

PELAGIC EGGS AND LARVAE OF THE DEEPSEA SOLE,
EMBASSICHTHYS BATHYBIUS (PISCES: PLEURONECTIDAE),
WITH COMMENTS ON GENERIC AFFINITIES

SALLY L. RICHARDSON¹

ABSTRACT

Two eggs of *Embassichthys bathybius* are 3.0 mm in diameter, pelagic, spherical, transparent, with a homogeneous yolk, narrow perivitelline space, and no oil globule. Embryos in late stage eggs have pigmentation characteristic of larvae, including pigment over the hindgut and three prominent postanal pigment bands. This pigment pattern and the high number of myomeres (>60) serve as distinguishing characters for larvae in the size series described from recently hatched specimens 9.8 mm standard length to a specimen beginning eye migration at 16.2 mm standard length.

Eggs and larvae of *E. bathybius* are extremely rare in extensive plankton and midwater trawl collections from the northeast Pacific with only eight specimens recorded to date. Occurrences were between March and June in the upper 185 m or less of the water column over bottom depths of 59-2,850 m.

Within the tribe Pleuronectini of the subfamily Pleuronectinae, larvae of *Glyptocephalus*, *Tanakius*, *Embassichthys*, and *Microstomus* form a distinct and logical group sharing similarities of a banded pigment pattern; angular, oblique jaw; elongate, slender form; and tendency toward a leptocephalus-like shape. If intense pigment banding and pronounced leptocephalus-like shape are derived characters, then the group is probably a naturally related one, with *Microstomus* the least and *Glyptocephalus* the most specialized.

The deepsea sole, *Embassichthys bathybius* (Gilbert), occurs in the northeast Pacific Ocean from Santa Catalina Island, southern California, to Pratt Seamount, Gulf of Alaska, in depths from 320 to 1,432 m but mostly >730 m (Miller and Lea 1972; Hart 1973). It grows to 47 cm and is reportedly uncommon (Miller and Lea 1972; Hart 1973). Life history data are minimal and nothing is known about its reproduction or early life.

Pelagic eggs and larvae of this species are described here for the first time based on collections taken off the Oregon coast. Knowledge of these early stages provides some insight into reproductive strategy as well as information on larval morphology which may be useful for examining systematic relationships.

METHODS

The pelagic specimens were collected (Table 1) with 70 cm bongos having 0.571 mm mesh nets and a 3.1 m Isaacs-Kidd midwater trawl with a 5 mm

mesh liner and a 0.5 m diameter cod end of 0.571 mm mesh. The bongos were towed obliquely through the water column. The midwater trawl was towed near the surface in the upper 10 m.

All material was preserved in 10% Formalin² and stored in 5% Formalin except the 16.2 mm larva which was transferred to 36% isopropyl alcohol.

Measurements made on larvae included:

Standard length (SL) = 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.

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

Eye diameter = horizontal diameter of pigmented portion of left eyeball.

Depth at cleithrum = vertical distance from dorsal body margin, excluding finfold or fin, to ventral tip of cleithrum.

¹School of Oceanography, Oregon State University, Corvallis, Oreg.; present address: Gulf Coast Research Laboratory, East Beach Drive, Ocean Springs, MS 39564.

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Collection data for eggs and larvae of *Embassichthys bathybius*.

Item	SL (mm)	Date	Gear	Lat. N.	Long. W	Distance from coast (km)	Bottom depth (m)	Depth of tow (m)
Eggs	—	22 May 1972	70 cm bongo	44°39.1'	124°45.7'	56	220	185-0
	—	20 March 1974	70 cm bongo	43°40.0'	124°33.0'	28	190	180-0
Larvae	9.8	27 March 1973	70 cm bongo	43°00.0'	125°01.7'	46	>1,000	102-0
	9.8	13 June 1972	70 cm bongo	44°39.1'	125°27.7'	111	2,850	120-0
	10.2	23 May 1972	70 cm bongo	44°39.1'	125°13.7'	93	1,300	165-0
	10.4	11 April 1972	70 cm bongo	44°39.1'	124°10.7'	9	59	48-0
	15.4	12 June 1972	70 cm bongo	44°39.1'	124°38.7'	46	330	115-0
	16.2	26 April 1965	3 m IKMT	44°39.1'	125°27.7'	93	1,300	≈10

Depth at anus = vertical distance from dorsal body margin, excluding finfold or fin, to anus.

