DEVELOPMENT AND DISTRIBUTION OF LARVAE AND PELAGIC JUVENILES OF OCEAN WHITEFISH, *CAULOLATILUS PRINCEPS*, IN THE CALCOFI SURVEY REGION

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ABSTRACT

Ocean whitefish larvae occurred in 88 tows taken on CalCOFI plankton surveys from 1954 to 1981. The robust larvae develop a distinctive array of spines and spiny ridges in the head region. The body becomes covered with minute spines, which develop on each scale. Larvae also have a characteristic pattern of melanistic pigmentation, which makes it possible to identify early stages that have not yet developed head spines.

Larvae occurred from Ensenada (CalCOFI line 100) to Magdalena Bay (line 140) and seaward to Guadalupe Island. Occurrences were concentrated off central Baja California; only 20% of the positive tows were north of Sebastian Viscaino Bay. It is apparent from the distribution of larvae that ocean whitefish populations off southern California are recruited from Baja California.

RESUMEN

Larvas oceánicas de *Caulolatilus princeps* estuvieron presentes en 88 arrastres de plancton realizados durante el programa CalCOFI entre 1954 y 1981. Estas robustas larvas desarrollan un claro conjunto de espinas y zonas espinosas en la región de la cabeza. El cuerpo se cubre con espinas diminutas, las cuales crecen sobre cada escama. Las larvas tienen, además, un patrón de pigmentación melánico característico que permite identificar estadíos tempranos que aún no han desarrollado espinas en la cabeza

Se encontraron larvas desde Ensenada (CalCOFI línea 100) hasta Bahía Magdalena (línea 140) y mar afuera de la Isla Guadalupe. Las larvas se concentraron frente a la zona central de Baja California; sólo un 20% de los arrastres con larvas ocurrió al Norte de la Bahía Sebastián Vizcaíno. La distribución de las larvas indica que las poblaciones oceánicas de *Caulolatilus princeps* en el Sur de California son formadas por reclutas provenientes de Baja California.

INTRODUCTION

The ocean whitefish, *Caulolatilus princeps*, ranges from Vancouver Island, British Columbia, to Peru and is a prominent coastal bottomfish off southern California and Baja California (Miller and Lea 1972; Dooley 1978). Southern California commercial passenger fishing boat catch from 1972 to 1983 ranged from 11,000 to 61,000 fish per year, with an average catch of 32,000 fish for the 12-year period[1]. Ocean whitefish ranked tenth in a survey of landings of the southern California private sport fishery (Wine 1978). Commercial landings declined steadily from a catch of 100,000 pounds in 1946 to less than 2,000 pounds in 1956 and have not increased appreciably since (Fitch and Lavenberg 1971). The species is an excellent food fish, and related species in the family Malacanthidae command a high market price, especially in Japan, where they are used for sashimi (S. Kato, National Marine Fisheries Service, Tiburon, California, pers. comm.).

What little is known about the biology of *C. princeps* is summarized in Fitch and Lavenberg (1971). Fourmanoir (1970) briefly described some juveniles taken from tuna and lancetfish stomachs. Kramer and Smith (1973) briefly summarized the distribution of ocean whitefish larvae from CalCOFI surveys of 1955-60. Johnson (1984) summarized rostral spination in *Caulolatilus* larvae in comparison with other malacanthid genera. Detailed descriptions of larvae and juveniles of other malacanthid species (Okiyama 1964; Fahay and Berrien 1981; Fahay 1983) show that in its early life history stages this family is among the most highly developed of all teleosts.

Larvae of *C. princeps* are relatively rare in California Cooperative Oceanic Fisheries Investigations (CalCOFI) plankton collections; however, this may result partly from their distribution off coastal Baja California, where sampling has been relatively low. The purpose of this paper is to describe the larvae and pelagic juveniles of *C. princeps* and summarize their distribution in CalCOFI samples taken during 1954-81.

MATERIALS AND METHODS

A total of 163 *C. princeps* larvae and 8 pelagic juveniles was available for study. Larval specimens ranged from 1.7 mm NL to 7.9 mm SL, and pelagic juveniles ranged from 15.5 to 44.5 mm SL. A developmental series was established to study general morphology,

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[1]Reports of fish caught by the California commercial passenger fishing boat fleet. California Department of Fish and Game, Marine Resources Division, Long Beach.

