorsal and anal rays by 6.6 mm. A broken band of melanophores develops in the proximal one-third of the dorsal and anal fins by 7.6 mm.

Scattered metallic yellow chromatophores were present over the head and body of newly hatched larvae. These chromatophores disappear soon after preservation in Formalin. No additional observations of chromatophore patterns were possible on larger field-collected larvae.

Pseudopleuronectes americanus

The eyes of *P. americanus* lack pigmentation at hatching (≈2.4 mm). Pigmentation begins to appear in the eyes of *P. americanus* at ≈2.9 mm, and the eyes are completely pigmented by 3.5 mm. Expanded external melanophores are scattered over the head of the smallest larva (2.4 mm). These melanophores are faint and may be difficult to see. Melanophores over the dorsolateral surfaces of the head disappear by ≈3.5 mm. A few melanophores remain on the upper and lower jaws and along the ventral midline of the head (gular and isthmus regions). No evidence of melanophore migration was observed in *P. americanus*. One to several internal melanophores are present along the anterior edge of the cleithrum often appearing under the operculum on larvae >2.6 mm. One or two

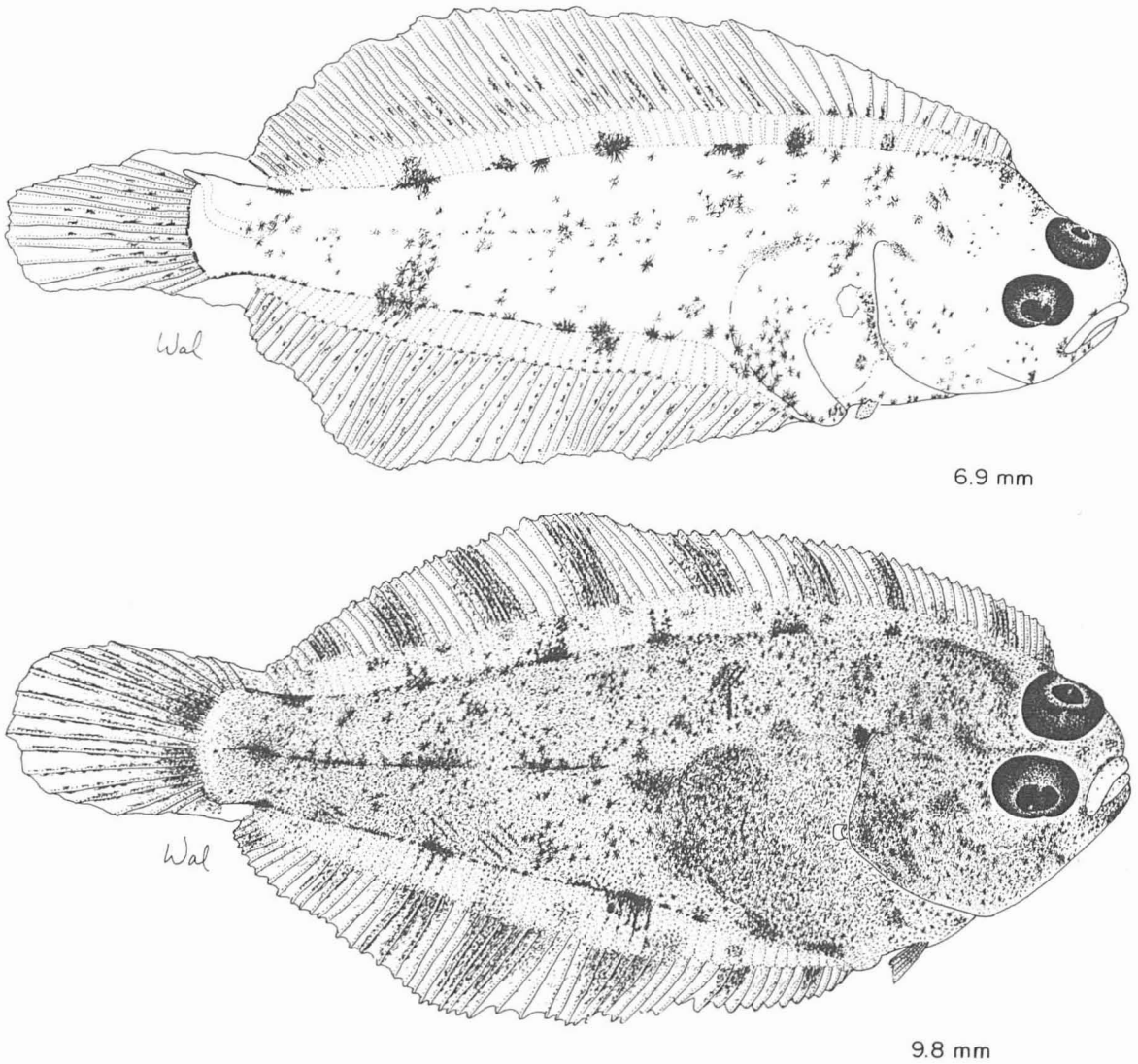

FIGURE 8.—Flexion, transforming, larva (6.9 mm) and postflexion, transforming, larva (9.8 mm) of *Pseudopleuronectes americanus*.

melanophores are present at the articulation of the lower jaw on larvae >3.4 mm. A few external melanophores appear on the snout and operculum of preflexion larvae >6.6 mm. Postflexion larvae (>5.8 mm) rapidly acquire a covering of external melanophores, characteristic of juveniles, as transformation proceeds.

External melanophores are scattered over the abdominal region of the smallest larva (2.4 mm) with greatest concentrations along the dorsal surface of the body and on the ventrolateral surface of the yolk sac. Internal melanophores are present in a patch over the posterior hindgut near the anus and over the middle of the gut. By 3.6 mm pigmentation disappears from the dorsolateral surface of the abdominal region, and the melanophores which had been scattered over the yolk sac are on the ventrolateral surfaces of the body. Some of these form a row which is often expanded and appears as a solid line between the anus and the cleithrum with some on the ventrolateral surface on each side of the line. Also, by 3.6 mm, one to several internal melanophores appear in the vicinity of the pectoral fin base posterior to the cleithrum. By 4.4 mm, internal melanophores are present over the notochord in this region. No further pigmentation changes occur until external melanophores begin to appear scattered over

TABLE 1.—Measurements (millimeters) of larval *Liopsetta putnami*. Specimens above dashed line are yolk-sac larvae.

