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**Development of Kelp Rockfish,
Sebastes atrovirens (Jordan and
Gilbert 1880), and Brown Rockfish,
S. auriculatus (Girard 1854), from
Birth to Pelagic Juvenile Stage, with
Notes on Early Larval Development
of Black-and-yellow Rockfish,
S. chrysomelas (Jordan and
Gilbert 1880), Reared in the
Laboratory (Pisces: Sebastidae)**

William Watson
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Abstract—Larval kelp (*Sebastes atrovirens*), brown (*S. auriculatus*), and black-and-yellow (*S. chrysomelas*) rockfish were reared from known adults, to preflexion stage, nine days after birth for *S. chrysomelas*, to late postflexion stage for *S. atrovirens*, and to pelagic juvenile stage for *S. auriculatus*. Larval *S. atrovirens* and *S. chrysomelas* were about 4.6 mm body length (BL) and *S. auriculatus* about 5.2 mm BL at birth. Both *S. atrovirens* and *S. auriculatus* underwent notochord flexion at about 6–9 mm BL. *Sebastes atrovirens* transform to the pelagic juvenile stage at about 14–16 mm BL and *S. auriculatus* transformed at ca. 25 mm BL. Early larvae of all three species were characterized by melanistic pigment dorsally on the head, on the gut, on most of the ventral margin of the tail, and in a long series on the dorsal margin of the tail. Larval *S. atrovirens* and *S. auriculatus* developed a posterior bar on the tail during the flexion or postflexion stage. In *S. atrovirens* xanthic pigment resembled the melanistic pattern throughout larval development. Larval *S. auriculatus* lacked xanthophores except on the head until late preflexion stage, when a pattern much like the melanophore pattern gradually developed. Larval *S. chrysomelas* had extensive xanthic pigmentation dorsally, but none ventrally, in preflexion stage.

All members of the *Sebastes* subgenus *Pteropodus* (*S. atrovirens*, *S. auriculatus*, *S. carnatus*, *S. caurinus*, *S. chrysomelas*, *S. dalli*, *S. maliger*, *S. nebulosus*, *S. rastrelliger*) are morphologically similar and all share the basic melanistic pigment pattern described here. Although the three species reared in this study can be distinguished on the basis of xanthic pigmentation, it seems unlikely that it will be possible to reliably identify field-collected larvae to species using traditional morphological and melanistic pigmentation characters.

Development of Kelp Rockfish, *Sebastes atrovirens* (Jordan and Gilbert 1880), and Brown Rockfish, *S. auriculatus* (Girard 1854), from Birth to Pelagic Juvenile Stage, with Notes on Early Larval Development of Black-and-yellow Rockfish, *S. chrysomelas* (Jordan and Gilbert 1880), Reared in the Laboratory (Pisces: Sebastidae)

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Introduction

Approximately 65 species of the viviparous rockfish genus *Sebastes* (Boehlert and Yoklavich, 1984; Moser, 1996b) occur in California waters (Eschmeyer et al., 1983; Eitner et al., 1999). Most are important sport and/or commercial fishery species (e.g., Lenarz, 1987; Lea et al., 1999; Aseltine-Neilson, 2000). A live-fish fishery that targets nearshore species, especially rockfishes, developed in the 1980s and has grown greatly (e.g., Walters, 2001). Many of the rockfishes targeted by this fishery are members of the *Sebastes* subgenus *Pteropodus*, which includes kelp (*S. atrovirens*), brown (*S. auriculatus*), gopher (*S. carnatus*), copper (*S. caurinus*), black-and-yellow (*S. chrysomelas*), calico (*S. dalli*), quillback (*S. maliger*), china (*S. nebulosus*), and grass (*S. rastrelliger*) rockfish (Hubbs and Schultz, 1933; Seeb, 1998). The effect of the fishery on stocks of the nearshore species is largely unknown, but it is not unreasonable to suppose that the depletion observed for other *Sebastes* species (e.g., Love et al., 1998; Ralston, 1998; Moser et al., 2000) may occur for these species as well. The

nearshore species recently were identified as requiring immediate fishery management attention, and they are included in the California Nearshore Fishery Management Plan of 2002 (Walters, 2001).

Management of nearshore stocks requires information on population sizes; however, fishery-dependent data on population trends have not been reliable (e.g., McKee-Lewis, 1998; Walters, 2001). Ichthyoplankton can provide a fishery-independent measure of population trends (e.g., Moser and Watson, 1990; Moser et al., 2000), and has been demonstrated to be a useful tool for estimating population size (e.g., Lasker, 1985; Ralston et al., 2003). For ichthyoplankton to be useful it must be possible to identify the larvae. *Sebastes* larvae are difficult to identify to species (e.g., Moser, 1996b) and currently no nearshore species is identified in ichthyoplankton samples. Published descriptions of complete larval development are available for only two of the *Pteropodus* species: *S. dalli* (Moser and Butler, 1981) and *S. rastrelliger* (Moreno, 1993; Laidig and Sakuma, 1998). Descriptions of partial developmental series are avail-

able for seven species: *S. atrovirens* (Moreno, 1993), *S. auriculatus* (DeLacy et al., 1964; Stahl-Johnson, 1985; Kendall¹), *S. carnatus* (Moreno, 1993), *S. caurinus* (DeLacy et al., 1964; Stahl-Johnson, 1985; Kendall¹), *S. chrysomelas* (Wold²), *S. maliger* (DeLacy et al., 1964; Kendall¹), and *S. nebulosus* (Kendall¹). However, the existing literature provides no characters that allow identification of larvae to species through all developmental stages. The purpose of this paper is to provide additional information on development of *S. auriculatus* and *S. atrovirens* from birth to pelagic juvenile stage, and early development of *S. chrysomelas*, based on laboratory-reared specimens. These are compared with larvae of the other *Pteropodus* species.

Materials and methods

Live adult *S. atrovirens* and *S. chrysomelas* were collected at San Miguel Island and *S. auriculatus* were collected near Point Conception, California, in March 1999. All fish were caught inshore (< 25 m depth) with hook and line or by SCUBA divers using dip nets. The fish were maintained aboard ship in two 500-l tanks with flow-through (19 l/min) ambient seawater (12–15°C), and transported to the laboratory in those tanks with the water inlets and outlets closed. In the laboratory the fish were held in 1700-l tanks with sand-filtered, UV-treated, flow-through (19 l/min) chilled seawater (11±1°C). Obviously gravid females (three *S. atrovirens*, one *S. auriculatus*) were isolated in separate, flow-through (7.5 l/min, 11±1°C) fiberglass tanks (360–680 l) that drained into fine-mesh (0.333 mm) collector baskets. All fish were fed to satiation twice weekly with thawed anchovy and squid, and formulated fish pellets (Bio-Oregon brood, 12 mm). The isolated, gravid females showed no interest in feeding until after parturition.

An *S. chrysomelas* and an *S. auriculatus* extruded larvae aboard ship. The larvae were placed in 5-l beakers (~ 300 larvae/l) maintained in water baths at 11.5°C (±0.5°C) with Lauda chillers (model RMS6). A small aquarium air pump provided light aeration and fluorescent lighting in the ship's wet lab provided constant illumination. Larvae were fed copepod eggs and microplankton, but insufficient quantities were available and the larvae survived only 4–5 days after yolk exhaustion.

In the laboratory larvae were gently manually expressed from one of the gravid *S. atrovirens* and the gravid *S. auriculatus*. The other two gravid *S. atrovirens* eventually released larvae naturally between noon and 3 PM for one, and sometime between 3:30 PM and 6:30 AM for the other. Manually expressed larvae were caught in 19-l buckets filled with 11°C seawater. Naturally spawned larvae were retained in the collector baskets and also were collected by partially draining the tanks and scooping larvae into 19-l buckets. All larval rearing was in static systems. Some larvae were stocked at ~ 200 larvae/l in black-plastic-wrapped, 5-l beakers in water baths cooled to 11°C with Lauda chillers. Others were stocked at ~ 50 larvae/l in various 19-l containers in a large water bath cooled to 11°C with an in-line titanium chiller (Aquanetics model AFC-4B). Fluorescent ceiling lights provided constant illumination, dimmed 16 h/day when containers were partially covered. Light aeration was provided to each rearing container with a thin pipette attached to an aquarium air pump (Tetra model G-M). Detritus and moribund or dead larvae were siphoned from each container and ~ 5–20% of the water exchanged with fresh seawater at about 1–2 day intervals. Streptomycin and penicillin (Sigma Chemical Co.) were added at a dosage of 50mg/l each as a prophylactic treatment at about 10–12 day intervals.

From the day after parturition through notochord flexion, larvae were fed about daily with the marine rotifer *Brachionus plicatilis*, reared on algae (*Tetraselmis* spp.). Wild plankton, predominantly copepod naupliar and copepodite stages and mollusc veligers, was added at irregular intervals, usually 2–3 times per week, depending on availability. Plankton was collected at the Scripps Institution of Oceanography pier using a 0.04 mm-mesh net. Plankton was filtered through a 0.15 mm-mesh sieve and the 0.04–0.15 mm fraction was fed to the larvae. Beginning late in the preflexion stage brine shrimp (*Artemia salina*) nauplii (Argent Labs) enriched with "HUFA" (Salt Creek, Inc.) were added to the diet, and the upper size limit of the wild plankton was increased to 0.3 mm. After notochord flexion, *Artemia* was the primary food, supplemented by wild plankton when available. *Tetraselmis* was added to the rearing containers occasionally to feed the prey organisms. Food densities varied according to availability, usually within the ranges of 5–12 *Brachionus*/ml, 5–10 *Artemia*/ml, and 4–6 plankters/ml. The 19-l rearing containers were of three different colors (white, blue, black). Larvae in white containers did not feed successfully and none survived more than a few days after yolk absorption. Feeding was observed in the blue and black containers, but survival was poor in the black containers and only modest in the blue containers. Survival in the 5-l beakers also was modest.

For the descriptive series 1–100 larvae (usually 1–3) were collected at intervals of ~ 1–2 days during the first

¹ Kendall, A. W., Jr. 1989. Additions to knowledge of *Sebastes* larvae through recent rearing. U.S. Dep. Commer. NOAA, NMFS, NWAFC Processed Report 89-21, 46 p. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115.

² Wold, L. 1991. A practical approach to the description and identification of *Sebastes* larvae. Unpubl. M.Sc. Thesis, Calif. State Univ., Hayward, 88 p. California State University, Hayward, 25800 Carlos Bee Blvd., Hayward, CA 94542.

two weeks and ~1–2 weeks thereafter. Specimens were preserved immediately in 2% sodium borate-buffered formalin. Totals of 96 *S. atrovirens* (4.4–14.6 mm, preflexion–late postflexion stage), 70 *S. auriculatus* (5.0–25.6 mm, preflexion–pelagic juvenile stage), and 110 *S. chrysomelas* (4.4–5.4 mm, preflexion stage) were used for description. Ten field-collected *S. atrovirens*, obtained from the Scripps Institution of Oceanography Marine Vertebrates Collection (SIO H51-239:14.4–23.7 mm, late postflexion–pelagic juvenile stage), were examined to complete that series. Other species examined for comparison were 20 *S. caurinus* (4.6–5.8 mm, preflexion stage) and 20 *S. rastrelliger* (4.8–6.4 mm, preflexion stage), reared at the Southwest Fisheries Science Center (SWFSC) experimental aquarium.

Most specimens were measured to the nearest 0.04 mm using a Wild M-5 binocular microscope equipped with an ocular micrometer (a few moribund, shrunken larvae were used only for pigment descriptions). Dimensions measured were body length (BL), preanal length (PAL), head length (HL), head width (HW), snout length (SnL), eye diameter (ED), body depth (BD), pectoral (P_1L) and pelvic (P_2L) fin lengths, and the lengths of several head and pectoral girdle spines. These included: the two longest preopercular (PPO2, PPO3), upper and lower opercular (UOP, LOP), interopercular (IOP), parietal (PA), nuchal (NU), tympanic (TM), pterotic (PT), preocular (PRO), postorbital (PSO), first and second lower infraorbital (LIO1, LIO2), nasal (NA), upper and lower posttemporal (UPST, LPST), and supracleithral (SC) spines (Fig. 1). Spine terminology follows Moser and Ahlstrom (1978); dimensions are defined by Moser (1996a). Larval lengths always refer to BL of preserved larvae. Seven *S. atrovirens*, measured immediately after preservation and again 30–60 days later when all measurements for the descriptions were made, shrank an average 2% (range 0–5%) during the interval. Nine *S. atrovirens* (4.4–14.6 mm) and six *S. auriculatus* (4.8–25.6 mm) were lightly stained with alizarin red S to aid in determining sequences of fin-ray and head spine formation. Occasionally, live or freshly preserved specimens (50 *S. atrovirens*, 62 *S. auriculatus*, 58 *S. chrysomelas*, mostly preflexion stage) were examined to document xanthophore patterns. Illustrations were made with the aid of a camera lucida.

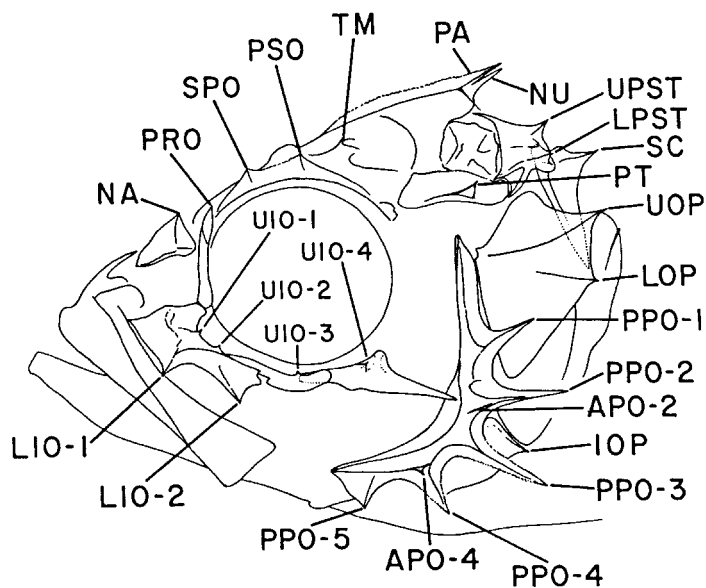


Figure 1

Locations of head spines referred to in the larval descriptions (modified from Ahlstrom and Moser, 1978). Abbreviations are: APO, anterior preopercular; IOP, interopercular; LIO, lower infraorbital; LOP, lower opercular; LPST, lower posttemporal; NA, nasal; NU, nuchal; PA, parietal; PPO, posterior preopercular; PRO, preocular; PSO, postocular; PT, pterotic; SC, supracleithral; SPO, supraocular; TM, tympanic; UOP, upper opercular; UPST, upper posttemporal.

Description

Kelp rockfish (*Sebastes atrovirens*)

Morphology Larval *S. atrovirens* were 4.4–4.9 mm at birth (mean, mode = 4.6 mm) and began notochord flexion at 6.1–6.9 mm, 32–49 days later (11.4–12.0°C). Flexion was completed just after 8.6 mm, ~60 days after birth. The largest reared specimen, 14.6 mm, was late postflexion stage; among the field-collected specimens, one (14.4 mm) was transformation stage, one (15.5 mm) was late postflexion stage, and the remainder (15.6–23.7 mm) were pelagic juveniles.

