Abstract. – Complete series of field-collected larvae were used to describe the post-yolksac development of two common southern California marine sculpins, *Clinocottus analis* and *Orthonopias triacis*. Characters diagnostic of *C. analis* include nape pigment, dorsal head pigment, heavy rows of dorsal gut melanophores, 18–33 postanal ventral melanophores (PAVM). Postflexion larvae develop multiple preopercular spines (9–12) and several post-temporal/supracleithral spines, and later stages also acquire a W-shaped patch of pigment on the body under the second dorsal fin. Characters diagnostic of *Orthonopias triacis* include a heavy cap of dorsoposterior gut pigment, 26–55 PAVM, occasionally one or two dorsocranial melanophores, and, rarely, one melanophore at the nape; postflexion *O. triacis* develop four preopercular spines. Comparison with other cottid species is included.

Field collection data (1978–85) indicate *C. analis* and *O. triacis* larvae both occur in greatest densities off rocky habitats along the 15m isobath. A key is provided for known preflexion marine sculpin larvae found in southern California.

Manuscript accepted 6 May 1992.
Fishery Bulletin, U.S. 90:454–468 (1992).

Post-yolksac larval development of two southern California sculpins, *Clinocottus analis* and *Orthonopias triacis* (Pisces: Cottidae)

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Clinocottus analis and *Orthonopias triacis* are two common marine sculpins (Pisces: Cottidae) of the rocky intertidal and subtidal areas of southern California (Miller and Lea 1972, Eschmeyer et al. 1983). The range of *C. analis* extends from Cape Mendocino, northern California, to Asuncion Pt., Baja California Sur; *O. triacis* extends from Monterey, central California, to San Geronimo I., central Baja California (Fig. 1).

A description of the embryology and larval development of *Clinocottus analis* was first attempted by Eigenmann (1892) who gave a preliminary description of the eggs and yolksac larvae of *C. analis* from reared eggs obtained in San Diego Bay CA, and subsequently by Budd (1940) from eggs obtained in Monterey Bay CA. In both studies the larvae died at the end of the yolksac stage. Bolin (1941) described the embryology and yolksac development of reared *Orthonopias triacis*.

Hubbs (1966) described many characteristics of *C. analis* embryology, especially in response to temperature, but gave no description of the larvae. Washington (1986) presented a description of a limited series of postflexion *C. analis* larvae and juveniles identified on the basis of meristic and morphological characters. A 7.0mm *O. triacis* was previously illustrated (Washington et al. 1984). No description, however, of a complete larval series of either species exists, despite the common occurrence of adults in California coastal waters and the existence of several partial descriptions of their larval development in the literature.

The following is a description of larval series for both *C. analis* and *O. triacis* based on field-collected specimens from southern California and Baja California, Mexico. Comparison with other cottid species and occurrence is discussed. A key to known southern California preflexion cottid larvae is included to summarize early-life-history information from many sources including Richardson and Washington (1980), Richardson (1981), Washington et al. (1984), Washington (1986), Feeney (1987), and Matarese et al. (1989). This work is intended to aid in identification and hopefully stimulate further research on the development of related species.

Materials and methods

A total of 145 larvae and 9 juveniles of *Clinocottus analis* and 322 larvae and 4 juveniles of *Orthonopias triacis* were studied. Specimens were examined from the Scripps Vertebrate Collection (SIO), the Southwest Fisheries Science Center (SWFSC), the California Academy of Sciences (CAS), and the Natural History Museum of Los Angeles County, Section of Fishes (LACM).

The SIO specimens (21) are preserved in 50% isopropanol and were collected in Baja California at Bahia Todos Santos (SIO H51-19B); the lot

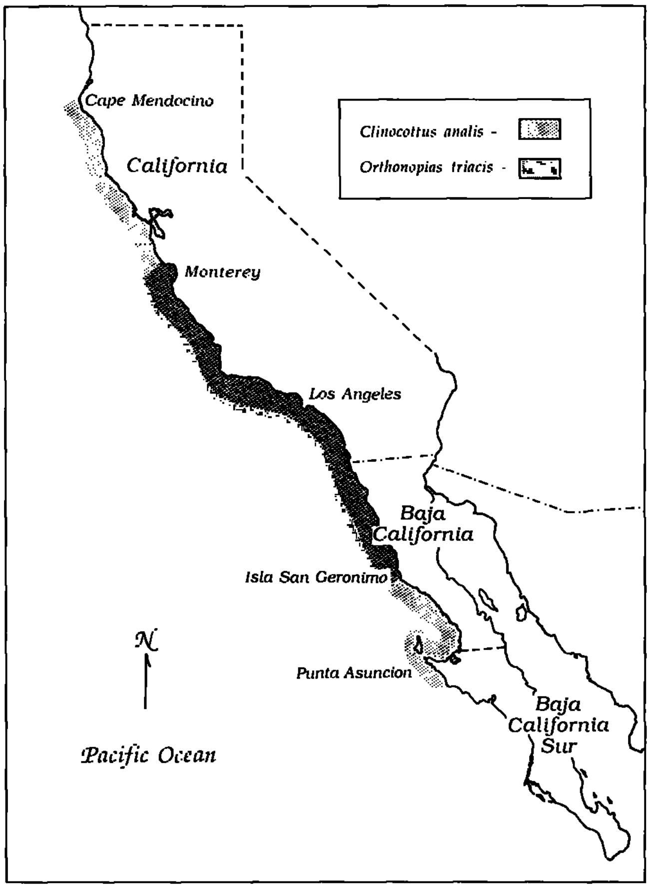

Figure 1
Geographic range of *Clinocottus analis* and *Orthonopias triacis*.

contained an excellent series of both *C. analis* and *O. triacis* postflexion larvae, the discovery of which became the impetus for the present study.

The SWFSC material (10 specimens) is preserved in 5% formalin; some specimens (6) were collected in Baja (6607-AX-110.32; 6806-JD-110.32; SWFSC/SIO H51-106), the remainder were collected in California. Two *C. analis* specimens (SWFSC/SIO H46-63) and two *O. triacis* (SWFSC 6607-AX-110.32) were cleared and stained.

CAS material included one lot of postflexion *C. analis* (SU 68789, 70% ethanol), collected in Monterey Bay, California.

LACM specimens (fixed in 5% formalin and preserved in either 5% formalin or 70% ethanol) were collected in coastal waters (<75 m depth) of the Southern California Bight between Pt. Conception and the Mexican border. Most specimens were collected during the Coastal Resources and 316b phases of the Ichthyoplankton Coastal and Harbor Studies (ICHS) Program and during the Bightwide Program; methods and station locations can be found in Brewer et al. (1981), Brewer and Smith (1982), and Lavenberg et al. (1986). Also, five postflexion *C. analis* specimens (LACM 45404-1, 45414-1–45417-1; in ethanol) were collected at the Catalina Island Marine Science Center (Ninos 1984). Six additional *C. analis* juveniles from the general LACM collection were used: four collected at Santa Barbara Island (LACM 31546-4), one at Catalina Island (LACM 35695-1), and one at Palos Verdes Peninsula (LACM 1993).

Morphometric data, including preanal length, body depth, pectoral length, head length, and eye diameter were measured from 50 *C. analis* and 54 *O. triacis* specimens. Data were entered into an "Excel" spreadsheet program on a Macintosh IIci. Means and standard deviation of morphometric measurements were computed using "SYSTAT." Frequency plots of melanophores vs. length were made using "SYGRAPH" and the "LOWESS" (locally-weighted least squares) scatterplot smoothing method (Wilkinson 1989).

Specimens were illustrated using a camera lucida attached to a Wild M3 stereomicroscope.