Standard length	Total length	Body depth at pectoral fin base	Body depth at anus	Maximum body depth at pectoral fin base	Maximum body depth at anus	Snout to anus length	Head length	Eye diameter	Upper jaw length	Snout length	Pectoral fin length
3.1	3.2	0.40	0.36	—	—	1.5	0.44	0.18	—	—	—
3.6	3.8	0.40	0.36	—	—	1.8	0.50	0.24	—	0.16	0.18
4.0	4.1	0.34	0.22	—	—	1.6	0.52	0.24	—	0.14	0.14
4.3	4.4	0.36	0.24	—	—	2.0	0.56	0.24	—	0.16	—
4.4	4.5	0.38	0.26	—	—	1.8	0.60	0.26	—	0.22	0.10
4.6	4.8	0.40	0.24	—	—	1.8	0.60	0.24	—	0.16	0.18
4.8	5.0	0.50	0.28	—	—	1.9	0.62	0.26	0.14	0.14	0.34
4.8	5.0	0.54	0.28	—	—	—	0.64	0.26	—	0.12	0.14
4.8	5.0	0.46	0.26	—	—	2.1	0.62	0.24	0.14	0.18	0.16
4.9	5.2	0.40	0.26	—	—	2.2	0.64	0.26	—	0.16	0.18
4.9	5.1	0.40	0.26	—	—	2.1	0.60	0.26	—	0.16	0.12
5.0	5.1	0.38	0.30	—	—	2.2	0.68	0.26	—	0.20	0.18
[1]5.2	5.3	0.46	0.32	—	—	2.2	0.74	0.26	0.20	0.18	0.30
[1]5.2	5.3	0.54	0.34	—	—	2.4	0.80	0.28	0.18	0.16	0.32
[1]5.4	5.7	0.62	0.40	—	—	2.4	0.80	0.29	0.16	0.12	0.38
[1]5.4	5.7	0.66	0.42	—	—	2.1	0.80	0.26	0.20	0.14	0.36
[1]5.5	5.8	0.82	0.62	—	—	2.1	0.96	0.30	0.18	0.10	0.52
[1]5.5	5.7	0.76	0.60	—	—	2.4	1.0	0.29	0.30	0.16	0.56
[1]5.7	5.9	0.74	0.60	—	—	2.4	1.1	0.28	0.26	0.12	0.52
[1]5.8	6.0	0.78	0.62	—	—	2.3	1.0	0.30	0.38	0.20	0.52
[1]5.9	6.2	0.74	0.44	—	—	2.4	0.96	0.27	0.28	0.16	0.44
[2]5.9	6.2	0.80	0.70	—	—	2.6	1.2	0.30	0.32	0.20	0.40
[1]5.9	6.2	0.78	0.56	—	—	2.3	1.1	0.30	0.36	0.18	0.40
[2]6.2	6.3	0.98	0.90	1.0	0.94	2.5	1.1	0.32	0.42	0.26	0.54
[1]6.3	6.6	0.78	0.56	—	—	2.5	1.0	0.30	0.32	0.16	0.48
[1]6.4	6.6	1.0	0.92	1.1	0.94	2.7	1.2	0.32	0.46	0.24	0.50
[1]6.5	6.7	0.74	0.52	—	—	2.7	1.1	0.32	0.30	0.16	0.46
[1]6.6	6.8	0.78	0.60	—	—	2.5	1.0	0.31	0.30	0.14	0.54
[2]6.6	6.9	1.0	0.80	1.1	0.86	2.7	1.2	0.33	0.40	0.20	0.46
[2]6.6	6.8	1.1	1.1	1.2	1.1	2.8	1.4	0.34	0.42	0.22	0.54
[2]6.7	6.9	0.92	0.80	0.96	0.86	2.7	1.0	0.32	0.40	0.20	0.44
[2]6.8	7.1	0.84	0.72	0.89	0.74	2.8	1.2	0.32	0.32	0.18	0.40
[2]6.9	7.1	0.92	0.76	0.96	0.80	2.6	1.2	0.34	0.40	0.20	0.50
[2]7.0	7.4	1.1	1.1	1.2	1.1	2.8	1.3	0.34	0.40	0.16	0.52
[2]7.0	7.3	1.2	1.1	1.2	1.2	2.8	1.4	0.32	0.40	0.20	0.50
[2]7.0	7.4	1.1	1.0	1.1	1.1	2.8	1.3	0.32	0.40	0.18	0.50
[3]7.1	8.1	1.5	1.4	1.6	1.5	2.6	1.5	0.36	0.44	0.26	0.60
[2]7.3	7.6	1.1	1.0	1.2	1.1	3.0	1.3	0.36	0.40	0.18	0.50
[2]7.3	7.5	1.1	1.0	1.2	1.1	2.8	1.3	0.34	0.40	0.20	0.48