Depth behind anus = vertical distance from dorsal body margin to ventral body margin, excluding finfold or fin, at point immediately behind anus where body depth decreases greatly compared with depth at anus.

Body lengths refer to standard length. Illustrations were made with the aid of a camera lucida.

IDENTIFICATION

The largest larva in the series, obviously a pleuronectid based on general body form and asymmetrical position of the left eye, had 60 myomeres (equivalent to vertebrae), 112 dorsal fin rays, and 97 anal fin rays. *Embassichthys bathybius* is the only pleuronectid occurring in the northeast Pacific which has these counts (Norman 1934; Miller and Lea 1972; Hart 1973). The larval series was linked together by the high number of myomeres and by pigment pattern, most notably three postanal pigment bands. Advanced embryos in the eggs had the same pigment pattern as the smallest larvae and the same high number of myomeres, providing positive identification.

DESCRIPTION

Eggs (Figure 1)

Two eggs identified as *E. bathybius* are spherical and transparent, 3.0 mm in diameter, with a homogeneous yolk, a relatively narrow perivitelline space, and no oil globule. The egg membrane is smooth and has a slight pinkish tinge in preserved material. Both eggs have well-developed embryos with three distinctive postanal pigment bands, including one at the tail tip. In the more advanced embryo (illustrated), the eyes are pigmented and the postanal bands are more intense. Pigment also occurs near the hindgut and extends out onto the yolk.

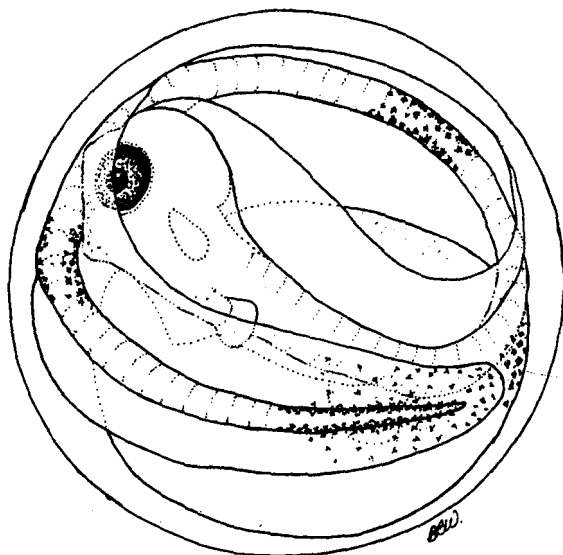


FIGURE 1.—Egg of *Embassichthys bathybius*, 3.0 mm in diameter.

Larvae (Figure 2; Table 2)

Six larvae identified as *E. bathybius* range from 9.8 to 16.2 mm SL. The two smallest specimens appear to be recently hatched, based on state of development compared with the most advanced embryo. A hatching size of about 9 mm (excluding shrinkage due to Formalin preservation) may be reasonable, based on the diameter-circumference relationship for a 3.0 mm diameter egg and the extent to which the advanced embryo encircles the yolk mass (Figure 1). The largest specimen, 16.2 mm, is beginning to undergo transformation as evidenced by the slight asymmetrical position of the left eye. The size at which the transformation process is complete is unknown.

Pigmentation on the smallest larvae is similar to that on the embryos, with melanophores present over the hindgut and in three bands postanally. Pigment in the anterior two of these three bands is generally more concentrated along the dorsal and

