Development and Distribution of Larvae and Pelagic Juveniles of Three Kyphosid Fishes (*Girella nigricans, Medialuna californiensis,* and *Hermosilla azurea*) off California and Baja California

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ABSTRACT: Complete developmental series are described for larvae and pelagic juveniles of three kyphosid fishes, *Girella nigricans* (Ayres), *Medialuna californiensis* (Steindachner), and *Hermosilla azurea* (Jenkins and Evermann), from California and Baja California coastal waters. Larvae of the three species have a similar compact body form, with *G. nigricans* being the most slender and *H. azurea* the most robust. They share a number of pigment characters: including dorsal, ventral, and lateral midline melanophore series; an embedded melanistic band through the eye region; and minute melanophores at the tip of the notochord. Unique pigment variations permit the identification of all developmental stages of these species. Each has a specialized pelagic juvenile stage with distinct pigmentation. The pelagic distribution of each species is described; larvae of *M. californiensis* are the most oceanic and those of *H. azurea* the most coastal of the three species. The ontogenetic characters of these species are consistent with the view that they are monophyletic.

The opaleye, *Girella nigricans*, occurs from San Francisco, California, to Cabo San Lucas, Baja California. It is a prominent member of near-shore rocky reef and kelp communities from southern California to central Baja California and ranges from the intertidal zone to about 30 m depth. The halfmoon, *Medialuna californiensis*, occurs from Vancouver Island, Canada, to the Gulf of California, but is rare north of Point Conception, California. Its preferred habitat is similar to that of *G. nigricans*, although it ranges deeper to 40 m. The zebra perch, *Hermosilla azurea*, is known from Monterey Bay, California, to the Gulf of California but prefers warmer waters and is rare north of southern California. It is found in shallow inshore areas to a maximum depth of 8 m (Miller and Lea 1972; Feder et al. 1974; Eschmeyer et al. 1983).

Opaleye and halfmoon are part of the incidental catch of the coastal purse seine fleet and are sold as "perch" in the fresh fish market (Fitch and Lavenberg 1971). Annual landings of opaleye average about 2½ tons with a maximum of 12 tons in 1973; halfmoon landings average about 7 tons annually with a maximum of 25 tons in 1968 (Heimann and Carlisle 1970; McAllister 1975). Halfmoon are seasonally abundant in the southern California commercial passenger fishing boat catch, ranking as high as fifth in numbers caught (Crook 1978). They also consistently rank among the top 10 species caught by the southern California private sport fishery (Wine 1982). Fewer opaleye are landed in these fisheries, reflecting the shallower distribution of this species; however, opaleye are a mainstay for rocky-shore anglers in southern California and are the second most important species in competitive spearfishing events (Pinkas et al. 1968; Fitch and Lavenberg 1971). Zebra perch are taken occasionally by southern California shore anglers and spearfishers (Limbaugh 1955; Feder et al. 1974).

Knowledge of the early life histories of opaleye and halfmoon is scanty. They spawn during spring and summer and their larvae appear in nearshore plankton tows during this period. Both species have a silvery pelagic juvenile stage, and both appear in small schools in nearshore areas and around floating masses of kelp. Halfmoon continue their juvenile development in these habitats, whereas opaleye enter tidepools at about 25 mm length and change abruptly to olive colored individuals which have one or two white spots on the back, lateral to the dorsal fin. They remain in the intertidal region until about

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75 mm length when they begin to seek deeper subtidal habitats (Limbaugh 1955; Fitch and Lavenberg 1971; Kramer and Smith 1973; Feder et al. 1974; Gruber et al. 1982; Walker et al. 1987; Waples 1987; Waples and Rosenblatt 1987). Information on zebra perch is limited; their larvae occur in nearshore plankton tows in summer and fall (Walker et al. 1987) and small juveniles are reported to school with those of opaleye in August (Lockley 1952; Limbaugh 1955; Feder et al. 1974).

The systematic placement of these species is unsettled. Hubbs et al. (1979) and earlier workers recognized separate families for each of them, placing G. nigricans in Girellidae, M. californiensis in Scorpididae, and H. azurea in Kyphosidae; other workers have grouped the three species in Kyphosidae (Robins et al. 1980). Johnson (1984) maintained separate families for these species in his survey of percoid ontogeny and included two of our original drawings (10.9 mm G. nigricans and 10.1 mm M. californiensis) in his review.

The purpose of this paper is to describe the larvae and pelagic juveniles of G. nigricans, M. californiensis, and H. azurea, summarize their distributions from California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys and other sources, and point out ontogenetic characters that may be useful in defining systematic relationships.

MATERIALS AND METHODS

Larvae and pelagic juveniles of G. nigricans and M. californiensis were obtained principally from CalCOFI plankton surveys, while those of H. azurea came from nearshore plankton samples off the San Onofre Nuclear Generating Station (SONGS) (Barnett et al. 1984). Totals of 213 larvae and 111 pelagic juveniles were available for G. nigricans; 253 larvae and 31 pelagic juveniles for M. californiensis; and 79 larvae and 6 pelagic juveniles for H. azurea. Additional larval specimens of G. nigricans were obtained from a batch of field-caught eggs reared by David Kramer in the experimental aquarium of the Southwest Fisheries Center from 1 to 28 June 1968. We reared several batches of G. nigricans larvae from field collections of eggs in May to July 1978 and in July 1979. None of these larvae survived more than one week; however, they were useful in defining early pigment patterns.

Developmental series were established to study general morphology, morphometry, and pigmentation; selected specimens were cleared and stained using the method of Potthoff (1984) to determine the sequence of ossification of fin rays, vertebrae, branchiostegal rays, and head spines. The descriptive methods and terminology follow Ahlstrom et al. (1976) and Johnson (1984). Prior to the completion of notochord flexion, body length was measured from the tip of the snout to the tip of the notochord and is designated notochord length (NL). In postflexion specimens body length was measured to the posterior edge of the hypural plate and is termed standard length (SL).

DISTINGUISHING FEATURES OF THE SPECIES

Larvae of the three species can be separated by melanistic pigment pattern (Fig. 1). Preflexion and flexion stage larvae of G. nigricans have one or two melanophores on the ventral midline of the gut. Hermosilla azurea usually have 3 or 4 (range, 1–6) evenly spaced melanophores in this region and M. californiensis larvae lack ventral gut melanophores during these stages. Preflexion and flexion larvae of G. nigricans and H. azurea have a series of evenly spaced melanophores along the ventral margin of the tail usually beginning at the first postanal myomere; in M. californiensis the series often is incomplete anteriorly (except in yolk-sac larvae). Larvae of M. californiensis usually have small melanophores dorsally and ventrally near the tip of the notochord. These melanophores are smaller, fewer, and often present only on the ventral margin in the other two species.

All three species are heavily pigmented along the dorsal and ventral margins through most of larval life and all three acquire a midlateral streak along the tail during notochord flexion. The streak originates more posteriorly in M. californiensis than in the other two species. In flexion larvae of M. californiensis and H. azurea, pigment spreads from the dorsal, lateral, and ventral series to form a band around the tail. This band originates more anteriorly

FIGURE 1.—Lateral, dorsal, and ventral views of early kyphosid larvae: (A–C) *Girella nigricans*, 5.7 mm NL, CalCOFI cruise 7805, station 90.28, surface tow; (D–F) *Medialuna californiensis*, 5.2 mm NL, CalCOFI cruise 6207–B, station 110.55, oblique tow; (G–I) *Hermosilla azurea*, 4.3 mm NL, MEC SONGS cruise I–80, surface tow.
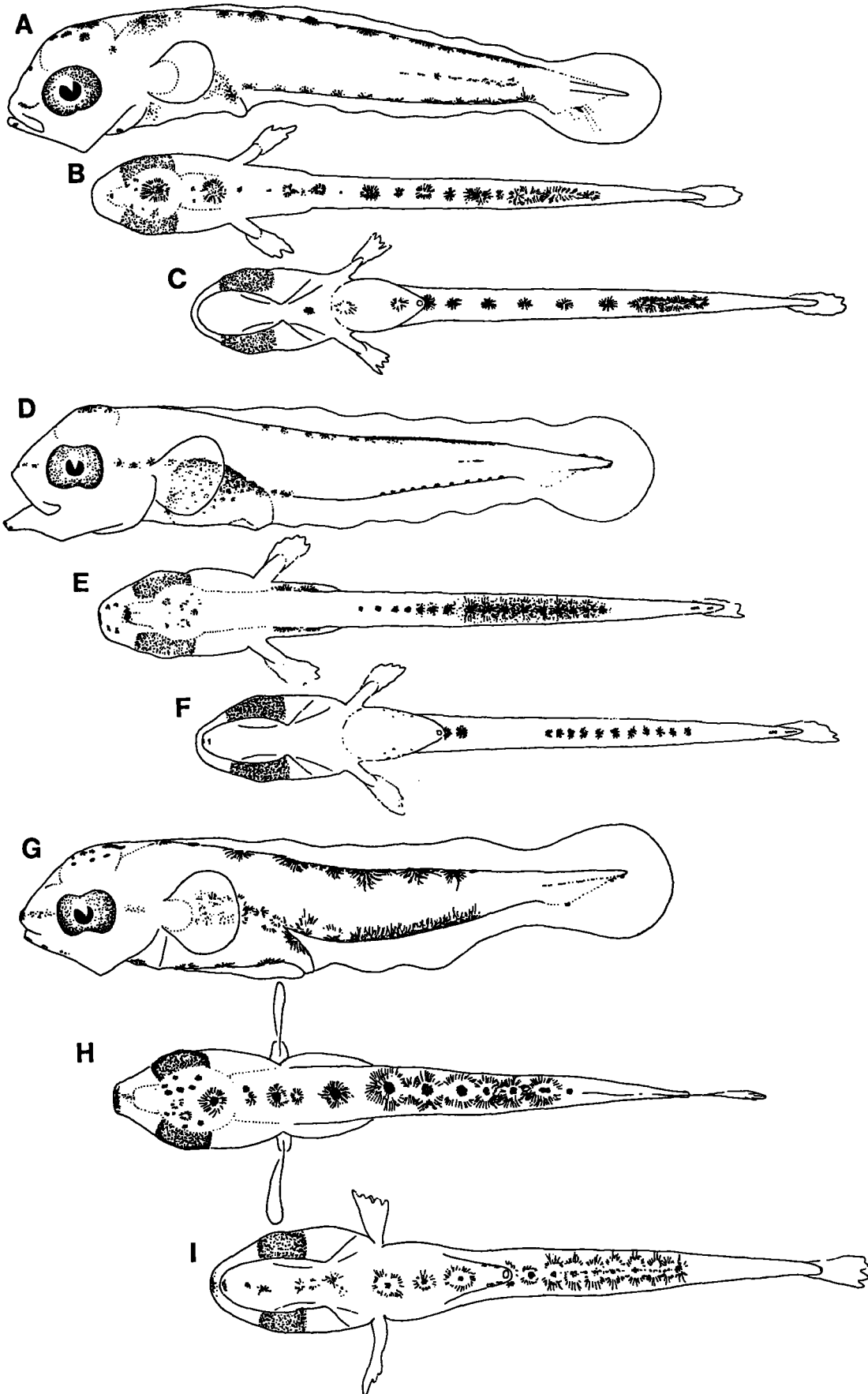
and is broader in the latter species, although in both species it subsequently expands anteriorly to completely cover the sides of the body. Late larvae and pelagic juveniles of all three species are heavily pigmented; *G. nigricans* maintains a strong midlateral stripe, *M. californiensis* becomes uniformly pigmented, and *H. azurea* develops a mottled or barred pattern.

The three species differ in body depth, with *G. nigricans* the most slender and *H. azurea* the most robust. Developmental events occur at a smaller size in *H. azurea* than in the other species. Notochord flexion occurs between 4.1 and 5.8 mm in *H. azurea*, and between 5.8 and 8.6 mm in *G. nigricans* and *M. californiensis*. Transformation to pelagic juveniles occurs at about 11–12 mm in *H. azurea*, ca. 17 mm in *G. nigricans* and ca. 12 mm in *M. californiensis*. Head spination is more developed in *M. californiensis* than in the other two species.

