EGGS AND LARVAE OF BUTTER SOLE, *ISOPSETTA ISOLEPIS* (PLEURONECTIDAE), OFF OREGON AND WASHINGTON

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ABSTRACT

Development of butter sole, *Isopsetta isolepis*, is described from egg through benthic juvenile, based on reared and field-collected specimens.

Isopsetta isolepis eggs are planktonic, spherical, and transparent with a narrow perivitelline space, homogeneous yolk, and no oil globule. Diameters of 80 reared eggs averaged 0.93 mm (range 0.90-0.99 mm). Using light microscopy, early and middle stage eggs are indistinguishable from those of three other pleuronectids, English sole, *Parophrys vetulus*, sand sole, *Psettichthys melanostictus*, and starry flounder, *Platichthys stellatus*, with which they cooccur. Pigment patterns distinguish late stage *I. isolepis* eggs from those of *Psettichthys melanostictus* and *Platichthys stellatus*. Because the late stages of *I. isolepis* embryos vary widely in degree and character of pigmentation, they often cannot be reliably separated from those of *Parophrys vetulus*.

Larvae are readily distinguished by three bands of melanistic pigment on the tail region of the body combined with myomere counts (39-42). Transformation from larva to juvenile takes place at about 18-23 mm. Larvae are abundant in nearshore coastal waters off Oregon and Washington in winter and spring, where they cooccur with larvae of *P. vetulus*. Recently transformed benthic juveniles of *I. isolepis* usually are found offshore rather than in the bay and nearshore habitats occupied by young juvenile *P. vetulus*.

This paper presents the first complete description of development of the butter sole, *Isopsetta isolepis* (Lockington), from egg through benthic juvenile. Larvae of this species are common in the ichthyoplankton off Oregon and Washington where they ranked fifth in overall abundance in April and May 1967 (Waldron 1972) and third in a coastal assemblage of larval fishes off Oregon in 1971-72 (Richardson and Pearcy 1977; Richardson[4]).

Isopsetta, a monotypic genus of the family Pleuronectidae, ranges from Ventura, Calif., to the Bering Sea (Miller and Lea 1972). It is usually found in coastal waters although it has been reported from the 274-366 m depth zone in western Alaska (Demory 1971; Miller and Lea 1972; Hart 1973). Adult butter sole ranked 11th and 7th in biomass of all flatfishes taken during trawl surveys off Oregon in 1971-72 and 1973-74 (Demory et al.[5]) and 6th in biomass of all flatfishes off Washington in both 1975 and 1976 (Barss et al.[6]). Because it is a relatively small, <55 cm TL (total length), slender fish (Miller and Lea 1972; Hart 1973), it is currently of only minor commercial importance.

Levings (1968) briefly described *I. isolepis* eggs as single, nonadhesive, transparent, spherical, without an oil globule, with a mean egg diameter of 1.013 mm, although he did not illustrate them. The eggs sank at salinities ≤26.61‰ but floated at salinities ≥28.03‰. Levings concluded that the eggs were demersal within Skidegate Inlet, British Columbia, where bottom salinities were 24.96‰. *Isopsetta isolepis* larvae 4.8, 7.9, 10.0, and 15.5 mm long from Puget Sound were sketched by Blackburn (1973) but were labeled *Lyopsetta exilis*. He also provided short descriptions.

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[4]Richardson, S. L. 1977. Larval fishes in ocean waters off Yaquina Bay, Oregon: abundance, distribution, and seasonality, January 1971 to August 1972. Oreg. State Univ., Sea Grant Coll. Prog., Publ. ORESU-T-77-003, 73 p.

[5]Demory, R. L., M. J. Hosie, N. TenEyck, B. O. Forsberg. 1976. Marine resource surveys on the continental shelf off Oregon, 1971-74. Oreg. Dep. Fish Wildl., Completion Rep., June 1976, 49 p.

[6]Barss, W. H., R. L. Demory, N. TenEyck. 1977. Marine resource surveys on the continental shelf and upper slope off Washington, 1975-76. Oreg. Dep. Fish Wildl., Completion Rep., September 1977, 34 p.

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METHODS

Eggs from ripe fish collected in Bellingham Bay, Wash., were artificially fertilized on 12 March 1974 and were reared at the Mukilteo field station of the Northwest and Alaska Fisheries Center (NWAFC), National Marine Fisheries Service (NMFS), NOAA, Seattle, Wash. The eggs were incubated in 0.6 or 1.0 l glass beakers containing local Puget Sound seawater maintained at 9°-10° C. Subsamples of eggs were preserved in Formalin[7] in eight time periods, 4, 9, 20, 24, 48, 72, 96, and 120 h, after fertilization. Subsamples of larvae were preserved for each of 13 time periods: at hatching (144 h or 6 d after fertilization) and at 2, 3, 4, 7, 9, 11, 14, 16, 18, 21, 23, and 25 d after hatching. Although rotifers (*Brachionus plicatilus*) were added to the containers at various levels (4, 8, and 16 rotifers/ml seawater), the larvae did not feed actively and all were dead by 22 April 1974.

Approximately 300 larvae were obtained from NWAFC collections made off coastal Washington in 1972. An additional 107 larvae were obtained from Oregon State University (OSU) ichthyoplankton collections taken off the Oregon coast from 1971 to 1972 (Richardson and Pearcy 1977; Richardson see footnote 4). Benthic juveniles were collected in beam trawls off the mouth of the Columbia River in June and September 1975 (Richardson et al.[8]).

Counts of meristic structures were made on 209 larvae (3.2-23.6 mm) and 7 juveniles (44-160 mm) taken from the OSU and NWAFC collections. Larvae were stained with Alizarin Red S using Taylor's (1967) enzyme method to determine sequence of ossification. Some (45) were subsequently restained with Alcian Blue and Alizarin Red using techniques described by Dingerkus and Uhler (1977). Counts were made of dorsal fin rays, anal fin rays, caudal fin rays, left and right pectoral fin rays, branchiostegal rays, gill rakers, vertebral centra, neural spines, and haemal spines. Fin rays and vertebrae were counted even if they were tinted only slightly with alizarin stain. Uptake and retention of alizarin in ossified structures may vary depending upon the length of time the specimens have been in preservative. Differential loss of stain may account for some of the variation observed in the onset of ossification of certain structures such as teeth.

Measurements were made using an ocular micrometer in a stereomicroscope. The greatest outside diameter and greatest yolk diameter were recorded for 80 eggs from the reared series, 10 for each of the eight time periods that eggs were preserved from 4 to 120 h after fertilization. Measurements were made on 63 reared larvae, 5 specimens (when available) from each of the 13 time periods after hatching (6 d after fertilization) that larvae were preserved to 25 d after hatching. Size range of reared specimens was 2.7-5.3 mm SL (standard length). Measurements also were made on 107 larvae from plankton collections including 5 specimens (when available) for each 1.0 mm size class interval from 2 to 23 mm SL (range 2.9-23.6 mm). Body measurements were made on larvae as follows:

Standard length – snout tip to notochord tip until notochord is fully flexed and the posterior margin of the forming hypural elements is vertical, then to posterior margin of hypurals.

Head length – snout tip to cleithrum.

Body depth at pectoral fin base – vertical distance from dorsal body margin to ventral body margin, excluding finfold or fins, at the pectoral fin base.

Body depth at anus – vertical distance from dorsal body margin, excluding finfold or fin, to anus.

Body depth behind anus – vertical distance from dorsal body margin to ventral body margin, excluding finfolds or fins, at point immediately behind anus where body depth decreases greatly compared to depth at anus.

Body depth at caudal peduncle – before formation of caudal fin, vertical distance from dorsal body margin to ventral body margin, excluding finfolds or fins, at the posteriormost myomere; after caudal fin formation, least depth of caudal peduncle.

Snout length – snout tip to anterior margin of right eye.

Eye diameter – horizontal distance across right eyeball.

Snout to anus length – distance along body midline from snout tip to vertical through posterior margin of anus.

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

[8]Richardson, M. D., A. G. Carey, Jr., W. A. Colgate. 1977. The effects of dredged material disposal on benthic assemblages off the mouth of the Columbia River. Final Rep., Dep. Army Corps Eng. Contracts DACW 57-75-C-0137 and DACW 57-56-C-0092, Vicksburg, Miss., 411 p.

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

Illustrations of eggs and larvae were made with the aid of a camera lucida. All specimens had been preserved in 5% Formalin. Illustrations of the caudal fin and skeletal structure were made from cleared and stained specimens.

VERIFICATION OF IDENTIFICATION

Reared eggs were fertilized from known parents, thus their identity was certain.