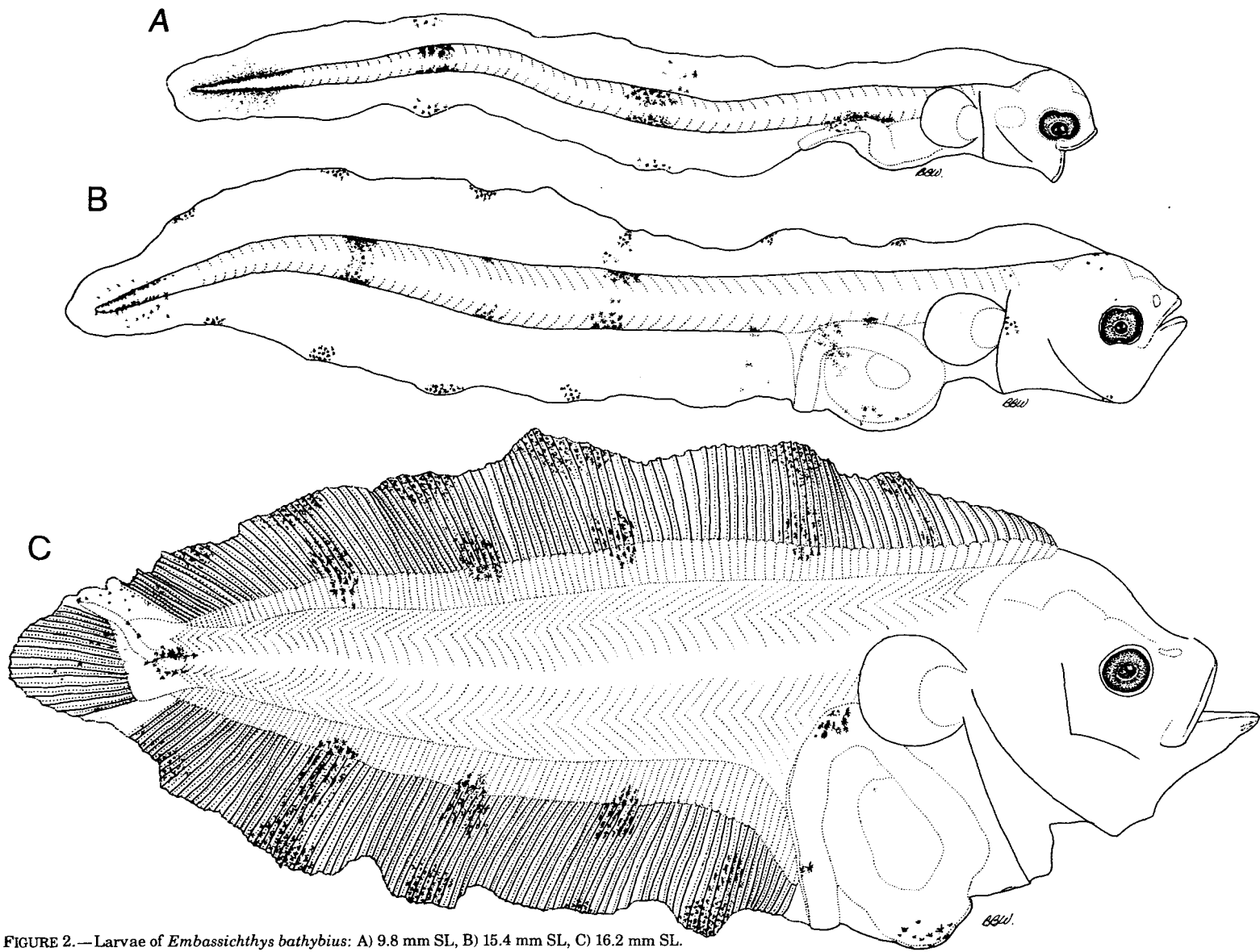


FIGURE 2.—Larvae of *Embassichthys bathybius*: A) 9.8 mm SL, B) 15.4 mm SL, C) 16.2 mm SL.

TABLE 2.—Measurements (millimeters) of selected body parts of larvae of *Embassichthys bathybius*.

SL	Head length	Snout to anus length	Eye diameter	Depth at cleithrum	Depth at anus	Depth behind anus
9.8	1.2	3.2	0.4	0.8	0.7	0.3
9.8	1.9	—	.5	1.3	—	.7
10.2	1.8	—	.5	1.2	—	.5
10.4	1.2	3.2	.4	.8	1.0	.5
15.4	2.0	5.3	.5	1.7	2.0	.8
16.2	3.7	6.4	.7	5.1	5.7	4.3

ventral body margins than laterally. Pigment also occurs on the finfold in the region of the bands, particularly at the finfold margins near the anterior two bands. During development, the most distinctive pigment additions occur along the fin fold (fin) margins, with seven patches forming along the dorsal fin and five along the ventral fin of the largest specimen. Pigment patches are also added to the dorsal and ventral body margins, generally in the vicinity of the fin fold (fin) patches, initially between the anterior two tail bands. With growth the original pigment bands become discontinuous laterally except for the one at the tail tip which eventually appears as a patch on the caudal peduncle. Some pigment is also added ventrally in the abdominal region.