TABLE 1
Measurements (mm) of Larvae and Pelagic Juveniles of *Caulolatilus princeps*

Station	Body length	Snout-anus length	Head length	Head width	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length
6107 123.45	2.6	1.0	0.59	0.42	0.13	0.27	0.68	0.19	0.19	—
6608 120.45	2.8	1.2	0.65	0.57	0.18	0.33	0.83	0.22	0.31	—
6608 120.45	3.0	1.6	0.80	0.56	0.24	0.33	0.86	0.21	0.37	—
5410 130.55	3.3	1.5	1.0	0.73	0.32	0.38	1.0	0.28	0.35	—
5707 120.35	3.7	1.8	1.1	0.80	0.32	0.40	1.2	0.27	0.48	—
5707 120.35	4.0	1.9	1.2	0.83	0.35	0.47	1.2	0.32	0.57	—
5907 133.45	4.2	2.0	1.2	0.95	0.30	0.48	1.3	0.33	0.62	—
6007 130.35	4.5	2.1	1.3	1.0	0.35	0.58	1.4	0.40	0.65	—
5908 123.55	4.7	2.3	1.5	1.2	0.36	0.60	1.5	0.37	0.64	0.02
5904 137.35	5.0	2.4	1.6	1.2	0.34	0.60	1.6	0.40	0.68	0.03
6107 133.35	5.3	2.7	1.7	1.2	0.30	0.65	1.8	0.50	0.69	0.05
H-5706 120.35	5.7	2.9	1.9	1.2	0.53	0.80	2.1	0.67	0.76	0.06
H-5706 120.35	6.1	3.4	2.2	1.3	0.55	0.87	2.3	0.70	0.82	0.04
5102 140.30	7.1	4.2	2.8	1.7	0.70	1.0	2.9	1.0	1.0	0.43
5302 100.30	7.9	4.7	3.1	1.8	0.93	1.2	3.2	1.3	1.0	0.71
6509 107.40	15.5	9.5	5.6	2.8	1.5	2.1	6.0	—	1.4	—
5706 130.60	16.9	10.0	5.9	3.1	1.6	2.1	6.3	3.0	1.5	2.2
5510 123.50	27.8	17.2	9.2	4.6	1.8	3.2	9.2	4.4	1.9	3.7
7510AX 130.30	33.9	18.8	10.3	5.4	2.2	3.9	10.1	5.8	2.3	4.3
6010B 117.30	44.5	25.8	12.7	6.1	3.2	4.0	12.8	7.5	2.8	6.2

Specimens between dashed lines are in the notochord flexion stage; those below the solid line are pelagic juveniles.

morphometry, and pigmentation. Additional specimens from the collection were used to define variability of these features. Subsequently, the series was stained with Alizarin Red-S and cleared in a graded series of KOH and glycerin to determine the sequence of formation of ossified fin rays, head spines, and scale patches. Most of the small specimens were poorly ossified because of calcium leaching in preservation and, for these specimens, only the appearance of unossified fin rays could be noted. The descriptive methods and terminology follow Ahlstrom et al. (1976) and Moser et al. (1977). Head spines are named for the bones from which they originate. Prior to the completion of notochord flexion, body length is measured from the tip of the snout to the tip of the notochord and is designated "NL." In postflexion specimens body length is measured to the posterior edge of the hypural plate and is termed "SL."

DESCRIPTION

General Morphology

Larvae of *C. princeps* are characterized by a robust body form and the development of larval features at a comparatively small size (Tables 1-3; Figures 1 and 2). Our smallest intact specimen (2.6 mm) has a relatively large head and a compact coiled gut with no evidence of yolk. At the beginning of notochord flexion (about 5.7 mm NL) the larva is highly robust and deep-bodied, with a massive head, triangular-shaped gut mass, and large eye. Notochord flexion is completed at about 7.0 mm SL, and this body form is maintained throughout the postflexion stage. Development of the larval morph is shown by changes in body proportions (Table 2). Relative snout-anus length, head length, head width, snout length, and body depth increase throughout the larval period. Each of these propor-

TABLE 2
Average Body Proportions (% ± Standard Deviation) for Larvae and Pelagic Juveniles of *Caulolatilus princeps*