Occurrence data are based on specimens taken during 1978–85 on ICHS and Bightwide cruises using a variety of sampling gears. During Coastal Resources collections (ICHS cruises, 1978–79) oblique bongo samples and discrete depth samples were taken monthly along a grid of 10 transects, each with 4 stations. The transects were evenly spaced along the coast from Point Conception to San Diego. The stations corresponded to bottom depths of 8, 15, 22, and 36 m. Additionally, 8 stations (4 sites each) were located in Los Angeles–Long Beach Harbor and San Diego Bay. Integrated water-column samples were collected by fishing a 70 cm bongo sampler from the bottom to the surface. Discrete depth samples were collected at the surface (manta sampler), at the mid-depth of the water column (70 cm bongo sampler) and at the bottom (70 cm bongo sampler equipped with wheels). All samplers had nets of 335 μ mesh Nitex, and attached flowmeters gave estimates of the volume of water filtered. During the 316b phase (ICHS cruises, 1979–80) the number of transects was increased to 20 and the number of stations was reduced to 2 (8 and 22 m) except for 4 "expanded" transects (Ormond Beach, Playa del Rey, Seal Beach, San Onofre), which retained 4 stations (8, 15, 22, and 36 m). For epibenthic sampling, the benthic bongo sampler was replaced by a larger "Auriga" sampler. Collections were taken monthly during the 316b phase. Samples were sporadically taken in 1981, but no data from them are used here.

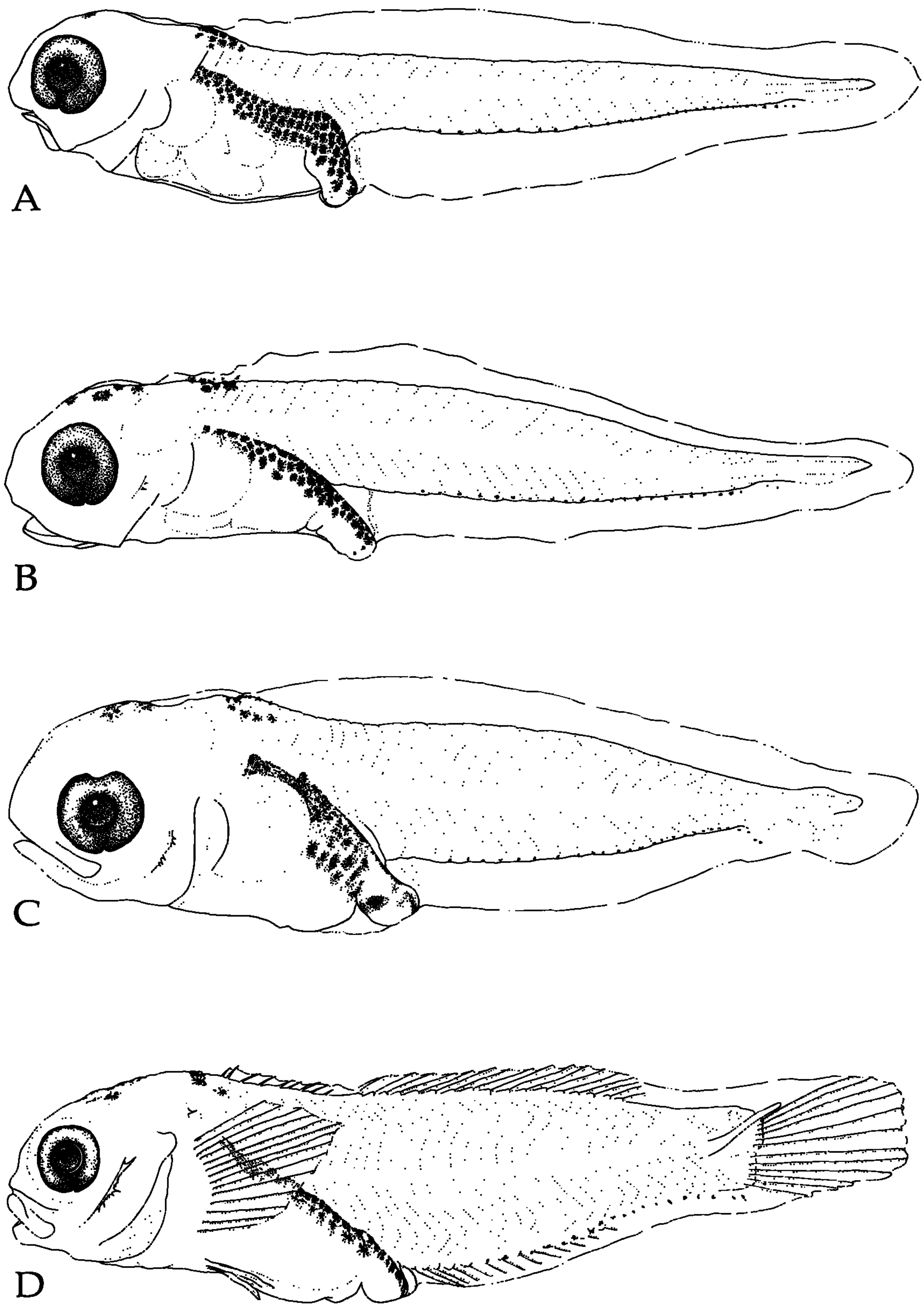

Figure 2
Field-collected *Clinocottus analis* larvae: (A) 3.9 mm (LACM KH #22), (B) 5.6 mm (LACM KH #22), (C) 5.6 mm (LACM 018-SO-36-AU-01), (D) 8.6 mm (SIO H51-19B).

The Bightwide program began in 1982 and samples were taken bimonthly at the four "expanded" 316b transects. During the Bightwide program, a fifth station (75m) was added to each transect. Only oblique bongo samples were taken during the Bightwide phase. Additional details are provided in Lavenberg et al. (1986).

Estimates of larval abundance (n/10 m^2 of sea surface) for each taxon were estimated (for methods, see Smith and Richardson 1977). These abundances were plotted against variables, such as transect, station depth, gear type and date, to determine patterns of local occurrence.

Table 1
Morphometrics of larvae and juveniles of *Clinocottus analis* and *Orthonopias triacis*, represented as a mean percentage of standard length ± the standard deviation, with range in parentheses.

Measurement stage	*Clinocottus analis*	*Orthonopias triacis*
Preanal length		
Preflexion	46.0±3.4(40.0–52.2)	38.8±3.0(31.5–44.8)
Flexion	47.1±2.2(44.6–48.5)	41.7±2.8(37.8–47.2)
Postflexion	50.5±2.1(46.9–54.5)	43.5±3.0(39.1–48.3)
Juvenile	47.3±1.1(46.0–48.4)	43.5±2.7(39.9–46.3)
Body depth		
Preflexion	24.8±2.2(19.7–29.7)	24.3±3.1(19.8–33.2)
Flexion	23.8±2.2(21.3–25.3)	24.3±2.9(19.8–28.5)
Postflexion	28.7±2.0(25.6–32.7)	25.9±2.4(22.1–29.5)
Juvenile	26.4±2.7(24.5–30.4)	23.6±1.6(21.7–25.3)
Pectoral length		
Preflexion	8.5±1.3 (6.6–11.3)	8.1±1.2 (6.1–11.3)
Flexion	8.9±2.0 (7.3–11.2)	10.2±2.6 (6.3–16.0)
Postflexion	27.8±4.3(16.9–32.5)	18.2±5.0(10.8–25.4)
Juvenile	35.4±1.8(33.0–36.8)	34.9±2.0(32.4–37.1)
Head length		
Preflexion	21.8±2.1(18.6–26.1)	21.2±1.7(18.0–24.4)
Flexion	23.3±0.7(22.5–23.8)	24.1±2.7(19.3–29.1)
Postflexion	30.2±1.8(25.6–32.8)	28.0±2.3(25.0–31.4)
Juvenile	36.6±4.4(33.8–43.2)	34.5±1.3(33.1–35.7)
Eye diameter		
Preflexion	10.7±1.1 (8.3–12.5)	10.0±0.8 (8.5–12.2)
Flexion	10.1±0.2 (9.9–10.2)	9.2±0.9 (7.8–10.7)
Postflexion	8.9±0.6 (8.0–10.5)	9.1±1.1 (8.1–10.8)
Juvenile	10.0±0.6 (9.4–10.7)	10.9±1.1 (9.9–12.4)