Initially the larvae are relatively long and slender with body depth at the anus 7% SL in the smallest larvae and 13% SL by 15.4 mm. Body depth increases considerably by 16.2 mm when it is 35% SL at the anus. Snout to anus distance is 31-34% SL until 16.2 mm when it increases to 40% SL. Between 15.4 and 16.2 mm a number of events occur including notochord flexion; dorsal, anal, and caudal fin development; and formation of pelvic fin buds. By 16.2 mm, the adult complement of dorsal (109-117) and anal (94-98) fin rays (Miller and Lea 1972) is attained but the caudal fin rays are not fully developed, based on the incomplete count of 8 + 8, and pectoral fin rays are not yet formed. No head or body spines are apparent on any of the larvae.

COMPARISON

The only other pleuronectids occurring in the northeast Pacific with >60 vertebrae are *Reinhardtius hippoglossoides* and *Glyptocephalus zachirus* (Norman 1934; Miller and Lea 1972; Hart 1973). Eggs of *R. hippoglossoides* are 4.0-4.5 mm in diameter (Pertseva-Ostroumova 1961) and those of *G. zachirus* are 1.98-2.34 mm (Pearcy et al. 1977) compared with about 3.0 mm for *E.*

bathybius. Larvae of *R. hippoglossoides* are lightly pigmented with melanophores lining the myosepta but never appearing as pronounced pigment bands on the body (Pertseva-Ostroumova 1961; Nichols 1971) as in *E. bathybius*. Small (<11 mm) larvae of *G. zachirus* have four postanal pigment bands (Ahlstrom and Moser 1975) compared with three in *E. bathybius*. The bands in *G. zachirus* extend with uniform intensity from dorsal to ventral body margins whereas those in *E. bathybius* are concentrated along the dorsal and ventral margins and are less intense laterally. With development these bands persist laterally in *G. zachirus* while the anterior two bands persist only near the body margins in *E. bathybius*. Small (<11 mm) larvae of *G. zachirus* also have a relatively shorter snout to anus distance (range = 25.3-27.2% SL; mean = 26.2% SL based on four specimens) than *E. bathybius* (range = 30.8-32.7% SL; mean = 31.8% SL based on two specimens). Freshly preserved larvae of *E. bathybius* possess scattered orange chromatophores on the body whereas larvae of *G. zachirus* have none. Eye migration begins at a smaller size in *E. bathybius* (at least by 16.2 mm) than in *G. zachirus* [34-35 mm (Pearcy et al. 1977)] indicating that final transformation to juvenile may take place at a smaller size in *E. bathybius* compared with 45 mm or larger (Pearcy et al. 1977) for *G. zachirus*.

OCCURRENCE

Because of the paucity of specimens of *E. bathybius* little can be said about temporal and spatial distribution. All were collected between March and June (Table 1) which may indicate a winter-spring spawning period similar to that of many species off Oregon (Pearcy et al. 1977; Richardson and Pearcy 1977). Additional documentation is needed to determine whether such spawning periodicity actually exists in the deep habitat (generally >730 m) of the adults.

Specimens were collected in the upper 185 m or less of the water column over bottom depths of 59 to 2,850 m, with the largest larva taken in a surface (upper 10 m) tow (Table 1). The wide ranging occurrences of the pelagic eggs and larvae between 9 and 111 km from the coast probably reflects drift and dispersal by currents.

The larvae appear to be rare, at least off Oregon, based on over 3,000 midwater trawl and plankton collections that have been taken in that region

(table 1 in Percy et al. 1977). Such rarity could reflect the reported rarity of adults, or may indicate that the principal spawning occurs outside our sampling area, or that the primary occurrence of eggs and larvae may be at depths (>200 m) below those commonly sampled.

The reproductive strategy of *E. bathybius* involves production of a large egg, probably with an associated reduced fecundity compared with an equivalent sized pleuronectid producing smaller eggs. The egg likely has a moderate pelagic life span lasting at least a few weeks, based on time to hatching for eggs of the related northeast Pacific species *Microstomus pacificus* [38 d at 7.5° C; 27 d at 10° C; 18 d at 12.5° C (Williams³)] which has eggs of 2.04-2.57 mm diameter (Percy et al. 1977). The larva of *E. bathybius* is well developed by the time it hatches and probably has an extended pelagic life lasting at least a few months, although size at which transformation is completed and growth rates are unknown. Percy et al. (1977) estimated that the related species *M. pacificus* and *G. zachirus* may have a pelagic phase lasting about 1 yr.