Stage	Snout-anus length / Body length	Head length / Body length	Head width / Head length	Snout length / Head length	Eye diameter / Head length	Body depth / Body length	Pectoral fin length / Body length	Pelvic fin base depth / Body length	Pelvic fin length / Body length
Preflexion	47.2±4.05	28.8±3.25	21.6±2.66	25.9±4.30	41.1±4.46	30.6±2.06	7.9±0.70	12.6±2.25	~1.0±0.00
Flexion	53.5±3.54	34.5±2.12	21.0±0.00	26.5±2.12	41.0±1.41	37.5±0.71	11.5±0.71	13.0±0.00	1.0±0.00
Postflexion	59.0±0.00	39.0±0.00	23.5±0.71	27.5±3.54	37.5±2.12	41.0±0.00	15.0±1.41	13.5±0.71	7.5±2.12
Juvenile	59.0±2.74	32.6±3.05	16.6±1.67	24.0±3.32	36.6±3.78	33.6±3.34	17.0±0.82	7.6±1.34	13.2±0.50

TABLE 3
Sequence of Development of Head Spines in Larvae of *Caulolatilus princeps*

	Body length (mm)													
Spine	.2.6	2.8	3.1	3.3	3.7	4.0	4.4	4.7	5.0	5.3	5.7	6.1	7.1	7.9
Preopercle margin—angle	—	+	+	+	+	+	(2)	(2)	(2)	(3)	(6)	B	(6)	(11)
Preopercle margin—upper series	—	1	1	2	2	3	3	3	4	4	4	5	5	6
Preopercle margin—lower series	—	—	1	2	3	3	4	3	4	4	5	5	5	5
Preopercle ridge—upper series	—	—	—	—	—	—	—	—	—	—	1	3	2	4
Preopercle ridge—lower series	—	—	1	1	2	2	4	3	4	4	5	6	6	6
Frontal—1st transverse ridge series	—	—	1	2	3	3	5	5	4	5	6	9	9	9
Frontal—2nd transverse ridge series	—	—	—	—	1	2	3	4	4	5	5	5	8	9
Frontal—3rd transverse ridge series	—	—	—	—	—	2	3	3	3	4	5	B	9	9
Frontal—secondary transverse ridges*	—	—	—	—	—	—	—	—	1	1	2	2	5	5
Frontal—longitudinal ridge series	—	—	—	—	—	1	3	3	3	3	4	B	7	8
Frontal—anterior longitudinal ridge series	—	—	—	—	—	1	2	3	3	4	4	5	5	7
Frontal—supraocular shelf series	—	—	—	—	1	3	4	4	4	6	7	10	10	13
Posttemporal—upper series	—	—	1	3	3	3	4	4	6	7	7	9	10	12
Posttemporal—lower series	—	—	—	—	1	2	2	2	2	4	3	3	5	5
Supracleithrum series	—	—	—	—	—	1	1	1	2	2	3	3	4	5
Dentary series	—	—	—	4	3	6	6	7	6	8	9	12	11	12
Pterotic series	—	—	—	—	—	—	1	1	1	1	2	4	4	5
Interopercle series	—	—	—	—	—	—	1	2	2	2	2	2	2	3
Subopercle series	—	—	—	—	—	—	—	—	—	—	1	1	1	2
Opercle	—	—	—	—	—	—	—	—	—	—	1	1	1	1
Nasal—lateral series	—	—	—	—	—	—	—	—	1	2	3	4	6	7
Nasal—median series	—	—	—	—	—	—	—	—	—	2	3	4	4	4
Nasal—ventral series	—	—	—	—	—	—	—	—	—	—	1	1	3	3
Lacrimal—upper series	—	—	—	—	—	—	—	—	—	—	4	4	6	8
Lacrimal—lower series	—	—	—	—	—	—	—	—	—	—	3	6	6	9
Extrascapular—upper series	—	—	—	—	—	—	—	—	—	—	—	—	2	2
Extrascapular—lower series	—	—	—	—	—	—	—	—	—	—	—	—	1	2

*Number of ridges indicated, not the number of spines.
Numbers of spines in each series are listed. Spinules on preopercular angle spine are enclosed in parentheses. Symbols: + = present; B = broken.

tions, except relative snout-anus length, decreases in pelagic juveniles as the body becomes more streamlined.

Larvae of *C. princeps* develop a remarkable array of head spines. Preopercular spines develop in larvae less than 3.0 mm NL. The spine at the angle of the preopercle develops first, then spines are added above and below it throughout the larval period (Table 3; Figures 1 and 2). The angle spine develops prominent spinules late in the larval period. A second preopercular series forms on a ridge anterior to the preopercular margin.