A series of larval specimens from plankton collections was linked together by pigment pattern. The left eye had begun to migrate in the largest specimens indicating that they were pleuronectids, the only right-eyed flatfishes occurring off Oregon and Washington. Positive identification was based on knowledge of early stages of all but one of the pleuronectids occurring in the area (Table 1) and on the following meristic characters for *I. isolepis* (Hart 1973; Ahlstrom[9]; this study):

Dorsal fin rays	= 78-92
Anal fin rays	= 58-69
Abdominal vertebrae	= 9-11, usually 10
Total vertebrae	= 39-42
Caudal fin rays	= 17-18, usually 18
Pectoral fin rays	= 11-13
Pelvic fin rays	= 6
Branchiostegal rays	= 7
Gill rakers	= 4-6 + 7-8

Additional confirmation was provided by larvae reared to yolk depletion, which were similar to the smallest specimens from the plankton samples.

DISTINGUISHING FEATURES

Early and middle stage eggs of *I. isolepis* are indistinguishable from those of English sole, *Parophrys vetulus*; starry flounder, *Platichthys stellatus*; and sand sole, *Psettichthys melanostictus*. Chorions of reared eggs are often noticeably striated, but this characteristic is not consistent among reared eggs and is rarely seen in eggs from the plankton. Thus, chorion sculpturing is not useful for identifying *I. isolepis* eggs.

[9]E. H. Ahlstrom, Senior Scientist, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, unpubl. data.

TABLE 1.—Pleuronectid flatfishes occurring off Oregon and Washington with references on early developmental stages.

Species	References
Atheresthes stomias	Pertseva-Ostroumova (1960, 1961)
Embassichthys bathybius	Richardson (in press)
Eopsetta jordani	Alderdice and Forrester (1971); Ahlstrom (unpubl. data); Richardson (in press)
Glyptocephalus zachirus	Ahlstrom and Moser (1975)
Hippoglossoides elassodon	Dekhnik (1959); Pertseva-Ostroumova (1961); Miller (1969); Alderdice and Forrester (1974) Forrester and Alderdice[1]
Hippoglossus stenolepis	Thompson and Van Cleve (1936); Pertseva-Ostroumova (1961)
Inopsetta ischyra	None
Isopsetta isolepis	Levings (1968); Blackburn (1973)
Lepidopsetta bilineata	Pertseva-Ostroumova (1961); Blackburn (1973); Richardson (in press)
Lyposetta exilis	Blackburn (1973); Ahlstrom and Moser (1975)
Microstomus pacificus	Hagerman (1952); Ahlstrom and Moser (1975)
Parophrys vetulus	Budd (1940)[2]; Orsi (1968); Blackburn (1973); Ahlstrom and Moser (1975); Misitano (1976)
Platichthys stellatus	Orcutt (1950); Yusa (1957); Pertseva-Ostroumova (1961) as *Pleuronectes stellatus*
Pleuronichthys coenosus	Budd (1940) (as *P. decurrens*); Sumida et al. (1979)
Pleuronichthys decurrens	Budd (1940) (as *P. coenosus*); Sumida et al. (1979)
Psettichthys melanostictus	Hickman (1959); Sommani (1969)

[1]Forrester, C. R., and D. F. Alderdice. 1968. Preliminary observations on the embryonic development of the flathead sole (*Hippoglossoides elassodon*). Fish. Res. Board Can., Tech. Rep. 100, 20 p.
[2]The 6.3 mm larva is not *P. vetulus*.

Late stage eggs are readily distinguished from other northeast Pacific pleuronectids with similar size eggs by means of pigment. Embryos in late stage *P. melanostictus* eggs have scattered yolk-sac melanophores, and those of *Platichthys stellatus* have pigmented finfolds, while *I. isolepis* embryos lack pigment in both places. *Isopsetta isolepis* embryos are most similar to those of *Parophrys vetulus*. While *I. isolepis* embryos usually have several isolated ventral tail melanophores, their number is quite variable, ranging from none to many, whereas *P. vetulus* embryos have so many ventral tail melanophores that the pigment appears almost continuous. The head and anterior trunk pigment of *I. isolepis* is more dendritic and melanophores are less numerous than on *P. vetulus*. Despite these differences, variation in both ventral tail and trunk melanophores, especially in *I. isolepis*, is so great that late stage eggs of the two species cannot always be reliably separated.

Most sizes of *I. isolepis* larvae can be easily distinguished from other flatfish larvae off Oregon and Washington by their body form together with their striking pigment pattern, most notably the three bands of melanophores on the body posterior to the abdominal cavity. After notochord flexion the posteriormost band lines the base of the caudal fin, but the two other bands remain apparent through transformation to benthic juvenile. No

other flatfiish larvae of similar form in the area have three such bands. The only other three-banded flatfish larva is deepsea sole, *Embassichthys bathybius*, but it hatches at about 9 mm, has over 60 myomeres, and a different elongate form (Richardson in press). The most similar appearing banded larval flatfish is the flathead sole, *Hippoglossoides elassodon*, which has four pigment bands.

Before the three pigment bands become obvious, i.e., in larvae <4 mm SL, larvae of *I. isolepis* are similar to those of *P. vetulus*. They usually are separable by the size and distribution of postanal ventral midline melanophores. Those of *I. isolepis* are small and appear more or less as a double row when viewed from the ventral surface; those of *P. vetulus* are enlarged and stellate and appear as a single row when viewed ventrally.

Newly transformed *I. isolepis* juveniles are also similar to *P. vetulus*. Before development of adult characters such as scales on the fins of *I. isolepis*, which will easily separate the two, *I. isolepis* can usually be distinguished by remnants of the larval pigment bands on the blind side. The number of gill rakers on the lower limb (Miller and Lea 1972) also will separate the two species (7-8 for *I. isolepis* and 10-13 for *P. vetulus*).

DEVELOPMENT OF EGGS (Figure 1)

Isopsetta isolepis eggs are spherical and transparent, with a narrow perivitelline space, a homogeneous yolk, and no oil globule. Although the eggs apparently sink at salinities ≤26.61‰ (Levings 1968), they are taken in our plankton samples, and live eggs floated in the rearing experiments (salinity ~26.9‰). Diameters of 80 reared eggs averaged 0.93 mm (0.90-0.99 mm), while yolk diameters averaged 0.76 mm (0.60-0.95 mm).

Embryonic development is typical of most teleosts with planktonic eggs. The stages of egg development we use correspond to the basic divisions of embryonic development used by Ahlstrom and Counts (1955), with detailed subdivisions of each stage (Naplin and Obenchain in press).

Pigmentation

Pigment first appears during the middle stage of embryonic development. At this time, distinct melanophores are scattered unevenly from the middle of the eyes posteriorly over the trunk. The

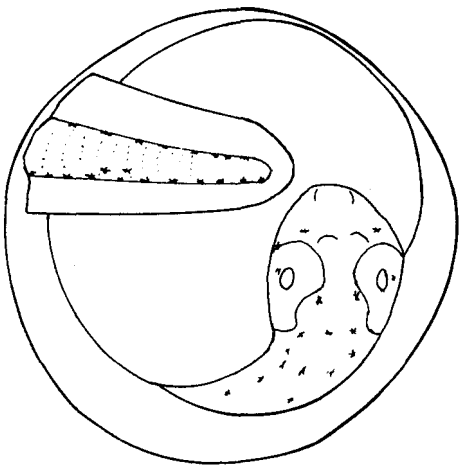

FIGURE 1.—*Isopsetta isolepis* eggs, late stage from plankton collections.

melanophores become more organized into two dorsolateral lines on the anterior somites, and diminish in size and frequency posteriorly. The dorsolateral lines are the site of melanophore formation, and pigment is present farther posteriorly as development continues.

The development of this species is unusual in that the anteriormost melanophores become increasingly dendritic and so fine that they gradually become less visible. By the time the embryos have reached the late stage (tail five-eighths of the way around the yolk), less head pigment is visible and the trunk is covered with very small but distinctly visible dendritic melanophores. Several distinct ventral melanophores lie at the juncture of the trunk and the yolk sac, and one or two isolated spots are on the yolk sac nearby. Most of the tail pigment is scattered dorsally in no obvious pattern, and several lateral melanophores are now in the ventral tail area.

When the tail is three-fourths of the way around the yolk, the head and trunk generally appear to be pigmented, although less distinctly than in the middle stage. Ventral trunk pigment is present, and some embryos may have one to three yolk-sac melanophores nearby. Scattered melanophores appear dorsally on the posterior trunk and on all surfaces of the tail. More lateral melanophores are present toward the tail tip.

From the time the tail is seven-eighths of the way around the yolk through hatching, little change in the pigment pattern occurs; however, the lateral tail melanophores have moved to become ventral. Dorsal and ventral tail pigment melanophores are

spread into thin lines between the margin of the body and finfold. The ventral melanophores are variable, ranging from no melanophores to many, and are separated at irregular intervals over the length of the tail, while the dorsal pigment can appear almost continuous. Near the tail tip the dorsal and ventral melanophores align, as in the early larvae, to form the precursor of the posteriormost band of pigment noted in the larvae.

