Abstract—Sequencing a portion of the cytochrome *b* gene of an unidentified *Sebastes* larval type long recognized in the California Current region demonstrated that it includes both whitespotted rockfish (*S. moseri*), also known as whitespeckled rockfish, and dwarf-red rockfish (*S. rufinanus*), two small unfished species first recognized in recent decades. Preflexion-stage larvae are moderately slender and compressed, with a short preanal length, moderately large head, short snout, and large eyes. There are no spines on the head until mid to late preflexion stage when the preopercular and pterotic spines form, followed quickly by the parietal and postocular spines. Pectoral-fin rays begin to form by mid preflexion stage and caudal-fin rays by late preflexion stage. Pigmentation is dorsally on the head, gas bladder, and gut, and posteriorly on the tail. The characteristic dorsal and ventral pigment patches on the tail are limited to its margins in *S. rufinanus* but commonly extend onto its dorso- and ventrolateral surfaces in *S. moseri*. Pectoral-fin pigment is present in some *S. moseri* but absent in all *S. rufinanus* during preflexion stage. Although not always distinguishable from one another, larval *S. moseri* and *S. rufinanus* are visually distinguishable through preflexion stage from other larval *Sebastes* species described to date, but it is unknown whether that remains true through postflexion stage.

Early larvae of the whitespotted rockfish (*Sebastes moseri* Eitner, 1999) and the dwarf-red rockfish (*S. rufinanus* Lea and Fitch, 1972) (Pisces: Sebastidae) identified by molecular methods

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Introduction

The rockfish genus *Sebastes* includes at least 97 species in the eastern North Pacific Ocean of which about 56 occur in the Southern California Bight (Love et al., 2002). Many of these are important in sport and commercial fisheries (e.g., Lenarz, 1987; Leet et al., 2001) and are well known, but some of the small, deep-water species that are not fished are relatively poorly known but can be numerically dominant (e.g., Thompson et al., 2016, 2017a; Field et al., 2021). Two of these diminutive species, whitespotted rockfish (*S. moseri*) (also known as whitespeckled rockfish, named in recognition of Dr. H Geoffrey Moser) and dwarf-red rockfish (*S. rufinanus*), were first recognized in the past few decades from specimens collected off southern California (Lea and Fitch, 1972; Eitner et al., 1999). Both species are small (<20 cm), school over rocky bottom, and reside primarily at 100–200 m depths off southern California (Love et al., 2022). Adult rockfishes exhibit a wide variety of life history traits as some are small and short-lived (maximum 13 years) while others are apex predators that can live for over 2 centuries (Love et al., 2002). Despite these differences, all *Sebastes* species are live-bearers and birth well-developed larvae that are ready to begin feeding at parturition. Larval rockfishes are readily obtained from pregnant females and commonly collected in plankton samples, particularly during late winter and spring (Moser et al., 1993). Larvae have been shown to be useful in estimating the spawning biomass of adults (e.g., Moser et al., 2000; Ralston et al., 2003; Ralston and MacFarlane, 2010), and because the adults of many species are economically important (e.g., Love et al., 2022), efforts have been made to improve our ability to identify the larvae (e.g., Kendall, 1991; Moser, 1996a). However, because larval *Sebastes* are difficult to rear (e.g., Kendall, 1991) and overlap considerably among species in meristic, morphological, and pigmentation characters (Moser, 1996a), only a few species can routinely be visually identified from eastern North Pacific plankton collections (Moser et al., 2000).

California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys have been conducted regularly in the California Current Ecosystem from 1951 through the present. The survey area initially extended from the Oregon–California border (approximately 42°N) to Cabo San Lucas, Baja California Sur, Mexico (approximately 22°54′N), but since 1985 has been limited to southern and central California (McClatchie, 2014). The larvae of 7 rockfish species are

sufficiently distinctive to be routinely identifiable to species in the plankton collections from these surveys (Moser et al., 2000). A distinctive but unidentified *Sebastes* larval type, characterized by having melanistic pigment on the trunk and tail limited to a short melanophore patch each on the dorsal and ventral margins far posteriorly on the tail, also has been recognized in samples collected between about Monterey, California, and Punta Baja, Baja California, Mexico, throughout the time series. Molecular genetic sequencing demonstrated that this unidentified larval type includes both *S. moseri* and *S. rufinanus*. The purpose of this paper is to describe pigmentation and morphology of molecularly identified preflexion through mid-postflexion stages of *S. moseri* and preflexion stage of *S. rufinanus*. Preflexion-stage larvae are about 90% of the rockfish larvae collected in standard plankton tows (e.g., Moser, 1996a); larger larval *S. rufinanus* were not collected in the samples analyzed for these descriptions.

Materials and methods

Details of the CalCOFI plankton sampling area, gear, and methods are widely available (e.g., Kramer et al., 1972; Ohman and Smith, 1995; Thompson et al., 2017b). An additional source of larvae was the 2002–2004 Cowcod Conservation Area survey of a newly established Marine Protected Area within the CalCOFI grid off southern California (Thompson et al., 2012). Briefly, both CalCOFI and Cowcod Conservation Area surveys include oblique plankton tows through the upper 212 m of the water column (to 15 m above the bottom in shallower water) at each of several stations arrayed along a series of transect lines using a 71-cm bongo frame equipped with 0.505-mm mesh nets. Samples from the starboard net are preserved in 5% sodium borate-buffered formalin and, beginning in 1997, those from the port net are preserved in 95–100% Tris-buffered ethanol to facilitate otolith and molecular analyses. Fish larvae are sorted from 100% of every ethanol-preserved sample.