Larvae were moderately slender at birth, with a rounded head, short snout, short preanal length, and sac-like integument enclosing the trunk and anterior part of the tail (Table 1; Figs. 2A, 3A). A little yolk and/or single oil globule were present at birth; absorption was completed 2–10 days later. The sub-dermal space gradually deflated during preflexion stage, and most body proportions gradually increased relative to BL throughout larval development (Table 1). Larvae had 25–26 myomeres (97% with 26): 6–8 preanal + 16–20 postanal (83% with

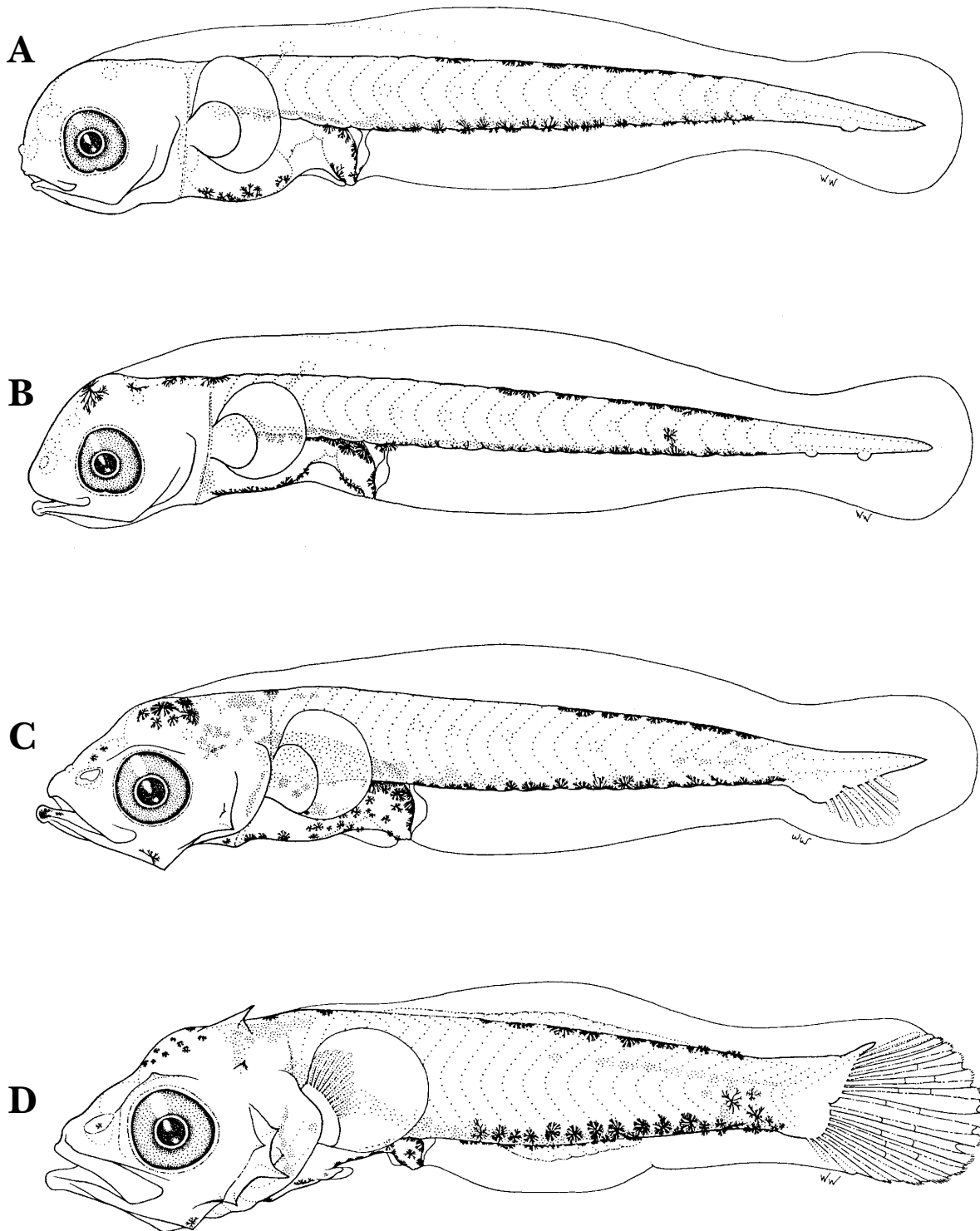


Figure 2

Kelp rockfish, *Sebastes atrovirens*, lateral view. (A) 4.6 mm preflexion stage, day 1; (B) 4.6 mm preflexion stage, day 23; (C) 6.9 mm early flexion stage, day 52; (D) 8.0 mm mid-flexion stage, day 58; (E) 8.6 mm early postflexion stage, day 80; (F) 14.6 mm late postflexion stage, day 82; (G) 14.4 mm field-collected pelagic juvenile (SIO H51-239). Neuromasts are shown (with dotted lines) only on the preflexion-stage larvae.

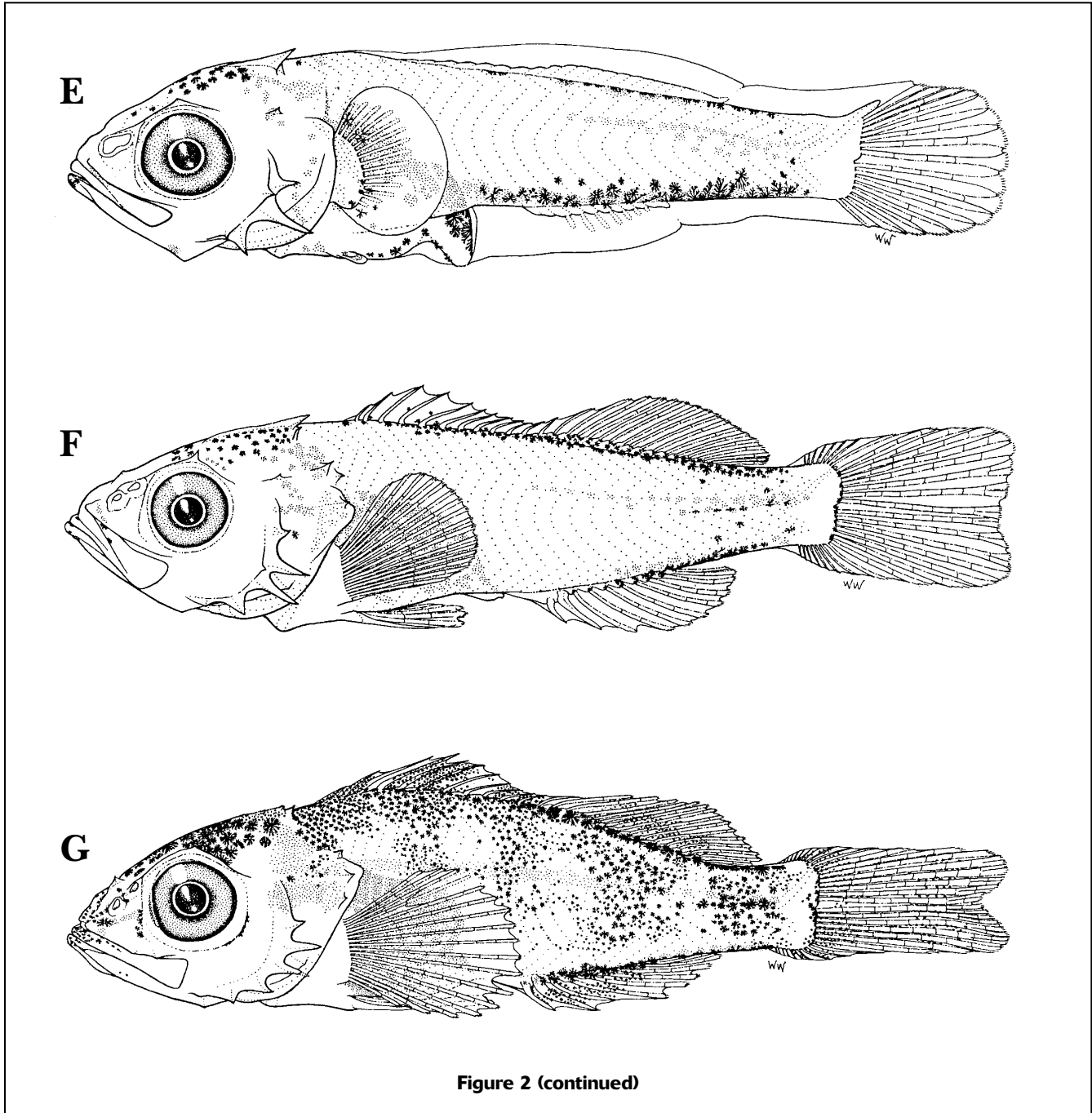


Figure 2 (continued)

7 + 19) through flexion stage, shifting to 12 + 14 by late postflexion stage.

Formation of the head spines began late in the preflexion stage (5.7 mm) with a preopercular spine (PPO3) at the angle of the posterior margin (Table 2). A much smaller spine (APO2) formed above and anterior to PPO3 at the end of preflexion stage. Simultaneously, or early in flexion stage (6.7–8.0 mm), a second posterior preopercular spine (PPO2) formed above PPO3. The third (lower) posterior spine (PPO4) formed by 7.1 mm

and the second anterior spine (APO4) formed by 8 mm. The last two preopercular spines, near its upper (PPO1) and lower (PPO5) ends, formed during postflexion stage by 11.9 and 14.6 mm, respectively. PPO3 was largest until mid- to late postflexion stage (ca. 11.9–14.6 mm), when PPO2 became nearly as long. In pelagic juveniles PPO2 was the longest spine (by ~ 20 mm), resulting from regression of PPO3. A small interopercular spine, which formed late in flexion stage, lacked a free distal end in some larvae and most pelagic juveniles.

Table 1

Summary of measurements of kelp rockfish, *Sebastes atrovirens*, given as percentages of body length in 1 mm size classes. For each measurement mean values are given above, ranges below; n = number of specimens. Notochord flexion occurs within the 6.1–9.0 mm size classes; all but one of the specimens > 15.0 mm are pelagic juveniles (15.5 mm specimen = postflexion larva).

Size range	n	PAL	BD	HL	HW	SnL	ED	P ₁ L	P ₂ L
4.1–5.0	71	37 36–43	18 14–20	20 18–23	11 10–14	4 3–7	7 7–8	5 3–7	0
5.1–6.0	4	41 40–43	18 17–19	24 22–26	13 11–16	6 5–8	8 7–9	6 5–7	0
6.1–7.0	6	41 40–43	17 11–20	26 24–28	14 13–15	7 5–9	9 8–10	7 6–7	0.1 0–0.3
7.1–8.0	2	44 43–45	23 21–24	29 27–30	15 14–17	7 7–7	10 9–10	8 8–8	1 1–1
8.1–9.0	1	51	26	31	17	8	11	10	1
11.1–12.0	1	54	27	34	22	12	11	13	10
14.1–15.0	2	55 55–56	27 26–27	33 31–34	16 15–18	10 9–11	11 10–11	20 18–22	15 13–16
15.1–16.0	3	57 56–58	27 27–28	35 34–35	15 14–15	12 11–12	11 10–11	21 21–22	17 16–18
17.1–18.0	1	57	27	34	15	10	11	23	18
20.1–21.0	1	59	27	34	15	10	10	27	20
21.1–22.0	3	59 58–59	28 28–29	34 33–35	15 15–15	9 9–10	11 10–11	27 26–28	19 19–20
23.1–24.0	1	59	29	33	15	10	10	26	19

Table 2

Summary of measurements of kelp rockfish, *Sebastes atrovirens*, head and pectoral girdle spines given as percentages of head length, in 1 mm size classes. For each measurement, mean values are given above, ranges below; n = number of specimens. Notochord flexion occurs within the 6.1–9.0 mm size classes; all but one of the specimens > 15.0 mm are pelagic juveniles (15.5 mm specimen = postflexion larva).

Size range (mm)	n	PPO2	PPO3	UOP	LOP	IOP	PA	NU	PT	PRO	PSO	LIO1	LIO2	NA	LPST	SC
4.1–5.0	71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5.1–6.0	4	0	1 0–1	0	0	0	0	0	0	0	0	0	0	0	0	0
6.1–7.0	6	0.3 0–2	5 2–6	0	0	<0.1 0–0.5	1 0–2	0	1 0–1	0	0.2 0–1	0	0	0	0	0
7.1–8.0	2	4 2–6	10 4–15	0	0	0.2 0–0.4	5 3–7	0	2 2–2	0	0	0	0	0	0	0
8.1–9.0	1	7	25	0	0	0	10	0	3	0	2	0	0	0	0	0
11.1–12.0	1	15	20	0	0	0.4	12	1	2	0	2	0	0	0	4	2
14.1–15.0	2	13 13–14	15 13–17	1 1–2	0.4 0–1	0.4 0.4–0.4	6 3–10	3 1–4	1 0–2	0	0.4 0–1	1 0–1	1 0–2	1 1–2	3 3–4	3 3–4
15.1–16.0	3	12 12–13	15 14–15	2 2–3	1 1–2	0.1 0–0.4	2 0.4–4	2 1–3	0	0	0	0.5 0–1	1 0.4–1	1 1–1	2 2–3	3 2–4
17.1–18.0	1	12	10	3	2	1	0.3	1	0	0	0	1	1	2	1	2
20.1–21.0	1	10	5	4	3	0	0	2	0	0.3	1	1	1	2	1	3
21.1–22.0	3	12 12–13	8 7–9	3 3–4	2 1–3	0.1 0–0.3	0	2 1–2	0	0.3 0–1	1 1–2	0.4 0–1	0.5 0.3–1	2 1–3	1 1–2	2 1–2
23.1–24.0	1	9	7	5	3	0	0	2	0	0.1	1	1	1	2	2	1

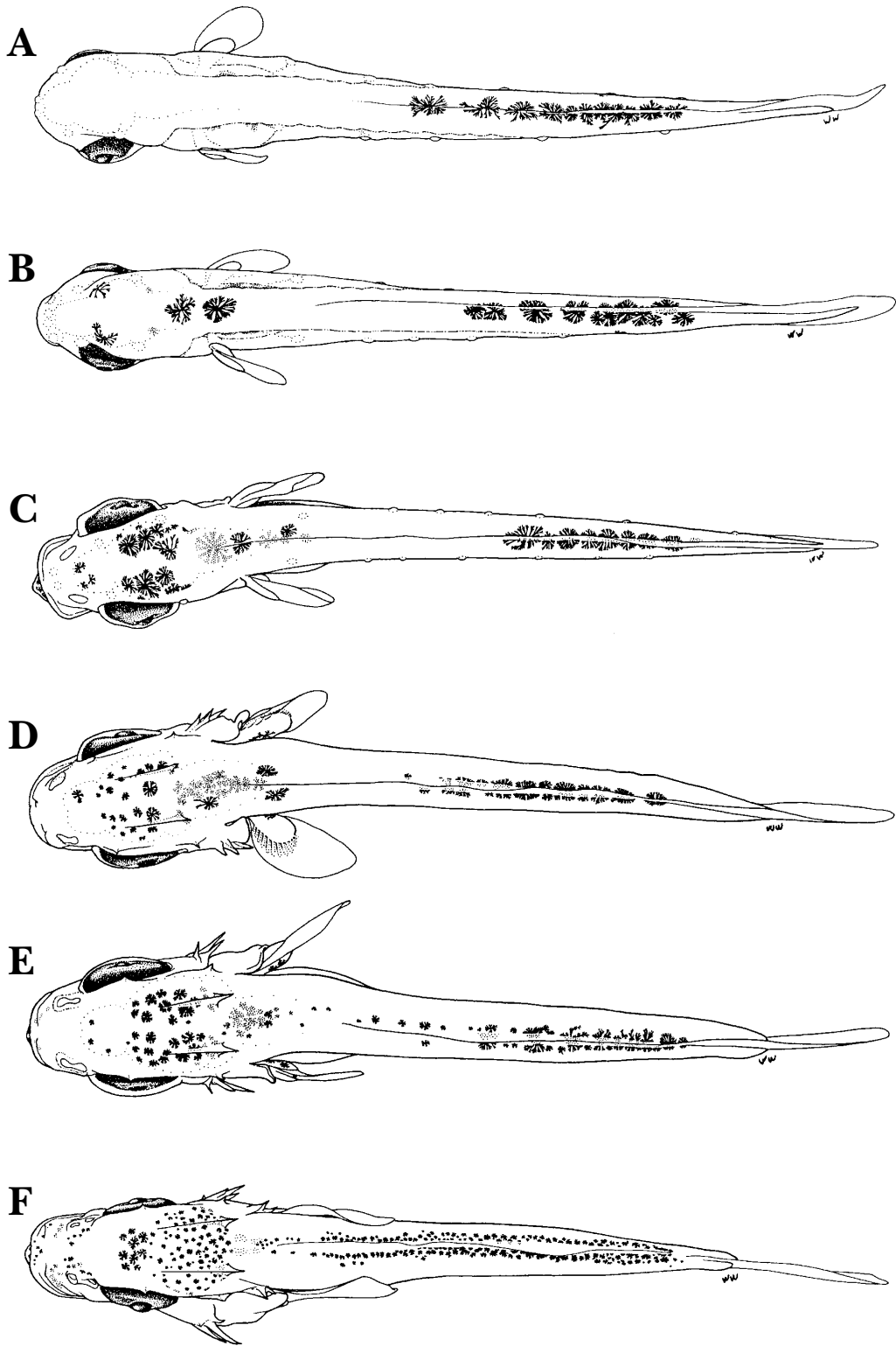


Figure 3

Kelp rockfish, *Sebastes atrovirens*, dorsal view. (A) 4.6 mm preflexion stage, day 1; (B) 4.6 mm preflexion stage, day 23; (C) 6.9 mm early flexion stage, day 52; (D) 8.0 mm mid-flexion stage, day 58; (E) 8.6 mm early postflexion stage, day 80; (F) 14.6 mm late postflexion stage, day 82. Neuromasts are shown only on the preflexion-stage larvae.