The reared embryos appear more lightly pigmented than wild-caught embryos. In the latter, it is possible that the marked fading of the head pigment may not occur until after hatching.

Morphology

Physical development of *I. isolepis* embryos progresses as in other fishes. At the time of initial pigment formation, the blastopore has closed and the embryonic body is gradually thickening on top of the yolk sac. During this stage, the eyecups are forming, but no lens tissue is discernible. About 12 somites have formed, and Kupffer's vesicle is still visible just anterior to the tail bud.

When the tail is five-eighths of the way around the yolk, the eyecups are well-formed and lenses are present. The brain has differentiated into a forebrain and a larger midbrain. The auditory vesicles are forming but are not yet hollow. About 27 somites are present, Kupffer's vesicle is no longer visible, and the small tail has a definite finfold.

By the time the tail has reached three-fourths of the way around the yolk, the auditory vesicles are well-formed and immediately apparent. The embryo now has about 37 somites. Hatching can occur when the embryo's tail has reached seven-eighths of the way around the yolk to full circle. At this point, the embryo has the full complement of somites or myomeres (39-42) and is morphologically similar to a newly hatched larva.

DEVELOPMENT OF LARVAE (Figures 2-5)

Pigmentation

Pigment on newly hatched larvae is scattered lightly on the head and snout, and appears on the dorsal, lateral, and ventral body surface above the abdominal cavity and also in the tail region. No pattern is obvious. The eyes are unpigmented.

In the head region, the eyes begin to darken by 4 d (about 3.8-4.0 mm) after hatching and are fully pigmented by 7 d (3.9-4.1 mm) in the reared larvae. Eyes in the smallest plankton specimen (2.9 mm) are pigmented. During early development, pigment over the head and snout disappears (by about 4 mm in reared larvae, 2.9 mm in planktonic larvae) except for a few internal melanophores above the otic capsule. Pigment appears on the lower jar and throat region by 4 or 5 mm and persists through the larval period. By about 6 or 7 mm several melanophores are present at the ventral angle of the preopercle. Later in development, scattered melanophores are added on the head (>10 mm) and on the upper jaw (>14 mm). Additional pigment is added to the entire head region on the eyed side during transformation (>17 mm).

In the abdominal region, melanophores disappear from the dorsal and lateral body surfaces above the gut cavity by the time larvae are about 4 mm long. Pigment is added again in this region during the transformation period when larvae are about 17 mm long. It is added first in two patches on the dorsal pterygiophores. More melanophores are then added laterally as well as on the dorsal pterygiophores, mainly along the myosepta, obscuring the original patches. A series of internal melanophores develops dorsal to the notochord above the abdominal cavity in larvae >10 mm. Melanophores are added along the ventral margin of the gut cavity by the time larvae are about 4 mm long. With development, additional melanophores extend over the ventral and posterior portions of the abdominal cavity appearing in a half-moon shape on most larvae >8 mm long. This pattern persists until transformation when the increase in body pigment on the eyed side obscures it.

In the tail region, three characteristic bands of pigment become obvious in reared larvae 4 d (3.9-4.1 mm) after hatching and are visible on the 2.9 mm plankton caught larvae. These are located on the body at positions roughly 50, 67, and 90% SL. In larvae <10 mm, these bands generally extend from dorsal to ventral body margins. With development the middle band becomes the most pronounced of the three. This middle band remains visible on the eyed side of some newly transformed benthic juveniles, and remnants of it persist on the blind side of juveniles as long as 35 mm. After notochord flexion (>14 mm), the posterior band is seen as a line of pigment at the base of the caudal fin. The anterior band becomes less pronounced and often does not extend above the lateral midline in larvae >14 mm. Along the notochord, a series of internal melanophores develops dorsal to

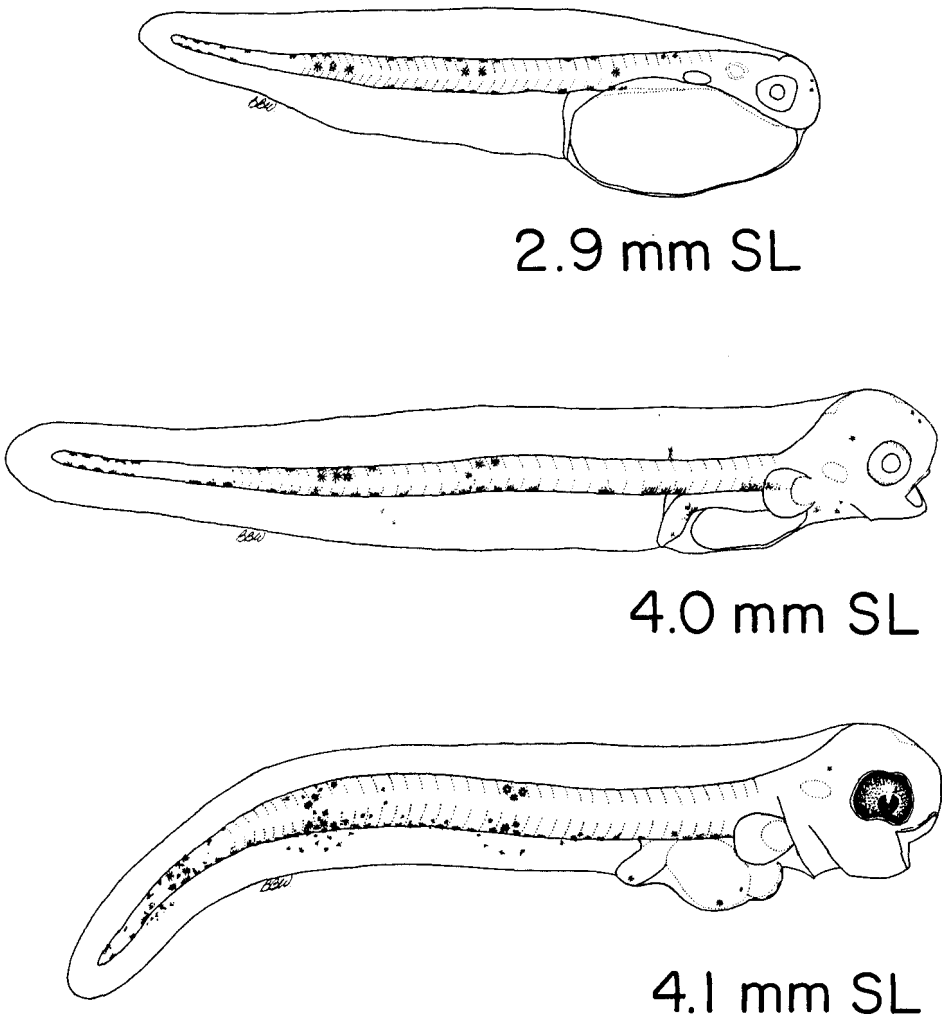

FIGURE 2.—*Isopsetta isolepis* larvae: 2.9 mm SL (reared, newly hatched, 144 h after fertilization); 4.0 mm SL (reared, 4 d after hatching); 4.1 mm SL (plankton specimen).

it, first in the region of the anterior two pigment bands in larvae about 6 or 7 mm long. Additional internal pigment spots then develop along the notochrod between the three pigment bands and anterior to them. This line of internal pigment spots is usually not continuous. It remains visible until the end of the transformation period. Along the ventral midline, pigment appears as a characteristic double row (viewed ventrally) of small melanophores in larvae >4 mm. This double row remains obvious until the onset of anal fin formation, about 14 mm, after which these melanophores appear to line the base of the anal fin, sometimes with one melanophore/fin ray. These melanophores become indistinct during transformation. On the ventrolateral body surface, melanophores are added just above the ventral midline row about the time the anal fin begins to form, around 10 mm. These melanophores eventually, by 12 mm, appear in the myosepta in a line midway between the lateral midline and the ventral margin of the body myomeres. Until the addition of pigment during transformation this line of melanophores is visible on the eyed side only, but is often visible on the blind side of newly transformed benthic juveniles. Along the margin of the ventral finfold a line of evenly spaced small melanophores is visible on newly preserved larvae >4 mm. This is often faded after a long period of preservation or is missing in plankton collected