Identification

Yolksac and small post-yolksac larvae of *Clinocottus analis* and *Orthonopias triacis* were identified by comparison with descriptions of reared larvae (Eigenmann 1892, Budd 1940, Bolin 1941). Larger preflexion and flexion larvae were associated to postflexion larvae and juveniles using pigment characters, number of preopercular spines, length of gut, and location of the anus. Washington (1986) was helpful in linking postflexion *C. analis* individuals to juveniles using melanophore patterns and meristics. For definition of terms, see Feeney (1987).

Results

Description of *Clinocottus analis* larvae

Distinguishing characters Distinguishing characters of *Clinocottus analis* preflexion larvae include heavy dorsoposterior gut pigment, nape pigment (usually with a nape bubble), 18–25 postanal ventral melanophores (PAVM), and melanophores on the head over the midbrain. Late preflexion larvae may develop up to 33 PAVM. Larger flexion and postflexion larvae develop multiple preopercular spines (9–12) similar to other *Clinocottus* and *Oligocottus* species (Washington 1986). Transforming larvae develop a W-shaped patch of pigment under the 2d dorsal and have an advanced anus. In juveniles, the preopercular spines coalesce to one bifurcate spine; small, prickly scales begin to develop under the 2d dorsal fin. The anus advances about halfway to pelvic fin origin.

Morphology *Clinocottus analis* yolksac larvae hatch at lengths of 3.7–4.5mm (Eigenmann 1892, Budd 1940); preserved field-collected larvae are found as small as 3.1mm (due to shrinkage during preservation). Larvae are robust with fully pigmented eyes at hatching. Dorsal gut diverticulae (wings) as seen in some *Artedius* (Washington 1986) are absent; however, sometimes a bump can be seen in that area.

The preanal length averages 46% of notochordal length (NL), which is closer to Eigenmann's illustration (est. 44%) than to Budd's illustration (est. 33%); the minimum preanal length from field-collected specimens was 40% NL (Table 1). During flexion the preanal length increases slightly to an average of 47%. In postflexion larvae, preanal length increases to an average 51.5% standard length (SL). In juveniles, the pectoral fin and head lengthen to an average 35 and 37% SL, respectively (Table 1).

In postflexion larvae, the anus is slightly advanced of the anal fin origin. In transforming postflexion larvae, the anus advances from the anal fin to about one-third the distance to the pelvic fin origin. In juveniles, the anus advances almost halfway to the pelvic fins.

At 9.8mm a cirrus appears on each dorsal orbit (Fig. 3B).

Fin development In postflexion larvae, fin elements start to form; the caudal rays become segmented. Pelvic fins appear as buds (Table 2). At 9.8mm, fin rays, including the pelvics, are well-formed.

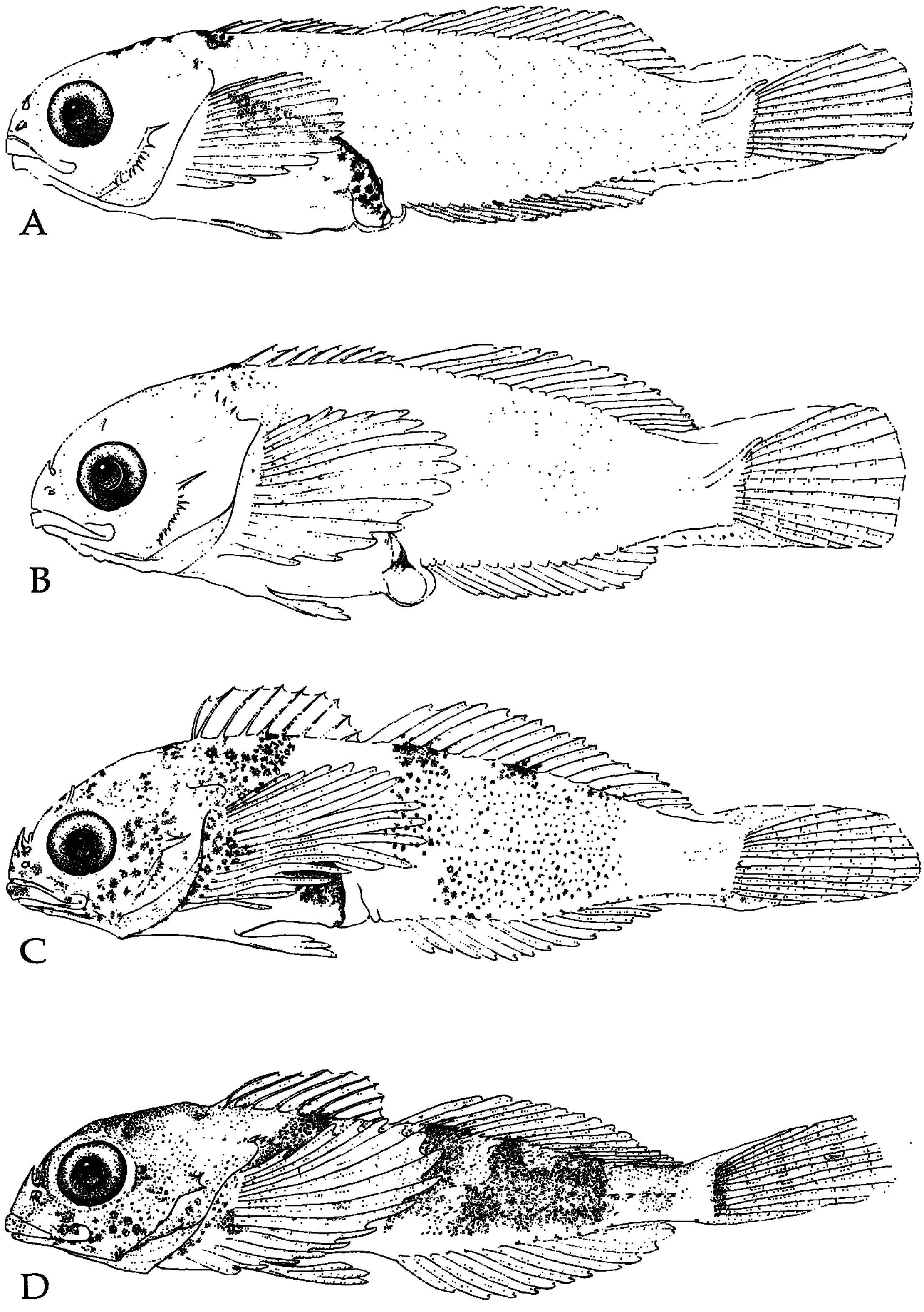

Figure 3

Field-collected *Clinocottus analis* larvae and juveniles: (A) 9.7 mm (SIO H51-19B), (B) 9.8 mm (SIO H51-19B), (C) 10.6 mm (LACM 008-88-22-MA-01), (D) 13.3 mm (LACM 45404-1).