[3]7.6	9.3	—	—	2.4	2.4	2.7	2.1	0.54	0.56	0.28	0.24

[1] = preflexion larvae; [2] = flexion larvae; [3] = postflexion larvae.

the abdominal region of preflexion larvae, >6.2 mm, as metamorphosis begins and the juvenile pattern of dense melanophore covering begins to develop.

A vertical band of concentrated melanophores of various sizes is present across the center of the postanal region in the smallest larva (2.4 mm). External melanophores are aligned in irregular rows on both sides of the ventral midline between the anus and the postanal band. A single irregular row of melanophores extends along the ventral surface from the vertical band nearly to the notochord tip. An irregular row is also present along the dorsal midline extending posteriorly nearly to the notochord tip. Only a few scattered melanophores appear laterally. A row of internal melanophores over the notochord is present on all larvae longer than ≈3.2 mm. The postanal band becomes less distinct, usually represented by only a few large stellate melanophores, in larvae >5.0 mm. Scattered external melanophores begin to appear over the lateral surfaces of preflexion larvae >5.6 mm and continue to increase in number through the larval period. Concentrated pigment spots develop along the dorsal and ventral body surfaces in transforming larvae >5.8 mm.

The fin folds of the smallest *P. americanus* larva are not pigmented. Various authors (Sullivan 1915; Breder 1924; Bigelow and Schroeder 1953; Lippson and Moran 1974) have illustrated small larvae with melanophores extending onto the dorsal and anal fin folds (probably no melanophores were centered on the fin folds) from the vertical postanal band. Their illustrations were of artificially reared larvae. I observed no melanophores extending onto the dorsal and anal fin folds of field-collected larvae; however, reared larvae commonly have somewhat increased pigment due mostly to light conditions which can be altered to change the size of melanophores (Milos and Dingle 1978). A few small melanophores appear along the margin of the pectoral fin fold at 3.5 mm and disappear

TALBE 2.—Measurements (millimeters) of larval *Pseudopleuronectes americanus*. Specimens above dashed line are yolk-sac larvae.