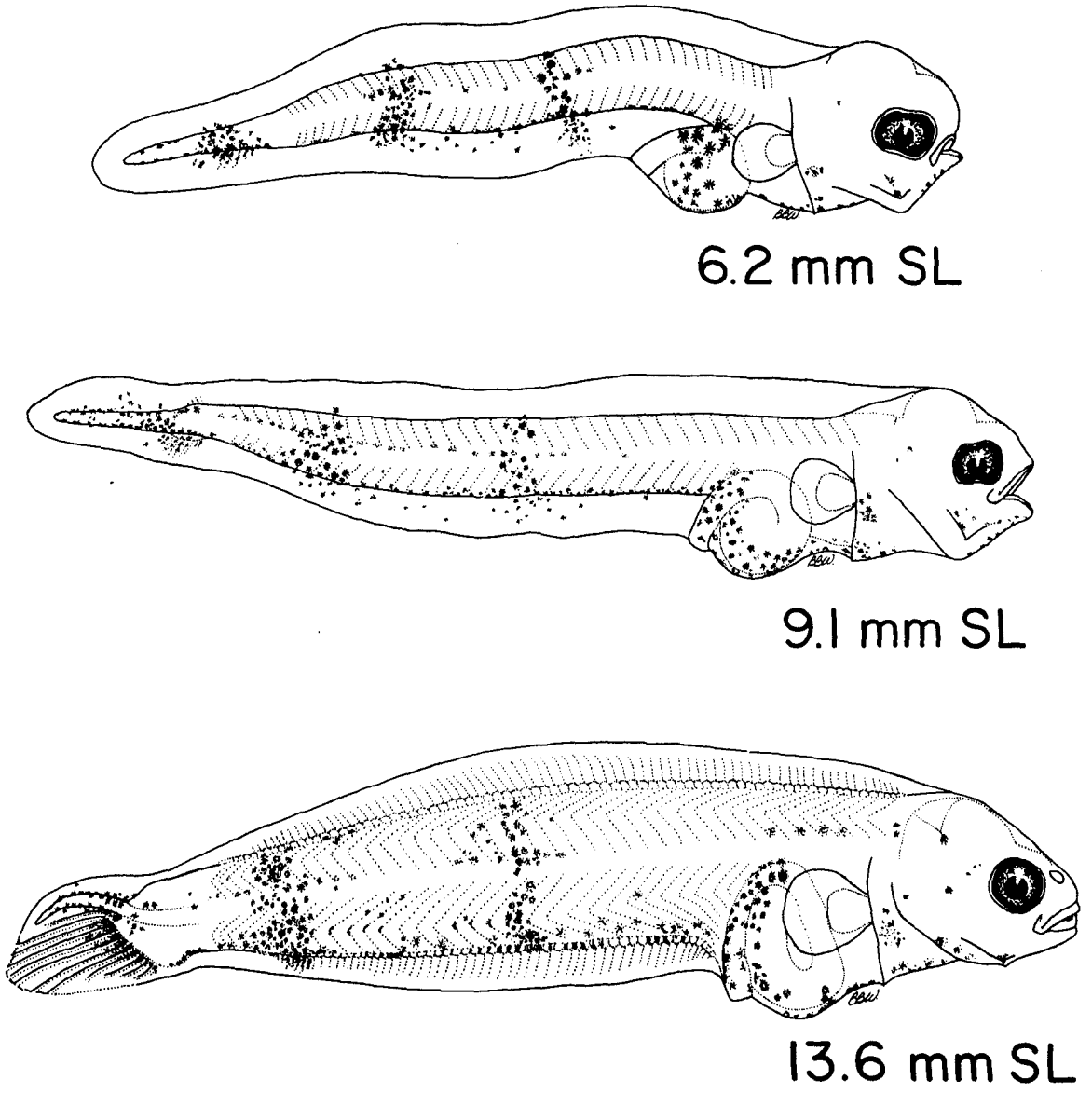

FIGURE 3.—*Isopsetta isolepis* larvae: 6.2 mm SL, 9.1 mm SL, and 13.6 mm SL.

specimens due to damaged finfolds. It is not visible on most specimens examined in this study, including the series illustrated. This line of melanophores has been seen on a few specimens up to 7.3 mm long. Additional pigment develops on the ventral finfold in the vicinity of the three pigment bands in larvae >4 mm and on the dorsal finfold near the posteriormost pigment band by the time larvae are 8 mm. This finfold pigment persists until caudal and anal fin formation. After the dorsal and anal fins are formed, by the time larvae are >15 mm, their margins are fringed with melanophores. However, the fin margins are often damaged on preserved planktonic specimens and the pigment fringing is not visible.

With transformation, at >17 mm, pigment is added to the eyed side in the tail region. Four or five clusters of melanophores appear along the dorsal pterygiophores and four along the ventral pterygiophores. These clusters eventually become obscured as more pigment is added. Increases in the number of melanophores along the bases of the

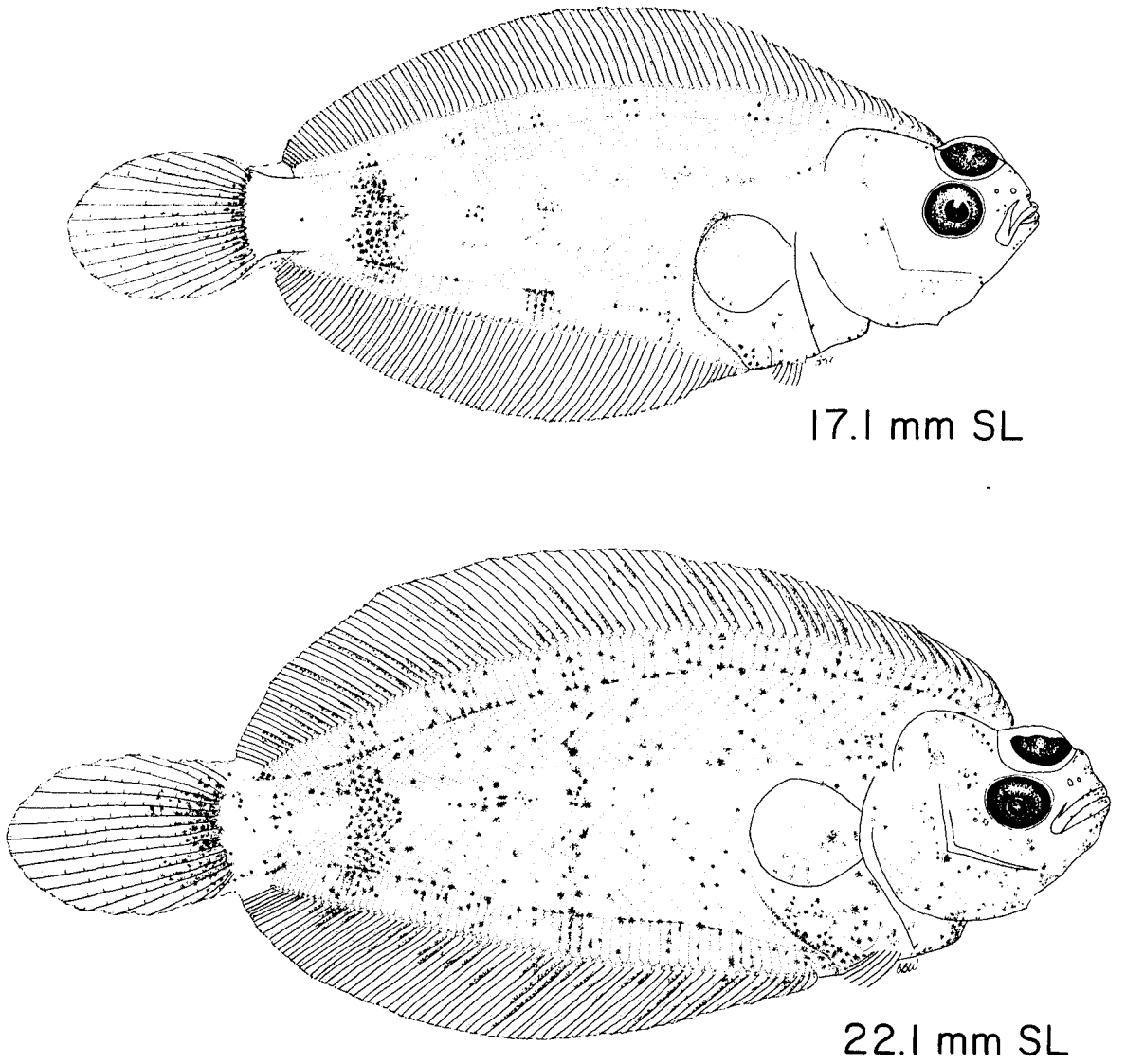

FIGURE 4.—*Isopsetta isolepis* larvae: 17.1 mm SL and 22.1 mm SL.

dorsal and anal pterygiophores give the appearance of solid lines of pigment. More melanophores appear on the body until all larval pigment is obscured. Additional pigment develops on the dorsal, anal, and caudal fins along the fin rays.