Spination Preopercular spines begin to develop in the late preflexion stage at ~5.5 mm NL; the 5.6 mm specimen (in Fig. 2B) has developed 2 spines. During flexion, the number of preopercular spines increases to 5 (Table 2, Fig. 2C).

In postflexion larvae, the preopercular spines number 6–12 (Table 2); the upper spine is elongated. A post-temporal/supracleithral spine appears at 8 mm (Fig. 2D).

By 9.7 mm, a pair of nasal spines appear (Fig. 3A). The dorsalmost preopercular spine elongates to about twice the length of other spines. The number of post-temporal/supracleithral spines increases to 3. At 9.8 mm, a small spine (not illustrated) may be present where the sensory canal forms over the parietal, anterior to the nape; the spine persists in specimens up to 11 mm SL (CAS SU 68789).

In juveniles, multiple preopercle spines (about 10) coalesce to 1 elongate, bifurcated uppermost spine and 2 convex undulations ventrally where the other spines had been. Larval post-temporal spines form the anteriormost part of the lateral line which later becomes decorated with a series of multispined scales. Smaller spines (prickles) form laterally below the 2d dorsal and lateral line.

Pigmentation In yolksac *Clinocottus analis*, about 140 dense melanophores in 6–7 rows line the dorsoposterior gut (peritoneal) membrane (Eigenmann 1892, Budd 1940). Nape melanophores number 11–15 with several extending onto a bubble of skin that is usually present at the anterior nape. A stellate melanophore can usually be found on the head over one or both sides of the midbrain. A row of 18–25 PAVM is present from about the 6th postanal myomere to the caudal area; the last 2–3 melanophores usually extend down into the finfold.

Post-yolksac larvae retain much of the appearance of the yolksac larvae (Fig. 2A). The number of PAVM may increase to 33, but usually ranges in the mid-20s, generally decreasing in larger larvae (Fig. 4).

Late preflexion larvae develop numerous head melanophores over the midbrain (Fig. 2B). One 4.6 mm specimen had 19 midbrain melanophores and one forebrain melanophore; however, the melanophores over the midbrain usually number 10–15 with no forebrain pigment. Melanophores sometimes form at the anus in this stage; however, these usually form in the postflexion stage. One 5.2 mm specimen had 5–6 melanophores in a circle around the anus.

By 9.7 mm, the number of PAVM has decreased to less than 23 (Fig. 4). In a 9.8 mm specimen (Fig. 3B), melanophores begin to form below the nape and laterally below the second dorsal fin.

Table 2

Meristics of larvae and juveniles of *Clinocottus analis* (specimens inside the two dashed lines are undergoing flexion of the notochord).

Size (mm)	D_1	D_2	A	P	V	PS	PCV	CV	TV	M	PAVM
3.1	–	–	–	–	–	0	–	–	–	35	29
4.2	–	–	–	–	–	0	–	–	–	33	28
5.6	–	–	–	–	–	2	–	–	–	34	24
5.2	–	–	–	–	–	?	–	–	–	34	25
5.6	–	–	–	–	–	5?	–	–	–	34	26
8.4	IX?	17?	13	15?	buds	6–8	–	–	–	32	21
9.7	IX	16	14	15	I,3	10	–	–	–	33	14
10.5	IX	17	14	15	I,3	10	–	–	–	31?	17?
10.9*	IX	17	13	15	I,3	11?	11	22	33	–	–
11.1	IX	17	13	15	I,3	9	–	–	–	32	9
11.4*	IX	17	14	15	I,3	11	11	22	33	–	–
13.3**	IX	16	13	15	I,3	1	11	21	32	–	11
15.1	IX	16	13	15	I,3	1†	–	–	–	–	14
15.8**	IX	16	13	15	I,3	1	11	21	32	–	8
21.0	IX	16	13	15	I,3	1†	–	–	–	–	8

D_1 dorsal fin spines; D_2 dorsal rays; A anal fin rays; P pectoral fin rays; V pelvic rays; PS preopercle spines; PCV precaudal vertebrae; CV caudal vertebrae; TV total vertebrae; M myomeres; PAVM postanal ventral melanophores

* cleared and stained larvae

** x-rayed

† The one preopercle spine has a double point.

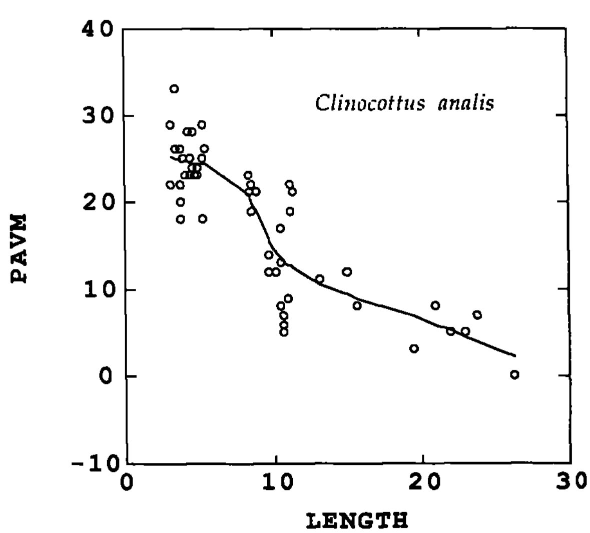

Figure 4

Frequency of postanal ventral melanophores (PAVM) vs. length (mm) with a LOWESS regression line at F = 0.5 (half the points included in a running window) for *Clinocottus analis* larvae and juveniles.

Transforming postflexion larvae develop a wide band of pigment under the second dorsal that is typically W-shaped and extends ventrally almost to the anal fin (Fig. 3C). Another band of dense pigment forms under the first dorsal fin and extends down across and onto the pectoral fin base. The head becomes heavily pigmented; about 15 large stellate melanophores (along with numerous small ones) extend across the preopercle and below the eye. Two or three melanophores appear on the posterior maxillary. Melanophores surround the nasal openings and spine. A band of pigment runs across the anterior upper lip (premaxillary). The lower jaw and chin also have pigment. The ventral gut is not pigmented. Several of the caudal rays are pigmented.

Juvenile *C. analis* continue to add pigment dorsolaterally while still retaining some of the larval pigmentation (Fig. 3D). The W-shaped patch is still present under the second dorsal, as well as a band of pigment under the first dorsal and across the pectoral fin base. The number of PAVM continue to decrease (Fig. 4). Two new patches of melanophores appear on the caudal peduncle and over the hypural plates. Melanophores appear in the dorsal, pectoral and caudal fins.

Meristics *Clinocottus analis* postflexion larvae have 6 branchiostegal rays and twelve (6+6) principal caudal rays which are consistent with adult counts. Other meristics are given in Table 2. Numbers of fin and vertebral elements match well with modes given by Howe and Richardson (1978).

Comparison with other species

Clinocottus analis larvae have no anterior gut pigment like *C. recalvus* larvae (Morris, 1951). *Clinocottus acuticeps* also has forebrain pigment and a longer trailing gut than *C. analis*, no early head pigment, fewer PAVM, and hindgut diverticulae (Washington 1986). *Clinocottus embryum* has fewer nape and PAVM. *Clinocottus globiceps* has anterior gut pigment and only four or five PAVM.