Standard length	Total length	Body depth at pectoral fin base	Body depth at anus	Maximum body depth at pectotal fin base	Maximum body depth at anus	Snout to anus length	Head length	Eye diameter	Upper jaw length	Snout length	Pectoral fin length
2.4	2.5	0.20	0.14	—	—	0.92	0.39	0.17	—	0.08	0.05
2.6	2.7	0.18	0.15	—	—	0.92	0.38	0.16	—	0.10	0.04
2.6	2.6	0.24	0.14	—	—	0.85	0.39	0.17	—	0.11	0.04
2.7	2.7	0.24	0.15	—	—	0.94	0.42	0.17	—	0.10	0.04
2.8	2.8	0.25	0.14	—	—	0.90	0.39	0.17	—	0.10	0.08
2.8	2.9	0.24	0.14	—	—	0.98	0.39	0.18	—	0.10	0.05
2.8	3.0	0.24	0.15	—	—	1.0	0.42	0.18	0.16	0.12	—
2.9	3.0	0.19	0.13	—	—	0.96	0.39	0.17	0.14	0.12	0.06
2.9	3.0	0.21	0.14	—	—	0.90	0.40	0.18	—	0.12	0.04
2.9	3.0	0.24	0.15	—	—	0.96	0.42	0.18	0.16	0.14	0.06
3.0	3.2	0.24	0.15	—	—	1.0	0.42	0.18	0.18	0.14	0.05
3.3	3.4	0.25	0.14	—	—	1.0	0.42	0.18	0.18	0.10	0.06
3.3	3.5	0.34	0.15	—	—	1.0	0.42	0.18	0.18	0.08	0.10
3.4	3.6	0.36	0.14	—	—	1.1	0.42	0.20	0.18	0.08	0.10
3.4	3.6	0.38	0.15	—	—	1.2	0.48	0.20	0.19	0.10	0.20
3.5	3.7	0.33	0.14	—	—	1.1	0.44	0.18	0.17	0.09	0.20
3.5	3.7	0.34	0.15	—	—	1.2	0.46	0.20	0.20	0.09	0.20
3.5	3.7	0.34	0.15	—	—	1.1	0.45	0.18	0.19	0.10	0.19
3.6	3.8	0.33	0.14	—	—	1.2	0.47	0.20	0.21	0.13	0.20
[1]3.7	3.9	0.48	0.24	—	—	1.4	0.66	0.24	0.26	0.12	0.30
[1]4.0	4.3	0.42	0.19	—	—	1.5	0.62	—	0.26	—	0.26
[1]4.2	4.3	0.60	0.30	—	—	1.5	0.76	0.27	0.26	0.18	0.32
[1]4.4	4.5	0.50	0.22	—	—	1.6	0.70	0.26	0.22	0.14	0.32
[1]4.4	4.5	0.50	0.22	—	—	1.5	0.68	0.24	0.22	0.15	0.30
[1]4.5	4.6	0.66	0.32	—	—	1.6	0.80	0.28	0.24	0.12	—
[1]4.5	4.6	0.70	0.35	—	—	1.7	0.82	0.27	0.26	0.18	0.30
[1]4.6	4.7	0.74	0.38	—	—	1.8	0.92	0.32	0.38	0.20	0.28
[2]4.8	4.9	0.80	0.46	—	—	1.8	0.88	0.31	0.30	0.18	0.30
[1]4.9	5.2	0.78	0.44	—	—	1.8	0.98	—	—	—	0.40
[1]4.9	5.2	—	—	—	—	2.0	1.1	0.34	0.32	0.20	0.45