Morphology

Newly hatched reared larvae, 144 h after fertilization, range in length from 2.68 to 2.92 mm ($\overline{X}$ = 2.78 mm, based on 50 specimens). The yolk sac extends along the anterior third of the body. The mouth is not yet formed. A moderate finfold extends from the head around the posterior part of the body to the anus. The otic capsule is visible on the head behind the unpigmented eye. The mouth is formed by 2 d (3.4-3.5 mm) after hatching. The yolk is nearly gone by 4 d (3.8-4.0 mm) and is no longer visible by 7 d (3.9-4.1 mm). By 11 d (3.3-4.1 mm) the previously straight gut begins to coil. The smallest larva identified from plankton collections is 2.9 mm. It has a formed mouth, no remnant of yolk, and its gut has begun to coil. The size discrepancy may be an artifact of preservation, or it may

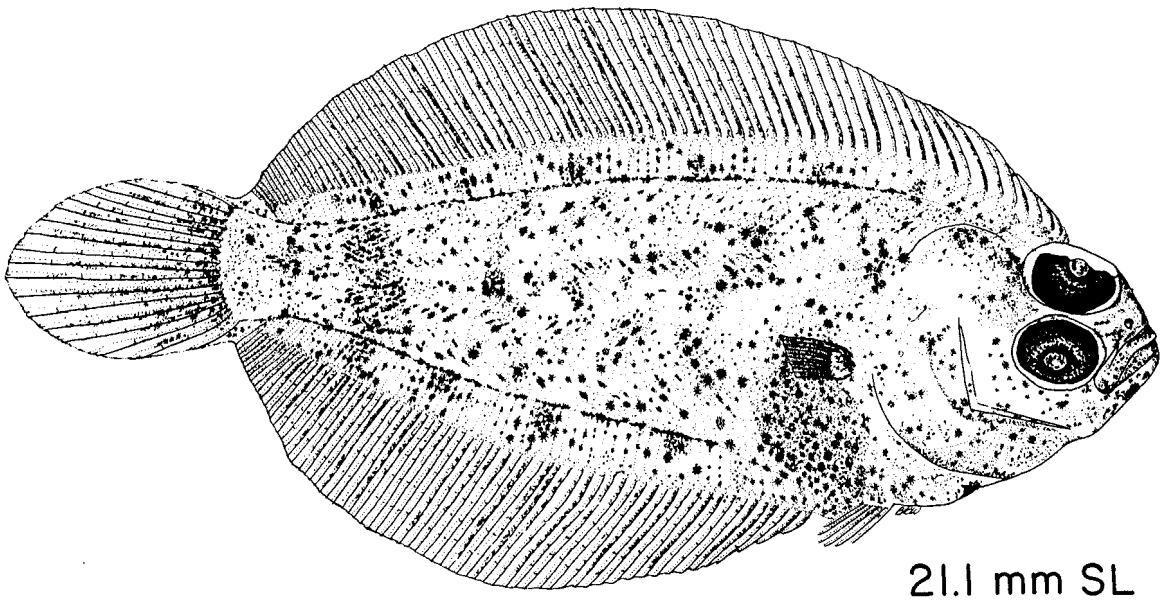

FIGURE 5.—Recently transformed benthic juvenile *Isopsetta isolepis*, 21.1 mm SL.

be due to the different environmental conditions of the reared and planktonic larvae. With development the gut continues to coil and the hindgut, which is initially directed posteriorly, comes to rest in an anteriorly directed position, by about 17 mm.

Notochord flexion begins by the time larvae are about 9 or 10 mm long and the notochord is fully flexed by about 14 mm. After flexion is complete, the tip of the urostyle continues to extend beyond the hypural plate, sometimes until larvae are 17 mm long. When larvae are about 12 or 13 mm long, near the end of notochord flexion, the left eye begins to migrate to the right side of the head. The left eye is visible on the ridge of the head, when viewed from the right side, in some larvae as small as 15 mm and consistently in specimens >17 mm. The left eye eventually migrates to the degree that it is directed upward, the most advanced position before complete transformation to benthic juvenile. This was the most advanced stage of eye migration of specimens taken in plankton tows and was observed in some, but not all, specimens >20 mm. The largest specimen collected in the plankton was 23.6 mm, but the most developed plankton specimen in terms of eye migration and increased pigmentation was 21.9 mm. The smallest specimen collected in a beam trawl was 18.0 mm, but its eye was on the dorsal ridge of the head directed upward and it had not completed transformation. The smallest benthic juvenile, in which the left eye had crossed over the middorsal ridge and juvenile pigment had intensified on the eyed side, was 18.5 mm.

With development (Tables 2, 3), relative head length increases considerably from mean values of 13-15% SL in preflexion larvae to 25% SL in postflexion larvae. Snout to anus length remains essentially constant with respect to standard length with mean values of 29-32%. Relative body depths at the pectoral fin base, at the anus, and behind the anus increase dramatically through the larval period with mean values nearly doubling in most cases between preflexion and flexion stages and doubling again between flexion and postflexion stages. The greatest rate of increase occurs in the depth behind the anus. Depth of the caudal peduncle also increases from 3 to 10% relative to standard length. Relative eye diameter is largest in preflexion larvae (29-36% HL (head length)) and decreases in flexion (24% HL) and postflexion (22% HL) larvae as does the relative length of the upper jaw (37-25% HL).

Ossification of Meristic Structures

Descriptions, based on cleared and stained specimens, depict only general trends of development because the size at which bones begin to ossify may vary among specimens and the uptake

TABLE 2.—Measurements (millimeters) of plankton caught larvae of *Isopsetta isolepis*. (Specimens between dashed lines are undergoing notochord flexion.)

Length interval (mm)	Sample size (*N*)	Mean length (mm)	Snout to anus	Head length	Snout length	Upper jaw length	Eye diameter	Body depth at pectoral fin base	Depth at anus	Depth behind anus	Caudal peduncle depth
2.9-3.0	2	2.90	0.95	0.45	—	—	0.20	0.30	0.20	0.15	0.10
3.1-4.0	[1]6	3.67	1.07	0.50	0.10	—	0.20	0.40	0.30	0.17	0.10
4.1-5.0	[2]4	4.63	1.28	0.55	0.10	—	0.25	0.40	0.35	0.23	0.10
5.1-6.0	[3]5	5.50	1.48	0.68	0.10	0.30	0.28	0.50	0.46	0.22	0.10
6.1-7.0	[4]5	6.58	2.04	1.02	0.12	0.40	0.30	0.72	0.72	0.34	0.12
7.1-8.0	[5]5	7.76	2.20	1.14	0.10	0.43	0.32	1.04	1.00	0.44	0.16
8.1-9.0	6	8.77	2.58	1.32	0.10	0.48	0.38	1.17	1.12	0.50	0.28
9.1-10.0	4	9.68	2.88	1.48	0.20	0.50	0.45	1.25	1.23	0.60	0.35
10.1-11.0	6	10.57	3.42	1.95	0.28	0.62	0.48	1.72	1.68	1.25	0.60
11.1-12.0	4	11.25	3.38	1.88	0.20	0.60	0.50	1.78	1.72	1.15	0.55
12.1-13.0	5	12.36	3.70	2.24	0.28	0.76	0.50	2.02	2.14	1.54	0.74
13.1-14.0	5	13.55	4.22	2.74	0.36	0.72	0.62	2.52	3.12	2.08	0.96
14.1-15.0	5	14.48	4.84	3.18	0.50	0.86	0.64	3.18	3.68	3.00	1.34
15.1-16.0	5	15.38	4.68	3.58	0.54	0.94	0.74	3.74	4.40	3.64	1.48
16.1-17.0	5	16.54	5.64	4.00	0.60	1.10	0.90	4.64	5.36	4.84	1.68
17.1-18.0	5	17.50	5.88	4.70	0.78	1.12	1.10	5.60	6.16	6.00	1.86
18.1-19.0	4	18.63	5.85	4.78	0.93	1.28	1.08	6.43	6.85	6.95	1.88
19.1-20.0	6	19.55	5.92	4.93	0.94	1.20	1.08	6.52	7.00	6.90	2.02
20.1-21.0	6	20.53	5.97	5.12	0.95	1.28	1.10	6.90	7.35	7.50	2.03
21.1-22.0	4	21.48	6.40	5.93	0.95	1.60	1.23	7.68	8.18	8.58	2.23
22.1-23.0	6	22.48	6.27	5.58	0.95	1.22	1.23	7.67	8.33	8.62	2.28
23.1-24.0	4	23.33	6.80	5.68	0.98	1.43	1.25	7.83	8.48	9.03	2.33

[1]*N* = 2 for snout length.
[2]*N* = 3 for snout length.
[3]*N* = 4 for snout length and 1 for upper jaw length.
[4]*N* = 1 for upper jaw length.
[5]*N* = 4 for upper jaw length.

TABLE 3.—Body proportions of *Isopsetta isolepis* larvae. Values given are percentages: mean ± standard deviation, and range in parentheses.