Dorsal and anal fin ray counts are distinct for all three species at about 10 mm SL. *Hermosilla azurea* has XI, 11 dorsal rays and III, 10 anal rays while these fin formulas are D: XII–XIV, 12–15, A: III, 10–13 for *G. nigricans* and D: IX–X, 22–27, A: III, 17–21 for *M. californiensis* (Miller and Lea 1972).

Girella nigricans
Figures 1–3

General Morphology

Our smallest yolk-sac larvae are ca. 3.0 mm, have unpigmented eyes, a rudimentary mouth, and a large oval yolk sac which extends from the head to ca. midintestine and contains a single posteriorly located oil globule (ca. 0.16–0.20 mm diameter). Larvae are 3.5–3.7 mm long when the yolk is completely absorbed. Preflexion larvae are moderately slender with a relatively short coiled gut which extends slightly less than 40% of body length (Tables 1, 2). A small gas bladder is positioned anteriorly above the gut. The head is relatively small, with a blunt snout, and with round to slightly elongate (horizontally) eyes (Fig. 2).

Development is gradual during flexion and postflexion with no abrupt changes in body form or proportions. Most body parts increase relative to body length throughout the larval period with snout-anus length, head length, and body depth showing the greatest changes (Table 2). A small blunt spine develops at the angle of the

preopercle in late preflexion larvae, and remains inconspicuous during later larval stages. No other head spines develop in larvae; however, one or more additional minute preopercular spines may appear in early pelagic juveniles. These specimens also develop an opercular and a minute supracleithral spine.

Notochord flexion begins at ca. 5.8 mm length and is completed by ca. 8.6 mm. Transformation into the pelagic juvenile stage is indicated by the appearance of scales (first seen in a 15.7 mm specimen), completion of fin ray elements, and attainment of juvenile pigment at about 17 mm (Fig. 3).

Fin Formation and Meristics

The first rays to calcify are the central principal caudal rays beginning late in the preflexion stage at ca. 5.8 mm (Table 3). The full complement of 9+8 principal rays is present midway through flexion and the procurrent rays begin to calcify at the end of flexion. The full complement of 10–12+9–10 procurrent rays is acquired in early pelagic juveniles (Table 3).

The dorsal and anal soft rays begin to calcify during flexion. Addition is posteriad with full complements attained in early postflexion. Dorsal and anal spines appear during early postflexion and are added in an anteriad direction. Full dorsal and anal fin complements (D: XII–XIV, 12–15; A: III, 10–13) are present in postflexion larvae 10.7 mm and larger.

The pectoral fins are initially rounded with rounded bases and retain this shape throughout the larval period; they become more elongate in pelagic juveniles. Calcification of rays begins midway through flexion; the upper rays are the first to appear and addition is ventrad. The full complement of 18–20 is present just before transformation into the pelagic juvenile.

The pelvic fins are the last to form. Fin buds appear midway through flexion and calcification of rays begins just after flexion is completed. The full complement of I,5 rays was present in specimens 10.7 mm and larger.

Initial vertebral ossification was not apparent in our stained series; however, the anteriormost 22 vertebral centra were already ossifying in a 6.7 mm larva. Ossification proceeds in a posteriad direction and the full complement of 27 vertebrae is present by the end of flexion. The branchiostegal rays begin to ossify late in preflexion and the full complement of six pairs of rays is present late in flexion.

TABLE 1.—Measurements (mm) of larvae and pelagic juveniles of *Girella nigricans*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Station	Body length	Snout-anus length	Head length	Head depth	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Predorsal length	Prepelvic length
6606–93.27	2.6	0.96	0.54	0.60	0.10	0.34	0.54	—	—	—	—
6307–83.39	2.7	0.86	0.51	0.44	0.08	0.28	0.46	0.14	—	—	—
8105–83.3.42	2.8	1.1	0.56	0.58	0.08	0.24	0.46	0.20	0.10	—	—
6606–93.27	2.9	1.2	0.65	0.74	0.09	0.22	0.60	0.20	0.10	—	—
8105–83.3.42	3.0	1.1	0.62	0.58	0.14	0.20	0.50	0.22	0.11	—	—
8105–83.3.42	3.1	1.1	0.64	0.64	0.16	0.20	0.56	0.30	—	—	—
6606–93.27	3.2	1.2	0.74	0.70	0.16	0.32	0.60	0.30	0.14	—	—
6509–120.40	3.4	1.4	0.45	0.48	0.11	0.26	0.45	—	—	—	—
6110–127.34	3.5	1.2	0.71	0.62	0.11	0.29	0.54	0.30	—	—	—
8105–83.3.42 .	3.6	1.2	0.72	0.66	0.12	0.26	0.60	—	—	—	—
SCBSIII 303	3.8	1.4	0.78	0.64	0.11	0.30	0.60	0.40	0.18	—	—
5710–123.37	4.1	1.8	1.0	0.80	0.22	0.34	0.79	0.60	0.22	—	—
SCBSIII 303	4.2	1.7	0.88	0.80	0.12	0.36	0.70	0.40	—	—	—
8105–103.3.29	4.3	1.8	1.0	0.80	0.22	0.42	0.78	0.46	0.18	—	—
5607–97.40	4.4	1.6	1.1	0.82	0.18	0.40	0.76	0.32	—	—	—
5708–127.34	4.5	1.8	0.86	0.84	0.23	0.33	0.80	0.44	0.16	—	—
8108–106.7.31	4.7	1.8	1.3	0.94	0.28	0.50	1.0	—	0.24	—	—
6310–87.32.5	4.8	2.0	1.2	0.96	0.24	0.42	0.84	0.60	0.22	—	—
6507–93.26	4.9	1.9	1.1	0.92	0.21	0.41	0.88	0.80	—	—	—
7805–90.28	5.8	2.0	1.4	1.1	0.32	0.52	1.0	0.60	0.36	—	—
5910–127.34	6.0	2.3	1.5	1.3	0.40	0.54	1.2	0.60	0.36	—	—
8107–83.3.42	6.1	2.3	1.5	1.2	0.36	0.56	1.3	0.60	0.34	3.2	—
8105–103.3.29	6.2	2.3	1.6	1.2	0.24	0.60	1.2	0.60	0.42	3.2	1.8
7805–90.28	6.3	2.4	1.5	1.2	0.36	0.60	1.2	0.64	0.36	3.3	—
8105–103.3.29	6.4	2.5	1.7	1.1	0.42	0.56	1.1	0.80	0.36	3.4	—
7805–90.28	6.5	2.3	1.6	1.2	0.32	0.60	1.2	0.88	0.40	3.3	1.5
8107–93.3.50	6.6	2.6	1.4	1.4	0.34	0.66	1.4	1.0	0.50	4.0	2.1
8107–93.3.50	6.7	2.7	1.8	1.5	0.46	0.72	1.5	0.80	0.30	3.7	2.1
7805–90.28	6.8	2.5	1.8	1.3	0.34	0.62	1.3	0.60	0.32	3.8	2.0
7805–90.28	7.0	2.8	1.9	1.4	0.40	0.68	1.4	0.82	0.40	4.0	2.0
7805–90.28	7.1	2.8	2.0	1.4	0.42	0.68	1.4	0.76	0.56	3.9	2.0
8105–103.3.29	8.2	3.6	2.4	1.7	0.48	0.88	1.8	1.1	0.42	3.8	2.7
8107–80.51	8.4	3.8	2.4	1.7	0.40	0.84	1.7	0.92	0.54	4.8	2.5
8105–86.7.35	8.6	3.7	2.5	1.8	0.60	0.88	1.9	1.2	0.56	4.0	2.8
8105–86.7.45	8.6	4.0	2.8	2.1	0.60	0.88	2.2	1.2	0.70	3.8	2.9
8105–86.7.33	10.7	5.5	3.1	2.2	0.64	1.1	2.5	—	0.68	3.9	3.4
7803–90.60	11.9	5.7	3.3	2.0	0.74	1.2	2.5	1.8	0.68	3.8	3.8
8108–96.7.35	14.8	8.1	4.9	3.8	1.0	1.6	3.8	2.6	0.80	5.7	5.2
8107–93.3.55	15.8	8.5	5.0	3.4	1.2	1.5	3.8	3.2	0.92	5.2	5.2
8107–93.3.55	16.5	8.3	5.2	3.7	1.2	1.6	4.1	2.8	1.0	6.0	6.0
8107–80.55	17.3	9.2	5.5	3.7	1.3	1.8	4.2	3.3	1.2	5.8	5.7
8108–103.3.30	18.4	10.3	5.8	4.5	1.5	1.8	5.0	3.4	1.2	6.8	6.7
8102–120.30	19.5	10.8	5.8	4.6	1.4	1.8	5.1	4.8	1.2	6.9	6.4
6612–123.36	23.2	12.0	6.9	5.8	1.8	2.2	6.7	5.0	1.6	8.2	7.7

TABLE 2.—Average body proportions (% ± standard deviation) for larvae of

Species/stage	Snout-anus length / Body length	Head length / Body length	Head depth / Body length	Snout length / Body length	Eye diameter / Body length
Girella nigricans					
Preflexion	38.2 ± 2.92	21.5 ± 3.07	19.3 ± 2.49	4.1 ± 1.06	8.7 ± 1.58
Flexion	38.9 ± 2.91	25.8 ± 2.15	19.8 ± 1.35	5.6 ± 0.82	9.6 ± 0.60
Postflexion	49.6 ± 4.15	30.7 ± 2.05	21.8 ± 2.88	6.8 ± 0.57	10.1 ± 0.42
Juvenile	54.1 ± 1.99	30.7 ± 1.13	23.6 ± 1.57	7.7 ± 0.43	9.7 ± 0.51
Medialuna californiensis					
Preflexion	39.6 ± 2.49	21.2 ± 3.23	19.1 ± 2.09	4.1 ± 1.23	8.4 ± 0.64
Flexion	44.3 ± 4.31	27.2 ± 3.88	21.8 ± 2.21	6.3 ± 0.86	10.7 ± 1.15
Postflexion	50.6 ± 4.13	30.5 ± 3.29	23.3 ± 1.46	6.0 ± 0.75	10.8 ± 0.33
Juvenile	56.5 ± 2.29	33.4 ± 1.75	27.2 ± 2.05	6.7 ± 0.92	10.6 ± 0.70
Hermosilla azurea					
Preflexion	51.0 ± 3.23	28.4 ± 3.10	23.5 ± 3.31	6.1 ± 1.66	11.0 ± 0.47
Flexion	54.2 ± 3.06	31.9 ± 3.90	24.0 ± 3.42	7.9 ± 1.46	11.6 ± 1.06
Postflexion	57.3 ± 1.03	31.7 ± 2.25	25.8 ± 1.72	7.5 ± 0.55	12.2 ± 0.75
Juvenile	58.0 ± 1.83	32.8 ± 1.89	25.8 ± 2.06	6.5 ± 0.58	11.2 ± 0.96

Pigmentation

Pigmentation of yolk sac and early preflexion larvae was described by Orton (1953) from specimens cultured in the laboratory. Newly hatched larvae have a few melanophores on the hindgut and in a short midventral row at the base of the tail. At about midway through yolk absorption, small melanophores appear on the ventral surface of the yolk sac (Fig. 2A); the row above the hindgut becomes heavier, extending forward to about the midpoint of the yolk sac; and the midventral tail series has increased to 7–11 melanophores, extending posteriad along most of the tail. A series of small melanophores appears on the dorsal midline along the posterior half of the tail, and several small melanophores are present above and below the tip of the notochord. Near the end of yolk absorption the eyes become pigmented; the dorsal gut pigment becomes heavier and extends over the entire gut; and the ventral tail melanophores enlarge, partly by aggregation, as do the melanophores on the dorsal margin of the tail.

In early preflexion larvae the ventral midline series of 5–8 large melanophores is continuous with the dorsal gut melanophores. A space separates the ventral tail series from one or more smaller melanophores near the tip of the notochord. The dorsal midline series consists of ca. 1–4 large melanophores posteriorly on the tail, with one to several small melanophores near the tip of the notochord. A large melanophore develops above the midbrain and one forms on the

nape. Internal pigment develops below each otic capsule, appearing as a continuation of the dorsal gut pigment. The series of small ventral gut melanophores coalesces into 3 pigment loci, each usually containing a single melanophore: 1) an embedded melanophore anterior to the liver, 2) a surface midventral spot just posterior to the liver, 3) a surface midventral spot just anterior to the hindgut (Fig. 1C).