DISCUSSION

The most recent, broad based review of the family Pleuronectidae that implied relationships was by Norman (1934) who recognized five subfamilies. Within the subfamily Pleuronectinae the genera fall into two main groups: one in which the mouth is moderate to large and the jaws and dentition are well developed on both sides [tribe Hippoglossini of Nelson (1976), with ca. 10 genera, 18 species]; the other in which the mouth is small and asymmetrical, with the jaws and dentition more developed on the blind side [tribe Pleuronectini of Nelson (1976) with ca. 16 genera, 42 species]. Norman (1934) stated "The group of Pleuronectine genera including *Microstomus*, *Embassichthys*, *Tanakius* and *Glyptocephalus* have generally been marked off from the remainder of the small-mouthed members [tribe Pleuronectini] of the subfamily as a primary division [within the tribe], distinguished by a generally more elongate body and by an increased number of vertebrae, fin-rays and of scales in a longitudinal series. Such an arrangement is clearly an artificial one, and it is doubtful whether

these [four] genera really form a natural group." He further said that *Embassichthys* is apparently closely related to *Microstomus* and *Glyptocephalus* is close to *Tanakius* whereas *Microstomus* is related to *Pseudopleuronectes* and *Tanakius* is apparently related to *Dexistes*.

Norman's (1934) discussion of intergeneric relationships was based mainly on external morphological features and therefore the phylogeny of the group was not really well defined. Additional evidence is needed to elucidate relationships. One source of additional information is the larval form of fishes which has been used to demonstrate or clarify systematic relationships in other groups of fishes, e.g., scoplarchids (Johnson 1974), gonostomatids (Ahlstrom 1974), myctophids (Moser and Ahlstrom 1974), myctophiforms (Okiyama 1974) marine teleosts in general (Ahlstrom and Moser 1976), bothids (Futch 1977), scombroids (Okiyama and Ueyanagi 1978), and serranids (Kendall 1979). Although larval characters that have been used are usually external morphological features such as body shape and form, spination, and melanistic pigmentation, character similarities have been consistently in agreement with intergeneric relationships.

With this paper, larvae of all species in the four pleuronectine genera mentioned by Norman (1934) are known (Table 3). Larvae are also known for 53 of the 60 pleuronectine species that occur in the North Pacific and North Atlantic (Ahlstrom and Moser 1979). With this knowledge it is possible to point out the similarity and distinctiveness of the larvae in the four-genus complex of *Microstomus*, *Embassichthys*, *Tanakius*, and *Glyptocephalus* which appear to form a logical group within the tribe Pleuronectini. Determination of whether this phenetically derived group is a

TABLE 3.—Selected references containing illustrations of larvae of species in the pleuronectid genera *Embassichthys*, *Glyptocephalus*, *Microstomus*, and *Tanakius*.

Species	References
<i>Embassichthys bathybius</i>	This paper
<i>Glyptocephalus cynoglossus</i>	Petersen 1904; Ehrenbaum 1905-09; Nichols 1971; Evseenko and Nevinsky 1975; Russell 1976.
<i>G. stelleri</i>	Dekhnik 1959; Pertseva-Ostroumova 1961; Okiyama 1963; Okiyama and Takahashi 1976.
<i>G. zachirus</i>	Ahlstrom and Moser 1975
<i>Microstomus achne</i>	Okiyama and Takahashi 1976
<i>M. kitt</i>	Nichols 1971; Russell 1976
<i>M. pacificus</i>	Hagerman 1952; Ahlstrom and Moser 1975
<i>Tanakius kitaharae</i>	Fujita 1965; Okiyama and Takahashi 1976

³S. Williams, Graduate student, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, unpubl. data, June 1976.

natural group comprised of related genera, in contrast with Norman's (1934) speculation, will depend on a detailed analysis of derived character states which is beyond the scope of this paper. However, based on other larval studies mentioned above, it seems probable that the larval similarities within the group may provide evidence to support the idea of intergeneric relationship. In an earlier study of larvae of *M. kitt*, *G. stelleri*, and *G. cynoglossus*, Pertseva-Ostroumova (1961) preliminarily concluded that larval evidence indicated a close relationship between *Microstomus* and *Glyptocephalus*.