Table 3

Fin-ray counts of reared kelp rockfish, *Sebastes atrovirens*. Abbreviations for fin rays are: D = dorsal, A = anal, P₁ = pectoral, P₂ = pelvic, C_{PRO} = principal caudal, C_{PRO} = procurrent caudal. Abbreviations for developmental stages are: Pr = preflexion, F = flexion, Po = postflexion.

BL (mm)	Stage	D	A	P ₁	P ₂	C _{PRO}	C _{PRO}
4.4	Pr (early)	0	0	0	0	0	0
5.4	Pr (mid)	0	0	0	0	0	0
5.0	Pr (late)	0	0	2	0	2 + 2	0
6.4	F (early)	0	0	6	buds	5 + 5	0
6.3	F (mid)	0	Anlage	—	buds	8 + 7	0
8.4	F (late)	anlage	Anlage	8	buds	8 + 7	0 + 1
8.8	Po (early)	anlage	5	12	3	8 + 7	2 + 3
11.2	Po (mid)	XIII, 14	III, 7	17	I, 5	8 + 7	5 + 6
14.6	Po (late)	XIII, 15	III, 7	16	I, 5	8 + 7	8 + 9

A small upper opercular spine formed late in postflexion stage, and transforming and pelagic juvenile specimens also had a smaller, lower opercular spine.

A short, low pterotic ridge formed on the otic capsule during late preflexion or early flexion stage (5.6–6.6 mm). A small pterotic spine formed on the ridge during flexion stage (6.1–7.1 mm) and persisted until late postflexion stage, but was absent in the pelagic juveniles. A pair of low, smooth parietal ridges formed during late preflexion or early flexion stage (5.7–ca. 6.9 mm) and became finely serrate by 11.9 mm. A parietal spine formed posteriorly on each ridge during late preflexion to mid-flexion stage (5.9–7.1 mm) and a small nuchal spine formed just behind each parietal spine by 11.9 mm. The parietal spine regressed during pelagic juvenile stage and by ~20 mm the nuchal spine was the only posterior spine on each parietal ridge. The postocular spine formed above the eye during notochord flexion at ca. 6.7–7.1 mm, and a smaller preorbital spine was present in pelagic juveniles ≥ ca. 21 mm. A lower infraorbital spine (LIO1) formed anteriorly on the lachrymal in some larvae ≥ 11.9 mm. Most pelagic juveniles had two lower infraorbital spines, but in some only the posterior spine (LIO2) was present. A pair of nasal spines formed at the end of the larval stage. Single supracleithral and posttemporal spines formed during postflexion stage, by 11.9 mm.

The principal caudal-fin rays formed first, beginning late in preflexion stage at 5.0–5.5 mm. The full complement (8+7) was completed late in flexion stage (ca. 8–8.5 mm), followed by formation of procurrent rays. These were added anteriorly from the last ray, and the full complement (10–11 + 9–11) was present by pelagic juvenile stage (Table 3). Pectoral-fin rays formed during late preflexion or early flexion stage, beginning at ~5–6 mm; addition of rays was ventrad and the full complement (16–18) was present in postflexion stage,

by 11.2 mm. Pelvic-fin buds formed during flexion stage at ca. 6.4–8.0 mm and rays formed in postflexion stage, beginning near 8.6 mm, with the full complement (I,5) present by 11.2 mm. Dorsal- and anal-fin anlagen formed during flexion stage, by ca. 8 mm, and segmented anal-fin rays formed late in the stage, by ca. 8.8 mm. Anal-fin spines and dorsal spines and segmented rays formed during postflexion stage; full complements (D: XIII, 13–15; A: III, 6–7) were present in both fins by 11.2 mm.

Pigmentation: Melanophores Larvae were moderately pigmented at birth (Figs. 2–4). Most lacked melanophores on the head and trunk (13% with a melanophore or two over the hindbrain, 18% with some on the trunk) but all had rows of melanophores dorsally and ventrally on the tail: usually 8–11 in a single dorsal row extending from myomere 9–17 through 21–23, and a broader ventral row, commonly of ~35–45 melanophores extending from myomere 7–8 through 22–24. Most larvae lacked melanophores laterally on the tail (pigment present in 20%, usually a melanophore ventrolaterally on one side between myomeres 21–23). The last 1–2 myomeres and notochord tip were unpigmented. The gut was heavily pigmented dorsally and there usually were 8–12 melanophores ventrally at mid-gut, with 1–2 on the hindgut adjacent to the anus.

Melanistic pigmentation gradually increased in all areas (Table 4). By day 2 or 3 melanophores were present above the myelencephalon and there usually were 2–3 melanophores over the midbrain area, increasing after about day 14 to ≥ 12 covering the area by the end of preflexion stage (Fig. 3). There usually were two melanophores above the hindbrain through mid-flexion stage (ca. 7 mm), increasing in number to cover the myelencephalon by ca. 8 mm. Melanophores formed laterally on the cerebellum beginning 2–3 days after

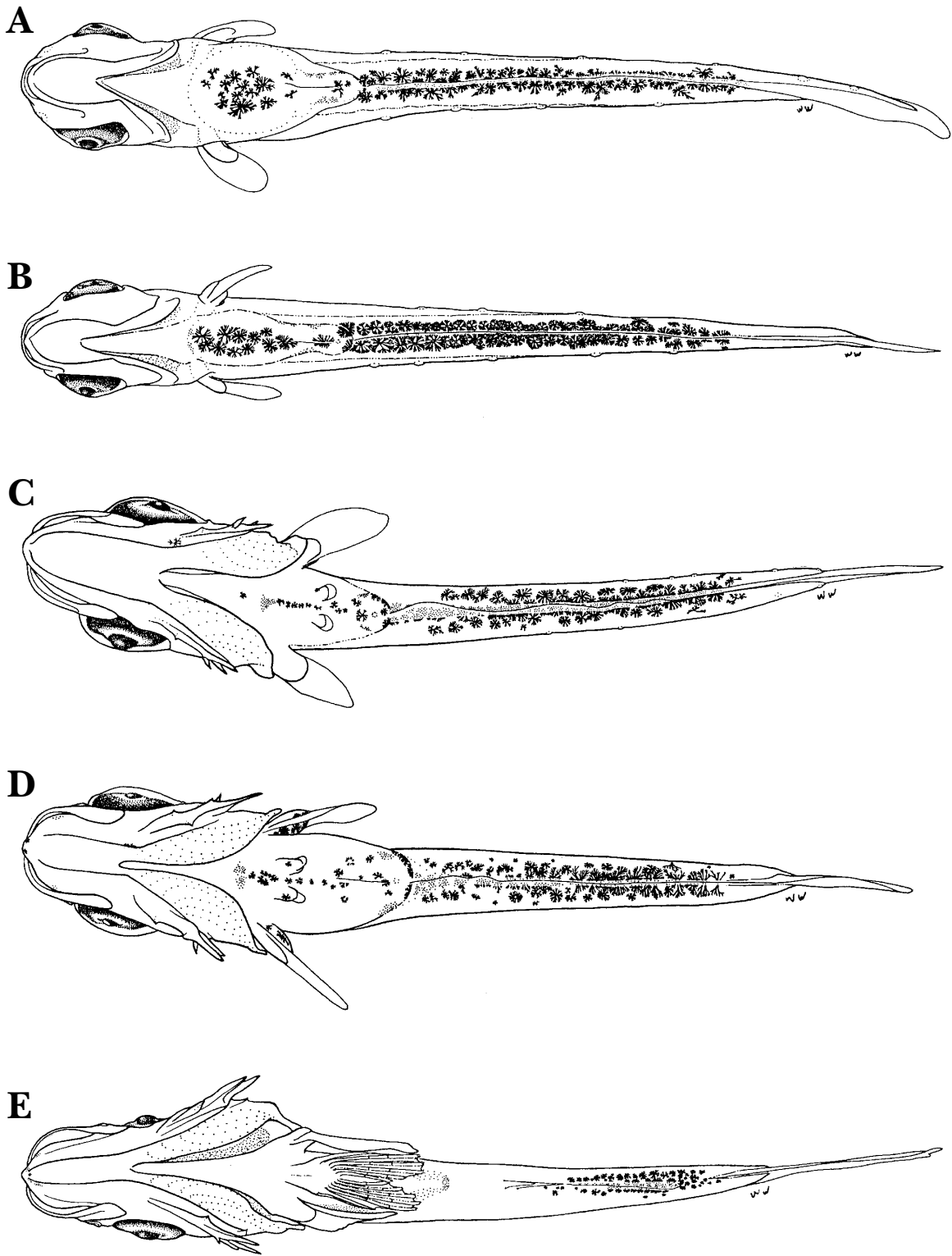


Figure 4

Kelp rockfish, *Sebastes atrovirens*, ventral view. (A) 4.6 mm preflexion stage, day 1; (B) 4.6 mm preflexion stage, day 23; (C) 8.0 mm mid-flexion stage, day 58; (D) 8.6 mm early postflexion stage, day 80; (E) 14.6 mm late postflexion stage, day 82. Neuromasts are shown only on the preflexion-stage larvae.

Table 4

Summary of melanophore distributions in larval kelp rockfish, *Sebastes atrovirens*. For number of melanophores, the range is given followed by the mode(s) in parentheses; for location of pigment, the area(s) where melanophores are located is given, followed by modal location(s) in parentheses (for trunk and tail pigment, location refers to the myomeres where melanophores are located). Modes are not given where clear modes were not apparent.

Pigment character	Larval stage		
	Preflexion	Flexion	Postflexion
HEAD			
Forebrain area			
Number	0–3 (0)	0–3 (3)	6–12
Location	dorsal, anterior margin	dorsal, anterior margin (dorsal)	dorsal–upper 50%
Midbrain area			
Number	0–31 (4)	16–many	many
Location	dorsal, posterior margin (dorsal, posterior margin)	dorsal, posterior margin (dorsal, posterior margin)	dorsal, posterior margin– upper 50%
Hindbrain area			
Number	0–6 (2)	several	many
Location	dorsal, lateral, ventral (dorsal)	dorsal, lateral, ventral (dorsal, lateral, ventral)	dorsal, lateral, ventral (dorsal, lateral, ventral)
Snout & upper jaw			
Number	0–1 (0)	0–2 (2)	several
Location	anterior nostril, premaxilla, maxilla	premaxilla, maxilla (premaxilla)	anterior nostril, premaxilla, maxilla
Lower jaw area			
Number	0–10 (0)	1–several	few
Location	dentary, articular, retroarticular, gular	dentary, articular, retroarticular (dentary, retroarticular)	dentary, articular, gular (dentary, gular)
Opercular area			
Number	0	0	several
Location			preopercle, opercle (opercle)
GUT AREA			
Dorsal			
Number	many	many	many
Location	mid- & hindgut (mid- & hindgut)	mid- & hindgut (mid- & hindgut)	mid- & hindgut (mid- & hindgut)
Lateral			
Number	0–several (0)	few–many (many)	many
Location	mid-gut area	upper 25%–≥90%	upper 50%–100%
Ventral			
Number	7–21 (10, 14, 16)	9–many	5–many
Location	mid- & hindgut (mid- & hindgut)	mid- & hindgut (mid- & hindgut)	mid- & hindgut (mid- & hindgut)
Isthmus			
Number	0–1 (0)	0–1 (0)	0
Location	near cleithra	near cleithra	
TRUNK & TAIL			
Dorsal, initial series			
Number	4–19 (10)	8–17 (13)	0–10
Location	1–17 to 21–23 (13–23)	1–17 to 21–23	1–4 to 20–24
Dorsal, secondary series			
Number	0	8–26	Many
Location		1–5 to 18–20	1–4 to 24
Ventral			
Number	~ 30–72 (46, 48, 49)	~ 49–70	Many
Location	6–9 to 22–24 (7–8 to 23)	7–8 to 23–24 (7–8 to 23–24)	8–17 to 24–25
Lateral			
Number	0–4 (0)	1–9 (4)	10– > 30
Location	10–24, horizontal septum, ventrolateral (19–24)	15–25, horizontal septum, dorsolateral, ventrolateral (24–25, horizontal septum)	2–26 horizontal septum, dorsolateral, ventrolateral (22–26)

continued

Table 4 (continued)

Pigment character	Larval stage		
	Preflexion	Flexion	Postflexion
Internal			
Number	0–4 (1)	Series	Many
Location	1–2 & 19–23, over &/or under notochord (19–21, over notochord)	1–24, over & under notochord (1–5 & 14–24, over notochord)	1–24, over & under vertebral column
FINS			
Pectoral			
Number	0–10	1–several	0–several
Location	inner & outer surfaces of base, proximally on membrane (inner surface of base)	inner & outer surfaces of base, proximally on rays (inner surface of base, proximally on rays)	inner surface of base
Pelvic			
Number	0	0–2 (0)	0–7
Location		base	base, rays I–2
Dorsal			
Number	0	0	0–many
Location			between spines, soft-ray bases
Anal			
Number	0	0–1 (0)	0–several
Location		last soft-ray base	soft-ray bases (soft-ray bases)
Caudal			
Number	0	0	9–several
Location			hypural margin, proximally on central rays

birth (present in 91%), gradually covering much of the lateral surface of the metencephalon and spreading posteriorly onto the myelencephalon by about mid-flexion. Basioccipital and/or pharyngobranchial melanophores usually formed late in preflexion stage (present in 16% ≤ 2 weeks and in 100% ≥ 3 weeks). A few melanophores formed on the anterior margin and/or dorsally on the forebrain in mid-preflexion stage (ca. 5.4 mm). Subsequently, forebrain pigment changed little until post-flexion stage, when more melanophores were added, covering the area by 14.6 mm. A melanophore formed near the mesial end of each premaxillary in 58% of late preflexion-stage specimens > 5.8 mm, commonly only on one side. One melanophore formed at the center of the upper jaw in 14% of specimens > 5.8 mm, and a few were present under the anterior end of each maxillary in all larvae > 7 mm. Some larvae ≥ 6.5 mm (22%) had ≥ 1 melanophore at the anterior nostrils. On the lower jaw pigmentation ranging from a melanophore at the tip to a series along the anterior half usually formed after day 3 (present in 11% ≤ 7 days and in 59% of older larvae, including 86% of those ≥ 5 mm). Some larvae (12%) had 1–2 melanophores anteriorly on the gular area. Most larvae ≥ 5.8 mm (71%) had 1–3 melanophores on the articular near the retroarticular, and some larvae

> ca. 6.5 mm (44%) had another 1–2 farther anteriorly on the ventral margin of the articular. The amount of articular pigment differed between left and right sides in 67% of the larvae. A melanophore formed on the isthmus near the cleithral symphysis in 20% of the larvae ≥ 5.7 mm. Pigmentation on the head increased during transformation–early juvenile stages, covering the upper 50–60% (sparsely laterally on the snout and opercle), extending over the jaws and onto the anterior gular area by 15.5–16 mm. The snout, jaws, and gular area were essentially fully pigmented by ~ 21 mm.

Melanophores spread ventrad from the dorsum of the gut, beginning at the anterior half of the mid-gut area, in mid–late preflexion stage (ca. 5.0–5.6 mm), and reached the ventrum in the anterior hindgut area by late preflexion to early flexion stage (ca. 5.4–8.0 mm). By late flexion stage the gut was largely covered. Nearly all larvae had ≥ 1 melanophore on the peritoneum just anterior to the liver; in some preflexion- and most later-stage larvae nearly the entire peritoneum was covered. The number of melanophores ventrally on the longitudinal midline of the gut increased a little during preflexion stage to 7–21 and by mid-flexion stage the ventral series usually was indistinguishable from the other gut pigment.