During preflexion the dorsal gut pigment expands to the lateral surface of the gut. The dorsal midline series increases anteriorly beginning in early preflexion, and soon extends from the head nearly to the tip of the tail. The smaller melanophores near the tip of the tail disappear or are reduced to one. Dorsal melanophores number 11–15. The smaller ventral spots at the notochord tip disappear, except for one, which persists in the finfold about halfway between the end of the ventral pigment series and the tip of the tail.

During late preflexion and flexion stages, pigment increases on the midbrain and appears on both the forebrain and hindbrain. Paired melanophores develop on the roof of the mouth below the nasal capsules and olfactory lobes, and one or more form at the tip of the lower jaw. As the pigment associated with the otic capsule increases, an embedded stripe passing through the eye region is formed (Fig. 2E). One or two surface melanophores appear posterior to the eye in the opercular region. Melanophores appear on the tip of the lower jaw, at the angle of the jaw, and later along the rami of the jaw. A large

Girella nigricans, Medialuna californiensis, and *Hermosilla azurea.*

Species/stage	Body depth / Body length	Pectoral fin length / Body length	Pectoral fin base depth / Body length	Predorsal length / Body length	Prepelvic length / Body length
Girella nigricans					
Preflexion	17.6 ± 1.98	9.7 ± 3.00	4.3 ± 0.69		
Flexion	19.8 ± 1.58	11.3 ± 1.79	6.0 ± 0.97	54.0 ± 3.69	29.4 ± 2.83
Postflexion	23.8 ± 1.77	16.3 ± 2.42	6.3 ± 0.89	37.7 ± 4.81	33.4 ± 1.68
Juvenile	26.6 ± 1.92	21.0 ± 2.78	6.6 ± 0.34	35.3 ± 1.43	33.8 ± 1.72
Medialuna californiensis					
Preflexion	17.0 ± 2.22	10.2 ± 1.29	4.7 ± 1.44		
Flexion	22.4 ± 2.49	12.2 ± 2.05	6.8 ± 0.83	44.8 ± 6.69	34.5 ± 2.43
Postflexion	24.2 ± 2.23	16.8 ± 3.46	6.6 ± 0.72	42.4 ± 5.80	33.8 ± 2.62
Juvenile	29.3 ± 0.71	22.0 ± 1.53	6.2 ± 0.74	38.1 ± 2.12	38.1 ± 1.13
Hermosilla azurea					
Preflexion	22.5 ± 2.59	12.0 ± 0.82	7.9 ± 1.12		
Flexion	24.5 ± 2.33	12.9 ± 2.23	9.1 ± 0.83	39.4 ± 1.99	36.6 ± 0.40
Postflexion	25.8 ± 1.17	16.4 ± 4.16	7.8 ± 0.98	40.3 ± 2.42	39.3 ± 2.42
Juvenile	31.2 ± 1.50	25.0 ± 2.45	7.2 ± 0.50	40.2 ± 1.26	38.5 ± 1.91

TABLE 3.—Meristics of cleared and stained specimens of *Girella nigricans.* Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Length (mm)	Principal caudal fin rays Superior	Principal caudal fin rays Inferior	Procurrent caudal fin rays Superior	Procurrent caudal fin rays Inferior	Branchiostegal rays Left	Branchiostegal rays Right	Pectoral fin rays Left	Pectoral fin rays Right	Dorsal fin rays	Anal fin rays	Pelvic fin rays Left	Pelvic fin rays Right	Vertebrae
5.8	3	3	—	—	3	3	—	—	—	—	—	—	—
6.0	6	6	—	—	4	4	—	—	—	—	—	—	—
6.5	8	7	—	—	5	5	—	—	—	—	—	—	—
6.7	8	7	—	—	5	5	—	—	—	—	—	—	22
7.0	9	8	—	—	5	5	—	—	—	—	—	—	24
7.2	9	8	—	—	6	6	6	6	5	—	—	—	26
7.9	9	8	1	1	6	6	10	10	13	10	—	—	27
8.2	9	8	1	1	6	6	9	10	12	10	1	1	27
9.1	9	8	1	1	6	6	14	14	—	—	I,4	I,4	27
10.7	9	8	5	5	6	6	17	17	XIII,14	III,12	I,5	I,5	27
11.7	9	8	6	5	7	7	17	17	XIII,15	III,11	I,5	I,5	27
12.0	9	8	5	5	6	6	18	18	XIII,13	III,11	I,5	I,5	27
15.7	9	8	10	9	6	6	20	20	XIII,12	III,11	I,5	I,5	27
21.8	9	8	12	9	6	6	19	19	XIV,13	III,11	I,5	I,5	27
22.0	9	8	10	10	6	6	18	19	XV,13	III,11	I,5	I,5	27
37.0	9	8	11	10	6	6	19	19	XIV,13	III,10	I,5	I,5	27

melanophore appears on the isthmus just anterior to the gut, often preceded by a series of several smaller spots. The pigment on the ventral surface of the gut may also increase to form a series of pigment dashes.

At this stage a line of midlateral pigment dashes develops on the tail, posteriorly between the dorsal and ventral midline pigment. The lateral row expands anteriad, reaching the trunk by the end of flexion. Pigment becomes heaviest posteriorly, and when midlateral, midventral, and middorsal melanophores are expanded in this region, an incomplete bar is formed. Concurrent with the development of the lateral midline pigment, internal series of melanophores form above and below the vertebral column and expand anteriorly in concert with the external lateral series.
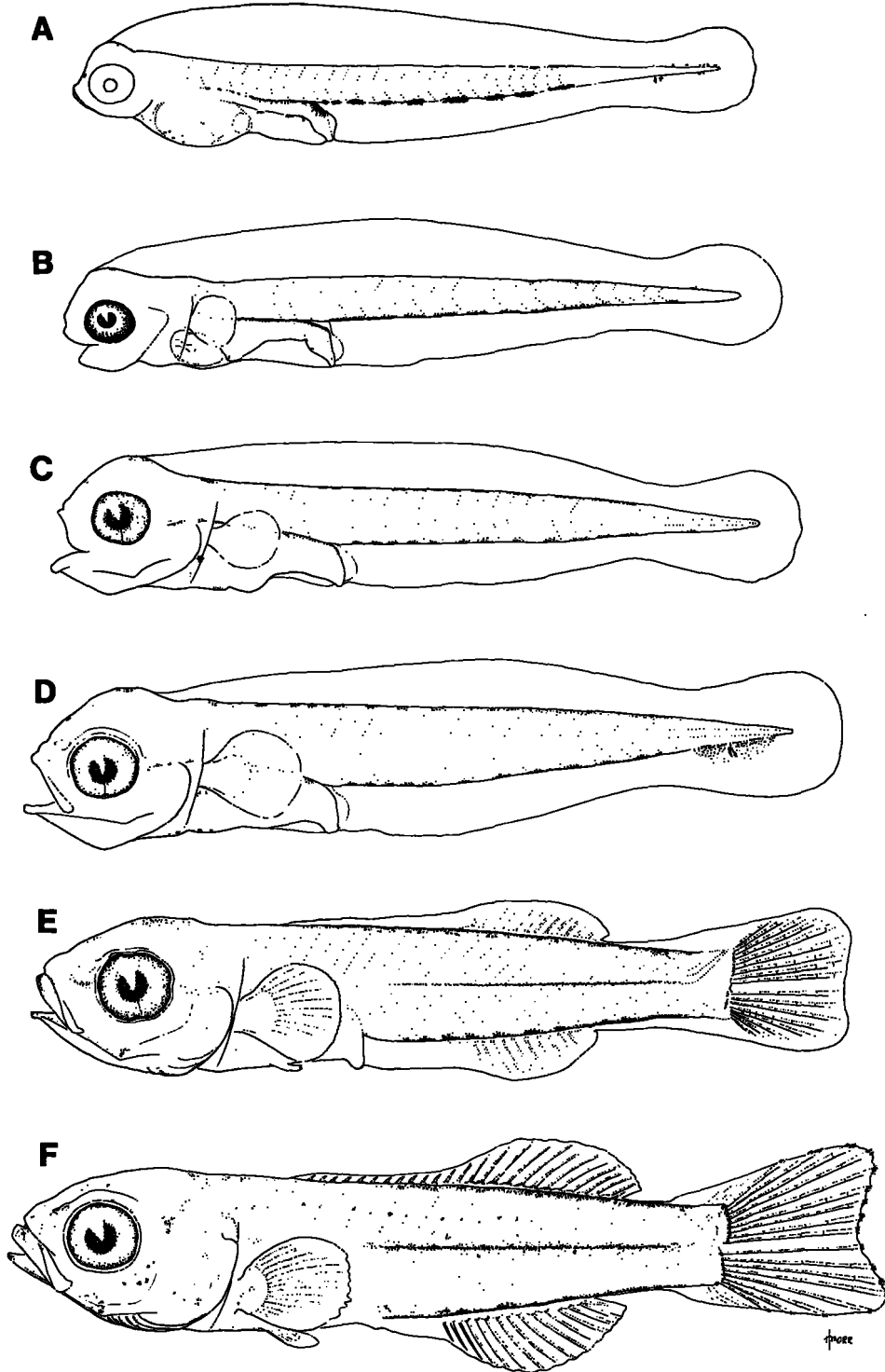
FIGURE 2.—Reared larvae of *Girella nigricans*: (A) 3.8 mm NL, day 1; (B) 3.8 mm NL, day 2; (C) 4.6 mm NL, day 8; (D) 5.3 mm NL, day 10; (E) 7.8 mm SL, day 18; (F) 10.9 mm SL, day 22.
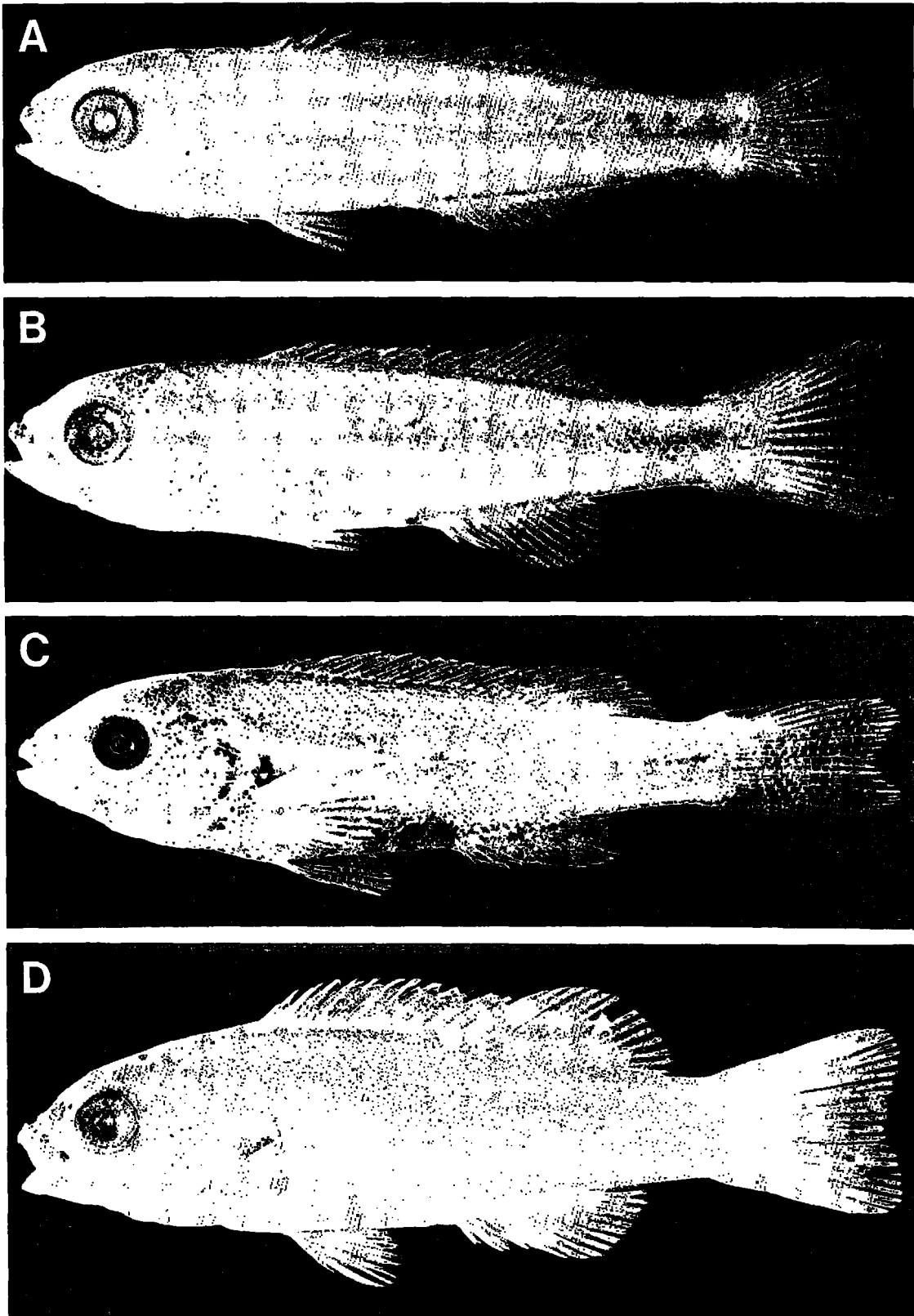
FIGURE 3.—Pelagic juveniles of *Girella nigricans*: (A) 15.8 mm SL, CalCOFI cruise 8197–JD, station 93.3.55, surface tow; (B) 17.3 mm SL, CalCOFI cruise 8107–JD, station 80.55, surface tow; (C) 22.8 mm SL, SIO Marine Vertebrate Collection, Cat. No. 76–295; (D) 29.0 mm SL, MEC SONGS cruise I–28, surface tow.