Preflexion *Oligocottus maculosus* have shorter guts (preanal averages 39.1% SL) than *C. analis* (Washington 1986). *Oligocottus snyderi* has no head pigment and few PAVM (~6). Larvae of *O. rubellio* (rosy sculpin) and *O. rimensis* (saddleback sculpin) have not been described. A 15.6 mm juvenile *O. rubellio* (LACM 42918-1) differs from *C. analis* juveniles by having more cirri on the head, no W-shaped pigment patch laterally, and no banding anywhere, just a fine covering of light melanophores. *Oligocottus rimensis* differs by having an elongate body and a high number of dorsal soft rays (16–19). A 17.1 mm *O. rimensis* (LACM 943) is developing saddles of pigment typical of adults but lacks the W-shaped patch of *C. analis*. *Oligocottus rimensis* has a single large preopercular spine (single pointed) and 3 smaller spines, similar to the "*Myoxocephalus*" group (Washington et al. 1984), i.e., 4 preopercle spines throughout their early development; the dorsal spine elongates in juveniles. *Oliocottus rimensis* juveniles also have no head cirri and the first pelvic ray appears double (split in two).

Clinocottus analis differs from some *Artedius* (*A. fenestralis*, *A. lateralis*, *A.* spp.) by having no large gut diverticulae (wings). Species of *Artedius* without wings (*A. creaseri*) differ by having anterior gut pigment and fewer PAVM (~10) (See Appendix 1).

Occurrence

Oblique bongo samples from coastal waters (8, 15, 22, 36, and 75 m depths) of the Southern California Bight taken during the period 1978–84 (see Lavenberg et al. (1986) for methods) indicate *C. analis* larvae (mostly preflexion) were captured at the greatest densities along the 15 m isobath off rocky tidepool areas in southern California, especially off Palos Verdes Peninsula and Gaviota in 1979–80. Larvae occurred during all months of the year, with peak abundance in July. Wells (1986) found that *C. analis* spawn throughout the year, with a peak in September–November in 1971–72, based on gonosomatic index values and the appearance of juveniles in the tidepools.

In discrete depth (neuston, middepth, epibenthic) samples taken in the Southern California Bight in October 1978 and June 1979–July 1980, 100% of the *C. analis* larvae (almost exclusively notochordal and flexion sizes) were caught in epibenthic samplers (benthic bongo or auriga nets) indicating the smaller larvae are near the bottom. Large postflexion individuals were common in neuston tows (manta nets) taken during the Coastal Resources Program (1978–79 except October; not fully sorted to date) at Coho Bay (Pt. Conception), and Playa del Rey and Seal Beach (stations on each side of Palos Verdes; no station at Palos Verdes) indicating larger postflexion, metamorphosing larvae are located near the surface. Ninos (1984) collected many larger postflexion larvae (~10 mm) during surface night-lighting at Catalina Island. At Palos Verdes, juveniles (<25 mm) are found back in the intertidal in small pools, separated from the larger adults (Wells 1986).

Description of *Orthonopias triacis* larvae

Distinguishing characters Distinguishing characters for *Orthonopias triacis* larvae include a heavy cap of pigment on the dorsoposterior gut, 26–55 PAVM, nape melanophores usually absent, no wings, short gut (preanal length 31.5–44.8% SL in preflexion larvae), and 4 preopercular spines in late-flexion and postflexion larvae. Postflexion larvae and juveniles have an anus advanced from the anal fin. Juveniles develop rows of spiny scales between the dorsal fin and lateral line.

Morphology *Orthonopias triacis* larvae hatch at 2.9–3.8 mm (Bolin 1941); field-collected larvae are as small as 2.6 mm (after preservation). At 4.3 mm, the caudal fin anlage is forming (Fig. 5B). Flexion occurs in larvae between 4.2 and 7.2 mm (Table 3).

In preflexion larvae, the preanal length averages 39% SL (Table 1). During flexion the preanal length increases to an average of 42% SL. Postflexion preanal length averages 43.5% SL. Small juveniles (13.2 mm, LACM W67-153, not illustrated) also have an average preanal distance of 43.5% SL.

In postflexion larvae, the anus starts to advance anteriorly from the developing anal fin. In larger postflexion larvae (Fig. 6C), a cirrus forms on the orbit. Small juveniles (13.2 mm, LACM W67-153, not illustrated) have a cirrus on the orbit and one in the interorbital space; they also have lateral line scales and scale bands under the dorsal fin.

Larger juveniles (Fig. 6D) have numerous cirri and spines on the head; a smaller cirrus forms on the maxillary and cirri develop between the preopercular spines. The anus is located about halfway to pelvic origin.

Fin development In postflexion larvae, complete rays are formed by 7.2 mm in all fins except the pelvics, which are present as buds (Table 3).

Spination Preopercular spines start to form in *Orthonopias triacis* during flexion at 4.2–5.8 mm (Fig. 5C, Table 3). Postflexion larvae typically have 4 preopercular spines of about equal size and equally spaced (Fig. 6B). Sometimes an accessory preopercular spine is present; a 7.3 mm larva possesses a smaller spine adjacent to the 2 large spine from the top.

Small juveniles (13.2 mm, LACM W67-153, not illustrated) still retain the 4 preopercular spines (Table 3). In larger juveniles (Fig. 6D, Table 3), preopercular spines are reduced to 3 and a bump where the ventralmost one used to be; the dorsalmost spine becomes bifurcate.

In large postflexion larvae (Fig. 6C), nasal spines are present. Three post-temporal/supracleithral spines appear above the opercular flap near the point where the lateral line will start to form. A small foramen is present on the parietals where a sensory canal forms.

Table 3

Meristics of larvae and juveniles of *Orthonopias triacis* (specimens inside the two dashed lines are undergoing flexion of the notochord).

Size (mm)	D_1	D_2	A	P	V	PS	PCV	CV	TV	M	PAVM
2.6	—	—	—	—	—	0	—	—	—	34	40
3.4	—	—	—	—	—	0	—	—	—	36	51
4.3	—	—	—	—	—	0	—	—	—	36	30
4.2	—	—	—	—	—	1	—	—	—	37?	43
4.9	—	—	—	—	—	2	—	—	—	34	35
5.5	—	—	—	—	—	2	—	—	—	35	35
6.5	—	—	—	—	—	4	—	—	—	35	27
7.2	—	—	—	—	—	4	—	—	—	34	28
6.8	IX?	16?	11?	14?	buds	5*	—	—	—	34	25
7.3	IX?	16?	12?	14?	buds	4	—	—	—	35	33
8.2**	IX	16	12	14	I,3	4	11	24	35	—	—
9.2	IX	16	12	14	I,3	4	—	—	—	35	7?
13.2	IX	17	12	15	I,3	4	—	—	—	—	1
17.2	IX	17	12	14	I,3	4	—	—	—	—	0
23.0†	IX	17	12	14	I,3	3††	11	24	35	—	8

* Second (from dorsum) preopercle spine has smaller spine next to it.
** cleared and stained larvae
† x-rayed
†† Dorsal preopercle spine has a double point.

Pigmentation Yolksac *Orthonopias triacis* have pigmented eyes at hatching, a cap of dense pigment on the dorsoposterior gut, and about 35 PAVM that start on the 3d or 4th postanal myomere. One or a pair of head melanophores is sometimes present (Bolin 1941).

The dorsoposterior gut pigment in field-collected larvae is composed of ~80–90 melanophores in a circular pattern (Fig. 5A). Small larvae (<4 mm) have 32–55 PAVM (Fig. 7); preflexion larvae >4 mm have 26–43 PAVM. One or two head melanophores over the midbrain occur in about 33% of preflexion larvae. Nape pigment is usually absent; one punctate melanophore occurs at the nape in about 25% of preflexion larvae.

Flexion larvae have similar pigment as above (Fig. 5D, 6A). The first few PAVM are formed as dashes of pigment at the start of the anal fin base (Fig. 6A). A 7.0 mm specimen (Washington et al. 1984) has at least 3 head melanophores and 1 nape melanophore, and seems to be just completing flexion. A 5.8 mm specimen (that may have shrunk to a greater extent because it was ETOH-preserved) completing flexion has 12 head melanophores and 2 nape melanophores (LACM 009-80-36-BB-01).