The minimum number of melanophores dorsally on the trunk and tail increased from 4–5 early in preflexion stage to 9–10 late in the stage, but the maximum remained ~ 19 (Table 4). These usually were in a single row of 7–10 melanophores extending from myomere 12–17 through 22–23. There commonly were 1–3 melanophores on the trunk and/or tail isolated from the dorsal series during preflexion stage (present in 68%), usually between myomeres 1–3 and 9–13: only on the trunk in 45%, only on the tail in 23%, and on both in 32% of the larvae having this pigment. During notochord flexion the dorsal melanophores became shallowly internal, beginning anteriorly, and by late postflexion stage (14.6 mm) none was visible externally. At about mid-flexion (ca. 7–8 mm) small melanophores formed between and adjacent to the original, larger dorsal melanophores on the tail, or both on the tail and at about mid-trunk. These small melanophores spread, extending from myomeres 1–4 through 20–24 during postflexion stage.

Most larvae lacked lateral melanophores on the trunk and tail during preflexion stage, but the proportion with some increased from ~ 17% early to ~ 36% late in the stage. When present, this pigment usually was a ventrolateral melanophore on one side in the vicinity of myomeres 19–24 until late in the stage when melanophores commonly formed on both sides, often with 1–2 on the horizontal septum (present in 60%) in the same area. All flexion- and later-stage larvae had ≥ 1 melanophore on the horizontal septum in the vicinity of myomeres 21–25. This pigment extended forward to mid-tail and expanded posteriorly during the pelagic juvenile stage but was obscured by other tail pigment after ~ 21 mm. Some flexion- and postflexion-stage larvae had melanophores dorsolaterally between myomeres 20–24 (25%) and ventrolaterally anywhere on the tail, commonly at myomeres 19–22 (38%). A bar formed here in transforming and early pelagic juvenile specimens. Late in postflexion stage melanophores spread ventrad from the dorsum, first in the vicinity of myomeres 7–9, then at myomeres 2–4. The anterior of these areas became a saddle extending from the nape to below the third dorsal-fin spine and ventrad nearly to the horizontal septum, by ~ 20 mm. The second became a saddle below D IV–VI or VII, extending to, or just below, the horizontal septum by ~ 20 mm. Two bars formed during transformation and early juvenile stages: below D IX–XI or XII, and below D 2 or 3–5 or 6; both neared the ventrum by ~ 20 mm. Thus, pelagic juveniles have five saddles and bars on the trunk and tail.

The number of ventral melanophores on the tail increased, with ~ 50–60 commonly present by the end of preflexion stage. These usually extended from myomere 7–8 to 23–24 and usually were continuous with the pigment dorsally on the gut, although a small unpigmented

gap sometimes separated the two areas (gap present in 25%). The ventral melanophores became internal, beginning anteriorly, during postflexion stage, with those on the caudal peduncle remaining at least partially external to at least early pelagic juvenile stage.

Melanophores formed internally above the notochord late in preflexion stage (by ca. 6 mm), beginning with 1–2 in the vicinity of myomeres 19–21 and often with another at myomere 1 or 2 (present in 60%), and spread from both sites to extend the full length of the vertebral column by the end of flexion stage. Melanophores formed under the notochord/vertebral column at about myomere 23 by late preflexion stage in some larvae, but were absent until postflexion stage in others (present in 45% ≥ 6 mm). These melanophores remained at myomeres 21–24 in some larvae, but extended the full length of tail in others, beginning at mid-flexion to postflexion stage.

One or more melanophores formed proximally on the mesial surface of one or both pectoral-fin bases late in preflexion stage (ca. 5.7 mm). During flexion stage melanophores covered the mesial surface in some larvae, but in others the fin bases were sparsely pigmented or even unpigmented (unpigmented in 10% of flexion- and postflexion-stage specimens). One to a few melanophores formed on the lateral surface of the pectoral-fin base in 23% of larvae ≥ 6 mm. A few melanophores formed proximally on some upper or lower pectoral-fin rays, or on both areas, in half of the late preflexion-stage and older larvae ≥ 6 mm; however, pectoral fin-ray pigmentation was not consistently present until pelagic juvenile stage, by ca. 20–21 mm. A little pigment was present on each pelvic-fin base in 30% of the late flexion- and postflexion-stage larvae, and a postflexion-stage specimen had a few melanophores proximally on the pelvic-fin rays (Table 4).

Melanophores first formed on the dorsal fin between dorsal spines II–V and at the bases of the segmented rays late in postflexion stage. Pigmentation increased rapidly, forming a dense bar at D I–III and sparser bars at D IV–V through VI–VII, D IX–XI or XII, and D 2–3 through 5–6, by early pelagic juvenile stage (< 16 mm). Fin bars first appeared just before the corresponding saddles and bars on the body. A distal band connected the second and third bars on the spinous dorsal, and the fourth bar extended posteriorly to about D 9, in pelagic juvenile stage by ca. 21 mm. All but about the distal 10–20% of the segmented-ray portion of the dorsal fin was pigmented by 23.7 mm. Melanophores formed at the bases of all, or all but the last segmented anal-fin rays, late in postflexion stage (≥ 14.6 mm). A band first appeared on the anal fin during transformation, tapering posteriorly from most of the length of A I down to the base of the last ray by early pelagic juvenile stage (< 16 mm). Melanophores formed on the hypural mar-

gin and, in one specimen, proximally on some central rays by 11.9 mm. Caudal fin-ray pigmentation in transformation stage was largely proximal on the principal rays at first, but extended nearly the full length of all principal rays and most procurvent rays by ca. 16 mm.

Pigmentation: Other chromatophores At birth xanthophores (yellow) were distributed much like the melanophores, but were more numerous than melanophores on the dorsum and less so on the ventrum. Xanthophores (2–4) covered much of the dorsal surface of the midbrain area and continued posteriorly as two rows to myomere 21–23, except that commonly there were none above the hindbrain. Xanthophores flanked the melanophores dorsally on the tail, expanding and spreading downward posteriorly. Ventrally on the tail, they formed a sparse row interspersed along the full length of the melanophore series in some larvae, but more commonly were posterior only, often expanded and spreading upward posteriorly. The expanded dorsal and ventral xanthophores commonly formed a bar at about myomeres 22–23 (present in 75%). On the gut, xanthophores were limited to the dorsum at midgut and anteriorly on the hindgut. The oil globule was golden yellow.

By late preflexion stage (ca. 5 mm) yellow pigment covered much of the midbrain area and was present internally in the otic capsule and anterolaterally on the hindbrain, but was absent externally over the hindbrain area in most larvae. By late flexion stage (ca. 8.8 mm) it covered the mid- and hindbrain, and extended anteriorly over the forebrain and posteriorly over the spinal chord to the antepenultimate vertebra. The entire dorsal and dorsolateral surfaces of the head were covered by late postflexion stage (15.2 mm). Series of small, orange xanthophores formed on the dentaries and articulars during preflexion stage, and during postflexion stage more formed at the bases and distally along the margins of the central two preopercular spines. A few (yellow) were present on the anterior preopercular margin of one flexion-stage specimen. By late postflexion stage dorsal xanthophores spread onto the snout, forming clusters on the premaxillary ascending processes and spreading along the proximal half of each maxilla. In the latter part of postflexion stage a few xanthophores (orange) formed anteriorly on the gular area, a few (yellow) formed at the bases of the supraclithral and posttemporal spines, and guanophores formed on the opercular area. By late postflexion (15.2 mm) the entire opercular area (except the preopercle) was bright silver.

External xanthic pigmentation on the trunk and tail changed little in preflexion stage. During notochord flexion xanthophores spread ventrolaterally from the dorsum at the first 1–3 myomeres and on the tail, ex-

tending progressively farther down the sides beginning at myomeres 14–18 and reaching the horizontal septum at about myomere 19–20. Xanthophores also proliferated ventrally on the tail during flexion stage, extending anteriorly and spreading dorsolaterally, reaching progressively farther up the sides posteriorly and meeting the dorsolateral pigment at about myomere 19, thus expanding the tail bar to about myomeres 19–24. The bar was predominantly yellow, with some orange pigment. During postflexion stage a xanthophore series formed on the horizontal septum of the tail, the bar spread anteriorly another 2–3 myomeres, and xanthophores covered (sparsely) the trunk to about myomere 5–6. A few xanthophores (yellow and orange) were present on the central hypural area in a flexion-stage specimen.

Xanthophores covered the gut during flexion and postflexion stages. Guanophores formed on the abdominal area during the latter part of postflexion stage; by late postflexion (15.2 mm) the entire area was bright silver. There were no xanthophores on the finfolds during preflexion stage; later a few formed on the pectoral fins near the bases of some rays in some larvae. A few xanthophores were present on the preanal finfold of a flexion-stage specimen.

Brown rockfish (*Sebastes auriculatus*)

Morphology Larval *S. auriculatus* were 5.0–5.3 mm long (mean 5.2 mm) at birth and completed yolk absorption in 9–13 days (5.4–5.8 mm). Notochord flexion began at 6–8 mm (32–45 days after birth) and was completed before 10 mm. Transformation to the pelagic juvenile stage was at ca. 25 mm, ~ 90 days after birth (11.5°C).

The *S. auriculatus* larvae were larger at birth and transformation but otherwise morphologically similar to *S. atrovirens* (Figs. 5–7; Tables 5–8). Larval *S. auriculatus* had 26–27 myomeres (92% with 26): 7–8 preanal + 18–20 postanal during preflexion stage (90% with 7 + 19), shifting to 10 + 16 in postflexion stage. Head and pectoral girdle spine development was similar in *S. auriculatus* and *S. atrovirens*, except that interopercular spines formed later, during postflexion stage, in *S. auriculatus* (Table 6), and pelagic juvenile *S. auriculatus* had tympanic spines (lacking in *S. atrovirens*), but lacked preorbital spines (present in *S. atrovirens*).

Principal caudal- and pectoral-fin rays began to form early in flexion stage (~ 7 mm) and full complements (8+7 and 15–19, respectively) were present by early postflexion stage (Table 7). Procurvent caudal-fin rays formed in postflexion stage; addition was anteriorly from the posterior-most rays and the full complement (9–11 + 9–12) was present by pelagic juvenile stage. Pelvic-fin buds formed early in flexion stage, and dorsal- and anal-fin anlagen in mid-flexion (Table 7), with all

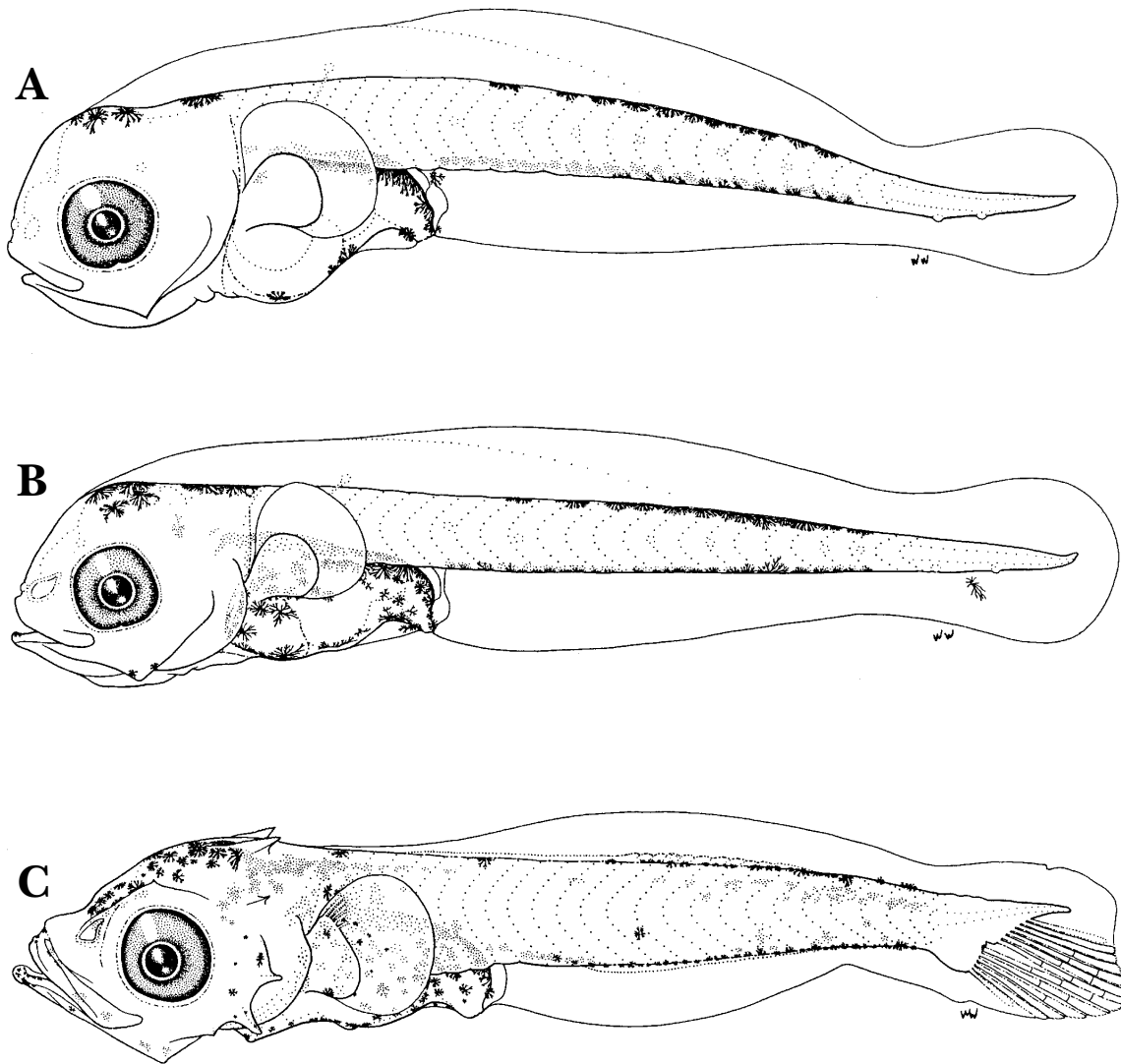


Figure 5

Brown rockfish, *Sebastes auriculatus*, lateral view. (A) 5.2 mm preflexion stage, day 1; (B) 5.8 mm preflexion stage, day 5; (C) 8.2 mm early flexion stage, day 45; (D) 10.6 mm postflexion stage, day 59; (E) 25.6 mm, pelagic juvenile, day 94. Neuro-masts are shown only on the preflexion-stage larvae.

fin-rays (I,5; XIII,12–15; III,5–8, respectively) present early in postflexion stage.

Pigmentation: Melanophores Larval *S. auriculatus* were moderately pigmented at birth (Figs. 5–7), most commonly with about seven melanophores dorsally on the head, 9–16 dorsally on the tail between myomeres 9–11 and 22–23, and a single row of 27–31 ventrally on the tail from myomere 9 through 23. The last 1–2 myomeres and notochord tip were unpigmented. At birth 45% had pigment on one or both sides of the tail, usually consisting of a melanophore between myomeres

18–21. All had heavy pigment dorsally on the gut, and about five melanophores ventrally at mid-gut plus one on the hindgut.