Item	Preflexion larvae with yolk (reared)	Preflexion larvae without yolk (reared)	Preflexion larvae without yolk (plankton)	Flexion larvae (plankton)	Postflexion larvae (plankton)
No. measured	20	42	[1]37	[2]20	50
SL	(2.7-4.0)	(3.4-5.4)	(2.9-9.0)	(10.5-14.2)	(13.5-23.6)
Head length/SL	15.0±2.7(10.6-19.6)	13.4±0.9(11.3-15.9)	14.2±2.0(10.2-17.2)	18.3±1.6(15.3-20.7)	24.9±2.1(20.7-29.4)
Snout to anus length/SL	32.4±3.8(28.3-39.3)	28.8±1.3(26.7-31.1)	29.2±2.9(22.9-34.4)	30.7±1.8(27.6-34.0)	31.0±3.0(23.2-35.8)
Depth at pectoral fins/SL	5.2±0.8(4.1-6.7)	9.2±1.0(7.4-11.6)	11.4±2.3(8.3-15.2)	16.6±1.7(12.9-18.5)	31.1±5.0(20.1-38.0)
Depth at anus/SL	9.8±1.2(8.2-12.0)	8.9±0.9(6.9-11.1)	10.3±2.8(5.7-15.6)	17.8±3.7(12.9-28.9)	34.1±4.4(23.2-40.2)
Depth behind anus/SL	4.3±0.7(2.8-5.9)	3.2±0.5(2.5-4.1)	5.1±1.3(2.9-7.8)	12.3±2.0(9.0-14.8)	33.4±6.7(18.8-41.3)
Caudal peduncle depth/SL	—	—	2.6±0.8(1.3-4.1)	6.0±1.1(4.4-7.4)	9.6±2.0(7.6-11.3)
Eye diameter/HL	32.8±2.6(30.2-38.1)	28.9±3.9(21.6-39.6)	35.6±9.1(25.0-50.0)	23.7±2.8(20.0-29.4)	21.8±2.2(17.5-26.2)
Snout length/HL	19.9±6.0(9.4-29.8)	28.1±4.1(20.8-34.0)	12.5±4.4(6.7-20.0)	13.7±2.8(8.7-21.0)	16.6±3.7(9.4-20.8)
Upper jaw length/HL	—	—	37.1±4.9(31.2-50.0)	31.6±5.9(24.0-47.6)	25.2±4.4(17.5-38.5)

[1]Except *N* = 29 for snout length and *N* = 16 for upper jaw length.
[2]Except *N* = 19 for snout length.

of stain may be affected by length of preservation. Terminology of bones generally follows Richardson and Joseph (1973) and Frame et al. (1978) except as noted.

Most of the meristic characters of *I. isolepis* larvae begin ossifying during notochord flexion (10-14 mm); only gill rakers and pectoral fin rays begin to ossify at larger sizes (Table 4; Figure 6). The following discussion roughly parallels the sequence of development of meristic characters, and we note their first appearance as well as the onset of ossification as indicated by the acceptance of Alizarin Red stain.

Paired conical teeth may be observed on the dentary of 5.3 mm larvae, and on the premaxillaries by 5.8 mm. Teeth continue to increase in number as the larvae grow. Teeth are consistently more numerous on the left (ultimately the blind) side of the head than the right side. The smallest specimen in which teeth accepted alizarin stain was 12 mm, possibly an artifact of preservation. Larval teeth develop in approximately two nonparallel rows. The outer row consists of conical, caninelike teeth, and the inner row is composed of smaller, curved teeth. Most teeth are ossified in 18 mm larvae. By transformation (ca. 20.0 mm), butter sole larvae possess approximately 37 larval teeth on the left dentary (27 in the outer row; 10 smaller teeth on an inner row) and about 37 large conical teeth on the left premaxillary arranged in

TABLE 4.—Development of meristic structures in *Isopsetta isolepis* larvae. Mean data are given for larvae in the specified length range. (Specimens between dashed lines are undergoing notochord flexion.)

SL (mm)	Sample size	Dorsal fin rays	Anal fin rays	Caudal fin rays	Pectoral fin rays		Pelvic fin rays		Neural spines			Haemal spines	Centra			Branchiostegal rays	Gill rakers	
					Left	Right	Left	Right	Abdom.	Caudal	Total		Abdom.	Caudal	Total		Upper	Lower
3.2-8.9	50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9.0-9.9	5	—	—	1.8	—	—	—	—	—	—	—	9.2	—	—	—	0.8	—	—
10.0-10.9	12	—	—	4.4	—	—	—	—	2.0	9.2	11.2	20.8	0.8	2.8	3.6	1.8	—	—
11.0-11.9	12	11.6	9.2	10.7	—	—	0.3	0.3	5.7	20.8	26.5	26.5	0.3	4.2	4.3	6.0	—	—
12.0-12.9	15	19.6	17.2	14.9	—	—	—	—	8.9	26.7	35.6	27.5	3.5	16.3	19.8	5.9	—	—
13.0-13.9	17	51.8	34.8	15.5	—	—	0.9	0.9	8.1	27.5	35.6							
14.0-14.9	18	45.0	36.8	14.6	—	—	0.4	0.4	9.1	27.1	36.2	27.0	4.9	19.0	23.9	6.1	—	—
15.0-15.9	17	52.9	46.8	15.4	—	—	2.2	2.2	8.2	24.8	33.0	24.8	6.4	22.0	28.6	5.6	—	—
16.0-16.9	10	72.2	55.0	18.0	—	—	2.1	2.1	9.9	30.5	40.4	30.5	9.9	31.8	41.7	7.0	—	—
17.0-17.9	11	89.7	67.5	18.0	0.5	0.5	4.5	4.5	10.0	31.2	41.2	31.2	10.0	32.2	42.2	7.0	—	—
18.0-18.9	15	87.3	66.9	18.0	0.7	0.7	5.0	5.0	9.9	30.9	40.8	30.9	9.9	31.9	41.7	7.0	—	0.3
19.0-19.9	9	87.9	67.9	18.0	0.3	0.3	6.0	6.0	9.9	31.2	41.1	31.0	9.9	32.0	41.9	7.0	—	—
20.0-20.9	9	88.0	68.1	18.0	1.8	1.8	6.0	6.0	9.9	30.9	40.8	30.8	9.9	31.7	41.6	7.0	—	1.7
21.0-21.9	4	88.8	67.8	18.0	2.3	2.3	6.0	6.0	10.0	30.8	40.8	30.8	10.0	31.8	41.8	7.0	—	1.0
22.0-22.9	5	91.2	68.8	18.0	5.0	5.0	6.0	6.0	10.0	31.0	41.0	30.8	10.0	31.8	41.8	7.0	—	2.8

two rows. The right dentary contains about 20 teeth (11 large conical teeth in the outer row and 9 smaller teeth in the inner row). The right premaxillary contains nine larger teeth and six smaller teeth. Teeth continue to increase in number after transformation. A 44 mm juvenile possessed about 40 teeth each on the left premaxillary and left dentary and 14 teeth on the right dentary and 10 teeth on the right premaxillary.

Neural spines ossify during notochord flexion (Table 4; Figure 6). The first neural spine to ossify lies just above the first haemal spine in the anterior abdominal region, and ossification proceeds posteriorly and anteriorly. The last two neural spines to ossify are those on the antepenultimate and penultimate vertebrae. Ossification is usually completed at about 16.5 mm. Haemal spines ossify from anterior to posterior beginning with the first haemal spine. The last two haemal spines to ossify are also on the antepenultimate and penultimate vertebrae.

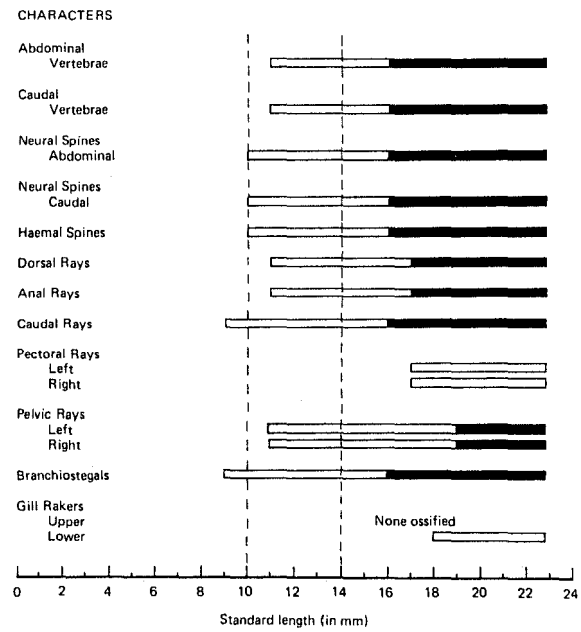

FIGURE 6.—Diagrammatic summary of the sequence of ossification of principal meristic structures in *Isopsetta isolepis*. Dashed vertical lines indicate size range in which notochord flexion occurs; open bars indicate meristic structure is undergoing ossification; solid bars indicate meristic structure is completely ossified.