The caudal melanophore (Fig. 2D) becomes located at the posterior hypural margin between the superior and inferior elements, and remains prominent during flexion. By the end of flexion it is accompanied by 1–5 more melanophores which outline the posterior edge of the hypural plate.

By the end of flexion the sides of the gut are covered with melanophores, the dorsal midline pigment is continuous to the head, and the lateral midline series extends slightly forward of the vent. A line of pigment extends along the isthmus; pigment outlines the jaw on its ventral surface; and pigment increasingly covers the snout, dorsal surface of the head, opercles, pectoral fin bases, and the walls of the gill chambers.

During postflexion and early juvenile stages

the amount of head and body pigment continues to increase. The lateral body stripe enlarges dorsad, ventrad, and anteriad. Small melanophores begin to outline the myosepta, initially in the epaxial zone and later in the hypaxial zone. Eventually the areas between the myosepta fill with melanophores and the entire body and head are covered (Fig. 3D). In addition to the development of melanistic pigment, early juveniles develop a layer of guanine which produces a silvery sheen on the lower half of the body. This silvery condition is retained throughout the pelagic phase and is lost abruptly when the pelagic young enter the tidepools at 25 mm length (Feder et al. 1974).

Fin pigment appears in early juveniles when the dorsal spines become outlined with mela-

TABLE 4.—Measurements (mm) of larvae and pelagic juveniles of *Medialuna californiensis*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Station	Body length	Snout-anus length	Head length	Head depth	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Predorsal length	Prepelvic length
5407–97.30	2.6	0.90	0.39	0.48	0.08	0.20	0.38	—	—	—	—
6607–87.55	2.8	1.2	0.60	0.58	0.08	0.22	0.44	0.30	0.14	—	—
7805–70.90	3.1	1.2	0.66	0.56	0.10	0.26	0.54	0.28	0.10	—	—
6606–90.60	3.3	1.2	0.50	0.50	0.08	0.23	0.44	0.24	0.10	—	—
6606–87.33	3.5	1.4	0.68	0.54	0.10	0.28	0.48	0.38	0.14	—	—
6907–93.30	3.8	1.6	0.84	0.74	0.22	0.32	0.68	0.44	0.18	—	—
6907–93.30	4.0	1.7	1.0	0.76	0.22	0.34	0.72	0.40	0.18	—	—
5104–107.70	4.3	1.7	0.98	0.90	0.19	0.38	0.80	0.42	0.14	—	—
6107–83.65	4.6	1.9	1.1	0.90	0.18	0.40	0.88	0.45	0.32	—	—
6207–100.45	5.0	1.9	1.2	0.96	0.24	0.44	0.84	0.60	0.20	—	—
6207–100.35	5.2	2.0	1.2	1.1	0.26	0.48	1.0	0.50	0.28	—	—
8105–100.70	5.5	2.2	1.2	1.2	0.32	0.50	1.1	0.60	0.40	—	—
5507–103.70	5.8	2.4	1.4	1.2	0.35	0.66	1.2	0.60	0.40	2.1	—
8105–100.35	6.0	2.4	1.2	1.2	0.32	0.58	1.2	0.60	0.35	—	—
6507–100.40	6.5	2.5	1.8	1.2	0.44	0.60	1.2	0.88	0.40	3.4	—
8105–100.70	6.7	2.9	1.7	1.7	0.40	0.80	1.6	0.76	0.56	3.5	—
8107–86.7.50	7.2	3.4	2.3	1.6	0.44	0.88	1.8	0.88	0.52	3.5	2.6
8108–100.40	7.9	4.0	2.4	1.8	0.64	0.88	2.0	1.3	0.48	2.9	2.8
7808–67.65	8.1	3.6	2.3	1.7	0.54	0.76	1.8	1.0	0.52	3.6	2.5
5907–103.50	8.4	4.1	2.5	2.0	0.48	0.88	2.0	1.0	0.60	3.6	3.0
7808–67.65	9.0	4.2	2.6	2.0	0.56	0.96	2.0	1.2	0.64	4.7	3.0
7808–67.65	9.2	4.1	2.4	2.0	0.42	0.96	2.0	1.3	0.64	4.1	2.9
7808–67.65	9.5	4.9	3.3	2.3	0.60	1.0	2.3	1.4	0.72	4.0	3.1
7808–93.45	9.8	5.2	3.2	2.4	0.64	1.1	2.5	1.9	0.64	4.1	3.1
5208–90.45	10.0	5.2	2.8	2.2	0.60	1.1	2.4	1.7	0.60	3.5	3.6
7808–93.45	10.8	6.0	3.5	2.7	0.72	1.2	3.0	2.4	0.62	4.2	4.1
5208–110.60	11.8	6.8	3.8	3.2	0.72	1.3	3.5	2.4	0.76	4.6	4.3
5208–110.60	12.9	7.3	4.2	3.1	0.72	1.3	3.6	2.8	0.84	5.0	5.1
7808–100.45	13.2	7.8	4.6	3.8	1.0	1.4	4.0	2.9	0.88	5.2	5.3
5208–90.45	13.5	7.8	4.7	3.8	0.96	1.5	4.0	3.3	0.96	5.3	5.2
7210–90.70	13.7	7.8	4.9	4.0	1.1	1.6	4.1	3.0	0.84	5.4	5.2
5208–90.45	17.9	9.7	5.6	4.8	1.1	1.9	5.3	4.3	0.96	6.5	6.7
7210–90.70	21.5	11.3	7.1	5.5	1.3	2.0	6.2	4.5	1.1	7.3	8.1

nophores. Gradually the fin membrane becomes covered with melanophores as does the basal half of the soft dorsal fin. Anal fin pigment is limited to a few anterior melanophores, and the caudal and the paired fins remain unpigmented.

Medialuna californiensis
Figures 1, 4, 5
General Morphology

The smallest yolk-sac larva in our collection is 2.6 mm long; it has a large oval yolk sac, a single posteriorly located oil globule (0.20 mm diameter), unpigmented eyes, and lacks a mouth (Fig. 4A). Larvae are ca. 3.0 mm long at the completion of yolk absorption; development is gradual with no abrupt changes in body form (Tables 2, 4).

The first head spines appear during flexion on the posterior preopercular margin near the angle. A 6.1 mm larva has 2 spines. The number of spines increases up to 6 in preflexion larvae and to 10–13 spines in juveniles up to 21.5 mm. In larger juveniles the spines are blunt and the posterior preopercular margin is smooth in a 33.7 mm juvenile. A single spine is present on the anterior preopercular ridge in a 6.5 mm larva. This spine is variously present or absent in flexion and postflexion larvae, and is absent in juveniles larger than 13.8 mm in our collections.

A single spine is present at the edge of the subopercle in larvae as small as 7.1 mm and is found on all postflexion larvae and juveniles up to a length of 21.5 mm. An interopercular spine is present in all postflexion larvae and in juveniles up to 18.2 mm. A supracleithral spine appears late in the postflexion stage (at 10.1 mm) and a posttemporal spine appears at 12.8 mm. Both spines are present in juveniles up to 21.5 mm but are absent in larger specimens. An opercular spine is present in juveniles between 12.8 and 21.5 mm. A cleithral spine is present on a single 18.2 mm juvenile.

Notochord flexion begins at ca. 5.8 mm and is completed at ca. 8.6 mm (Table 5). Transformation into the pelagic juvenile occurs at ca. 12 mm (Fig. 5).

Fin Formation and Meristics

The first rays to form are the principal caudal rays early in flexion (Table 5). The full complement of 9+8 rays is present at midflexion, when the procurrent rays begin to develop. The full complement of 11–13 + 10–11 procurrent rays is present in early juveniles.

Dorsal, anal, and pectoral rays begin to calcify during midflexion in the manner described for *G. nigricans*. Full complements of dorsal (IX–X, 22–27) and anal (III, 17–21) rays form in early postflexion larvae (Table 5). The full complement

TABLE 5.—Meristics of cleared and stained specimens of *Medialuna californiensis*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