Numerous spinous ridges develop on the frontal bone. Each begins with one or two broad-based spines and gradually adds spines to form a serrate ridge. Initially a transverse ridge forms above the eye; two additional transverse ridges form posterior to it, and two longitudinal ridges form anterior to it. Later in the larval period several secondary transverse ridges develop anterior to the original three; these curve forward to form a pattern that appears heart-shaped from dorsal view. The longitudinal ridges become aligned with the lateral ridges of the nasal bone. These series of ridges are joined anteriorly by a transverse ridge at the point of fusion of the nasal bones to form a long troughlike structure that projects beyond the upper jaw. In addition to these ridges, a spinous supraocular shelf forms at the margin of the frontal bone and projects laterally over the eye. A spinous ridge develops on the pterotic bone posterior to the supraocular shelf, and, late in the larval period, ridges develop on the extrascapular bone in the epiotic region (Table 3; Figures 1 and 2).

Ornate spinous ridges develop on the posttemporal and supracleithral bones early in the larval period. The upper series on the posttemporal forms first and becomes antlerlike at full development (Table 3; Figures 1 and 2). The lower posttemporal and supracleithral ridges are less ornate, and fuse to form a continuous structure.

Ventrally on the head, spinous ridges develop on the upper and lower margins of the lacrimal bone and along the ventral margin of the dentary bone. Two spines form on the subopercle, three form on the inter-