Pigmentation increased on all areas (Table 8). The upper ~25–50% of the midbrain area was covered by early flexion stage (Figs. 5, 6). Pigmentation over the myelencephalon increased from the initial 0–4 (usually 2–3) melanophores to nearly cover it by flexion stage, and melanophores formed laterally on the cerebellum by day 2–3 and covered much of the metencephalon by early flexion stage. Melanophores formed at the anterior margin of the forebrain as early as day 4 in some

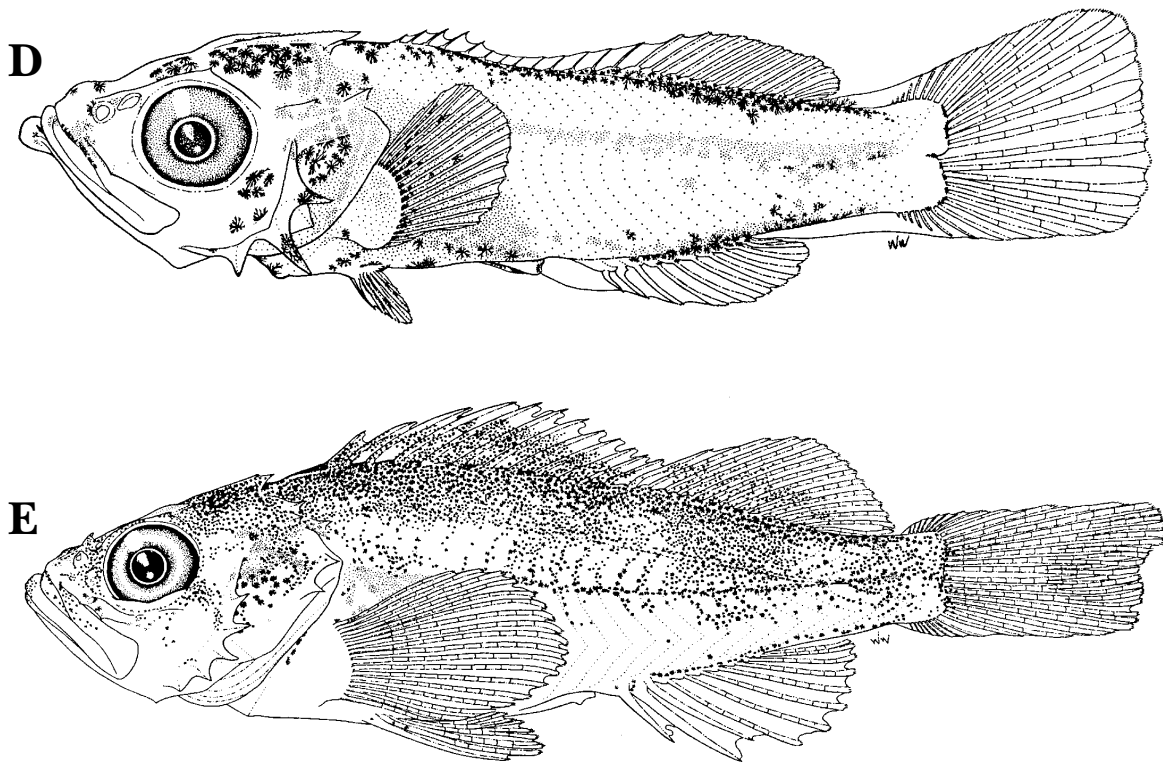


Figure 5 (continued)

Table 5

Summary of measurements of brown rockfish, *Sebastes auriculatus*, given as percentages of body length in 1 mm size classes. For each measurement mean values are given above, ranges below; n = number of specimens. Notochord flexion occurs within the 6.1–9.0 mm size classes; the 25.6 mm specimen is a pelagic juvenile.

Size range	n	PAL	BD	HL	HW	SnL	ED	P ₁ L	P ₂ L
4.1–5.0	2	41	26	24	14	5	9	5	0
		39–42	26–26	23–24	14–14	5–5	9–9	4–6	0–0
5.1–6.0	56	40	23	23	13	6	9	5	< 0.1
		38–48	16–26	22–32	12–17	5–9	8–12	4–9	0–0.4
6.1–7.0	1	42	19	27	14	8	10	8	0
7.1–8.0	2	47	22	30	15	9	10	8	1
		46–48	20–23	29–31	15–16	9–9	10–11	8–8	1–1
8.1–9.0	1	44	20	28	13	9	9	8	0.4
10.1–11.0	1	55	27	35	21	11	12	8	6
25.1–26.0	1	62	28	34	20	10	9	24	18

larvae, but not until flexion stage in most. Forebrain melanophores were primarily dorsal during flexion stage, covering much of the upper half by late postflexion stage. Melanophores formed on the basioccipital by day 2, usually posteriorly on its dorsal and/or ventral margins. In ~ 50% of preflexion-stage larvae \geq 4 days old

this pigment spread forward and/or posteriorly under the anterior end of the notochord to the level of future vertebrae 1–3.

After the first week 58% of preflexion-stage larvae, and all later-stage specimens, had melanophores anteriorly near the bases of the premaxillary ascending

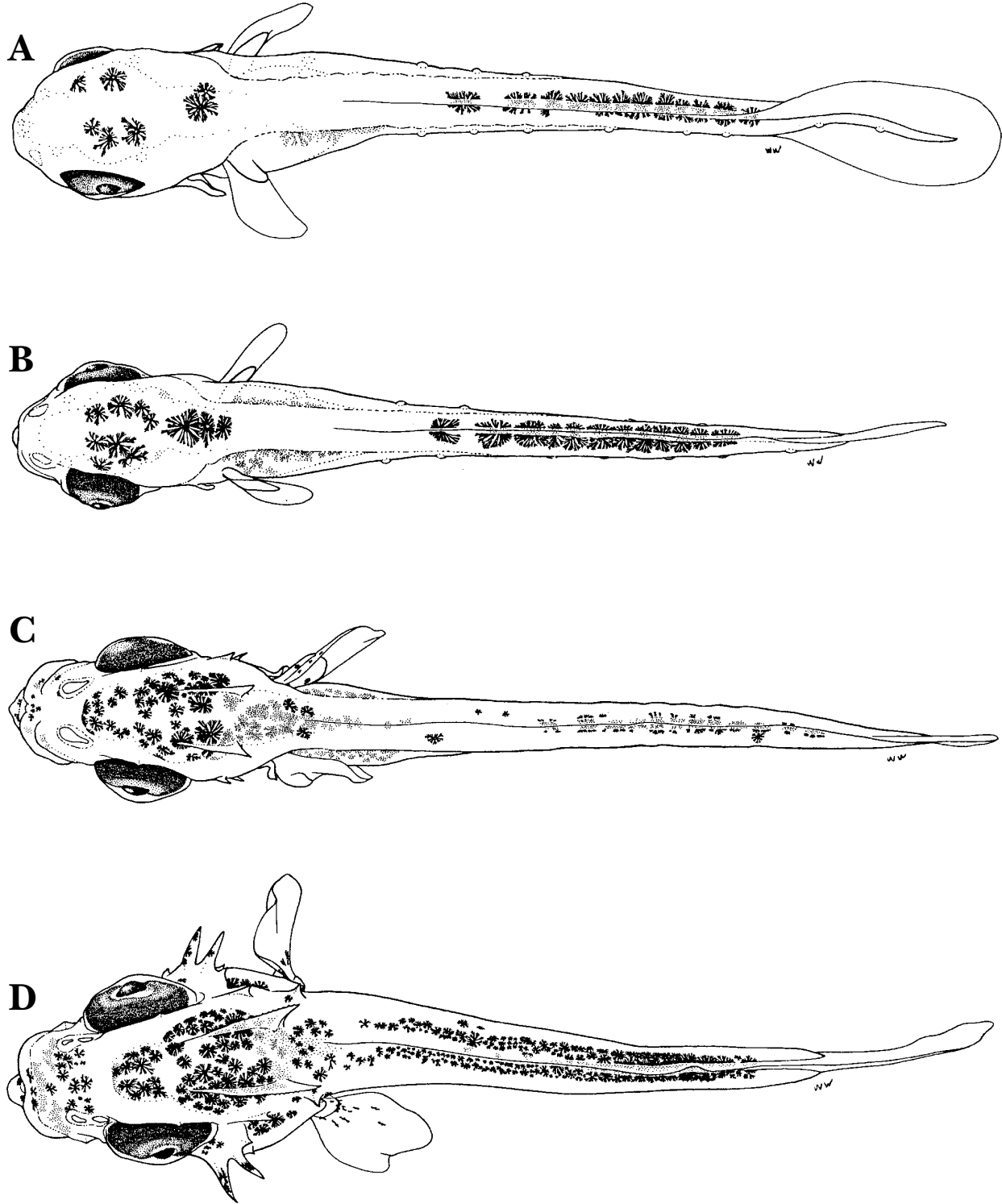


Figure 6

Brown rockfish, *Sebastes auriculatus*, dorsal view. (A) 5.2 mm preflexion stage, day 1; (B) 5.8 mm preflexion stage, day 5; (C) 8.2 mm early flexion stage, day 45; (D) 10.6 mm postflexion stage, day 59. Neuromasts are shown only on the preflexion-stage larvae.

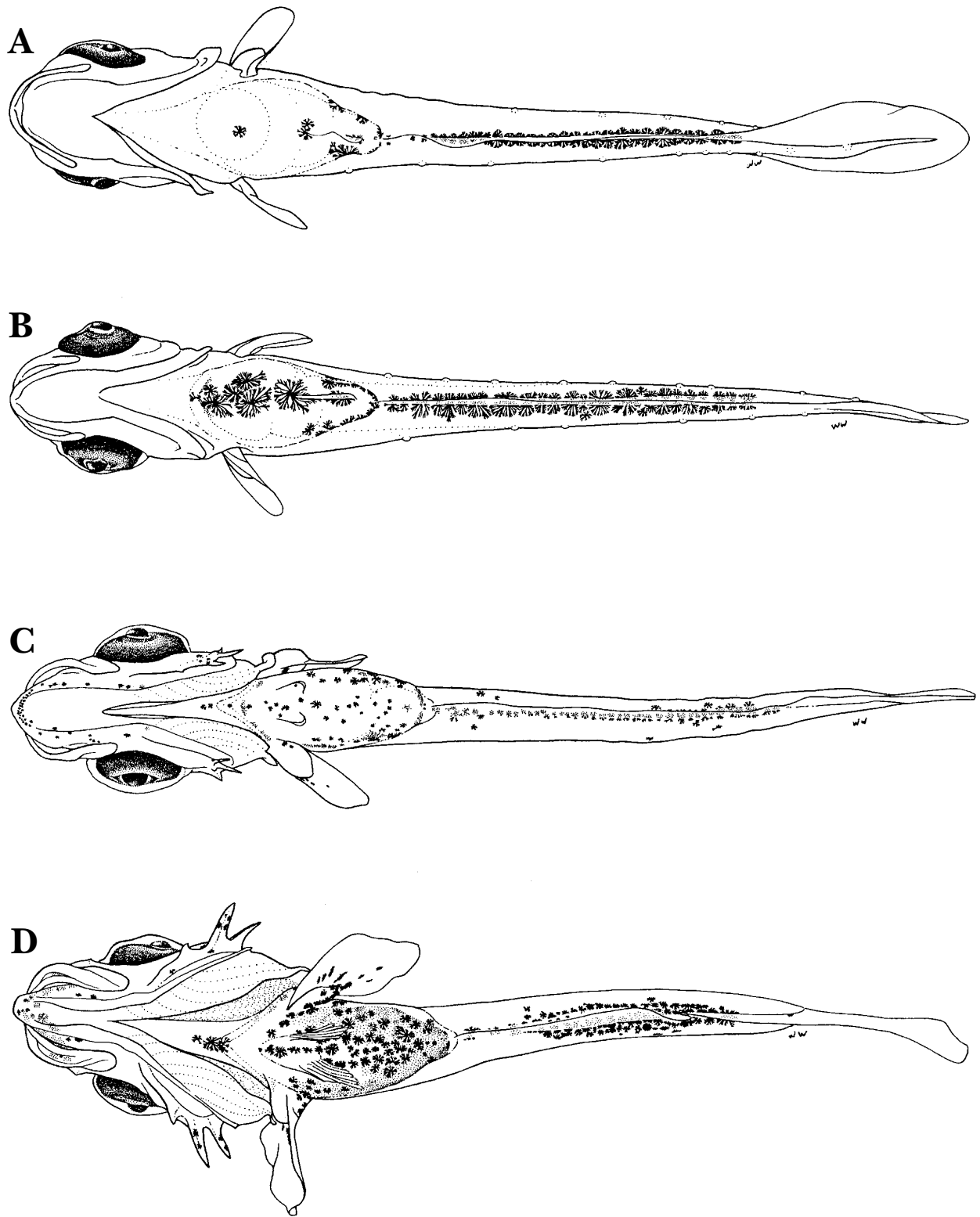


Figure 7

Brown rockfish, *Sebastes auriculatus*, ventral view. (A) 5.2 mm preflexion stage, day 1; (B) 5.8 mm preflexion stage, day 5; (C) 8.2 mm early flexion stage, day 45; (D) 10.6 mm postflexion stage, day 59. Neuromasts are shown only on the preflexion-stage larvae.

Table 6

Summary of measurements of brown rockfish, *Sebastes auriculatus*, head and pectoral girdle spines given as percentages of head length, in 1 mm size classes. For each measurement mean values are followed by ranges in parentheses. Number of specimens is given in parentheses for each size class. Notochord flexion occurs within the 6.1–9.0 mm size classes; the 25.6 mm specimen is a pelagic juvenile.

Spine	Size range						
	4.1–5.0 (2)	5.1–6.0 (56)	6.1–7.0 (1)	7.1–8.0 (2)	8.1–9.0 (1)	10.1–11.0 (1)	25.1–26.0 (1)
PPO2	0	< 0.1 (0–2)	2	6 (5–7)	7	13	11
PPO3	0	0.1 (0–5)	8	11 (10–12)	11	18	12
UOP	0	0	0	0	0	0	4
LOP	0	0	0	0	0	0	1
IOP	0	0	0	0	0	1	0
PA	0	0.1 (0–4)	3	6 (6–7)	5	11	0
NU	0	0	0	0	0	2	3
PSO	0	< 0.1 (0–0.5)	1	1 (1–1)	1	2	2
PT	0	< 0.1 (0–2)	3	4 (3–5)	4	4	1
TM	0	0	0	0	0	0	2
LIO1	0	0	0	0	0	1	1
LIO2	0	0	0	0	0	0.5	0.5
NA	0	0	0	0	0	0	2
UPST	0	0	0	0	0	0	2
LPST	0	0	0	0	0	3	1
SC	0	0	0	0	0	0	3

Table 7

Fin-ray counts of reared brown rockfish, *Sebastes auriculatus*. Abbreviations for fin rays are: D = dorsal, A = anal, P₁ = pectoral, P₂ = pelvic, C_{PRI} = principal caudal, C_{PRO} = procurrent caudal. Abbreviations for developmental stages are: Pr = preflexion, F = flexion, Po = postflexion, PJ = pelagic juvenile.

BL (mm)	Stage	D	A	P ₁	P ₂	C _{PRI}	C _{PRO}
4.8	Pr	0	0	0	0	0	0
7.0	F (early)	0	0	3	buds	5 + 5	0
7.2	F (mid)	anlage	anlage	6	buds	5 + 5	0
6.7	F (late)	anlage	anlage	14	buds	6 + 6	0
10.6	Po	XII,14	III,7	18	I,5	8 + 7	5 + 5
25.6	PJ	XIII,13	III,7	18	I,5	8 + 7	9 + 9

processes, and on the ascending processes in ~ 33% of the flexion-stage and older larvae. A melanophore was present on each maxilla in a preflexion-stage specimen (13 days), and most (86%) flexion-stage and later larvae had some pigment anteriorly under the maxillae. The snout usually was unpigmented into flexion stage (two flexion-stage larvae had a melanophore at the anterior margin of the nasal capsule), but by mid-postflexion stage melanophores nearly covered it to the level of mid-eye (Fig. 6). Melanophores formed on the lower jaw between days 3–7, usually anteriorly and laterally, but often not in both locations. About 75% of preflex-

ion-stage larvae ≥ 5 days old had 1–2 melanophores on the lower margin of the articular, and later-stage larvae commonly had them along its full length. A melanophore was present on the retroarticular, usually on its inner surface, in 43% of preflexion larvae ≥ 11 days old and in 89% of later-stage larvae. A late preflexion-stage specimen had a melanophore anteriorly on the gular membrane, and one each of flexion and postflexion stage had several. About 75% of preflexion-stage larvae ≥ 7 days old had 1–2 melanophores on the isthmus near the cleithral symphysis, and all later-stage larvae typically had 2–3. Larvae ≥ 7 days old usually had a melanophore

Table 8

Summary of melanophore distributions in larval brown rockfish, *Sebastes auriculatus*. For number of melanophores, the range is given followed by the mode(s) in parentheses; for location of pigment, the area(s) where melanophores are located is given, followed by modal location(s) in parentheses (for trunk and tail pigment, location refers to the myomeres where melanophores are located). Modes are not given where clear modes were not apparent.