| Length (mm)	Principal caudal fin rays Superior	Principal caudal fin rays Inferior	Procurrent caudal fin rays Superior	Procurrent caudal fin rays Inferior	Branchiostegal rays Left	Branchiostegal rays Right	Pectoral fin rays Left	Pectoral fin rays Right	Dorsal fin rays	Anal fin rays	Pelvic fin rays Left	Pelvic fin rays Right	Vertebrae
6.1	6	5	—	—	4	4	—	—	—	—	—	—	12
6.5	9	8	—	—	6	6	—	—	—	—	—	—	21
7.1	9	8	1	1	7	7	10	10	20	II,16	—	—	24
7.4	9	8	1	1	7	6	8	8	19	14	—	—	24
8.1	9	8	—	1	6	6	6	6	9	9	—	—	24
8.6	9	8	2	2	7	7	10	10	VI,22	II,18	—	—	25
9.1	9	8	3	3	7	7	14	14	IX,22	III,18	—	—	25
9.5	9	8	4	4	7	7	14	14	VIII,22	III,17	I,2	I,2	25
10.1	9	8	5	5	7	7	14	14	X,24	III,19	I,4	I,4	25
11.0	9	8	6	6	7	7	17	17	X,23	III,18	I,5	I,5	25
12.8	9	8	9	8	7	7	18	18	X,24	III,19	I,5	I,5	25
13.8	9	8	11	10	7	7	17	17	X,25	III,19	I,5	I,5	25
18.2	9	8	13	11	7	7	18	18	X,25	III,19	I,5	I,5	25
21.5	9	8	12	11	7	7	18	18	X,25	III,19	I,5	I,5	25
27.6	9	8	12	11	7	7	18	17	X,23	III,18	I,5	I,5	25
33.7	9	8	12	11	7	7	19	20	X,23	III,18	I,5	I,5	25
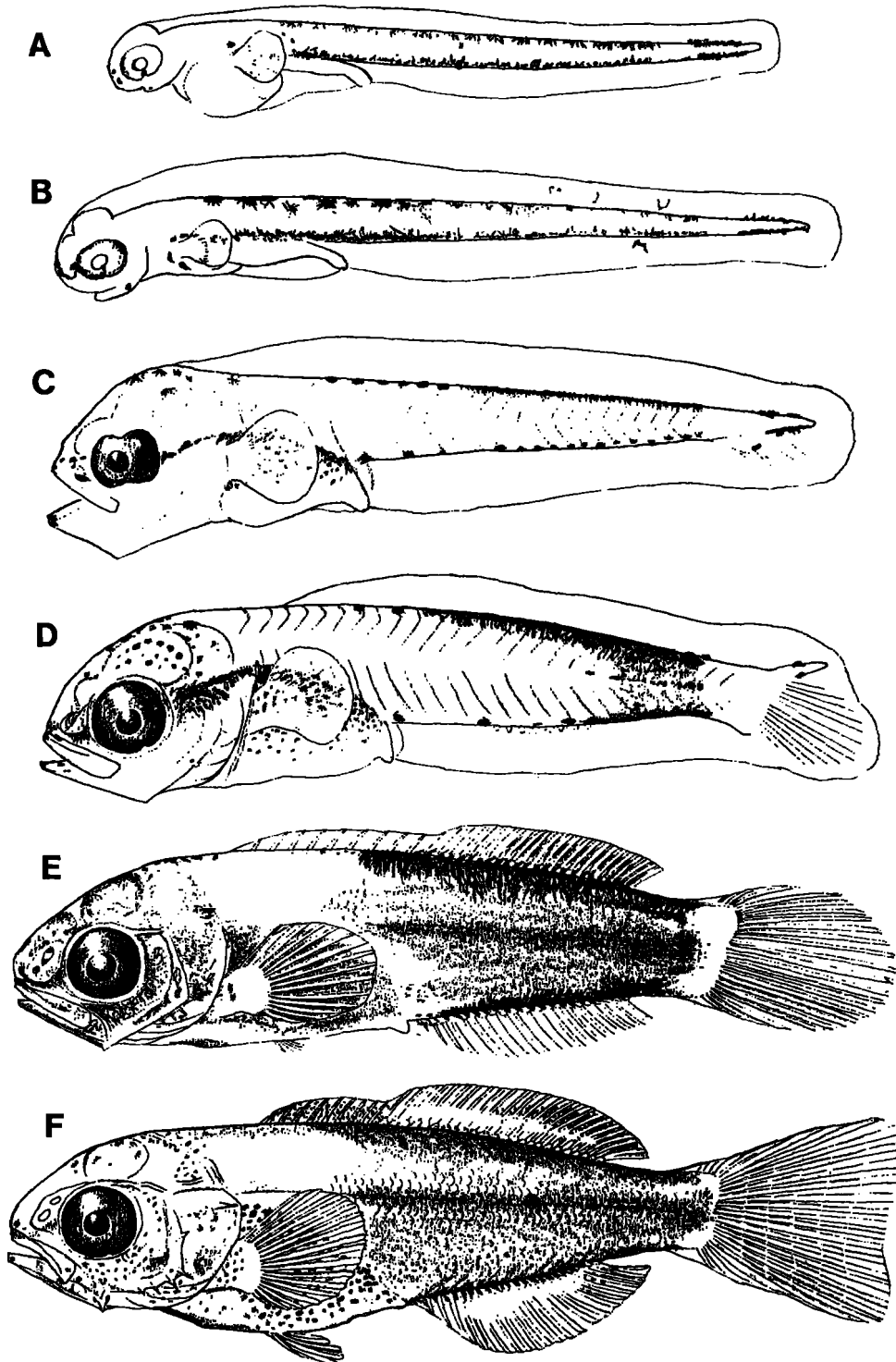
FIGURE 4.—Larvae of *Medialuna californiensis* from CalCOFI oblique plankton tows: (A) 3.0 mm NL, cruise 5004, station 120.90; (B) 3.5 mm NL, same station as above; (C) 4.7 mm NL, cruise 4906, station 102.75; (D) 6.8 mm NL, cruise 4907, station 92.68; (E) 10.1 mm SL, cruise 5007, station 100.70; (F) 11.8 mm SL, cruise 4910, station 82.77.
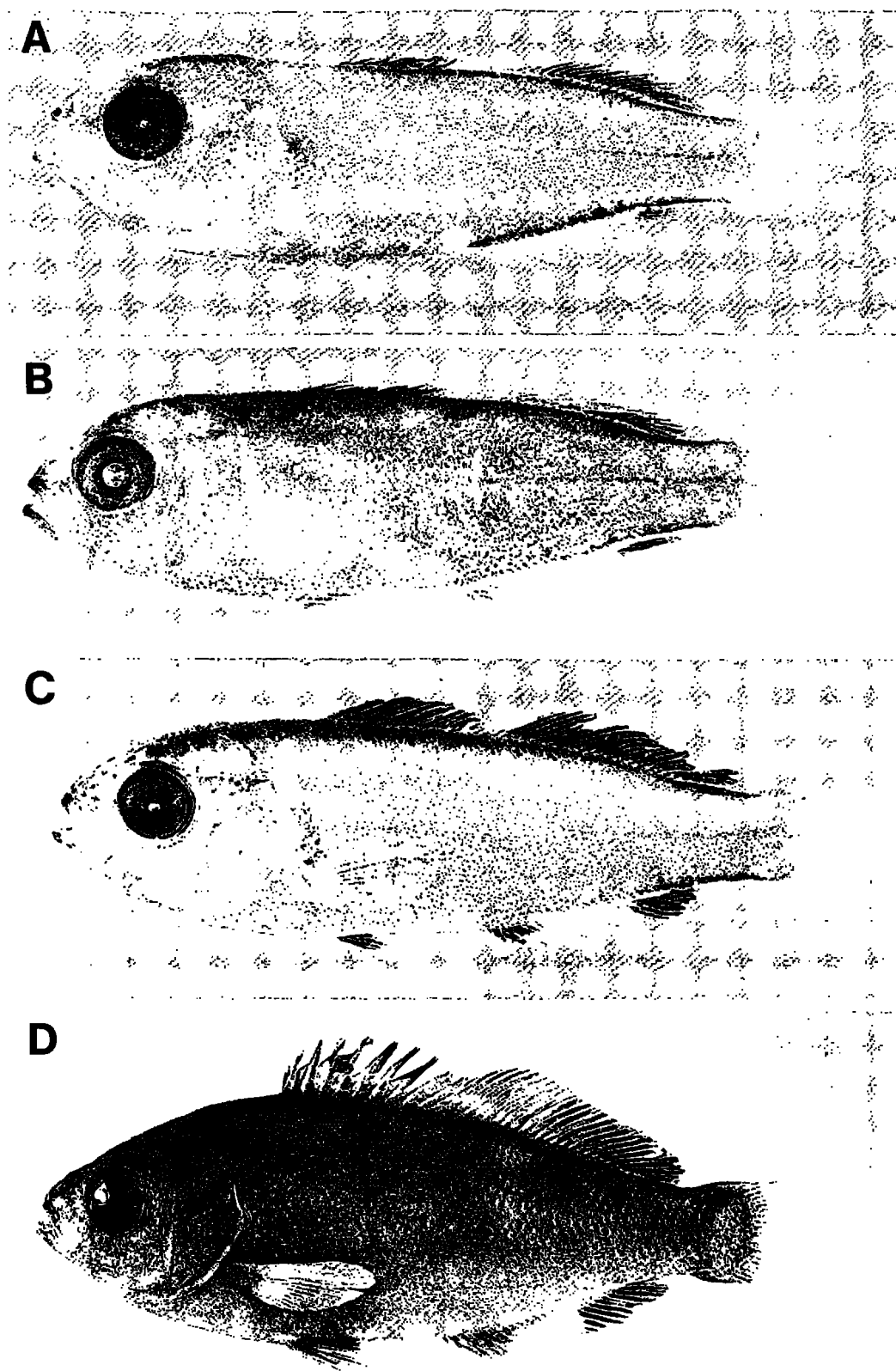
FIGURE 5.—Pelagic juveniles of *Medialuna californiensis*: (A) 13.2 mm SL, CalCOFI cruise 7808, station 100.45, surface tow; (B) 17.9 mm SL, CalCOFI cruise 5208, station 90.45, surface dipnet; (C) 20.5 mm SL, CalCOFI cruise 5407-H, station 130.60, surface dipnet; (D) 46.0 mm SL, SWFC DSJ midwater trawl, off Catalina Island, 31 October 1968.

of 17–20 pectoral rays appears at transformation. Pelvic rays begin to calcify late in postflexion and all are calcifying at transformation. Initial vertebral ossification occurs early in the flexion stage and the full complement of 25 vertebrae is present at the end of flexion. Calcification of branchiostegal rays begins late in preflexion and the full complement of 7 pairs is present in some midflexion specimens.

Pigmentation

The earliest yolk-sac larvae in our collections have extensive dorsal and ventral midline pigment. The dorsal midline has an irregular row of 30–40 melanophores between the notochord tip and the midgut region. More than 40 melanophores form an irregular series along the entire ventral margin of the tail, extending some distance forward above the gut. Melanophores in these rows coalesce to ca. 30 in each, before the eyes become pigmented. At initial eye pigmentation there are ca. 20 larger, regularly arranged melanophores in each row with a gap separating a line of 5–7 smaller melanophores that outline the dorsal and ventral margins of the notochord tip. Melanophores also appear at the dorsal surface of the gut, at the gular region, and on the snout.

At the end of the yolk-sac stage the melanophores in the dorsal and ventral rows coalesce to as few as 18 in the dorsal row and to 16 in the ventral row. A melanophore forms at the nape and, in some specimens, is continuous with the dorsal midline series. The zone of melanophores covering the dorsal surface of the gut extends forward into the head below the otic region. Embedded melanophores form in the snout region below the forebrain and some appear above the midbrain. The ventral gut melanophores move internally anterior to the gut mass. A melanophore is present at the tip of the lower jaw.

The midline melanophores coalesce further during early preflexion (15–18 dorsally and 12–15 ventrally). The short rows at the notochord tip are also reduced (2–3 dorsally and 1–3 ventrally). Melanophores are added above the brain and cover the optic lobes. Snout and otic pigment increase to give the appearance of a band through the eye, similar to that formed in *G. nigricans* and *H. azurea* (Fig. 1D, 4C). The dorsal gut melanophores increase to form a shield which extends laterally over the gut; the ventral surface of the gut remains unpigmented.

Midlateral melanophores begin to form posteriorly on the tail in preflexion larvae as small as 3.8 mm. The series consists of 1–2 (up to 4) melanophores during most of the preflexion period. During this period the dorsal midline series recedes posteriad to above the hindgut and a gap develops in the ventral series posterior to the large melanophore embedded above the anus. In late preflexion and flexion larvae the ventral series is restricted to the posterior half of the tail and contains 6–10 melanophores. Melanophores are added to the lateral series during flexion and a short bar is formed when these, together with the midline melanophores above and below, are expanded. By the end of flexion it is difficult to distinguish individual melanophores in any of the midline series. The melanistic shield on the gut covers all but the ventral midline. The dorsal surface of the head is fully pigmented and a patch of melanophores forms on the opercle. The notochord tip usually has 1–2 small melanophores dorsally and ventrally in flexion larvae, 0–2 in postflexion specimens, and 0–2 in some pelagic juveniles up to 14.5 mm in length.

The dorsal and ventral midline pigment series extend forward in postflexion larvae, the ventral series reaching the anus at ca. 9.5 mm and the dorsal series reaching the head at ca. 10.5 mm. The lateral midline series reaches the anal fin origin at ca. 9.0 mm and extends to above the midgut in transforming larvae. A covering of superficial melanophores develops on the tail and advances anteriad with the midline series. The entire body, except for the anterior trunk region, is pigmented by the end of postflexion and only a small portion of the upper trunk lacks melanophores in transforming specimens. Melanophores are added to the opercular and preopercular regions, the lower jaw, gular region, and isthmus. The entire head and gut are pigmented by the beginning of transformation.

The distinctive fin pigmentation of pelagic juveniles begins to form in late postflexion larvae when the membrane between the posterior dorsal soft rays becomes pigmented (Fig. 4E, 4F). By the end of transformation the membrane between the dorsal spines also becomes pigmented, leaving an unpigmented zone in the middle of the fin. Also, at this stage a melanistic zone develops posteriorly on the anal fin (Fig. 5A). A patch develops over the anal spines and basally on each pelvic fin in 14.0 mm pelagic juveniles; juveniles up to about 40 mm are characterized by this interrupted pattern on the median fins (Fig. 5C). In 40–50 mm juveniles the

entire dorsal fin is pigmented except for an area on the anterior half of the soft dorsal. The pelvic fins are completely pigmented at 50 mm. The pectoral and caudal fins are unpigmented in larvae and pelagic juveniles.

Hermosilla azurea
Figures 1, 6, 7

General Morphology

The size and state of development at hatching are unknown. The smallest larva examined, 2.5 mm, had pigmented eyes, a functional mouth, and no remnants of yolk or oil droplets. Preflexion larvae are moderately robust, with a coiled gut extending slightly beyond midbody (Tables 2, 6) and with a small swimbladder over the anterior gut. The head is moderately large, with a blunt snout, and with round to slightly elongate (horizontally) eyes. Development is

gradual with no abrupt changes in body form or proportions. Most body parts showed small increases in size relative to the standard length (Table 2). Among the largest proportional changes are the increases in snout-anus length and in body depth (Fig. 6).