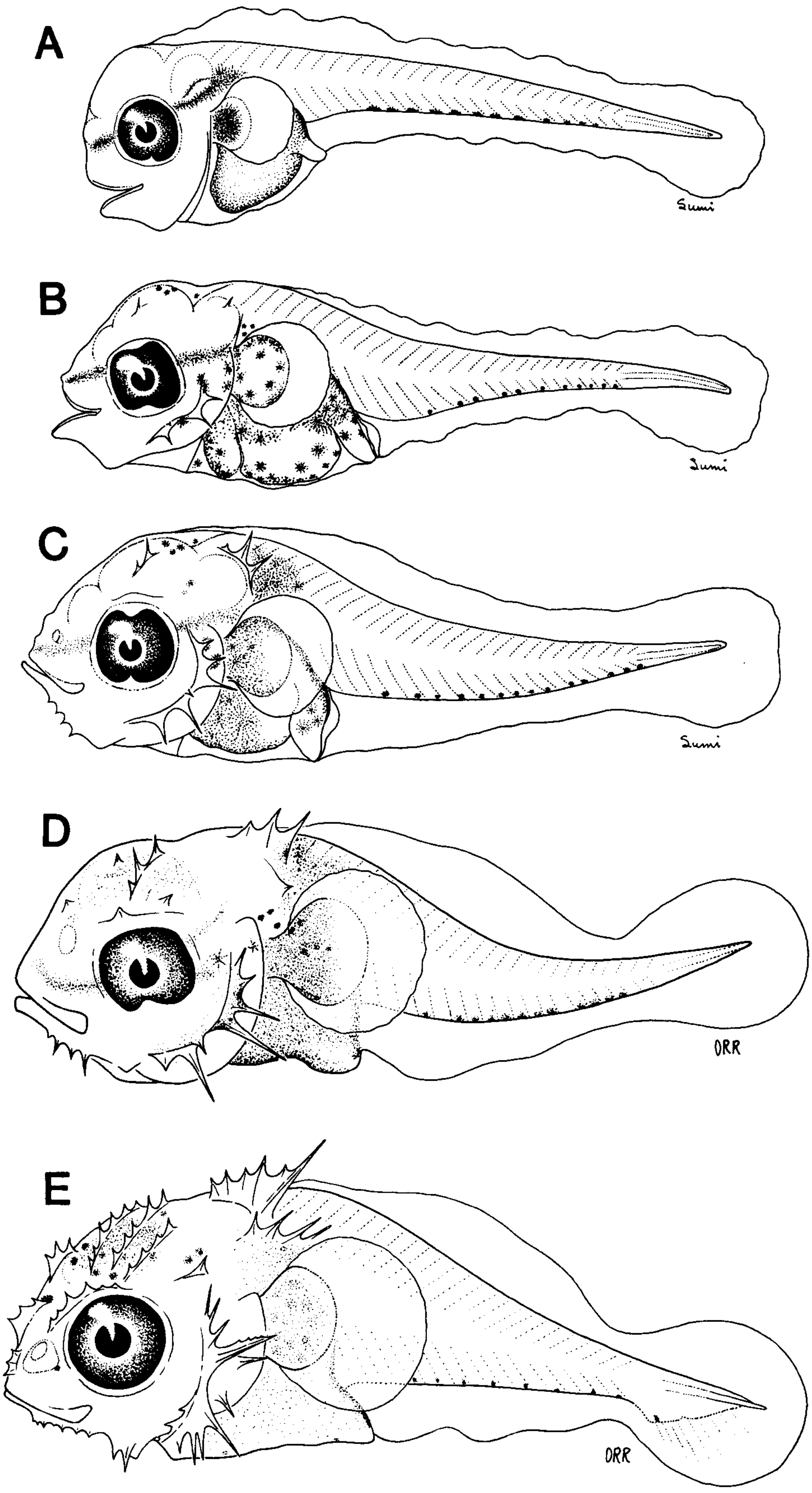

Figure 1. Preflexion larvae of *Caulolatilus princeps:* (*A*) 2.6 mm; (*B*) 3.0 mm; (*C*) 3.3 mm; (*D*) 3.8 mm; (*E*) 5.3 mm.