Pigment character	Larval stage		
	Preflexion	Flexion	Postflexion
HEAD			
Forebrain area			
Number	0-1 (0)	2-several	several
Location	anterior or lateral	dorsal-upper 50% (dorsal)	upper 50%
Midbrain area			
Number	1-11 (3-4)	several	several
Location	dorsal, lateral (dorsal)	upper 25-50%	upper 50%
Hindbrain area			
Number	0-6 (3-4)	several	several
Location	dorsal, lateral (dorsal)	upper 25-50%	upper 50%
Snout & upper jaw			
Number	0-3 (0, 1)	0-4 (0, 2)	2-many
Location	premaxilla, maxilla (premaxilla)	nasal capsule, premaxilla, maxilla (premaxilla, maxilla)	anterior nostril-upper 50%, premaxilla, maxilla
Lower jaw area			
Number	0-8	5-several	many
Location	dentary, articular, retroarticular, gular (dentary)	dentary, articular, retroarticular, gular (dentary, articular, retroarticular)	dentary, articular, retroarticular, gular (dentary, articular, retroarticular)
Opercular area			
Number	0-1 (0)	3-many	many
Location	preopercle	preopercle, opercle	preopercle, opercle
GUT AREA			
Dorsal			
Number	several	many	many
Location	full length	full length	full length
Lateral			
Number	0-several	several	many
Location	mid-gut/hindgut area	entire area	entire area
Ventral			
Number	3-23	(indistinguishable from general gut pigmentation)	(indistinguishable from general gut pigmentation)
Location	mid- & hindgut		
Isthmus			
Number	0-2	1-4	2-3
Location	near cleithra	near cleithra	near cleithra
TRUNK & TAIL			
Dorsal, initial series			
Number	0-20 (16)	11-15 (12, 14)	10-13
Location	1-17 to 22-24 (1 & 11-22)	10-13 to 22-25 (12 to 22-25)	1-11 to 23-24
Dorsal, secondary series			
Number	0	several	many
Location		1-23	1-24
Ventral			
Number	16-35 (28)	28-40	≥ 44
Location	7-9 to 22-25 (9-23)	7-8 to 23-24 (8-23)	10-25
Lateral			
Number	0-4 (1)	2-9 (9)	3-many
Location	12-23 (20)	1-3 & 8-24 (1 & 10 to 20-21)	1-26 (13-24)
Internal			
Number	0-2 (0)	series	series
Location	18-24, over or under notochord, or lateral (20-22, over notochord)	1-24, over & under notochord/vertebral column	1-25, over, under & lateral to vertebral column

continued

Table 8 (continued)

Pigment character	Larval stage		
	Preflexion	Flexion	Postflexion
FINS			
Pectoral			
Number	0	0–several	10–many
Location		inner & outer surfaces of base, proximally on blade or rays (inner & outer surfaces of base)	inner & outer surface of base, on rays
Pelvic			
Number	0	0–2 (0)	0–several
Location		base	base, rays
Dorsal			
Number	0	0	0–many
Location			soft-ray bases
Anal			
Number	0	0–5 (0)	0–several
Location		finfold near origin of anlage	soft-ray bases
Caudal			
Number	0–1 (0)	0–1 (0)	0–several
Location	finfold near hypurals	proximally on a central ray	proximally on principal rays

on the lower (anterior) part of the preopercle, and 55% of flexion-stage and later specimens had one near the preopercular angle and/or on the upper part of the preopercle. Most (78%) flexion- and postflexion-stage larvae had melanophore(s) at the base(s) of ≥ 1 posterior preopercular spine(s), commonly at PPO3. The opercular melanophore patch characteristic of pelagic juveniles began to form during postflexion stage. By pelagic juvenile stage the upper half of the head was nearly fully pigmented, most densely on its upper quarter, with a light peppering over the jaws and gular area, and a more or less prominent patch near the upper end of the opercle (Fig. 5E).

A melanophore or two formed on the peritoneum just anterior to the yolk and/or oil globule during the first day in most larvae, and spread ventrad to become continuous with the ventral pigmentation on the gut by late preflexion stage (Fig. 5). Melanophores began to spread ventrad from the dorsum of the gut (especially in the posterior mid-gut/anterior hindgut vicinity) on about day 3, and nearly reached the ventrum by late preflexion stage. By late flexion stage most of the gut was pigmented, more sparsely ventrolaterally. Beginning about day 7, some melanophores in the vicinity of the gas bladder extended up to the notochord. The number of melanophores ventrally on the gut gradually increased during preflexion stage, forming a broad longitudinal row by day 4 and becoming indistinguishable from the other gut pigmentation by late flexion stage (Fig. 7).

The location and number of dorsal melanophores on the tail changed little during preflexion stage (Figs. 5,

6): larvae commonly had 12–16 melanophores between myomeres 11–22 (Table 8), mostly in a single row, except the row commonly was doubled posteriorly at one or two myomeres. The dorsal melanophores typically were more widely spaced anteriorly. Some preflexion-stage larvae ≥ 7 days old (58%) also had some dorsal pigment on the trunk, usually a melanophore at the first myomere. Early in flexion stage an irregularly spaced dorsolateral row of smaller melanophores formed on each side of the initial series, usually originating simultaneously in the vicinities of myomeres 1–3 and 7–10. By mid-flexion stage the dorsolateral melanophores spread posteriorly on the trunk and formed in the vicinity of myomeres 14–23, and by late flexion they filled in between sites and merged into the original marginal series posteriorly. During postflexion stage the original marginal series became shallowly internal and the number of dorsolateral melanophores increased, forming a 2–3 melanophore-wide band on each side of the dorsal margin from the nape to mid-caudal peduncle (Fig. 6D). By 10.6 mm this pigmentation was sparse at the first 1–2 myomeres but dense along the bases of the segmented dorsal-fin rays.

The proportion of larvae with lateral melanophores on the tail rapidly increased after birth to 100% within two weeks. The number of lateral melanophores increased to 2–9 on each side by flexion stage (Table 8), then changed little through mid-postflexion stage (Fig. 5D). These melanophores were dorso- and ventrolateral, and on the horizontal septum, usually between myomeres 10–21, with most between myomeres 18–21.

About 10% of preflexion-stage larvae ≥ 7 days old and just over half of flexion-stage larvae also had 1–2 melanophores dorsolaterally or on the horizontal septum in the vicinity of myomeres 1–3. In the latter part of postflexion stage melanophores spread forward on the horizontal septum, extending along its full length by pelagic juvenile stage (Fig. 5E). Others spread from the dorsum onto the sides of the trunk and tail, combining with the lateral pigment to cover much of the upper half of the body (densest on the upper quarter), and formed five saddles and bars in early pelagic juvenile stage (Fig. 5E). The first saddle extended diagonally from below D I–III to the posttemporal area, the second from below D IV–VIII to near the horizontal septum, the third from below D IX–XII to just below the horizontal septum, the fourth (a bar) from below D 2–11 nearly to the ventrum, and the last bar covered much of the caudal peduncle. Pigmentation in the saddles and bars was densest dorsally and increasingly sparse ventrad.

The number of ventral melanophores on the tail increased with development (Table 8). These were mostly in a single row, although the proportion of larvae with the row doubled at some myomeres posteriorly increased to just over 40% by flexion stage. Melanophores in the ventral row usually were small anteriorly, progressively more expanded posteriorly to about myomere 20–22, then progressively more contracted again (Fig. 7). Early in postflexion stage smaller melanophores formed, interspersed with the original series, and by mid-postflexion stage the original melanophores were shallowly internal except on the caudal peduncle. The smaller melanophores formed a 1–2 melanophore-wide row on each side of the anal-fin base in the latter part of postflexion stage (Fig. 7D).

Larvae rarely had internal pigment in the trunk or tail during the first 2–3 days, but 58% of preflexion-stage larvae ≥ 7 days old had 1–2 melanophores, usually above the notochord at about myomeres 20–22. During flexion stage a series of melanophores formed above the spinal cord, initially in the vicinities of myomeres 1–2, 15–17, and 21–24. Two or three melanophores formed under the notochord at myomeres 19–21 early in flexion stage, and spread forward to myomeres 14–18 and posteriorly to myomere 23 by late in the stage. Others spread forward dorsally along the notochord to myomeres 14–16, and some formed over the first 1–4 vertebrae by late flexion stage. A few formed elsewhere internally, primarily dorsally and ventrally in the vicinity of myomeres 18–23, during postflexion stage.

A preflexion-stage larva had a ventral melanophore in the caudal finfold (Fig. 5B); others lacked fin pigmentation before flexion stage (Table 8). During flexion stage melanophores formed on the inner surface of the pectoral-fin base, usually proximally on its lower part, and some usually formed on the lateral surface.

A few formed on the pectoral-fin blade, usually on its upper half, during early- to mid-flexion stage. One or two melanophores formed on each pelvic-fin base in some flexion- and postflexion-stage larvae (44%) and beginning about mid-postflexion stage, up to several formed on the membranes between the pelvic-fin rays. Melanophores formed on the bases of the segmented dorsal-fin rays at about mid-postflexion stage, but none formed on the fin rays or membranes before late postflexion or transformation stage. In the 25.6 mm pelagic juvenile all but about the distal 20–40% of the spinous dorsal fin and proximal 25% of the segmented ray portion of the fin were pigmented (except none on the last ray). A flexion-stage specimen had a few melanophores anteriorly on the anal finfold, but otherwise the anal fin was unpigmented before mid-postflexion stage, when melanophores formed at the bases of the segmented rays. The pelagic juvenile had a few melanophores at A III–1, and one each proximally on some other segmented rays. One or two melanophores were present on the lower hypural margin in some flexion-stage larvae, and by mid-postflexion stage there were several on the hypural margin. By pelagic juvenile stage a narrow bar extended along the hypural margin, and there were several melanophores proximally along each principal caudal-fin ray and a few farther distally on the fin.

Pigmentation: Other chromatophores Xanthophore and melanophore patterns differed from one another through mid-preflexion stage, but became more alike in older larvae. At birth, most larvae had a few yellow xanthophores dorsally over the midbrain, occasionally 1–2 over the hindbrain, and none elsewhere. The oil globule was pale yellow. By day 2 xanthophores usually were present over the hindbrain, and by day 3 a third of the larvae had 1–2 over the forebrain. During the latter part of preflexion stage xanthophores proliferated dorsally and spread dorsolaterally on the head, and in flexion stage they were present over the forebrain, spread ventrolaterally to the level of the eyes and otic capsule, and spread posteriorly to myomeres 1–2. By early postflexion stage nearly the entire brain area and posteriorly to about myomere 3 was densely covered, a few xanthophores were scattered on the upper half of the opercular area, and a few were present on the snout and along the mesial ends of the maxillaries, premaxillaries, and dentaries. Pigmentation gradually increased in these areas. The opercular area and isthmus became silvery in pelagic juvenile stage.

Xanthophores formed on the trunk and tail during the latter part of preflexion stage. A row of irregularly spaced chromatophores formed along each side of the dorsal margin posteriorly to about the end of the melanophore series (myomere 23–25), with a few laterally, resulting in a bar in the vicinity of myomeres

19–23. Some of the dorsal xanthophores flanked the melanophore row and others were interspersed among them; the majority on the trunk and flanking the melanophores were orange while most of those interspersed among the melanophores were yellow. Two rows of irregularly spaced xanthophores extended forward along the ventral margin from myomere 24–25 to anywhere between mid-tail and the first postanal myomere. Ventral xanthophores were predominantly yellow, and those in the tail bar were an ~ 50:50 mixture of orange and yellow. During notochord flexion pigmentation increased in all three areas, extending the full length of the tail ventrally, and spread laterally from the dorsum and ventrum, apparently beginning at the tail bar and progressing cephalad. A few xanthophores formed on the horizontal septum of the posterior half of the tail in flexion stage. In postflexion stage the tail bar broadened to myomeres 18–19 through 24–25. By pelagic juvenile stage xanthophore and melanophore patterns on the trunk and tail were essentially the same, except that xanthophores were scattered along the myosepta on the lower half of the tail where melanophores lacked. Xanthophores were dense in the saddles and bars.

Xanthophores formed dorsally on the gut at the end of preflexion stage and surrounded it except at the terminus of the hindgut in flexion stage. A few formed on the lower half of the cleithrum during postflexion stage. The abdominal area became silvery by pelagic juvenile stage.

The pectoral and caudal were the first fins to acquire xanthophores: during flexion stage a few (yellow) formed on the outer surface of the pectoral-fin base and proximally on the finfold, and 1–2 (orange) formed at the base(s) of the central caudal-fin rays. More formed on one or both surfaces of the pectoral-fin bases and proximally on some rays in postflexion stage. Xanthophores formed on the hypural margin in postflexion stage, and along all but the distal 10–25% of each principal caudal-fin ray by pelagic juvenile stage. Those on the dorsal and anal fins corresponded to melanophore patterns, but in the pelagic juvenile they extended a little farther distally on the soft-ray portion of the dorsal fin, and formed a stripe on the anal fin that extended from the middle of the second spine to the base of the next to last ray, with few accompanying melanophores. There were a few xanthophores proximally on the pelvic fins in pelagic juvenile stage.

Black-and-yellow rockfish (*Sebastes chrysomelas*)

Morphology Larval *S. chrysomelas* were 4.4–4.8 mm (mean 4.6 mm) at birth and completed yolk absorption 3.5–5 days later at 4.6–5.4 mm (mean 5.1 mm). Neither notochord flexion nor development of the head spines

and fin rays began before the last larvae died on day 9. The larvae were morphologically similar to *S. atrovirens*: moderately slender with rounded head and short snout, short preanal length, and slightly inflated, sac-like integument enclosing the trunk and anterior part of the tail (Table 9; Fig. 8). The larvae had 25–27 myomeres (97% with 26): 6–8 preanal + 18–20 postanal (68% with 7 + 19, 26% with 6 + 20).

Pigmentation: Melanophores Larvae were moderately pigmented at birth (Fig. 8). Initially, the head was unpigmented except for 1–2 melanophores dorsally on the myelencephalon in 72% of the larvae. All larvae had a row of melanophores dorsally on the trunk and tail, usually 11–20 (mode 17) between myomeres 6–10 and 22–24 (modes 7 and 9 through 23). The first 1–4 melanophores in the series were more widely spaced than the others in 64% of the newly born larvae. In half of the newly born larvae the dorsal melanophores were in a single row; in the others the row was doubled at ≥ 1 myomere(s), usually between myomeres 19–22. At birth some larvae (16%) had a melanophore on or near the horizontal septum on one side of the tail (usually the left) between myomeres 11–14; the others lacked lateral melanophores. About 45–61 (mean 53) melanophores were arrayed in a 1–3 melanophore-wide row (most with a 1–2 melanophore-wide row) ventrally on the tail, usually from myomere 7 through 23 or 24. The notochord tip was unpigmented. The pigment ventrally on the tail nearly always was continuous with that over the gut. The gut was heavily pigmented dorsally from near the level of the cleithra to the terminus. Ventrally, the gut was moderately pigmented, usually with 11–14 (mode 13) melanophores covering most of the mid-gut area and one on the hindgut adjacent to the anus. The gut was unpigmented laterally.

Pigmentation changed only a little in the remaining days, except on the head. The proportion of larvae with melanophores over the myelencephalon increased to 100% by day 4, but the number of melanophores remained 1–3 (modally 2). A melanophore or two formed over the cerebellum by day 4 in some larvae ≥ 5.3 mm (27%), and another 1–2 were added on each side of the cerebellum in a few larvae \geq five days old (14%). One to three melanophores were present over the midbrain area in 24% of larvae $>$ four days old. The number of melanophores ventrally on the tail increased slightly, to 47–69 (mean 58). One melanophore was present on the peritoneum at the anteroventral margin of the liver in 10% of the 3–4 day old larvae, and in 34% of older larvae.

Pigmentation: Other chromatophores Xanthophore patterns at birth were not recorded. On day 4, xanthophores (yellow) were continuous on the dorsum from

Table 9

Summary of measurements of black-and-yellow rockfish, *Sebastes chrysomelas*, given as percentages of body length in 1 mm size classes. For each measurement mean values are given above and ranges below; *n* = number of specimens.

Size range	<i>n</i>	PAL	BD	HL	HW	SnL	ED	P ₁ L	P ₂ L
4.1–5.0	78	35	16	20	10	5	7	5	0
		33–38	14–18	19–22	9–11	4–6	6–8	4–5	
5.1–6.0	25	36	15	19	10	5	6	4	0
		34–37	14–16	19–20	9–10	4–6	6–7	4–5	

the midbrain area to the end of the dorsal melanophore series (myomere 22–24) in 70% of the larvae, increasing to 80% by one week. In the remainder, the series was interrupted at myomeres 6–7 through 8–12. The dorsal xanthophores on the trunk and tail were irregularly spaced in two rows flanking the median melanophore row, with a few interspersed among the melanophores. No xanthophores were present on the gut at day 4, but by one week some had formed dorsally or dorsolaterally on the hindgut (present in 50%) and by day 9 ~ 90% of the larvae had 1–2 xanthophores on the peritoneum at or near the anterior margin of the liver. Most larvae (~ 90%) had a xanthophore near the center of the otic capsule, and at day 9 three-quarters had 1–2 xanthophores at or near the pharyngobranchial location. All larvae lacked ventral xanthophores.