Larvae acquire only a few small head spines. The first spine may develop at the angle of the posterior preopercular margin as early as late preflexion (3.7 mm), or may be delayed until early flexion (always present by 4.7 mm); 19% of preflexion larvae had this spine. During flexion 1–3 additional small spines develop along the posterior preopercular margin and up to 3 (usually 0 or 1) small spines are acquired along the anterior preopercular ridge. Postflexion larvae may develop up to 4 very small spines along the posterior margin of the subopercular, and usually lose the anterior preopercular spines. Juveniles lack both the preopercular and the subopercular spines.

TABLE 6.—Measurements (mm) of larvae and pelagic juveniles of *Hermosilla azurea*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Station	Body length	Snout-anus length	Head length	Head depth	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Predorsal length	Prepelvic length
SONGS	2.5	1.2	0.56	0.64	0.08	0.28	0.44	0.28	0.16	—	—
	2.8	1.4	0.76	0.72	0.20	0.32	0.60	—	0.24	—	—
	3.0	1.6	0.84	0.72	0.16	0.36	0.64	0.32	0.28	—	—
	3.2	1.8	1.0	0.88	0.24	0.36	0.80	—	0.24	—	—
	3.4	1.7	0.92	0.56	0.16	0.36	0.72	0.40	0.28	—	—
	3.6	1.8	1.1	0.72	0.28	0.40	0.88	0.44	0.24	—	—
	3.8	2.1	1.2	0.96	0.32	0.44	1.0	—	0.24	—	—
	4.0	1.8	1.1	0.92	0.24	0.44	0.88	0.56	0.36	—	—
	4.4	2.1	1.1	0.92	0.28	0.44	0.92	0.52	0.36	—	—
	4.6	2.4	1.4	1.2	0.24	0.52	1.2	0.60	0.40	—	—
SONGS	4.1	2.2	1.4	1.0	0.36	0.48	1.0	0.42	0.40	—	—
	4.3	2.4	1.4	0.88	0.36	0.52	1.0	0.64	0.44	1.7	—
	4.5	2.4	1.3	1.1	0.28	0.52	1.1	0.48	0.40	1.6	—
	4.7	2.3	1.2	1.0	0.28	0.48	1.0	0.60	0.40	1.8	—
	5.0	2.6	1.6	1.2	0.40	0.60	1.3	0.48	0.48	2.0	—
	5.2	3.0	1.9	1.6	0.52	0.68	1.4	0.80	0.44	2.1	1.9
	5.4	3.2	2.0	1.4	0.48	0.68	1.5	0.80	0.48	2.3	2.0
	5.8	3.1	1.6	1.3	0.40	0.60	1.4	0.80	0.52	2.4	2.1
SONGS	6.4	3.6	1.9	1.6	0.52	0.76	1.6	1.0	0.60	2.6	2.4
SONGS	6.5	3.7	2.2	1.7	0.52	0.80	1.6	0.88	0.60	2.7	2.4
SONGS	8.6	4.9	2.5	2.2	0.68	1.0	2.2	1.7	0.68	3.3	3.4
8108–106.7.35	9.2	5.3	3.0	2.1	0.68	1.2	2.3	—	0.68	3.6	3.4
SONGS	9.6	5.5	2.9	2.6	0.68	1.1	2.5	2.0	0.64	3.7	3.9
8108–106.7.31	10.8	6.4	3.7	3.0	0.80	1.4	3.0	1.2	0.76	4.7	4.6
SONGS	14.3	8.6	4.3	3.7	1.0	1.6	4.2	4.0	0.96	5.8	5.3
SONGS	15.7	9.2	5.4	3.8	1.0	1.9	5.0	4.0	1.2	6.3	5.8
8108–120.25	17.0	9.5	5.8	4.2	1.2	2.0	5.4	4.2	1.2	7.1	6.9
SONGS	21.5	12.2	7.1	5.8	1.2	2.2	6.8	4.7	1.6	8.3	8.3

Developmental milestones occur at a relatively small size in *H. azurea*: notochord flexion begins at ca. 4.1–4.6 mm and is complete at ca. 5.9–6.3 mm; transformation to the juvenile occurs at ca. 10.8–14.3 mm (Fig. 7). Although spinous scales have been reported to occur in larvae of some Kyphosidae (Johnson 1984), juvenile *H. azurea*, as well as *G. nigricans* and *M. californiensis*, lack spines on their scales.
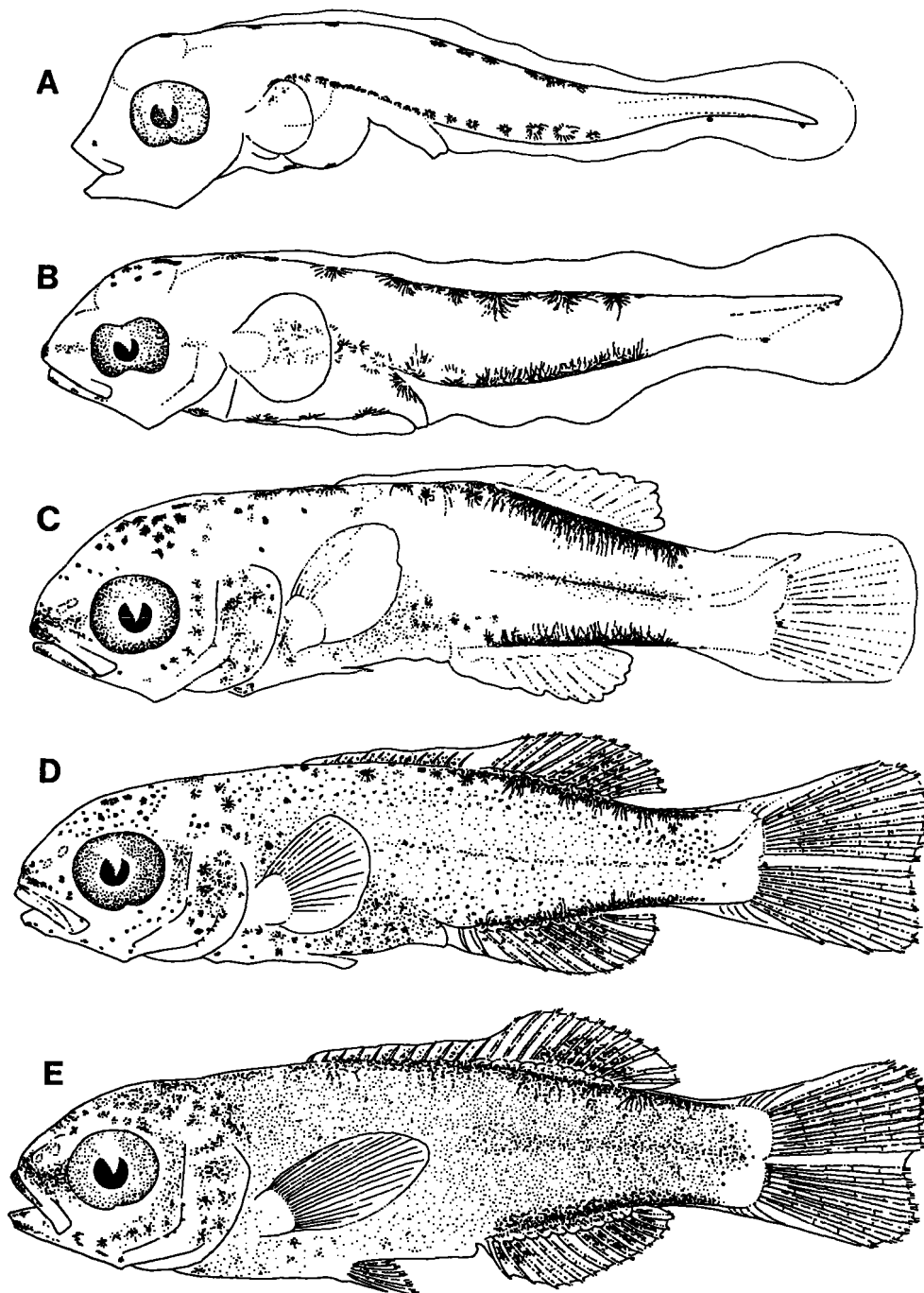

FIGURE 6.—Larvae of *Hermosilla azurea* from MEC SONGS (A–D) and CalCOFI (E) Cruises: (A) 2.6 mm NL, I–74, I-80, D–SONGS, oblique tow, 11 August 1980; (B) 4.3 mm NL, I-80, D–SONGS, surface tow, 22 September 1980; (C) 6.4 mm NL, I–53, E–LS, surface tow, 21 September 1979; (D) 8.7 mm SL, I–90, B–LS, surface tow, 27 August 1982; (E) 9.9 mm SL, 8108–NH, station 106.7.31, surface tow.
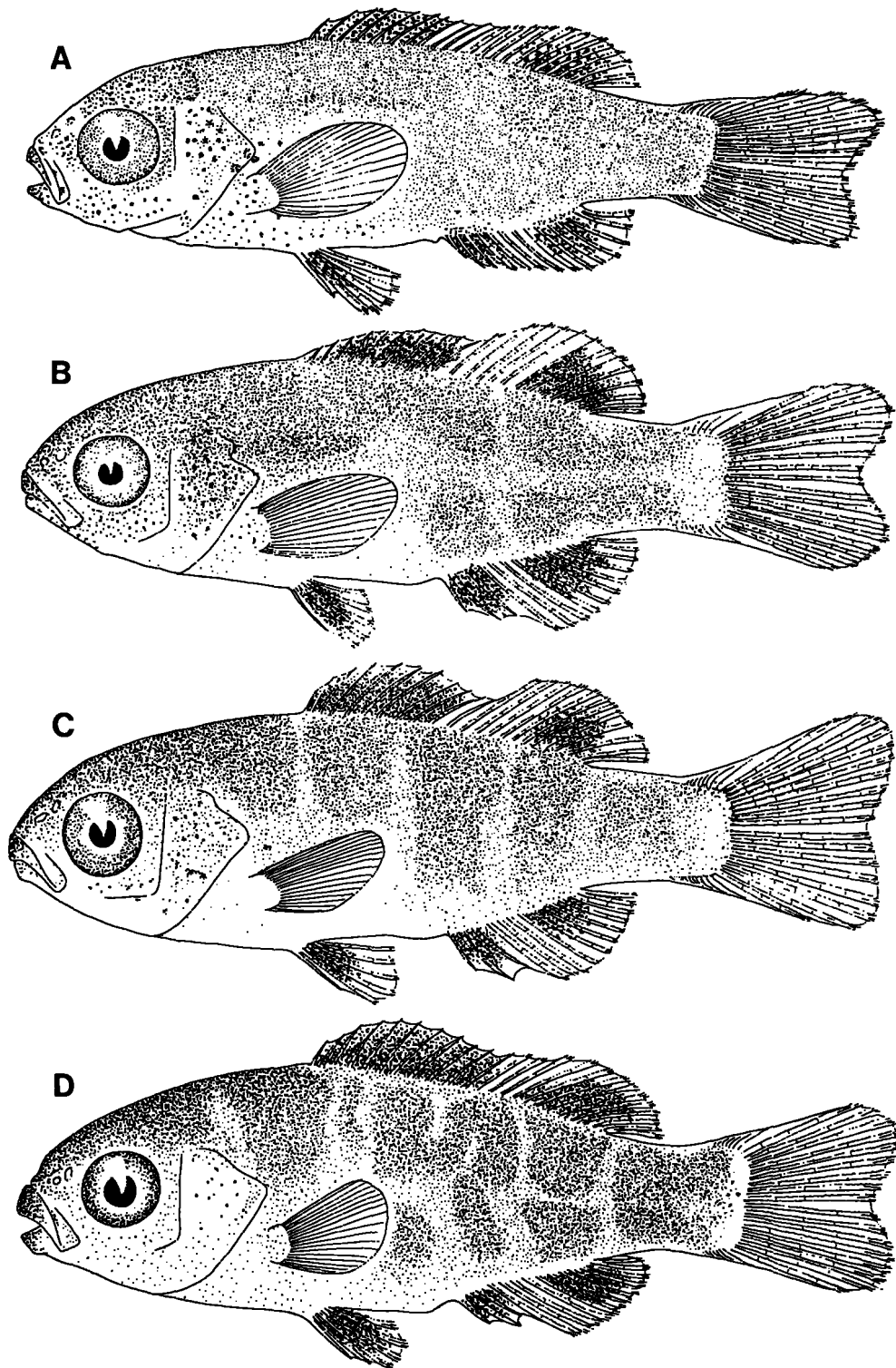
FIGURE 7.—Pelagic juveniles of *Hermosilla azurea* from MEC SONGS (A, B, D) and CalCOFI (C) surface tows: (A) 15.0 mm SL, I–35, C–1–N, 2 October 1978; (B) 16.0 mm SL, I–35, E–1–N, 2 October 1978; (C) 17.7 mm SL, 8108–NH, station 120.25; (D) 21.4 mm SL, I–35, B–1–N, 2 October 1978.