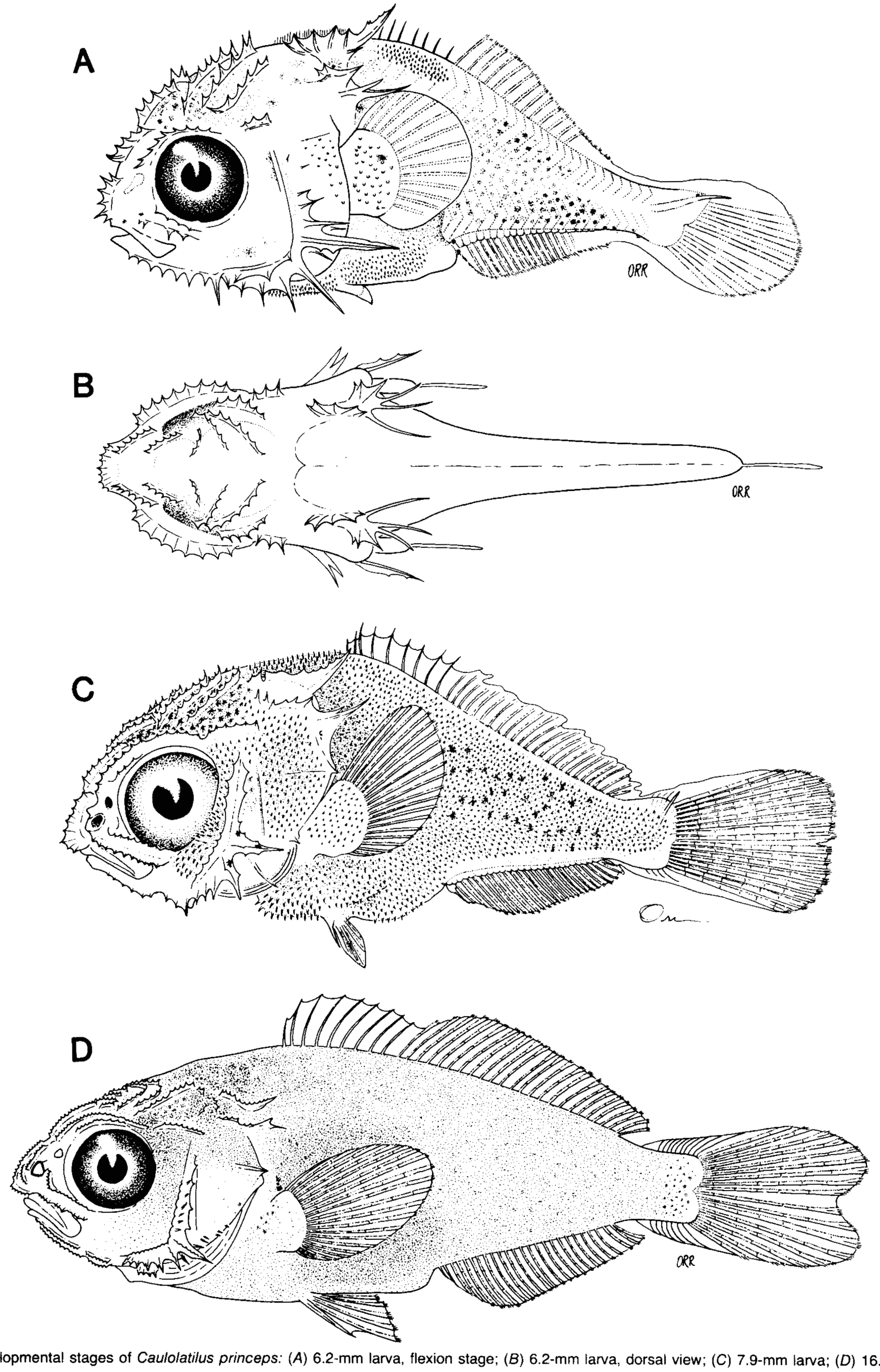

Figure 2. Developmental stages of *Caulolatilus princeps:* (*A*) 6.2-mm larva, flexion stage; (*B*) 6.2-mm larva, dorsal view; (*C*) 7.9-mm larva; (*D*) 16.8-mm pelagic juvenile.

TABLE 4
Meristics of Stained Specimens of *Caulolatilus princeps*

Length (mm)	Principal caudal fin rays Superior	Principal caudal fin rays Inferior	Procurrent caudal fin rays Superior	Procurrent caudal fin rays Inferior	Branchio-stegal rays Left	Branchio-stegal rays Right	Pectoral fin rays Left	Pectoral fin rays Right	Anal fin rays	Dorsal fin rays	Pelvic fin rays Left	Pelvic fin rays Right	Vertebrae
3.7	—	—	—	—	1	1	—	—	—	—	—	—	—
4.0	—	—	—	—	4	4	—	—	—	—	—	—	—
4.1	—	—	—	—	3	3	—	—	—	—	—	—	—
4.2	—	—	—	—	4	4	—	—	—	—	—	—	3
4.4	—	—	—	—	5	5	—	—	—	—	—	—	6
4.5	(1)	(1)	—	—	5	5	—	—	—	—	—	—	7
4.7	(1)	(1)	—	—	5	5	—	—	—	—	—	—	7
5.0	(1)	(1)	—	—	5	5	—	—	—	—	—	—	9
5.1	(4)	(4)	—	—	6	6	(6)	(5)	(7)	(VIII,4)	—	—	13
5.3	4	4	—	—	6	6	(5)	(5)	(7)	(VIII,5)	—	—	14
5.7	(6)	(6)	—	—	6	6	(7)	(7)	(I,12)	(VIII,10)	—	—	15
6.1	(8)	(7)	—	—	6	6	—	(12)	(I,17)	(IX,17)	—	—	17
7.1	9	8	—	—	6	6	12	12	II,22	IX,20	I,3	I,3	27
7.9	9	8	4	4	6	6	19	19	II,25	IX,24	I,5	I,5	—
15.5	9	8	13	11	6	6	19	19	II,25	IX,24	I,5	I,5	—
16.8	9	8	11	11	6	6	18	18	II,24	IX,25	I,5	I,5	—
17.1	9	8	12	12	6	6	19	19	II,25	IX,26	I,5	I,5	—
38.6	9	8	13	12	6	6	19	19	II,25	IX,26	I,5	I,5	—

Specimens between dashed lines are undergoing notochord flexion. Numbers in parentheses indicate unstained fin elements.

opercle, and the opercle has one. In pelagic juveniles the spines on the ridges become less prominent, but the ridges increase in number as multiple ridges develop at the supracleithral shelf, lacrimal, dentary, and preopercular bones.

In addition to head spines, larvae of *C. princeps* develop spinous scales on the head and body. These appear initially in flexion-stage larvae as patches of small conical spines lacking the ossified scale. Flexion-stage larvae develop the following patches: (1) a linear patch on each side of the nape, (2) a linear patch on each side of the spinous dorsal fin, (3) a patch on the opercle, (4) one on the outer surface of the pectoral fin base, (5) one on the ventral midline posterior to the isthmus, (6) a rounded patch on the posteroventral surface of the gut, (7) an elongate patch on the trunk extending posteriad along the midlateral region of the tail. All of these patches enlarge in postflexion larvae, and the supporting scales become ossified. The patches at the nape and fin base enlarge to fill in the body region above the lateral line; the trunk patch enlarges to fill in the area below the lateral line. The gut patch extends anteriad and dorsad to cover the gut area, and the ventral midline patch expands in a broad triangular shape to cover that region. A patch also forms on the cheek posterior to the eye.