Discussion

Larval *S. atrovirens*, *S. auriculatus*, and *S. chrysomelas* are much alike, but exhibit some differences in xanthic and melanistic pigmentation, at least during the preflexion stage. Xanthophore patterns become increasingly alike between *S. atrovirens* and *S. auriculatus* after preflexion stage, and melanophore patterns become increasingly alike among most *Pteropodus* species after preflexion stage. Larval *S. auriculatus* lack dorsal xanthophores on the trunk and tail until late preflexion stage, while the other two have extensive dorsal xanthic pigmentation from birth. Larval *S. chrysomelas* lack lateral and ventral xanthophores on the tail for at least the first nine days, and *S. auriculatus* lack them until late preflexion stage, in contrast to *S. atrovirens* which have them ventrally, and often laterally, from birth. Larval *S. atrovirens* also have more extensive xanthic pigmentation on the jaws and gut than the other two. These differences suggest that xanthophore patterns could be useful for species identifications. However, xanthic pigmentation has not been documented for all the *Pteropodus* species and it is unknown how many have unique patterns. Preflexion-stage *S. caurinus* have a pattern much like that of

S. atrovirens, but usually have a little xanthic pigment on the upper jaw (lacking in *S. atrovirens* before postflexion stage). During at least the first week larval *S. rastrelliger* apparently lack xanthophores and thus resemble *S. auriculatus*, which have only a few xanthophores before late preflexion stage. Xanthophores rarely persist longer than a few days in the usual formalin or alcohol preservatives and their utility for identifying field-collected larvae currently is limited. (Attempts to stabilize the xanthic pigment in larval *S. atrovirens* using solutions of 0.1–10.0% ionol in ethanol and in formalin were unsuccessful.) Nevertheless, documentation of xanthophore patterns may prove to be a valuable exercise if future research leads to a method for stabilizing this pigment in preserved specimens.

Melanophore patterns differ among larval *S. atrovirens*, *S. auriculatus*, and *S. chrysomelas* during the preflexion stage primarily in the location of the dorsal series, and in the number of melanophores and width of the ventral series on the tail. Dorsal melanophores on the trunk are rare in *S. auriculatus* but more common in the other two (~ 40–50% of specimens). Larval *S. dalli* (Moser and Butler, 1981), *S. caurinus* (Stahl-Johnson, 1985), *S. carnatus* (Moreno, 1993), *S. rastrelliger* (Moreno, 1993), and *S. nebulosus* (Kendall¹) also usually have melanophores dorsally on some of the trunk myomeres. Larval *S. auriculatus* usually have fewer ventral melanophores on the tail than *S. atrovirens* and *S. chrysomelas*, averaging 30 in a single row; essentially the same pattern is displayed by larval *S. dalli* (Moser and Butler, 1981). Larval *S. chrysomelas* typically have the most ventral melanophores among the three, averaging 55 in a 1–3 melanophore-wide series; essentially the same pattern is displayed by *S. carnatus* (Moser, 1967). Larval *S. atrovirens* are intermediate, with an average 45 melanophores in a 1–2 melanophore-wide series, and their range (28–62 melanophores) overlaps both *S. auriculatus* and *S. chrysomelas*. Larval *S. rastrelliger* initially have a ventral series like *S. auriculatus*, with 19–46 (mean 30) melanophores mostly in a single row, but the number increases and by 4–5 days after birth there are 48–61 (mean 52) in a 1–3 melanophore-wide series, much like *S. chrysomelas*.

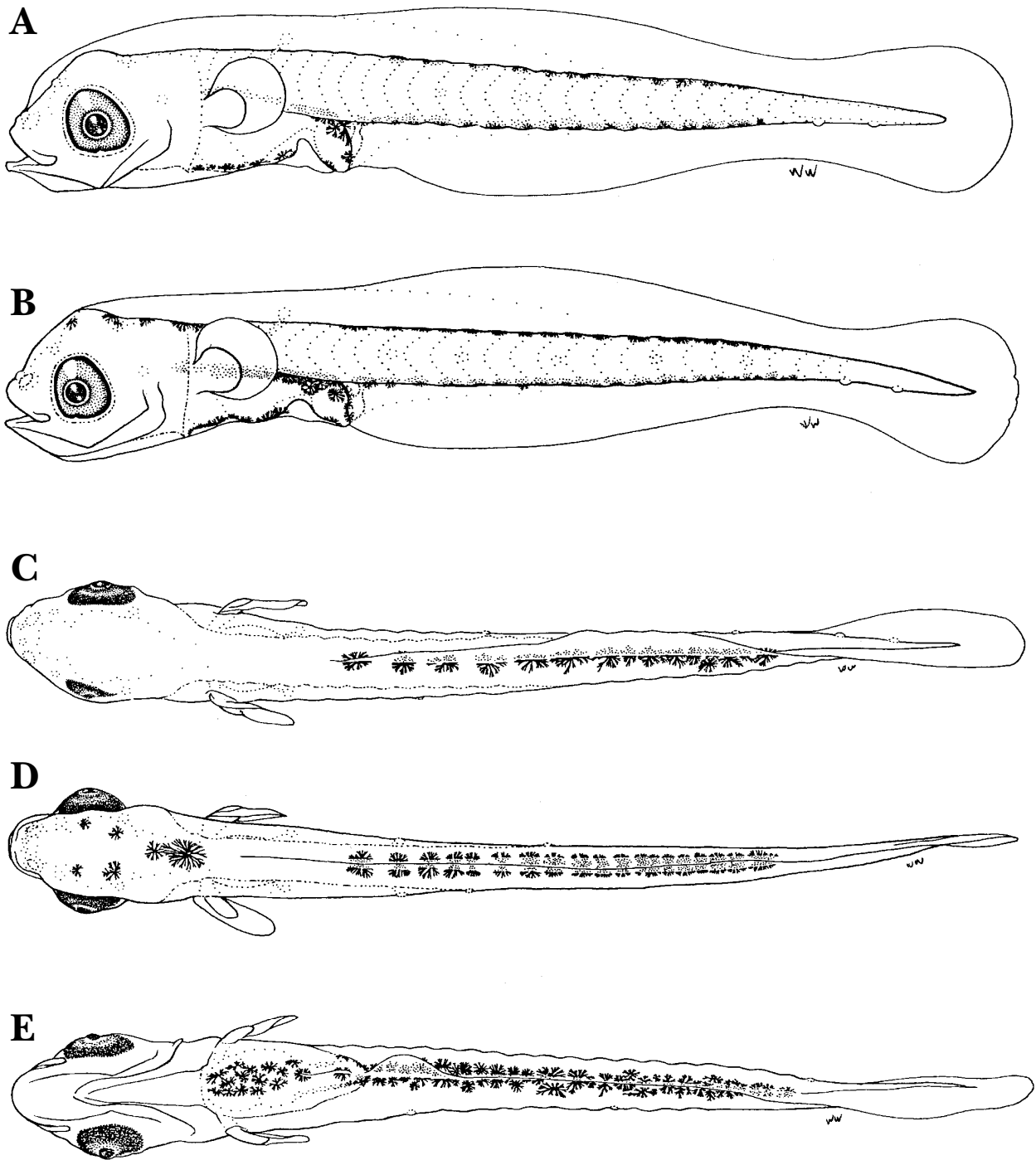


Figure 8

Black-and-yellow rockfish, *Sebastes chrysomelas*, preflexion stage. (A) 4.6 mm, day 1, lateral view; (B) 5.3 mm, day 6, lateral view; (C) 4.6 mm, day 1, dorsal view; (D) 5.3 mm, day 6, dorsal view; (E) 5.3 mm, day 6, ventral view.

Table 10

Trunk and tail melanophores of preflexion-stage *Sebastes* larvae, subgenus *Pteropodus*. Under number of melanophores, the mean is given above and range below; for location of pigment, the myomere number at the modal location is given above and range below. SWFSC refers to larvae reared at Southwest Fisheries Science Center.

Species	Source	Dorsal		Lateral		Ventral	
		Number	Location	Number	Location	Number	Location
<i>S. atrovirens</i>	SWFSC	11	12–23	< 1	20	42	8–23
	group 1	8–19	1–23	0–1	20	28–49	8–24
	SWFSC	11	11–22	< 1		44	8–23
	group 2	6–15	1–23	0–2	10–23	37–52	7–24
	SWFSC	9	15–23	< 1		48	7–23
<i>S. auriculatus</i>	SWFSC	4–15	1–23	0–4	11–22	38–62	6–24
		13	11–22	1	20	30	9–23
<i>S. caurinus</i>	Moser, 1967	0–20	9–22	0–4	12–23	16–35	9–23
		16				55	
		11–23				49–63	
<i>S. caurinus</i>	SWFSC	19	7–23	< 1	11	42	7–24
		15–27	1–24	0–1	11–21	32–57	7–24
		23					
<i>S. chrysomelas</i>	SWFSC	18–32					
		16	7, 9–23	< 1	10	55	7–24
<i>S. dalli</i>	Moser & Butler, 1981	8–25	2–24	0–2	2–22	45–69	7–25
		14		2		38	
<i>S. rastrelliger</i>	SWFSC	7–19	12–23	0–6		29–49	9–24
		44	1, 7–23	1	12	57	8–23
<i>S. nebulosus</i>	Kendall ¹	26–55	1–24	0–3	2–24	43–82	7–24
		ca. 50	5–23				ca. 7–23

Larval *S. caurinus* also initially have a predominantly single row of ~ 30–50 (mean 40) melanophores ventrally on the tail, but within a week the number increases to ~ 35–60 (mean 45) in a 1–3 melanophore-wide series.

Intraspecific variation in pigmentation can be relatively large. For example, preflexion-stage larvae from one *S. atrovirens* had 28–49 (mean 42) ventral melanophores on the tail and 8–19 (mean 11) in the dorsal series, those from another had 37–52 (44) and 6–15 (11), respectively, and those from a third had 38–62 (48) and 4–15 (9), respectively (Table 10). In a single batch of *S. auriculatus* the number of dorsal melanophores on the trunk and tail in preflexion stage ranged from 0 (in 2%) to 19. Preflexion-stage *S. caurinus* reared at SWFSC (March–April 1999) typically were more lightly pigmented, especially dorsally, than those described by Stahl-Johnson (1985), although the same batch also contained larvae as heavily pigmented. Marliave et al.³ described similar variation in a single batch of

S. caurinus, and we observed the same variability in *S. chrysomelas*.

Given the similar melanophore patterns among *Pteropodus* species and the variability within species, the instability of xanthic pigment in the usual preservatives, and the morphological similarity among species, it seems likely that unless a new method for preserving xanthic pigment is developed, reliable species identifications of field-collected larvae will not be possible using traditional morphological and pigment characters. However, because larval *Pteropodus* do have a common basic pattern of melanistic pigmentation during the preflexion stage (Fig. 9), identification of the subgenus may be possible. The principal elements of the pattern are the long dorsal melanophore row on the tail that often extends onto the trunk (Fig. 10), the long ventral melanophore row on the tail that originates at the last preanal or first postanal myomere (Fig. 11), and little or no pigment on the pectoral fins. Occasionally an individual may have a shorter dorsal row (occupying ≤ 5–6 myomeres), or a ventral row that originates at the second postanal myomere. The basic pattern may be diagnostic for *Pteropodus* although larvae of some other species (e.g., squarespot rockfish *S. hopkinsi*;

³ Marliave, J. B., D. I. Kent, and C. M. Brenton. 1997. Pigment polymorphism in sibling larvae of *Sebastes caurinus*. Abstr., 77th Ann. Meeting Amer. Soc. Ichthyol. Herpetol., Seattle, WA, 26 June–2 July 1997. Available from University of Washington, College of Fisheries, Seattle, WA 98195.

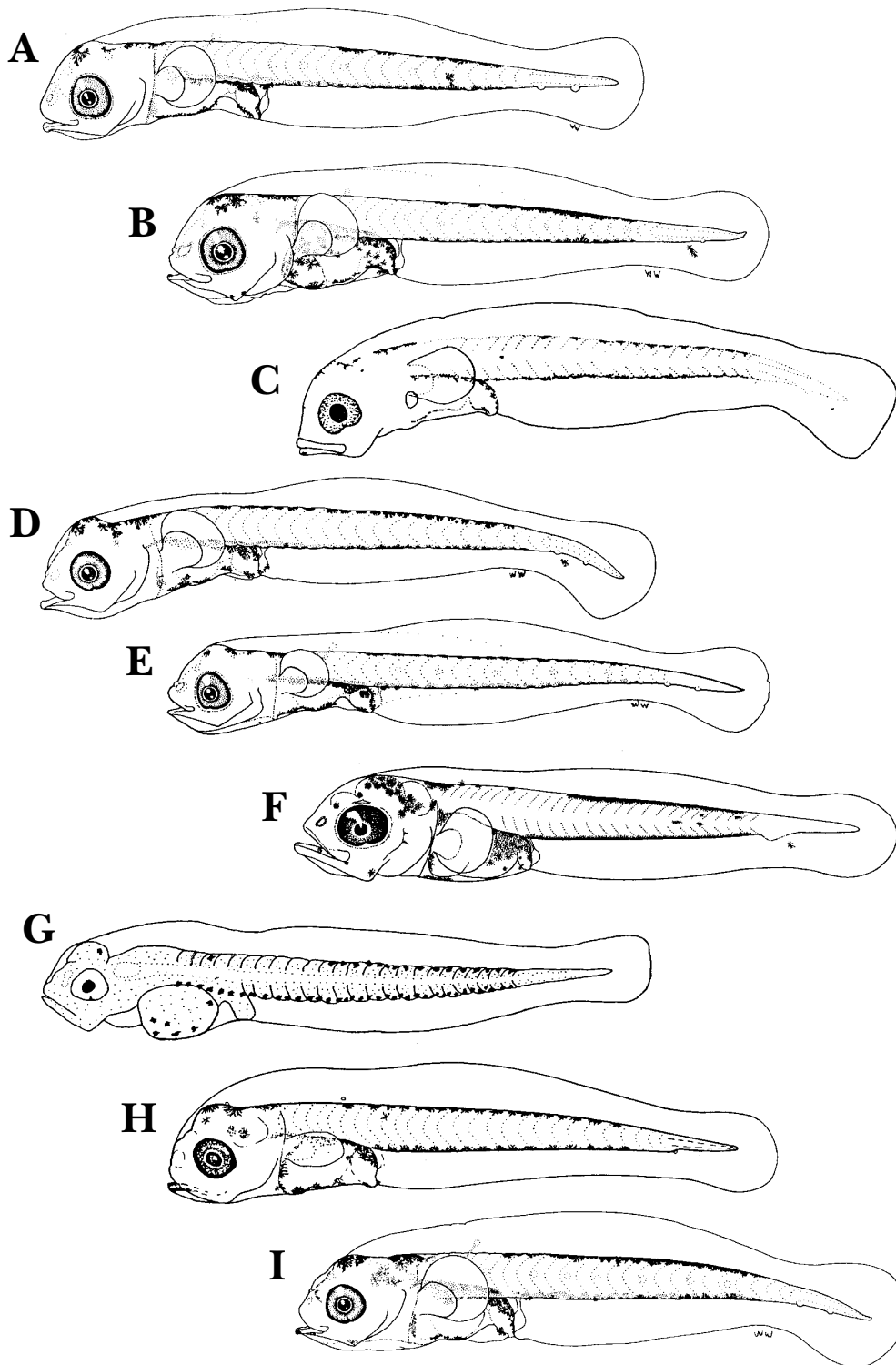


Figure 9

Preflexion-stage larvae of the *Sebastes* subgenus *Pteropodus*, lateral view. (A) *Sebastes atrovirens*, 4.6 mm; (B) *S. auriculatus*, 5.8 mm; (C) *S. carnatus*, 4.3 mm (Moreno, 1993); (D) *S. caurinus*, 5.2 mm; (E) *S. chrysomelas*, 5.3 mm; (F) *S. dalli*, 6.2 mm (Moser and Butler, 1981); (G) *S. maliger*, ca. 5 mm (DeLacy et al., 1964); (H) *S. nebulosus*, 5.7 mm (Kendall¹); (I) *S. rastrelliger*, 5.6 mm.