Fin Formation and Meristics

The first rays to calcify are the central principal caudal rays beginning in preflexion at about 4.1 mm (Table 7). The full complement of 9+8 principal rays is acquired during flexion at ca. 5.6 mm. Procurrent rays also may begin to calcify during flexion, as early as 5.6 mm, although more commonly they are not apparent until postflexion at ca. 6.4–6.5 mm. The full complement of 10+10 procurrent rays is completed early in the juvenile stage, by 14.3 mm.

The first dorsal and anal rays form simultaneously, early in flexion, beginning by 5.2–5.3 mm. Dorsal rays are added from anterior to posterior, with the full complement of 11 present by 5.6 mm, before the end of flexion. Dorsal spines calcify from posterior to anterior, beginning in flexion at 5.6 mm, with the full complement of 11 present in postflexion larvae by 9.4 mm. Anal rays are added from anterior to posterior, with the full complement of 10 present in flexion larvae ca. 5.3 mm long. Anal spines are added from posterior to anterior, beginning during flexion at ca. 5.6 mm; the third anal spine calcifies from the first anal ray; all three spines are present early in the juvenile stage, by 14.3 mm.

The pectoral fins initially are rounded with rounded bases, but begin to elongate during flexion when the first upper rays calcify. Addition of pectoral fin rays is from top to bottom of the fin, beginning at ca. 5.2 mm, with the full complement of 15 present by the early juvenile stage. The pelvic fins are the last to begin calcifying in the flexion stage by ca. 6.4 mm. The full complement of I, 5 rays is present by 9.4 mm.

Branchiostegal rays begin to ossify in preflexion larvae at about 4.1 mm; the full complement of 7 rays on each side is ossifying during flexion at ca. 5.2 mm. Vertebral ossification begins by 4.6 mm, just before flexion. Ossification is from anterior to posterior; all 25 centra are ossifying by the end of flexion.

Pigmentation

Preflexion larvae are relatively heavily pigmented, principally over the gut and along the dorsal and ventral midlines. In the smallest specimen examined (2.5 mm), the dorsal midline pigment consisted of a single row of 7 large stellate melanophores irregularly arranged from the midbrain to myomere 20. The number of melanophores in this dorsal row increases, so that by the beginning of flexion the dorsal and upper dorsolateral surfaces of the trunk and tail (except the last 4 or 5 myomeres) are almost completely pigmented. Dorsal and dorsolateral pigmentation on the trunk and tail becomes in-

TABLE 7.—Meristics of cleared and stained specimens of *Hermosilla azurea*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Dorsal fin rays	Anal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right			Left	Right	
2.6	—	—	—	—	—	—	—	—	—	—	—	—	—
4.1	1	1	—	—	—	—	—	—	—	—	—	—	—
4.1	—	—	—	—	2	2	—	—	—	—	—	—	—
4.6	6	5	—	—	4	4	—	—	—	—	—	—	15
4.6	6	6	—	—	5	5	—	—	—	—	—	—	15
4.6	6	5	—	—	4	4	—	—	—	—	—	—	16
4.9	4	5	—	—	4	4	—	—	—	—	—	—	16
5.2	7	7	—	—	6	6	—	—	7	8	—	—	21
5.2	6	6	—	—	5	5	—	—	—	—	—	—	20
5.3	8	8	—	—	6	6	—	—	5	8	—	—	21
5.3	8	8	—	—	6	6	—	—	10	10	—	—	22
5.6	9	8	1	1	6	6	6	6	III,11	I,10	—	—	23
6.0	9	8	—	—	6	6	8	8	V,11	II,10	—	—	25
7.4	9	8	3	3	6	6	13	12	X,11	III,10	3	3	25
9.4	9	8	6	6	7	7	15	15	XI,11	III,10	I,5	I,5	25
22.2	9	8	10	10	7	7	15	15	XI,11	III,10	I,5	I,5	25

creasingly dense and spreads posteriorly; at the end of flexion the last three myomeres are usually unpigmented but acquire pigment by the end of the larval stage.

Midbrain pigment increases in concert with the dorsal trunk and tail pigment, covering the area over the midbrain and spreading anteriorly to the snout and posteriorly over the hindbrain. Thus, by the beginning of flexion, larvae are nearly completely pigmented along the upper surface (Fig. 1H). Snout and nape pigment are usually lighter than the remaining dorsal pigment.

Preflexion larvae have a single melanophore at the roof of the mouth; during flexion more melanophores may be added in this area. A melanophore first appears below the otic capsule in the preflexion stage (by 2.6 mm) and one develops under the anterior midbrain by 3.1 mm. Melanophores proliferate in these areas to give the appearance of a stripe through the head by, or during, flexion.

Pigment first appears on the dorsal surface of the hindbrain by 2.8 mm (one melanophore), and rapidly increases to essentially cover the dorsal surface of the hindbrain by early flexion (ca. 4.8 mm). This pigment subsequently extends posteriorly as a series of melanophores over the vertebral column.

One or two melanophores first appear at the tip(s) of the upper and/or lower jaw(s) between 2.8 and 3.1 mm. Melanophores spread along the upper jaw beginning late in preflexion or early in flexion, and along the lower jaw beginning midway or later through flexion. At ca. 2.8 mm a single melanophore appears on the gular membrane; by the beginning of flexion 3–4 additional melanophores form a longitudinal series evenly spaced along the membrane (Fig. 1G).

A single melanophore appears on the opercle late in preflexion or early in flexion (by 4.4 mm). Melanophores proliferate here to form a large pigment patch midway through flexion, and subsequently extend dorsally, ventrally, and anteriorly to cover the entire opercular area, usually by the end of flexion or early in postflexion.

The smallest specimens examined had a continuous double row of melanophores, which extended over the dorsal surface of the gut and swimbladder, and posteriorly as a single row nearly to the end of the hindgut. These specimens also had 1–6 melanophores evenly spread along the ventral midline of the gut from the anterior midgut to the anterior hindgut. The dorsal gut pigment increases, extending as far as halfway down the front and sides of the gut by the beginning of flexion, and completely covers the sides of the gut by the end of flexion. This pigment continues to spread ventrally, from anterior to posterior, meeting the midline series in postflexion larvae (between 8.6 and 9.6 mm). The series of melanophores along the ventral midline of the gut changes little during larval development. Modal numbers of melanophores in the series were 3–4 (range of 1–6) for preflexion larvae and 4 (range of 2–6) for flexion larvae.

Initially, ventral midline pigment on the tail consists of a single row of 7–10 large melanophores between the first and the 13th postanal myomeres. Usually 2 or 3 (1–4) small melanophores lie under the notochord tip; later these become located along the hypural margin (Fig. 6B, 6C). Occasionally, the first one or two postanal myomeres are unpigmented in preflexion larvae (14% of the preflexion specimens lacked pigment here), but thereafter the first postanal myomeres are always pigmented. The ventral melanophores enlarge and may increase in number during preflexion, so that by ca. 3.5 mm a melanistic band extends along the tail to ca. myomere 20 or 21.

A series of 1–3 small melanophores appears on the lateral midline of the tail at the 14th–20th myomeres late in preflexion or early in flexion (ca. 3.7–4.3 mm). Melanophores proliferate to form a band as do the ones along the dorsal and ventral midlines. Further enlargement of the ventral, lateral, and dorsal bands results in a nearly continuous tail bar during mid to late flexion. Subsequent proliferation of melanophores in this region and over the gut and trunk results in complete body pigmentation, except for the last 3–5 myomeres, by ca. midway through postflexion. Pigmentation is complete by transformation.

The dorsal and ventral midline pigment begins to spread onto the bases of the middle and posterior dorsal and anal soft rays during flexion at ca. 5.4 mm. By late flexion or early postflexion the membranes between dorsal rays 5 or 6 to 10 or 11 and between anal rays 5, 6 or 7 to 9 or 10 are pigmented. During postflexion, the base of the entire dorsal fin becomes heavily pigmented and near the end of the larval stage the membranes between the dorsal spines become pigmented (by ca. 9.6 mm). Pigmentation does not develop on the membranes between dorsal soft rays 1–5 during the larval period, and is very sparse there in juveniles. The base

of the entire anal fin is pigmented by 8.6 mm; the anal spines and membranes are heavily pigmented by 9.6 mm, as are the membranes between anal soft rays 5 to 9 or 10. The membranes between anal soft rays 1–5 are usually unpigmented in larvae, and only sparsely pigmented in juveniles.

Caudal fin pigment is usually restricted to the melanophore(s) at the distal hypural margin during the larval stage. Small melanophores may be acquired along the proximal edges of some of the principal caudal rays in small juveniles.

The first pigment on the paired fins consists of a single melanophore on the lower proximal external surface of the pectoral fin base. This melanophore may appear as early as 4.8 mm, but is not consistently present before ca. 8.6 mm. Pectoral pigment subsequently changes little, except that beginning at ca. 9.6 mm, melanophores appear at the bases of the upper pectoral rays. The pelvic fins are unpigmented in larvae but become heavily pigmented in small juveniles.

Transforming specimens are uniformly pigmented except for the residual melanistic bands at the dorsal and ventral margins and along the lateral midline of the tail. Between 11 and 14 mm, a series of faint bars begins to appear, one anterior to the dorsal fin, one below the spinous dorsal, one below the transition from spinous to soft dorsal, one below the soft dorsal, and one at the caudal peduncle (Fig. 7C). The bars are usually interrupted along the lateral midline and variously developed below the midline, giving a mottled appearance. The mottled appearance is intensified when the bars begin to subdivide and ultimately produce the 12 bars found in late juveniles and adults.

DISTRIBUTION

Girella nigricans

A total of 71 occurrences of *G. nigricans* larvae were recorded from CalCOFI oblique plankton tows during the period 1951–81 (Fig. 8). Larvae were not found on survey cruises during 1951, 1953, 1955, and 1972. Identification of some shorefish species was of variable competency during the early years of CalCOFI and this may explain the apparent absence of *G. nigricans* larvae in 1951, 1953, and 1955. Larvae ranged from San Luis Obispo, CA (cruise 6907, station 77.48) to San Cristobal Bay, Baja California (cruise 5810, station 137.23)—the former

station is the only record north of Pt. Conception, CA. Thirty-eight percent of the total occurrences were between Pt. Conception and the Mexican border and 62% were off Baja California. Larvae ranged seaward to ca. 330 km (cruise 6407, station 93.70); however, 80% of the occurrences were from station 40 shoreward on the CalCOFI survey lines (typically <110 km from the coast). Numbers of larvae sorted from each sample were low, ranging from 1 to 5, with a mean of 1.35 per positive tow. The standardized mean number per positive tow was 4.0 with a range of 0.3–17.5[1]. *Girella nigricans* is a highly seasonal spawner with 80% of the larvae occurring in summer months (June, 27%; July, 45%; August, 8%). Larvae were not taken in January–March.

The importance of the surface layer as a habitat for *G. nigricans* larvae has not been assessed; however, the addition of surface (Manta net) tows on CalCOFI stations during the 1978 and 1981 surveys has provided some information. Larvae occurred in nine surface tows in 1978 and in 11 tows during 1981. These occurrences compare with those from three positive oblique tows in 1978 and one in 1981 and suggest that 1) *G. nigricans* larvae may occur frequently in the neuston and 2) they are undersampled by oblique tows. The mean size of larvae taken in surface nets is nearly twice that of larvae taken in oblique tows. The mean larval length from surface tows during 1978–81 was 7.1 mm ± 3.7 SD (range = 2.6–16.5 mm). The mean for oblique tows during 1978–81 was 3.8 mm ± 1.69 SD (range = 2.2–15.0 mm).