In early pelagic juveniles the entire body is covered with scales that have one to several spines located on their posterior regions. The head is also covered, except for the frontal ridge region and the ventral region. In late-stage pelagic juveniles each scale has typically 4-6 spines in a cluster at the posterior central region of the scale.

Fin Formation/Meristics

The first elements to ossify are the branchiostegal rays at about 3.7 mm NL (Table 4). Specimens larger than 5.0 mm NL have the full complement of 6 branchiostegal rays. The sequence of initial ossification of fin rays could not be determined because of calcium leaching during preservation; however, the appearance of unstained rays could be noted, and these are indicated in Table 4. Principal caudal rays appear at about 4.5 mm NL, and the full complement of 9 + 8 rays is present in early preflexion larvae. Procurrent caudal rays begin forming late in the postflexion stage; the full complement is formed in pelagic juveniles (Table 4). Dorsal and anal fin rays appear in 5-mm larvae, and the full complements (D. VIII-IX, 23-26; A. I-II, 23-25) are present in our largest larva (7.9 mm SL).

The pectoral fins have a large rounded base and blade in preflexion larvae. Rays begin to form in 5-mm larvae and are fully formed by the end of the larval period. The pelvic fins are the last to develop and are fully formed in postflexion larvae (Table 4). Vertebrae begin to ossify in 4-mm larvae; all centra (27) are ossifying by the end of the notochord flexion.

Pigmentation

The melanistic pigment pattern present on the smallest larvae of *C. princeps* persists throughout most of the larval period. Melanophores cover all surfaces of the gut and continue dorsally and internally to the anterior region of the trunk (Figure 1). The trunk pigment continues internally through the otic region to the base of the neurocranium and extends forward to the snout. Before the larvae reach 3.0 mm NL, melanophores appear on the nape region, the lateral and medial surfaces of the pectoral fin base, the preopercular-opercular region, the cardiac region, and on the optic and cerebellar lobes of the brain. Pigment on all of these regions intensifies during the remainder of the larval period.

A postanal series of melanophores along the ventral midline is present in the smallest larvae available (Figure 1). The series begins on the third to fifth postanal myomere and extends posteriad to the caudal fin anlage. There are typically 11-14 melanophores in the series; occasional specimens have as few as 9. At the end of the preflexion stage, the hypaxial musculature begins to mask the anterior melanophores in the series; coalescence further reduces the number so that they are not visible in specimens larger than 7.0 mm SL.

The principal change in pigmentation during later larval stages is the gradual posteriad extension of the trunk pigment to cover the entire body. This begins at about 5.0 mm NL, when the region dorsal to the gut becomes covered with large melanophores. This melanistic sheath extends posteriad to about half the distance to the caudal fin in flexion-stage larvae. The pigment sheath covers the entire body posteriad to the hypural region in the largest larva (7.9 mm SL). At this stage only the ventral region of the head and the jaws are unpigmented. The hypural region is fully pigmented in 40-mm juveniles.

DISTRIBUTION

A total of 88 occurrences of *C. princeps* larvae can be documented for CalCOFI plankton surveys during 1954-81. All but 10 of these are from the 1954-69 period, when coverage of the stations off central and southern Baja California was most complete. Ocean whitefish larvae were not identified in survey collections from 1951 through 1953; however, 7 large larvae were found in these collections during the present study. The paucity of occurrences in the surveys of 1972, 1975, and 1978 reflects the limited station coverage in central and southern Baja California during the summer months.

Larvae of *C. princeps* were taken as far north as Ensenada, Baja California, (CalCOFI line 100) and south to Magdalena Bay, Baja California, (CalCOFI line 140). Lack of larvae from stations south of line 140 reflects the infrequent occupancy of stations on CalCOFI lines 143-157. The fact that only 20% of the occurrences were north of Sebastian Viscaino Bay emphasizes the warm-water affinity of ocean whitefish. Larvae were concentrated in a band within about 100 miles of the coast, although some were found at nearly twice that distance—as far seaward as station 70 on some lines (Figure 3). Pelagic juveniles were even more closely associated with the coast.