Characters shared by larvae of members of this four-genus complex and not found in other members of the Pleuronectini include pigment pattern (preflexion larvae) consisting of three or four post-anal pigment bands which may be continuous (from dorsal to ventral body margin) or discontinuous (concentrated only near the dorsal and ventral body margins); elongate, slender form of reflexion larvae; angular jaw with strongly oblique appearance; and tendency toward a leptocephaluslike shape with development. Among genera, similarities are greatest between *Glyptocephalus* and *Tanakius* which share the characters of continuous postanal pigment bands that, later in development, become concentrated mediolaterally; pigment addition as ventral patches between bands; preopercular spines; and pronounced leptocephaluslike shape. *Embassichthys* most closely resembles *Glyptocephalus* and *Tanakius*, having continuous postanal pigment bands initially which later become discontinuous, persisting only at the body margins; pigment addition as dorsal and ventral patches between bands; no head spination; a moderate leptocephaluslike shape. *Microstomus* is most distinct with postanal pigment bands discontinuous and not prominent; occipital spines in two of three species; much less tendency toward long leptocephaluslike shape with dorsoventral deepening of body instead. If strong pigment banding and pronounced leptocephaluslike shape can be shown to be derived character states, which they appear to be considering the rest of the Pleuronectini, this group of genera may indeed be related, with *Microstomus* being least specialized and *Glyptocephalus* most specialized.

Additional observations on head spine patterns, extremes in larval form, and eye position in relation to caudal fin development may prove to be useful in future studies assessing relationships

within this group of genera. Evseenko (1979) theorized that the presence of head spines in flatfish larvae was indicative of their percoid ancestors and that a reduction in head spines within a genus was a derived character state. Both *M. achne* and *M. pacificus* of the North Pacific have prominent occipital spines (Hagerman 1952; Okiyama and Takahashi 1976) while *M. kitt* of the northeast Atlantic reportedly has none (Russell 1976; Evseenko 1979). This tends to offer support for the concept of a North Pacific origin of the genus *Microstomus* with *M. kitt* being a more specialized, derived form. All three species of *Glyptocephalus* reportedly have preopercular spines (Ahlstrom and Moser 1975; Russell 1976; Okiyama⁴) although total number and relative size have not been well documented for each species. It would be interesting to see if a reduction in preopercular spination occurs in *G. cynoglossus* of the North Atlantic, following a pattern similar to *M. kitt*.

Both egg size and size at transformation reach maxima in species of this generic complex in the northeast Pacific. Eggs of *E. bathybius* are about 3.0 mm in diameter and those of *M. pacificus* and *G. zachirus* are ≥ 2.0 mm (Pearcy et al. 1977). Larval lengths of up to 89 mm in *G. zachirus* and 65 mm in *M. pacificus* prior to transformation have been reported (Pearcy et al. 1977). The latter species develops an extremely deep bodied, highly compressed specialized larval form. The large egg size and size at transformation may possibly reflect an environmentally induced, specialized adaptation to the upwelling system (or deep habitat in the case of *E. bathybius*) and associated circulation patterns of the region.

Patterns of eye migration in relation to caudal fin development vary among genera. In *G. zachirus* the caudal fin forms entirely before the left eye begins to migrate whereas in *M. pacificus*, the eye begins to migrate as notochord flexion begins (Pearcy et al. 1977). Relatively few specimens of *G. zachirus* have been collected with the left eye on the middorsal ridge suggesting that once eye movement is initiated it proceeds rapidly, with transformation completed shortly thereafter. This is in contrast to *M. pacificus* where a large number of specimens in a wide size range (10-63 mm SL) have been collected with the eye on the middorsal

⁴M. Okiyama, Professor, Ocean Research Institute, University of Tokyo, 1-15-1, Minamidai, Nakano-ku, Tokyo 164, Japan, pers. commun. April 1979.

ridge (Pearcy et al. 1977). These patterns have not been investigated fully in the other species and genera in the group although our limited *E. bathybius* series indicates eye migration may begin with notochord flexion. Larvae of *G. zachirus* appear to maintain symmetry until they are ready to settle and then transform rapidly, while asymmetry begins earlier and persists longer in the pelagic phase in *M. pacificus* and possibly the other genera. Perhaps the delay in eye migration in *Glyptocephalus* is a specialization associated with the prolonged pelagic period of all species in this genus.

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