Medialuna californiensis

A total of 150 occurrences of *M. californiensis* larvae were recorded on CalCOFI oblique plankton tows during 1951–81 (Fig. 8). Larvae occurred on all surveys except during 1953; the apparent absence during 1953 probably was a result of identification error. Larvae ranged from off Monterey Bay, CA (cruise 5707, station 67.55) to off Pt. San Jaunico, Baja California (cruise 6507, station 133.50). There were only five occurrences north of Pt. Conception, CA, during the 30 yr period; only one of these was near the coast (Fig. 8). Except for two stations,

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[1] Standardized number adjusts for percent of sample sorted and standard haul factor to give the number of larvae under 10^2 m of sea surface (see CalCOFI ichthyoplankton data reports cited in Ambrose et al. 1988).
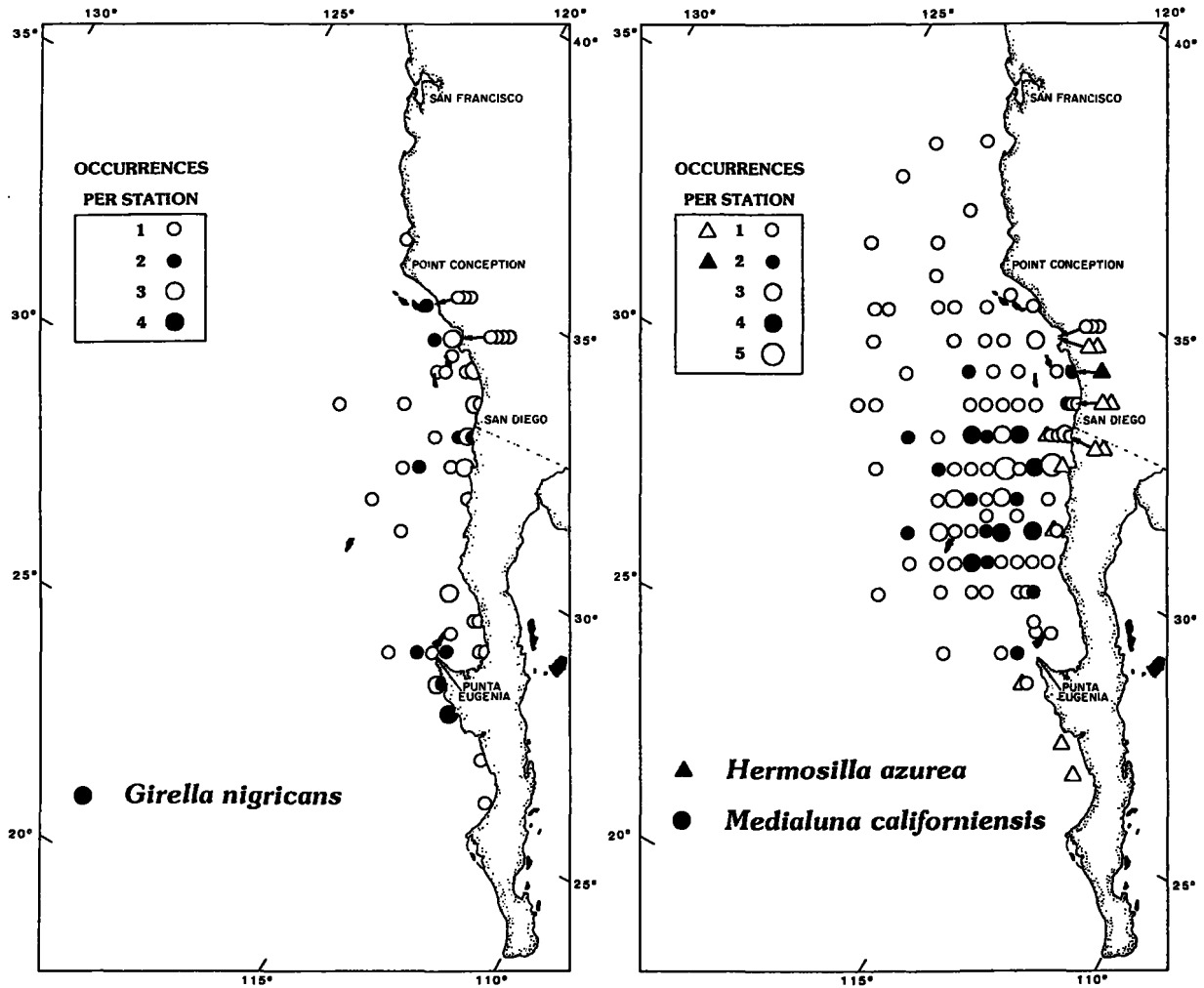
FIGURE 8.—Pooled numbers of occurrences of *Girella nigricans*, *Medialuna californiensis*, and *Hermosilla azurea* larvae taken in CalCOFI tows from 1951 to 1981. Occurrences for *G. nigricans* and *M. californiensis* represent oblique tows and those for *H. azurea* are both oblique and surface tows.

all the remaining larvae were taken between Pt. Conception, CA and Pt. Eugenia, Baja California; 28% of these occurrences were off California and the remainder were off Baja California.

In contrast to *G. nigricans* larvae, those of *M. californiensis* occur well offshore to a distance of ca. 500 km (cruise 5505, station 93.95); 71% of the occurrences were seaward of Station 40 (>110 km from the coast on most lines). Numbers of larvae ranged from 1 to 11 with a mean of 1.42 per positive tow, slightly higher than for *G. nigricans*. The standardized mean number per positive tow was 4.94 with a range of 1.0–30.7. Like *G. nigricans*, the occurrence of *M. californiensis* larvae was highly seasonal with 53% taken in July and 90% in June–August. Larvae did not occur in November–March.

Larvae of *M. californiensis*, like those of *G. nigricans*, utilize the neuston habitat and may be undersampled by oblique tows. *Medialuna californiensis* occurred only once in the oblique tows during 1978 and once in 1981, whereas there were five positive Manta tows in 1978 and three in 1981. The mean size of larvae taken in surface tows during 1978–81 was almost twice that in the oblique tows (7.0 mm ± 2.60, range = 2.6–11.0 mm versus 3.9 mm ± 1.18, range = 2.3–9.4 mm).

Hermosilla azurea

Larvae of *H. azurea* have a nearshore shallow distribution (Fig. 8). We can document only two occurrences of this species in the entire CalCOFI time series of oblique tows (cruise 6907, station 93.30, two specimens; station 97.29, four speci-

mens). Since this species was first identified during the course of the present study, it is possible that other misidentified specimens reside in the collections. They were not, however, confused with G. *nigricans* or M. *californiensis* since we have reexamined all identifications of these species. Larvae of H. *azurea* occurred in Manta net samples at three stations during the 1978 survey and at nine stations on the 1981 survey. Occurrences ranged from Santa Monica Bay, CA (cruise 8107, station 86.7.33) to Pt. San Juanico, Baja California (cruise 7807, station 133.23). Occurrences were shoreward of station 36 on each CalCOFI line (4–42 km from the coast).

Larvae of H. *azurea* were well represented in the SONGS plankton collections of MEC Analytical Systems. The shallow distribution of H. *azurea* larvae was clearly demonstrated in the SONGS collections. Surface tows accounted for 87% of the larvae and oblique tows for 14%. Larvae occurred principally in the outer section of the SONGS transect (1.9–7.2 km from the coast; ca. 18–75 m depth). Larval occurrence was highly seasonal, with 62% of the total number taken in August and >99% in July–September.

SYSTEMATICS

Johnson (1984) discussed kyphosid fishes in his review of percoid systematics and ontogeny. He considered Girellidae, Kyphosidae, and Scorpididae to be distinct families and redefined the latter to include only four genera (*Scorpis*, *Medialuna*, *Labracoglossa*, and *Bathystethus*). Evidence from adult anatomy that led to these decisions was deferred to a forthcoming review (Johnson and Fritzsche, in press). Johnson (1984) pointed out the similarity of girelline and scorpidine larvae and presented this as evidence for considering them sister groups; he now believes girellines, scorpidines, and kyphosines form a monophyletic group (G. D. Johnson[2]).

A principal problem in assessing ontogenetic characters of teleost fishes is a lack of information for all but a few taxa under consideration. This is especially true for percoids and for this group of percoids. In addition to our description of *Girella nigricans*, ontogenetic series are known for two other species of *Girella* (G. *punctata* eggs, larvae, and juveniles [Mito 1958a]; G. *melanichthys* larvae [Okiyama

1988]). Developmental stages of the other girelline genus (*Graus*) are unknown. Other than our description of *Medialuna californiensis*, the only scorpidine larval series description is that of *Labracoglossa argentiventris* (Hattori 1964). Developmental stages of two of the four kyphosine genera are known. In addition to our description of larvae and pelagic juveniles of *Hermosilla azurea* there are descriptions of developmental stages of at least three species of *Kyphosus* (K. *cinerascens* larvae and juveniles, [Mito 1958b; Okiyama 1988]); K. *sectatrix* transforming larvae and juveniles [Moore 1962]; K. *incisor* transforming larvae and juveniles [Moore 1962]; K. *vaigensis* or *bigibbus* eggs [Watson and Leis 1974]; K. *vaigensis* or *bigibbus* larvae [Miller et al. 1979; Leis and Rennis 1983]). Developmental stages of *Sectator* have not been described.

The literature on development stages of these fishes does not provide sufficient descriptive detail to adequately assess ontogenetic characters. In this paper we present detailed descriptions of representatives of the three putative families to establish a basis for character comparisons. The striking feature of the three larval series is their similarity. The fact that the three species were confused with one another during the history of CalCOFI surveys attests to this in a practical sense. Our more rigorous study of their morphologies and pigment patterns has allowed us to identify each specimen correctly, while reinforcing the similarities perceived by early CalCOFI workers. These similarities are 1) a general percoid body form with a *Girella-Medialuna-Hermosilla* grade in degree of robustness; 2) dorsal and ventral midline melanophore series, with unique variations for each species; 3) lateral midline melanophore series, with unique variation; 4) an embedded melanistic band through the eye region; 5) minute melanophores at the tip of the notochord which become associated with the hypural margin of the caudal fin; 6) an anteriad progression of general body pigmentation late in the larval period; and 7) head spination with a *Girella-Hermosilla-Medialuna* grade in degree of development. This morph is not unique among percoids (see Leis and Rennis 1983; Johnson 1984); however, the coherence of these and other more subtle characters among these three eastern Pacific species supports the argument that they represent sister groups.

The pattern of lateral pigmentation is more variable in kyphosine larvae than in girellines and scorpidines. We can recognize three pat-

terns of lateral body pigment in kyphosines. The pattern in *H. azurea* larvae is essentially like that in *Girella* and *Medialuna*. It begins as a midlateral series on the tail and fills in the unpigmented region above, below, and anteriad to it. In *Kyphosus sectatrix* and *K. incisor* lateral pigment extends along the entire epaxial region of the body (Moore 1962). In *K. cinerascens* and *K. vaigensis* (*bigibbus?*) larvae a broad zone of lateral body pigment expands to cover unpigmented regions above, below, anteriad, and posteriad to it (Mito 1958b; Leis and Rennis 1983).

Ontogenetic divergence among kyphosid fishes is greater during the pelagic juvenile stage than in larvae. The silvery pelagic juveniles of *Girella*, which transform abruptly to olive benthic juveniles, are well known. Apparently, *Medialuna* not only has a silvery pelagic juvenile too, but also has a strongly variegated pattern on the dorsal and anal fins. The pelagic juveniles of *H. azurea* are strongly mottled. This feature is shared with other kyphosines, some of which exhibit a striking pattern of pale spots (*K. sectatrix* and *K. incisor* [Moore 1962]; *K. cinerascens* [Mito 1958b]; *K. vaigensis* (*bigibbus?*) [W. Watson, pers. obs.]).

Ontogenetic stages of kyphosid fishes provide a promising array of systematic characters. The utility of these characters in assessing phylogenetic relationships is limited by our present inability to identify shared derived character states through outgroup comparison. The solution to this problem awaits a broader knowledge of ontogeny in kyphophids and other groups in the percoid series.

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