[1]5.1	5.3	0.85	0.54	—	—	2.0	1.0	0.33	0.32	0.14	0.44
[1]5.2	5.4	0.96	0.64	—	—	2.0	1.0	0.34	0.38	0.24	0.44
[2]5.3	5.5	0.94	0.56	—	—	2.1	0.98	0.33	0.34	0.22	0.44
[1]5.4	5.5	0.90	0.60	—	—	2.1	1.1	0.33	0.35	0.18	—
[2]5.6	5.7	1.1	0.82	—	—	2.3	1.2	0.34	0.40	0.24	0.48
[1]5.7	5.8	1.1	0.78	—	—	2.1	1.2	0.34	0.40	0.22	0.45
[1]5.7	5.8	1.1	0.72	—	—	2.2	1.1	0.34	0.40	0.26	0.46
[2]5.8	6.1	1.1	0.70	—	—	2.3	1.2	0.36	0.36	0.20	0.52
[2]6.0	6.2	1.1	0.80	—	—	2.3	1.3	0.36	0.36	0.20	0.48
[2]6.2	6.3	1.3	0.88	—	1.0	2.4	1.3	0.36	0.42	0.26	0.55
[2]6.3	6.4	1.3	0.98	1.4	1.2	2.4	1.4	0.40	0.48	0.26	0.54
[2]6.3	6.4	1.3	0.88	—	1.1	2.4	1.4	0.36	0.44	0.28	0.50
[2]6.4	6.5	1.2	0.86	1.3	1.1	2.4	1.3	0.34	0.40	0.20	0.48
[2]6.5	6.7	1.2	0.84	1.3	1.0	2.6	1.4	0.38	0.42	0.26	0.42
[3]6.6	6.7	1.3	0.96	1.4	1.2	2.5	1.4	0.38	0.42	0.22	0.52
[3]6.6	6.8	1.4	1.1	1.6	1.5	2.4	1.6	0.39	0.48	0.28	0.58
[2]6.8	6.9	1.3	1.0	1.4	1.3	2.5	1.5	0.38	0.40	0.26	0.50
[2]6.9	7.2	1.3	0.96	1.4	1.2	2.6	1.5	0.40	0.46	0.27	0.52
[2]7.0	7.3	1.4	1.1	1.5	1.2	2.7	1.5	0.41	0.44	0.28	0.64
[2]7.1	7.3	1.3	0.94	1.4	1.2	2.6	1.3	0.39	0.44	0.24	0.58
[2]7.3	7.8	1.7	1.4	1.8	1.7	2.6	1.8	0.46	0.44	0.32	0.54
[2]7.4	7.7	1.4	1.1	1.5	1.2	2.4	1.5	0.38	0.44	0.26	0.50
[3]5.7	—	1.7	1.2	1.8	1.6	2.0	1.6	0.48	0.49	0.22	—
[3]6.0	—	1.7	1.3	1.7	1.7	2.4	1.7	0.46	0.48	0.34	0.40
[3]6.2	—	1.9	1.3	2.2	1.8	2.3	1.7	0.46	0.46	0.38	0.34
[3]6.4	—	2.2	1.5	2.4	2.1	2.3	1.7	0.54	0.51	0.34	0.10
[3]6.6	7.7	1.6	1.3	1.8	1.7	2.4	1.8	0.46	0.44	0.38	0.42
[3]6.6	—	1.7	1.4	1.8	1.9	2.5	1.8	0.48	0.44	0.34	0.41
[3]6.9	8.2	1.9	1.5	2.1	2.1	2.3	1.8	0.50	0.46	0.40	0.30
[3]7.0	8.4	1.9	1.5	2.0	2.1	2.4	1.8	0.46	0.42	0.36	0.30
[2]7.0	8.4	2.2	1.7	2.4	2.4	2.2	2.0	0.58	0.56	0.44	0.10
[3]7.1	8.5	2.0	1.5	2.1	1.8	2.4	1.9	0.51	0.40	0.40	0.20
[3]7.3	7.9	2.5	1.8	2.8	2.2	2.4	2.0	0.62	0.38	0.38	—