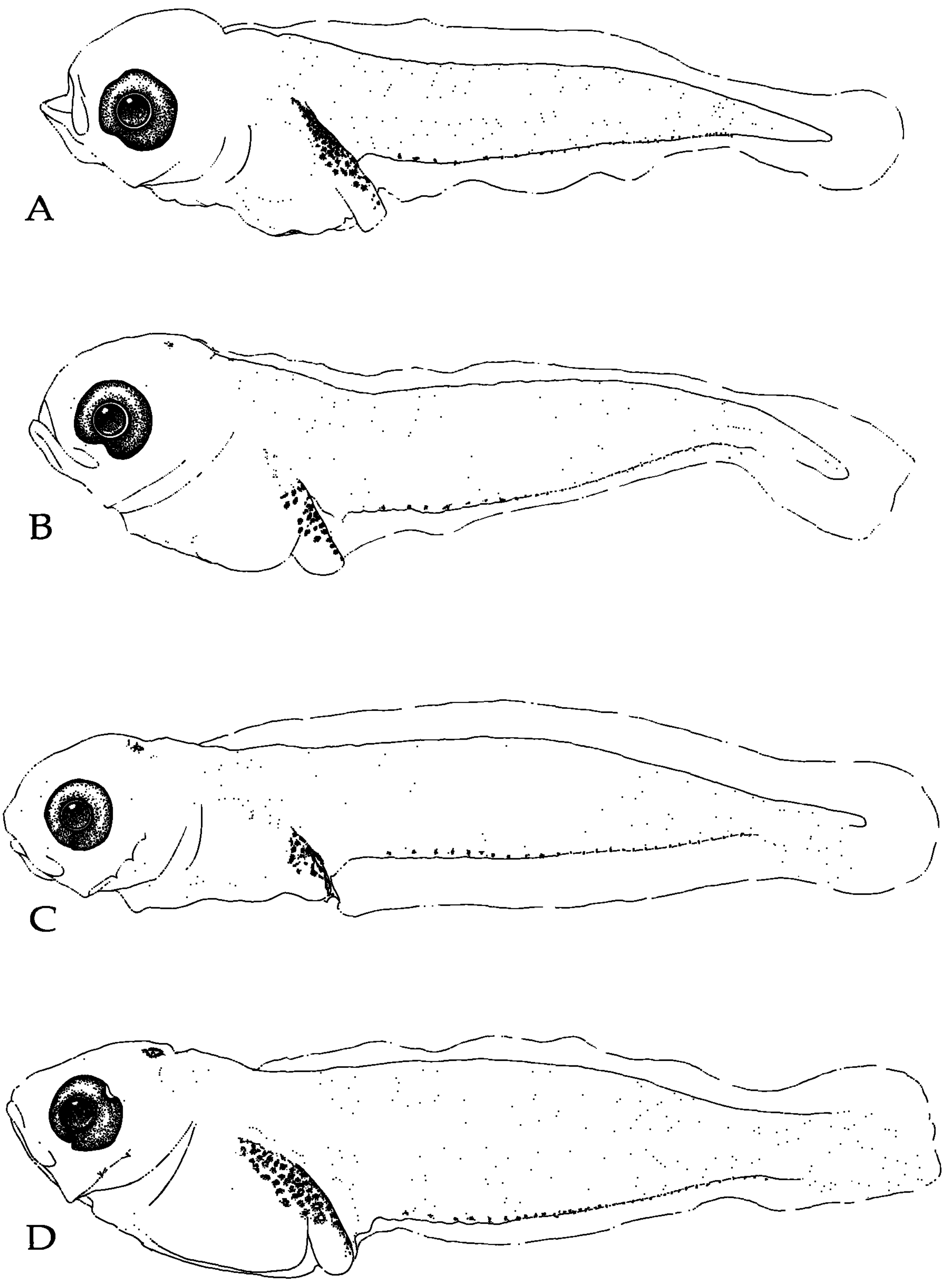

Figure 5
Field-collected *Orthonopias triacis* larvae: (A) 3.3 mm (LACM 026-PV-22-OB-02p), (B) 4.3 mm (LACM 026-PV-15-OB-01p), (C) 5.8 mm (SIO H51-19B), (D) 5.5 mm (LACM 012-80-08-BB-01).

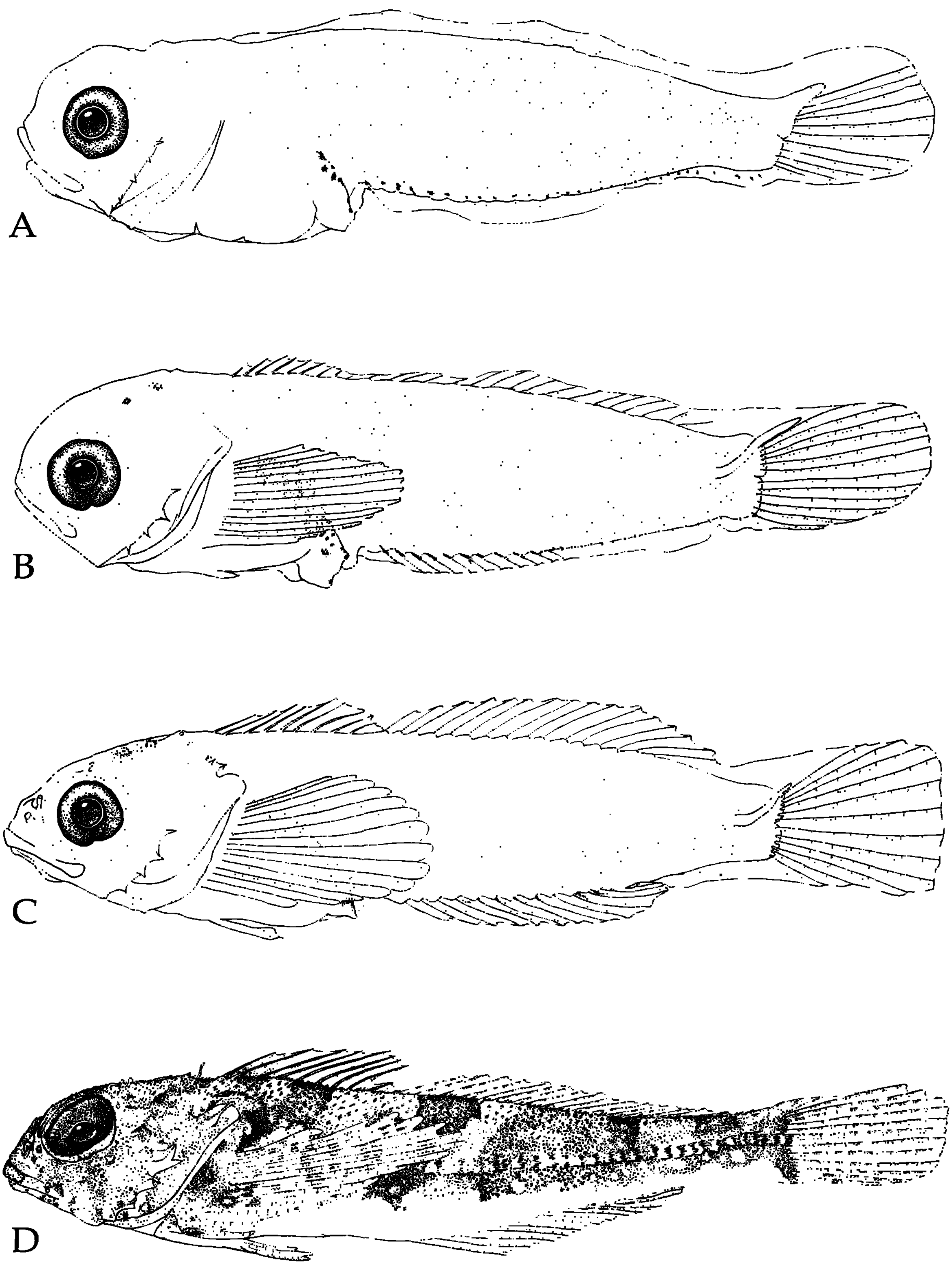

Figure 6

Field-collected *Orthonopias triacis* larvae and juveniles: (A) 5.9 mm (LACM 026-PV-15-OB-01p), (B) 7.2 mm (LACM 012-88-36-BB-01), (C) 9.2 mm (SIO H51-19B), (D) 23.0 mm (LACM 9423-8).