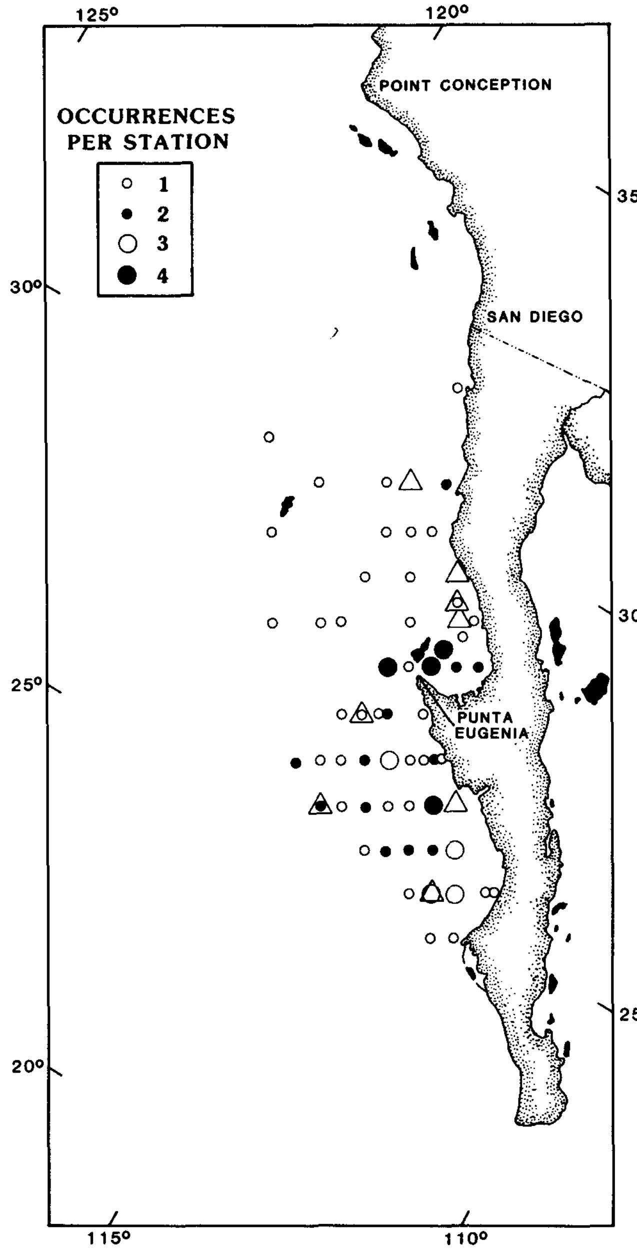

Figure 3. Pooled numbers of occurrences of *Caulolatilus princeps* larvae (circles) and pelagic juveniles taken in standard CalCOFI tows from 1954 to 1981. Triangles indicate single occurrences of pelagic juveniles.

Larvae occurred principally in summer: 33% of the occurrences were in July, 25% in August. Larvae were taken in all other months except December, with the number of occurrences ranging from two to eight. Juvenile occurrences were highly clustered seasonally, with 6 of the 8 specimens coming from October cruises.

The number of specimens per tow was small ($\bar{x}$ = 1.85 ± 2.69SD), with 72% of the positive tows represented by a single larva. Larval size ranged from 1.7 mm NL to 7.9 mm SL ($\bar{x}$ = 4.3 mm NL ± 1.093SD), with a paucity of postflexion specimens: only 9 of the 126 measured specimens were larger than 6.0 mm SL. The 8 pelagic juveniles were taken on separate tows; their length measurements were 15.5, 16.8, 17.1, 27.8, 33.9, 38.6, 43.2, and 44.5 mm SL.

It is apparent from the distribution of ocean whitefish larvae that populations in southern California, and perhaps northern Baja California, are recruited from central and southern Baja California. This pattern is seen in other transboundary species like white seabass, yellowtail, and bonito. Although ocean whitefish larvae do not occur off southern California, adults of this population may contribute to production of larvae off central and southern Baja California by periodic migration. Alternatively, they may spawn unsuccessfully in southern California or may be reproductively inactive. A study of the seasonal changes in the gonads of southern California ocean whitefish could solve a part of this puzzle.

ACKNOWLEDGMENTS

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