In the axial skeleton the first centrum to ossify (as early as 11 mm) supports the first haemal spine. Ossification proceeds both anteriorly and posteriorly, with the urostyle ossifying before the antepenultimate and penultimate vertebrae. All centra are ossified by 17 mm.

The first caudal supports to ossify are hypurals[10] 2 and 3 in larvae as small as 12 mm. Hypural 1 is ossified by 13 mm and hypural 4 at about 15 mm. The epurals ossify last at about 16 mm. We interpret the caudal complex of *I. isolepis* to consist of four hypurals (two below and two above the medial axis) and two epurals. One is a normal-sized epural that supports the uppermost caudal ray, and the other epurallike bone is reduced in size and supports no rays (Figure 6H). No uroneurals are present.

Fin rays begin to ossify during notochord flexion (10-14 mm) in the dorsal, anal, caudal, and pelvic fins. Ossification is completed in the following order: caudal, dorsal, anal, pelvic, and pectoral fins (Table 4; Figure 6). Pectoral fin rays were not fully ossified in the largest stained larva, 22.8 mm.

The anlage of the base of the caudal fin begins to form by 5.5 mm (Figure 7A). Incipient caudal rays are evident from 5.5 to 8.8 mm. By 10.5 mm (Figure 7 B) the notochord begins to flex and hypurals 1-3 develop, supporting about eight incipient rays. At about 12.7 mm the notochord is usually fully flexed and three hypurals are evident, supporting 10 differentiated but unossified caudal rays (Figure 7C). By 14.3 mm (Figure 7D), hypurals 1-3 are ossified and some caudal rays have started ossifying, beginning at the center of the fin and proceeding dorsally and ventrally. The full complement of 18 rays is consistently ossified by 16.4 mm (Figure 7E). By 18.0 mm (Figure 7F) all four hypurals and both epurals are ossified. By 22.8 mm (Figure 7G) the caudal fin essentially resembles that of a juvenile (Figure 7H) and nearly all elements of the caudal complex are ossified. The 18 rays, consisting of (from ventral to dorsal) 3 unbranched rays, 12 branched rays, and 3 unbranched rays, are carried on the hypurals as follows: epural 1, 1 ray; hypural 4, 2 rays; hypural 3, 6 rays; hypural 2, 5 rays; hypural 1, 4 rays.

Incipient dorsal fin rays may be observed in the proximal portion of the finfold at midbody by 10.5 mm. Ossification of dorsal rays begins at midbody by 11 mm and proceeds anteriorly and posteriorly. By 17.5 mm the dorsal rays reach their full complement and are completely ossified.

The anal fin develops in a manner analagous to the dorsal fin and nearly simultaneously. Rays begin to differentiate at midbody with formation progressing both anteriorly and posteriorly. Ossified rays begin at midbody at about 11 mm and the full complement may be ossified by 17.5 mm.

Pelvic fin buds may be observed on larvae as small as 10 mm, although not consistently until notochord flexion is complete at about 14 mm, and individual rays may begin ossifying by 11 mm. The full complement of six rays is ossified by 19 mm.

Pectoral fin buds are visible above the yolk sac in newly hatched reared larvae. Larval pectoral fins are present in the smallest stained larvae examined (3.2 mm). The rays begin to differentiate by 13.5 mm and individual rays begin ossifying as transformation occurs by about 17 mm. The full complement of pectoral rays was not attained in the largest larva examined, 22.8 mm, but is fully developed in a 44 mm juvenile.

Branchiostegal rays begin to accept alizarin stain at about 9.5 mm. The adult complement of seven rays may be differentiated, but not ossified, by 13.6 mm. All rays are ossified by 16 mm.

Gill rakers on the first ceratobranchial begin forming at about 7 mm. A maximum of six rakers was formed in the largest stained larva examined (22.8 mm). No rakers were formed on the epibranchials of this specimen. The adult complement of four plus seven gill rakers is present on a 44 mm juvenile.

Of the median fin supports, pterygiophores supporting anal and dorsal fin rays begin ossifying at about 19 mm. These pterygiophores are completely ossified by 22.8 mm (Figure 8).

Scales form sometime between 22.8 mm (largest stained larva) and 44 mm (smallest stained juvenile).

OCCURRENCE

Off Oregon, larvae of *I. isolepis* are distributed mainly in the near coastal zone within 18 km of shore, with abundance peaks at 6-9 km (Richardson 1973, see footnote 4; Richardson and Pearcy 1977). Smaller numbers of larvae have been taken as far as 56 km offshore (Richardson and Pearcy 1977; Laroche and Richardson 1979), inside the mouth of Yaquina Bay (Pearcy and

[10]We follow Moser and Ahlstrom's (1970) definition of hypurals ". . . all bones of hypaxial origin associated with ural centra [are defined] as hypurals, including the lowermost bone."

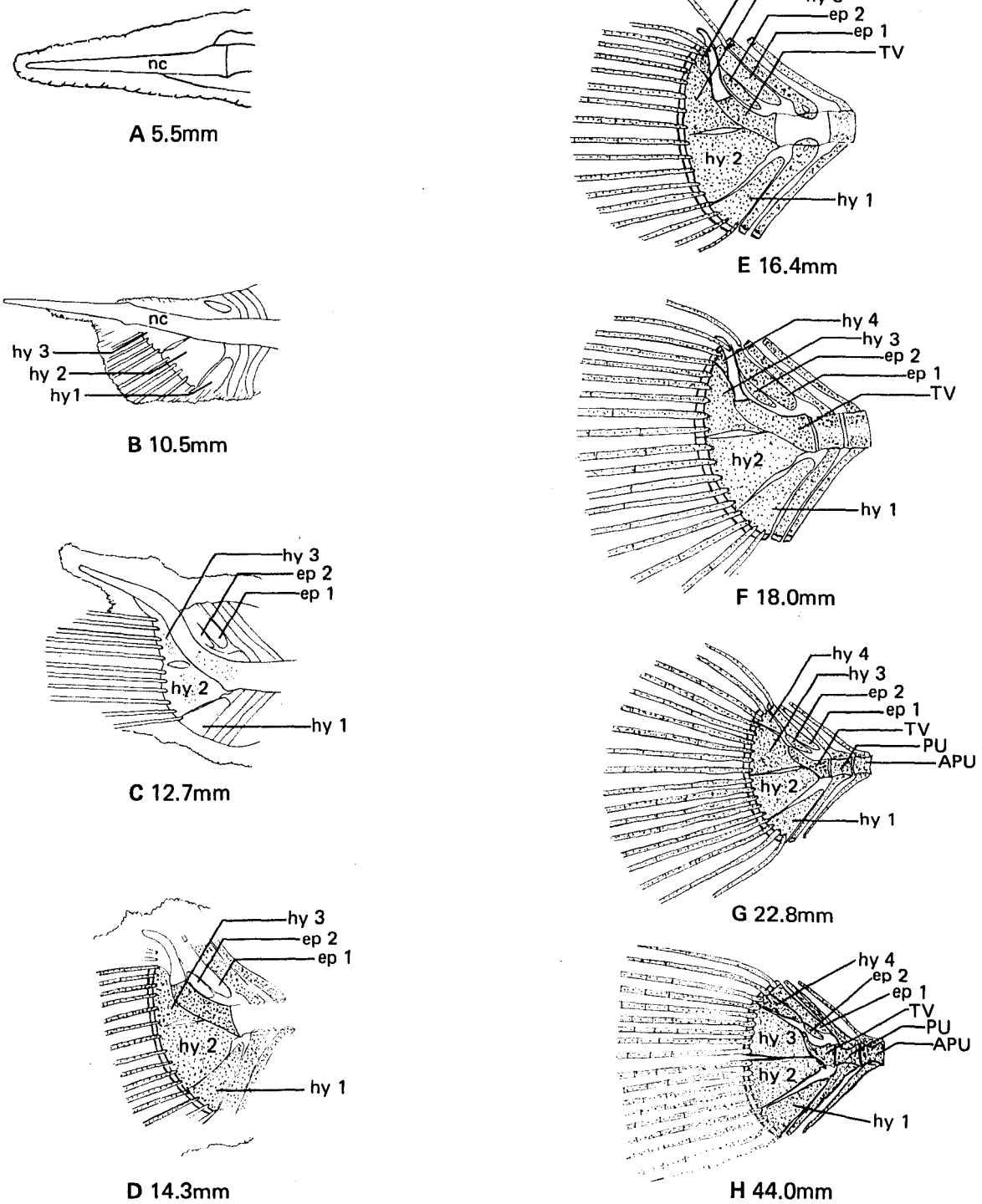

FIGURE 7.—Development of the caudal fin of *Isopsetta isolepis*: 5.5 mm SL, 10.5 mm SL, 12.7 mm SL, 14.3 mm SL, 16.4 mm SL, 18.0 mm SL, 22.8 mm SL, and 44.0 mm SL. Ossified elements are stippled. hy = hypurals; ep = epurals; nc = notochord; APU = antepenultimate vertebrae; PU = penultimate vertebrae; TV = terminal vertebrae.