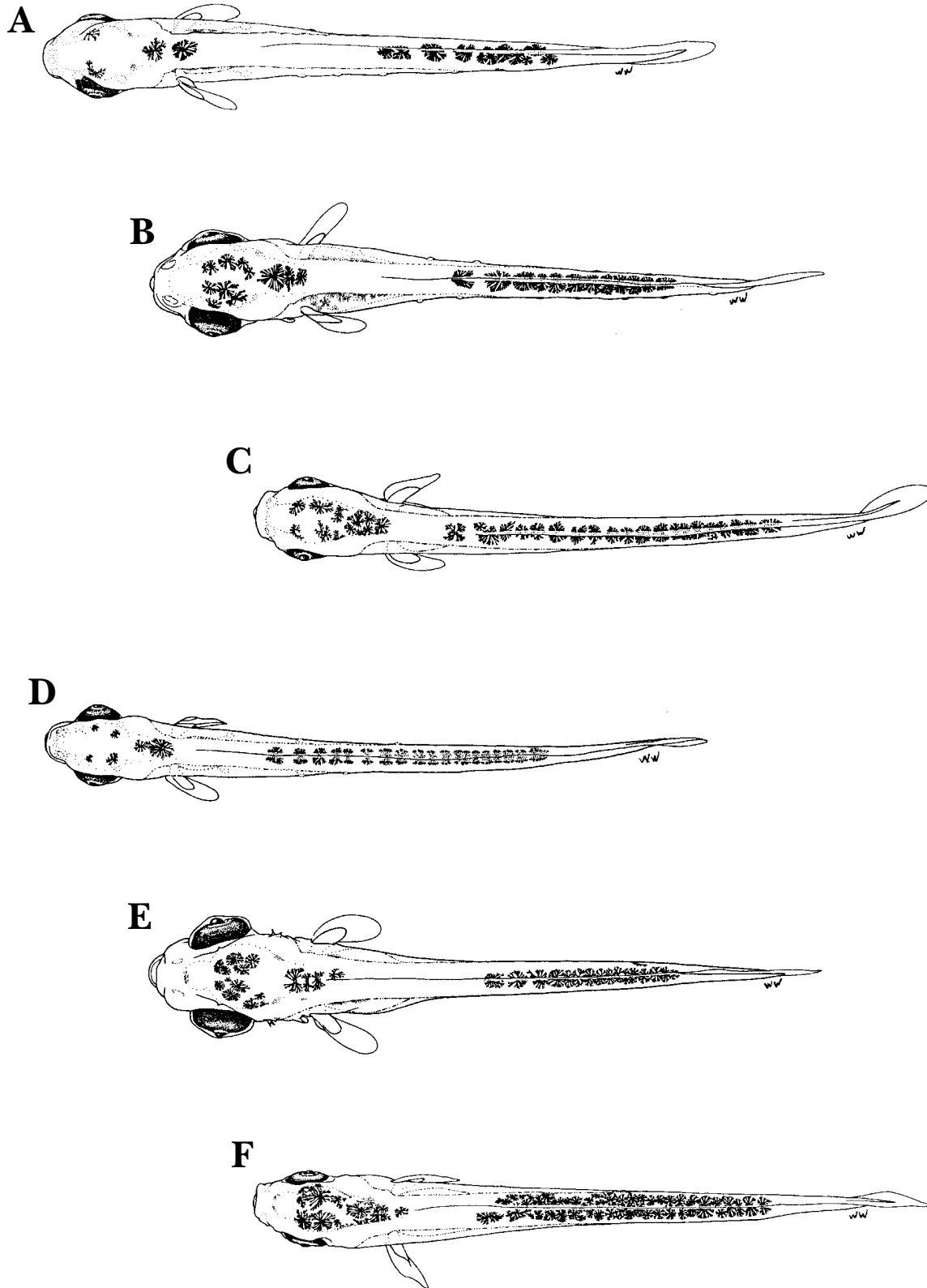


Figure 10

Preflexion-stage larvae of the *Sebastes* subgenus *Pteropodus*, dorsal view. (A) *Sebastes atrovirens*, 4.6 mm; (B) *S. auriculatus*, 5.8 mm; (C) *S. caurinus*, 5.2 mm; (D) *S. chrysomelas*, 5.3 mm; (E) *S. dalli*, 6.2 mm; (F) *S. rastrelliger*, 5.6 mm.

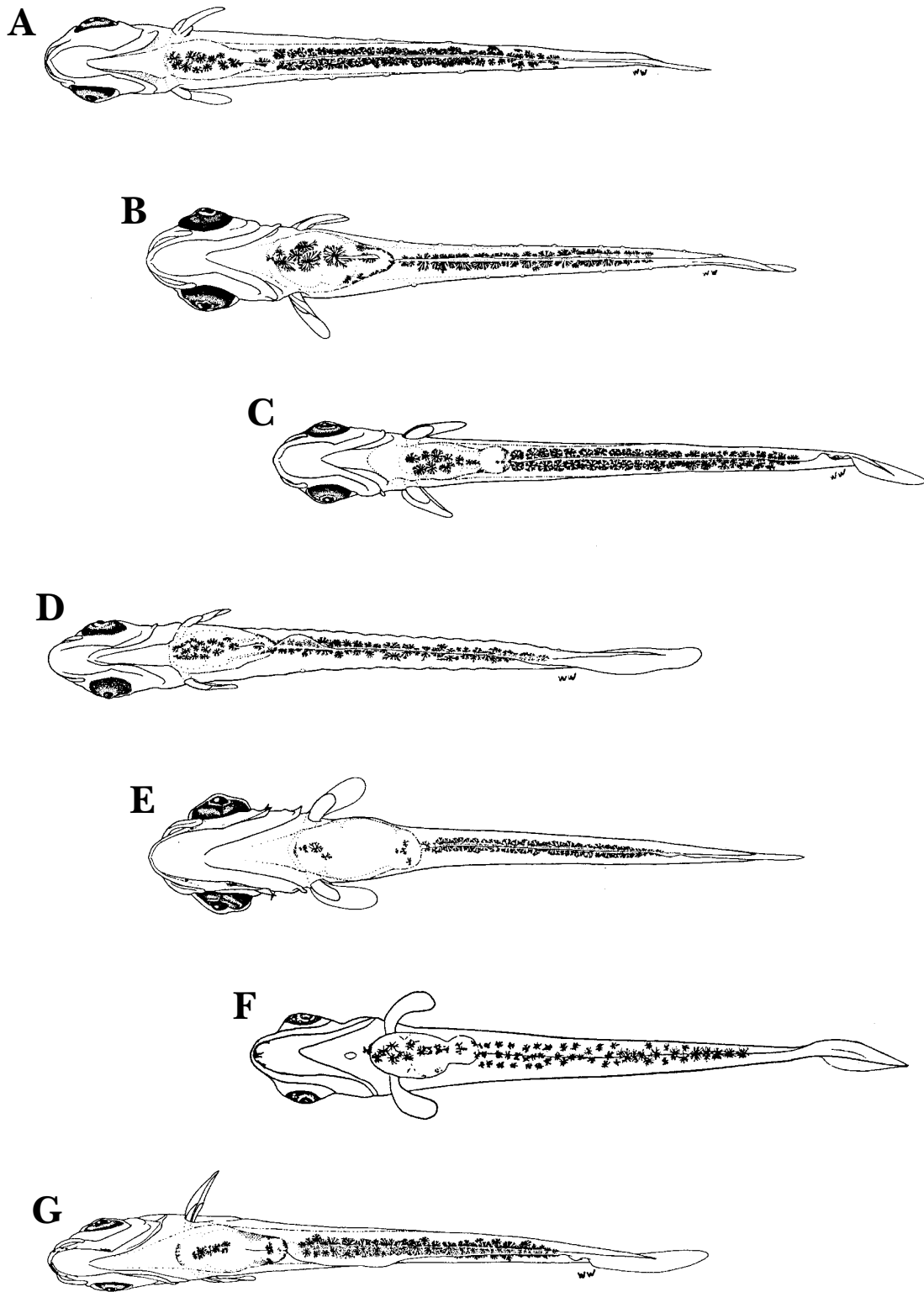


Figure 11

Preflexion-stage larvae of the *Sebastes* subgenus *Pteropodus*, ventral view. (A) *Sebastes atrovirens*, 4.6 mm; (B) *S. auriculatus*, 5.8 mm; (C) *S. caurinus*, 5.2 mm; (D) *S. chrysomelas*, 5.3 mm; (E) *S. dalli*, 6.2 mm; (F) *S. nebulosus*, 5.7 mm (Kendall¹); (G) *S. rastrelliger*, 5.6 mm.

Taylor⁴) can display a similar pattern. During flexion and postflexion stages pigmentation of *Pteropodus* and several other species converge on a common pattern with melanophores on most or all of the dorsal margin, on the horizontal septum of the tail (especially posteriorly, often with a saddle or bar posteriorly), and posteriorly on the ventral margin of the tail. However, it may be possible to distinguish preflexion-stage larvae of the subgenus as a whole from other *Sebastes* larvae based on the *Pteropodus* pattern. Clearly, it is unlikely that every preflexion-stage *Sebastes* larva could be unequivocally assigned to *Pteropodus* or “other” categories: lightly pigmented *Pteropodus* would be excluded from that category and unusually pigmented non-*Pteropodus* would be erroneously included. Probably ~ 75% of the preflexion-stage *Pteropodus* would be correctly identified and perhaps fewer than ~ 25% of non-*Pteropodus* larvae incorrectly classified based on larval pigmentation patterns. The likelihood of correctly classifying *Pteropodus* larvae using pigmentation diminishes rapidly after the preflexion stage. Nevertheless, because ~ 90% of the larval *Sebastes* collected in standard oblique bongo net tows off California are preflexion stage (Moser, 1996b), if the pigmentation method for larval identification is validated and confidence bounds on the technique established, probably using molecular methods, it may be possible to generate an index of larval *Pteropodus* abundance as a fishery-independent measure of population trends for this group of nearshore rockfishes as a whole.

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Literature cited

- Aseltine-Neilson, D.
2000. Recreational fishery. In (L. Rogers-Bennett, ed.), Review of some California fisheries for 1999: Market squid, Dungeness crab, sea urchin, prawn, abalone, Pacific sardine, Pacific herring, Pacific mackerel, reduction, white seabass, and recreational, p. 22–24. Calif. Coop. Oceanic Fish. Invest. Rep. 41:8–25.
- Boehlert, G. W., and M. Yoklavich.
1984. Reproduction, embryonic energetics, and the fetal-maternal relationship in the viviparous genus *Sebastes* (Pisces: Scorpaenidae). Biol. Bull. 167:354–370.
- DeLacy, A. C., C. R. Hitz, and R. L. Dryfoos.
1964. Maturation, gestation, and birth of rockfish (*Sebastes*) from Washington and adjacent waters. Wash. Dep. Fish., Fish. Res. Pap. 2:51–67.
- Eitner, B., C. Kimbrell, and R. Vetter.
1999. *Sebastes moseri* (Scorpaeniformes: Scorpaenidae): a new rockfish from the eastern North Pacific. Copeia 1999:85–92.
- Eschmeyer, W. N., E. S. Herald, and H. Hammann.
1983. A field guide to Pacific coast fishes of North America, 336 p. Houghton Mifflin, Boston.
- Hubbs, C. L., and L. P. Schultz.
1933. Descriptions of two new American species referable to the rockfish genus *Sebastes*, with notes on related species. Univ. Washington Publ. Biol. 2:15–44.
- Laidig, T. E., and K. M. Sakuma.
1998. Description of pelagic larval and juvenile grass rockfish, *Sebastes rastrelliger* (family Scorpaenidae), with an examination of age and growth. Fish. Bull. 96:788–796.
- Lasker, R.
1985. An egg production method for estimating spawning biomass of pelagic fish: Application to the northern anchovy, *Engraulis mordax*. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36, 99 p.
- Lea, R. N., R. D. McAllister, and D. A. Van Tresca.
1999. Biological aspects of nearshore rockfishes of the genus *Sebastes* from central California, with notes on ecologically related sport fishes. Calif. Dep. Fish Game Fish Bull. 177, 109 p.
- Lenarz, W. H.
1987. A history of California rockfish fisheries. In B. R. Melteff (ed.), Proceedings of the International Rockfish Symposium, p. 35–41. Univ. Alaska Sea Grant Rep. 87-2.
- Love, M. S., J. E. Caselle, and W. Van Buskirk.
1998. A severe decline in the commercial passenger fishing vessel rockfish (*Sebastes* spp.) catch in the Southern California Bight, 1980–1996. Calif. Coop. Oceanic Fish. Invest. Rep. 39:180–195.
- McKee-Lewis, K.
1998. Live fishes. In (B. Eitner, ed.), Review of some California fisheries for 1997, p. 17–18. Calif. Coop. Oceanic Fish. Invest. Rep. 39:9–24.
- Moreno, G.
1993. Description of early larvae of four northern California species of rockfishes (Scorpaenidae: *Sebastes*) from rearing studies. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 116, 18 p.
- Moser, H. G.
1967. Reproduction and development of *Sebastes paucispinis* and comparison with other rockfishes off southern California. Copeia 1967:773–797.
1996a. Introduction. In (H. G. Moser, ed.), The early stages of fishes in the California Current region, p. 1–72. Calif. Coop. Oceanic Fish. Invest. Atlas 33.
1996b. Scorpaenidae: Scorpionfishes and rockfishes. In (H. G. Moser, ed.), The early stages of fishes in the California Current region, p. 733–795. Calif. Coop. Oceanic Fish. Invest. Atlas 33.
- Moser, H. G., and E. H. Ahlstrom.
1978. Larvae and pelagic juveniles of the blackgill rockfish,

⁴ Taylor, C. A. Personal comm. Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093-0203.

-
- Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. J. Fish. Res. Bd. Canada 35:981–996.
- Moser, H. G., and J. L. Butler.
1981. Description of reared larvae and early juveniles of the calico rockfish, *Sebastes dallii*. Calif. Coop. Oceanic Fish. Invest. Rep. 22:88–95.
- Moser, H. G., and W. Watson.
1990. Distribution and abundance of early life history stages of the California halibut, *Paralichthys californicus*, and comparison with the fantail sole, *Xystreurys liolepis*. In (C. W. Haugen, ed.), The California halibut, *Paralichthys californicus*, resource and fisheries, p. 31–84. Calif. Dep. Fish Game Fish Bull. 174.
- Moser, H. G., R. L. Charter, W. Watson, D. A. Ambrose, J. L. Butler, S. R. Charter, and E. M. Sandknop.
2000. Abundance and distribution of rockfish (*Sebastes*) larvae in the Southern California Bight in relation to environmental conditions and fishery exploitation. Calif. Coop. Oceanic Fish. Invest. Rep. 41:132–147.
- Ralston, S.
1998. The status of federally managed rockfish on the U.S. west coast. In (M. M. Yoklavich, ed.), Marine harvest refugia for west coast rockfish: a workshop, p. 6–16. U.S. Dep. Commer., NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-255.
- Ralston, S., J. R. Bence, M. B. Eldridge, and W. H. Lenarz.
2003. An approach to estimating rockfish biomass based on larval production, with an application to *Sebastes jordani*. Fish. Bull. 101:129–146.
- Seeb, L. W.
1998. Gene flow and introgression within and among three species of rockfishes, *Sebastes auriculatus*, *S. caurinus*, and *S. maliger*. J. Heredity 89:393–403.
- Stahl-Johnson, K. L.
1985. Descriptive characteristics of reared *Sebastes caurinus* and *S. auriculatus* larvae. Can. Tech. Rep. Fish. Aquat. Sci. 1359: 65–76.
- Walters, K.
2001. Live fishes. In (L. Rogers-Bennett, ed.), Review of some California fisheries for 1999: Market squid, Dungeness crab, sea urchin, prawn, abalone, Pacific sardine, Pacific herring, Pacific mackerel, reduction, white seabass, and recreational, p. 22–24. Calif. Coop. Oceanic Fish. Invest. Rep. 41:8–25.

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