Postflexion PAVM pigment takes the form of dashes at the base of each anal ray. At least 3 melanophores can be found on the head over the midbrain. In larger postflexion larvae, the number of PAVM is greatly reduced (Fig. 7).

Small juveniles (13.2 mm, LACM W67-153, not illustrated) have numerous melanophores over the midbrain. Few or no PAVM may be present (Fig. 7). In the 13.2 mm juvenile, a dark patch of melanophores on the pectoral fin base extends to and around the pelvic girdle and meets at the ventral midline. Bands of pigment extend down from the dorsum and stop just ventral to lateral line.

In larger juveniles (Fig. 6D) a patch of melanophores is present on the pectoral fin base, but may not be continuous across the pelvic girdle as it is in the 13.2 mm juvenile. Light circles appear in the dense pigment below the lateral line.

Meristics Meristics for *O. triacis* (Table 3) are comparable to published accounts. Modes for the fin elements matched those given in Howe and Richardson (1978). Vertebrae (35) were 1 greater than the mode (34) in Howe and Richardson. Branchiostegal rays (BR) form during flexion; a 5.6 mm FL larva had 5 visible BR. In postlarvae and juveniles, branchiostegal rays = 6, PCR = 6+6.

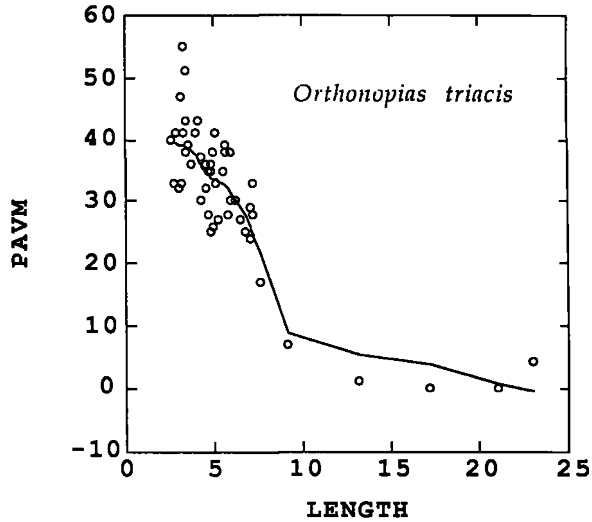

Figure 7
Frequency of postanal ventral melanophores (PAVM) vs. length (mm) with a LOWESS regression line at F = 0.5 (half the points included in a running window) for *Orthonopias triacis* larvae and juveniles.

Comparison with other species

Orthonopias triacis are similar to *Artedius meanyi* larvae (Washington 1986) by possession of 4 preopercular spines, a short compact gut, and an eye cirrus; *A. meanyi* postflexion larvae and juveniles also develop small, prickly scales on the head and below the dorsal fin. *Artedius meanyi* differ in having far fewer PAVM (<13), pigment in the dorsal finfold, anterior gut melanophores, and in undergoing flexion at a larger size (6.2–9.4 mm). *Artedius meanyi* and *O. triacis* were put in the "*Myoxocephalus*" group by Washington et al. (1984) due to the presence of 4 preopercular spines.

Orthonopias triacis larvae are similar to others within the "*Myoxocephalus*" group, including *Icelinus* and *Chitonotus*, in having no heavy nape pigment and a high number of PAVM; *Icelinus quadriseriatus* has 25–63 PAVM (Feeney 1987) and *Chitonotus* has 24–45 PAVM (Richardson and Washington 1980). *Orthonopias triacis* lacks ventral gut pigment (see Appendix 1).

Orthonopias triacis can not be assigned to the "*Artedius/Clinocottus/Oligocottus*" group, as tentatively suggested by Richardson (1981), because it lacks the multiple preopercular spine pattern, gut diverticulae, and trailing gut. *Clinocottus analis* postflexion larvae (this paper) are similar to *O. triacis* because of the advanced anus and presence of head pigment, nasal spines, post-temporal/supracleithral spines, cirri over the eye, and similar meristics. *Clinocottus analis* differs in having multiple (>5) preopercular spines, a 'W' shaped pigment patch on the side of the body, and a longer gut (preanal = 46.0–54.5% SL vs. 39.1–48.3% SL in *O. triacis*).

Orthonopias triacis larvae initially have more PAVM than *C. analis*; however, the number of PAVM decreases with length more quickly than *C. analis* (Figs. 6, 7); linear regressions (not shown) of *O. triacis* PAVM have a greater negative slope (−2.413 vs. −1.161) than *C. analis*. Linear regression lines were not used, however, in the final plots (Figs. 6, 7) because LOWESS smoothing (Wilkinson 1989) indicates that the relationship between PAVM and length may be nonlinear, especially in *O. triacis*. Additional large postflexion and juvenile specimens need to be examined to verify this relationship.

Occurrence

During 1978–84, *O. triacis* larvae (like *C. analis*) were collected in highest densities off Palos Verdes and other rocky areas, at the 15 m isobath during the entire year, peaking in spring and summer. Approximately 72% of the larvae in discrete depth tows were collected in epibenthic tows and none in neuston tows. Flexion larvae were rarely collected. Postflexion individuals have not been found in the 1978–79 neuston tows as were

C. analis. Postflexion/metamorphosing individuals apparently do not exhibit neustonic behavior like *C. analis*. Juvenile *O. triacis* have been collected subtidally on reefs and off rocky areas (LACM collection data).

Conclusions

Clinocottus analis larvae can be grouped with the "*Artedius*" group of cottid larvae based on the high number of preopercular spines (9–12) (Washington et al. 1984). The advanced anus of postflexion larvae is typical of *Clinocottus*. Swank (1988) showed that *Clinocottus analis* is more closely related to other species within the genus rather than to *Oligocottus maculosus*; *C. analis* was found to be the most divergent in the genus. Larval characters presented here lend support to her conclusions. *Clinocottus analis* larvae share many characters with other *Clinocottus*, but still have some significant differences, i.e., a high PAVM count and development of prickly spines on the body.

Orthonopias triacis larvae can be grouped, along with *A. creaseri*, *A. meanyi*, *Chitonotus*, and *Icelinus*, in the "*Myoxocephalus*" group (Washington et al. 1984) because of the presence of four preopercular spines. Body morphology of *O. triacis* is most similar to *A. meanyi*.

Orthonopias triacis and *C. analis* preflexion larvae co-occur in the same areas (15 m isobath near rocky habitats), but can be easily distinguished using pigment and morphological characters. Larger postflexion larvae can be distinguished by the number of preopercular spines.

Acknowledgments

I thank the following for their help: David Ambrose, Daniel Cohen, Pamela and Lissette Feeney, Javier Gago, Robert Lavenberg, Gerald E. McGowen, Geoffrey Moser, Margaret Neighbors, Debra Oda, Brenda and Jim Rounds, Jeremyn Schmitz, Helga Schwarz, Jeffrey Seigel, Camm C. Swift, H.J. Walker, Brian White, William Watson, and the Natural History Museum of Los Angeles County.