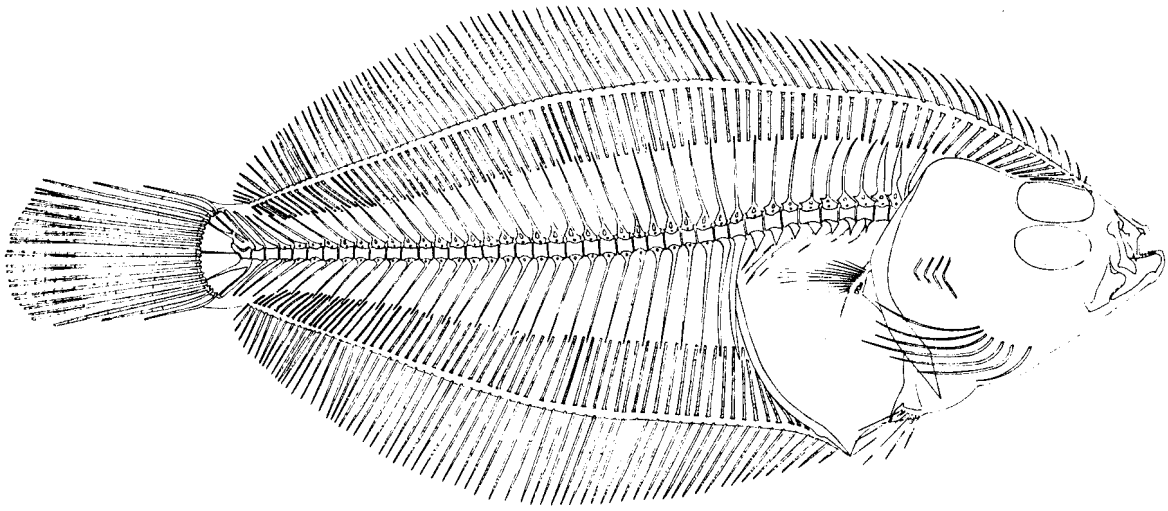

FIGURE 8.—Juvenile *Isopsetta isolepis*, 44 mm SL, showing details of skeletal structure.

Myers 1974), and in the Columbia River (Misitano 1977). A similar coastal distribution is indicated off Washington with reduced numbers occurring in Puget Sound (Waldron 1972; Blackburn 1973). Thus spawning takes place primarily in coastal areas rather than bays and estuaries.

Larvae occur in the plankton off Oregon mainly in winter and spring (Waldron 1972; Misitano 1977; Richardson see footnote 4) although in 1971 larvae were taken in every month of the year except September, November, and December (Richardson see footnote 4). In 1972 they were taken in every month sampled, March through August (Richardson see footnote 4). In 1971, abundance peaked in May, and in 1972, smaller abundance peaks were observed in March and May (Richardson see footnote 4). Spring occurrences of larvae have been reported off Washington and in Puget Sound (Waldron 1972; Blackburn 1973).

Monthly length-frequency distributions and median lengths of larvae collected off Oregon indicate winter-spring spawning (Figure 9). Small larvae <5 mm were taken January through May 1971, October 1971, and March and April 1972. Median lengths increased progressively from 2 to 16 mm in January through June 1971 and from 4 to 16 mm in March through June 1972.

Based on available data, *I. isolepis* apparently settles to the bottom in coastal areas and remains near the coast during the early juvenile period. Newly transformed juveniles (18-38 mm) have been collected off the mouth of the Columbia River in depths of 34-56 m (Table 5). Juveniles in this size range have not been reported from bays, estuaries, and nearshore coastal areas where juvenile *Parophrys vetulus* have been found (Westrheim 1955; Kendall 1966; Beardsley 1969; William Johnson's data listed in Pearcy and Myers 1974; Peden and Wilson 1976; Laroche and Holton 1979; Cummings and Schwartz[11]; Higley and Holton[12]; Krygier[13]). Although Misitano (1977) reported that both *I. isolepis* and *P. vetulus* use the Columbia River as a nursery area, he was referring to fish >85 mm long (>95 mm for *I. isolepis*). Thus, smaller *I. isolepis* juveniles apparently use offshore coastal areas during their first year of life as opposed to the bay, estuarine, and near coastal nursery habitats of *P. vetulus*.

TABLE 5.—Data from beam trawl collections of juvenile *Isopsetta isolepis* taken off the mouth of the Columbia River, 1975.

Date	Location (Lat. N, long. W)	Depth (m)	Specimens (no.)	SL of larvae	
				Median (mm)	Range (mm)
26 June	46°11.5′, 124°07.6′	37	86	24	18-38
26 June	46°09.5′, 124°06.3′	40	7	21	18-24
14 Sept.	46°09.5′, 124°05.0′	34	5	24	22-26
15 Sept.	46°09.3′, 124°08.0′	56	11	25	20-28

[11]Cummings, E., and E. Schwartz. 1971. Fish in Coos Bay, Oregon, with comments on distribution, temperature, and salinity of the estuary. Oreg. Fish Comm., Res. Div., Coastal Rivers Invest. Inf. Rep. 70-11, 22 p.

[12]Higley, D. L., and R. L. Holton. 1975. Biological baseline data, Youngs Bay, Oregon, 1974. Final Rep. Alumex Pacific Aluminum Corp., 1 November 1973 through 30 April 1975. Oreg. State Univ., Sch. Oceanogr. Ref. 75-6, 91 p.

[13]E. Krygier, Research Assistant, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. June 1978.

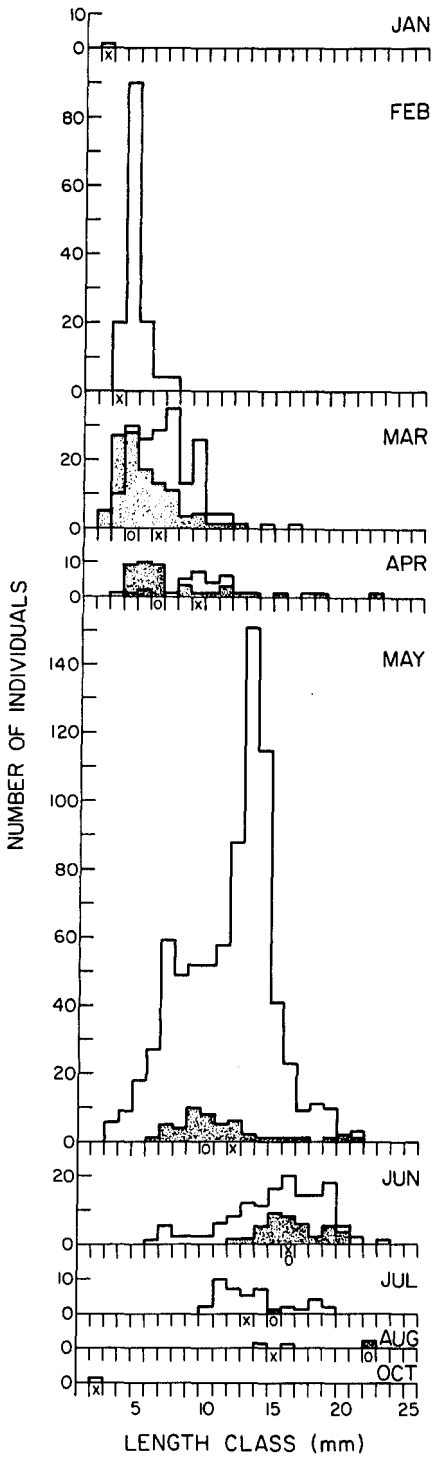

FIGURE 9.—Length-frequency histograms of *Isopsetta isolepis* larvae collected in 70 cm bongo nets off Oregon in 1971 (unshaded) and 1972 (shaded). X = median length of larvae in 1971; 0 = median length of larvae in 1972.

The habitat separation of newly transformed benthic juveniles of *I. isolepis* and *P. vetulus* is interesting since spawning times overlap for the two species and the larvae are codominants in coastal waters off Oregon (Richardson and Pearcy 1977). Habitat separation also has been noted in large (>10 mm) larvae; *P. vetulus* is more abundant in neuston samples relative to plankton samples than *I. isopsetta* (Laroche and Richardson 1979). Ratios of relative abundance of *P. vetulus* to *I. isolepis* in plankton samples was 2:1 compared with 36:1 in neuston samples. Thus the two cooccurring species appear to be utilizing different parts of the water column. Smaller larvae might be segregated similarly by depth, but we have no data on vertical distribution to substantiate this idea. Feeding studies, which may help verify these habitat differences and provide evidence for resource partitioning between these morphologically similar larvae, remain to be conducted.

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