[1] = preflexion larvae; [2] = flexion larvae; [3] = postflexion larvae.

again in flexion larvae by ≈6.4 mm. Scattered melanophores appear on the anal fin fold at 3.6 mm, and a few appear at the center of the dorsal fin fold at ≈4.2 mm. These melanophores remain through the larval period with pigment bars, characteristic of juveniles, developing on the dorsal and anal fins in flexion and postflexion larvae >7.3 mm. By 4.4 mm a few melanophores appear on the fin fold at about the notochord flexion point. These melanophores increase in number with development and are visible on the caudal fin during and after development of the caudal fin rays.

TABLE 3.—Body proportions of larval *Liopsetta putnami* and *Pseudopleuronectes americanus*. Values given are percentage of standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses. Number of specimens measured may be derived from Tables 1 and 2.

Item	*Liopsetta putnami*	*Pseudopleuronectes americanus*
Body depth at pectoral fin base/SL:		
Yolk sac	9.4± 1.61(7.6-12.9)	8.8±1.23(6.6-11.2)
Preflexion	12.5± 1.74(8.8-13.8)	15.2±2.87(10.5-19.3)
Flexion	15.4± 2.14(12.4-20.5)	19.3±1.49(16.7-23.3)
Postflexion	23.6±11.38(15.5-31.6)	28.6±3.85(21.2-34.2)
Body depth at anus/SL:		
Yolk sac	6.4± 2.08(5.2-11.6)	4.8±0.61(3.9-5.9)
Preflexion	9.2± 2.22(6.2-14.4)	8.6±2.99(4.8-13.7)
Flexion	13.5± 1.99(11.0-16.7)	13.9±2.11(9.6-19.2)
Postflexion	25.6± 8.41(19.7-31.6)	21.3±1.83(16.7-24.3)
Maximum body depth at pectoral fin base/SL:		
Yolk sac	9.4± 1.61(7.6-12.9)	8.8±1.23(6.6-11.2)
Preflexion	12.6± 1.89(8.8-16.6)	15.2±2.87(10.5-19.3)
Flexion	15.6± 1.52(13.1-17.6)	20.2±1.80(16.7-24.7)
Postflexion	28.1± 7.50(22.8-33.4)	31.1±4.45(24.2-38.4)
Maximum body depth at anus/SL:		
Yolk sac	6.4± 2.08(5.2-11.6)	4.8±6.09(3.9-5.9)
Preflexion	9.2± 2.28(6.2-14.7)	8.6±2.99(4.8-13.7)
Flexion	14.1± 2.00(10.9-17.0)	16.1±3.35(10.6-23.3)
Postflexion	26.8± 7.67(21.4-32.1)	28.8±3.17(22.7-34.3)
Snout to anus length/SL:		
Yolk sac	43.6± 3.62(39.1-50.0)	33.3±2.03(30.3-37.7)
Preflexion	41.2± 2.46(37.9-46.2)	37.6±1.72(34.1-40.8)
Flexion	40.5± 1.67(36.6-44.1)	37.9±1.95(32.4-41.1)
Postflexion	36.0± 0.78(35.5-36.6)	35.4±2.39(24.2-28.6)
Head length/SL:		
Yolk sac	13.2± 0.53(12.2-14.2)	13.9±1.05(12.4-16.0)
Preflexion	15.4± 4.31(14.2-18.8)	18.7±2.03(15.5-22.4)
Flexion	18.3± 1.63(14.9-21.2)	21.0±1.61(18.3-24.7)
Postflexion	24.4± 4.60(21.1-27.6)	27.0±1.22(24.2-28.6)
Eye diameter/HL:		
Yolk sac	41.9± 2.87(38.2-48.0)	43.1±1.81(40.0-47.6)
Preflexion	31.2± 3.57(25.5-37.5)	33.4±2.55(31.1-37.1)
Flexion	26.8± 2.28(24.3-32.0)	28.3±2.71(25.0-33.7)
Postflexion	24.8± 1.20(24.0-25.7)	27.1±2.36(24.0-31.4)
Upper jaw length/HL:		
Yolk sac	22.6± 0.00(22.6)	41.0±2.80(35.9-44.7)
Preflexion	28.2± 5.96(18.8-38.3)	34.5±4.18(30.0-41.9)
Flexion	31.5± 3.57(26.7-40.0)	31.3±2.47(26.7-34.7)
Postflexion	28.0± 1.84(26.7-29.3)	26.0±3.67(19.0-30.6)
Snout length/HL:		
Yolk sac	27.5± 4.69(18.8-36.7)	25.2±4.71(19.0-33.3)
Preflexion	16.6± 3.72(10.4-24.3)	19.8±3.37(14.0-24.0)
Flexion	16.2± 3.05(12.3-20.0)	18.3±1.92(15.4-22.4)
Postflexion	15.3± 2.83(13.3-17.3)	19.8±2.40(13.8-22.4)
Pectoral fin length/SL:		
Yolk sac	3.8± 1.38(2.4-7.1)	3.0±1.75(1.4-5.9)
Preflexion	7.8± 1.30(5.8-10.2)	7.7±0.92(6.1-9.2)
Flexion	7.1± 0.74(5.9-8.5)	7.8±0.85(6.2-9.1)
Postflexion	5.0± 2.55(3.2-6.8)	4.7±2.48(0.8-8.8)

Melanophore numbers on the caudal fin membrane increase through flexion and postflexion periods with the entire fin becoming covered with melanophores, including an intense pigment patch near the fin base, by 9.8 mm.

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