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Appendix 1: Key to known southern California sculpin larvae (preflexion stage)

Comments: The following key is provided as a guide to identifying known Southern California sculpin larvae. Some larvae may not key out exactly due to variation in pigment or because they are a species that is not described yet (see table at end of key). Types (e.g., *Artedius* type 16) are named as they are labeled in the LACM collection. Equivalent types in literature are noted.

1 Wings (gut diverticulae) present 2

Wings absent (or as bumps only) 4

2(1) Postanal ventral melanophores 3–12 3

Postanal ventral melanophores 22–32 .... ***Artedius lateralis***

3(2) Nape pigment present; myomeres 32–35 .... ***Artedius* type 16**
(= *Artedius* type 3 (Washington 1986); may be either *A. corallinus* or *A. notospilosus*)

Nape pigment absent; myomeres 36–37 .... ***Artedius* type A**
(= undescribed; has wings like other *Artedius*, no nape pigment, and only 3–8 PAVM)

4(1) Body covered with melanophores 5

Body melanophores restricted to ventral midline, gut, nape or head region 9

5(4) ~26–28 myomeres; stubby body (hatches at 6–7 mm) .... ***Rhamphocottus richardsonii****

36–41 myomeres; elongate body 6

6(5) Elongate pectoral fin (>20% of the body); pigment extending into dorsal and anal finfold (hatches at ~7–9 mm) .... ***Nautichthys oculofasciatus****

Pectoral fins not elongate (<15% of body); no pigment extending into fins 7

7(6) Lateral body relatively unpigmented; preanal length 36–42% of notochordal length .... ***Hemilepidotus spinosus***

Lateral body covered with melanophores; preanal length ~44–46% of notochordal length 8

8(7) Series of elongate melanophores present along the lateral midline; pointed snout .... ***Radulinus* sp.**

No distinct series of elongate melanophores along the lateral midline; blunt snout .... ***Scorpaenichthys marmoratus***

9(4) Otic capsule pigment present (may be present in *Paricelinus hopliticus*) 10

Otic capsule pigment absent 11

10(9) Nape pigment present (several melanophores); dorsal gut pigment not in bands .... ***Oligocottus/Clinocottus* type D**
(= *C. recalvus* (Morris 1951) or *C. globiceps* or *O. maculosus* (Washington 1986). These specimens are most similar to larger *C. recalvus* from same locality; however, they share characters with all three species (e.g., otic capsule pigment) or with one species (e.g., nape bubble like *O. maculosus*).

Nape pigment absent (or 1 melanophore occipitally); dorsal gut pigment in bands .... ***Leptocottus armatus***

11(9) Nape pigment present 12

Nape pigment absent (rarely present in *Orthonopias* triacis and flexon *Chitonotus pugetensis*) ... 19

12(11) Anterior gut pigment present; ventral gut pigment present 13

Anterior gut pigment absent; ventral gut pigment absent 14

13(12) Myomeres 40–42; postanal ventral melanophores ~37–38; pigment on snout .... ***Paricelinus hopliticus****

Myomeres 27–30; postanal ventral melanophores <15; pigment on snout absent .... ***Enophrys taurina*?**
(= undescribed; only one specimen collected, similar to *E. bison* description (Richardson and Washington 1980) except for scattered ventral gut pigment)

14(12) Postanal ventral melanophores 5–14 15

Postanal ventral melanophores 15–33 16

15(14) Preanal myomeres 7-9; head pigment usually absent; gut pigment light and scattered .... ***Oligocottus synderi***

Preanal myomeres 10–12; head pigment present; gut pigment heavy .... ***Oligocottus/Clinocottus* type B**
(= undescribed; looks much like *C. analis* but has only 10–14 PAVM)

16(14) Nape melanophores <6 17

Nape melanophores >6 18

17(16) Postanal ventral melanophores 15–21; dorsal gut pigment light to moderate .... ***Clinocottus embryum****

Postanal ventral melanophores 21–33; dorsal gut pigment heavy .... ***Artedius harringtoni***

18(16) Head pigment absent; dorsal gut pigment moderate; nape melanophores ~18 .... ***Oligocottus/Clinocottus* type C**
(= undescribed; no head pigment, 17–31 PAVM; lighter pigment than *C. analis*, may be *O. maculosus*)

Head pigment present (except in smallest larvae (<3.0 mm)); dorsal gut pigment heavy; nape melanophores <17 .... ***Clinocottus analis***

19(11) Postanal ventral melanophores 7–18 20

Postanal ventral melanophores ≥24 21

20(19) Ventral gut pigment absent; preanal myomeres 8–10 .... ***Artedius creaseri***

Ventral gut pigment present; preanal myomeres 11–12 .... ***Cottus asper***

21(19) Ventral gut pigment present 22
Ventral gut pigment absent .... ***Orthonopias triacis***

22(21) ~5 parallel lines (striations) of pigment oriented horizontally on posterior gut .... ***Synchirus gilli****
No parallel lines of pigment on posterior gut 23

23(22) Two or more prominent anterior gut melanophores present 24
Anterior gut melanophores absent (or one only) 26

24(23) Dorsal head pigment absent; jaw angle pigment present 25
Dorsal head pigment present (except in larvae ~3.5 mm or smaller); jaw angle pigment usually absent .... ***Chitonotus pugetensis***

25(24) Anterior gut melanophores ~2; myomeres 33–37 .... ***Icelinus/Chitonotus***
(= not a type, but a category for ambiguous or damaged specimens that may be either *Icelinus* or *Chitonotus*)
Anterior gut melanophores ~10; myomeres 38–40 .... ***Icelinus* type A**
(= undescribed; probably *I. tenuis* based on high myomere counts (38–40))

26(23) Jaw angle (quadrate) pigment present .... ***Icelinus quadriseriatus***
Jaw angle pigment absent .... ***Icelinus/Chitonotus***

*I have not examined larvae of this type; characters were taken from the literature.

Appendix table

The following larvae have not been described and are probably unknown, which should be taken into consideration when using the key, especially if the larva(e) do not key out exactly.

Taxa	Comments
Artedius corallinus	15–16 dorsal rays; *A.* type 3?; intertidal (see Washington 1986).
Artedius notospilotus	*A.* type 3? (Washington 1986).
Icelinus burchami fuscescens	Rare; found in deep water (126–549 m); 16–18 dorsal rays.
Icelinus cavifrons	X–XI dorsal spines (>98%); IX dorsal spines (<2%).
Icelinus filamentosus	15–18 dorsal rays.
Icelinus fimbriatus	Rare; found at moderate depths (60–265 m); X–XI dorsal spines.
Icelinus oculatus	Rare; found in deep water (109–274 m); X–XI dorsal spines; 37 vertebrae.
Icelinus sp. nov.	X dorsal spines; rare?
Leiocottus hirundo	16–17 dorsal rays; recent occurrence on reefs in Santa Barbara area and Santa Cruz I., California.
Oligocottus rimensis	16–19 dorsal rays; juveniles lack 'W'-shaped pigment on side; intertidal.
Oligocottus rubellio	Juveniles lack 'W'-shaped pigment on side; intertidal.
Psychrolutes phrictus	Rare, found in deep water (839–2800 m), 22–26 pectoral rays; may = "cottoid A" (Richardson and Washington 1980).
Radulinus vinculus	Rare; southern range limit is Anacapa I.
Zesticelus profundorum	Rare; 25–26 vertebrae; deep water (88–2580 m).