Initial molecular identification of a larva of the unknown *Sebastes* type demonstrated that it was the then newly described *S. moseri* and prompted a search of the ethanol-preserved collections for additional specimens, some of which subsequently proved to be *S. rufinanus*. In total, we obtained 187 *S. moseri* (2.4–8.9 mm, preflexion through mid postflexion stage) and 90 *S. rufinanus* (2.6–5.8 mm, preflexion stage) from the 1997–2013 CalCOFI and Cowcod Conservation Area surveys (Suppl. Table 1).

Prior to molecular analysis, we recorded the pigmentation pattern and various measurements for each larva using a Wild M5 Stereomicroscope (Wild Stereo Microscopes, now manufactured by Leica Microsystems Inc., Wetzlar, Germany) equipped with an ocular micrometer. These measurements, including body length (BL), preanal length, head length, head width, snout length, length of the pectoral-fin blade, eye diameter, and body depth, are defined by Moser (1996b). All larval lengths given here refer to body length, all proportions are expressed as percentages of BL, and all descriptions of larval pigmentation refer only to melanistic pigment. Measurements were not adjusted to account for larval shrinkage in ethanol. Literature reports indicate shrinkage in the range of 3–6% in alcohol preservative (e.g., Theilacker, 1980; Moku et al., 2004; Fey and Hare, 2005), suggesting that these changes were likely not important for our purposes. Small fish larvae are also commonly distorted by fixation in alcohol, and not all specimens were used for the descriptions or measurements; thus, we used 117 *S. moseri* (2.4–8.9 mm, preflexion through mid postflexion stage) and 73 *S. rufinanus* (2.6–5.8 mm, preflexion stage) for the pigmentation descriptions. We used 93 *S. moseri* (2.4–8.9 mm, preflexion through mid postflexion stage) and 49 *S. rufinanus* (2.6–5.8 mm, preflexion stage) for morphometric measurements. We illustrated representative specimens selected from among the least distorted larvae of each species using the Wild microscope with a camera lucida. After molecular analysis, we recorded counts of myomeres, head spines, and fin-rays.

For molecular analysis, we extracted DNA from an eyeball or caudal muscle following the protocol described by Hyde et al. (2005), and we sequenced a 625-bp section of the mitochondrial cytochrome *b* gene. Primers included GluRF2 5′ AAC CAT CGT TGT TAT TCA ACT ACA AGA ACC and CB3RF2 5′ CGA ACA GGA ART ATC AYT CTG G for the initial PCR and CBINR3 5′ ATG AGA ART AGG GGT GGA AGC T as an internal sequencing primer following the protocol of Thompson et al. (2016). We compared the resulting sequence data to a reference library of 374 independent haplotype sequences from all northeast Pacific Ocean *Sebastes* species (J. Hyde, unpubl. data; Hyde and Vetter, 2007) with MEGA software, vers. 11 (Tamura et al., 2021), to measure genetic distance and construct a phylogenetic tree using a Kimura 2-parameter model and the neighbor-joining algorithm with 1000 bootstrap replicates. All genetic assignments to the 2 species were unambiguous.

Results

Identification

Larval sequences clustered (>90% bootstrap support) in 2 monophyletic clades with reference sequences (Hyde

and Vetter, 2007) for *S. moseri* or *S. rufinanus*. Despite being understudied due to only rare observations and collections, we found a significant number of unique haplotypes for both species, with *S. moseri* having 40 unique haplotypes (GenBank OQ944383–OQ944422), including the early sequenced data of the unknown larval type FL1 (*moseri* haplotype 40 OQ944422), and *S. rufinanus* having 21 unique haplotypes (GenBank OQ944423–OQ944443), including the early sequenced data of the unknown larval type LT22 (*rufinanus* haplotype 19 OQ944441). Intraspecific divergence for larval *S. moseri*, 0.97%, and larval *S. rufinanus*, 1.62%, are similar to intraspecific variability observed for other *Sebastes* species (e.g., Hyde et al., 2008; Hyde and Vetter, 2009). Net interspecific divergence from other *Sebastes* species was 2.0–8.9% for *S. moseri* and 2.0–8.6% for *S. rufinanus*; net divergence between the 2 species was 2.0%.

Descriptions

Sebastes moseri Eitner, 1999

The smallest larva available, 2.4 mm, had no yolk or oil globule remaining. Notochord flexion begins after 6.2 mm but before 6.8 mm and is completed after 7.1 mm but before 8.8 mm. During preflexion stage (Fig. 1A) larval *S. moseri* are moderately slender (mean body depth 18.4%, range 15.8–23.4%) and compressed (mean head width 8.5%, range 6.9–13.3%), with a short preanal length (mean preanal length 37.9%, range 33.6–47.3%). The head is moderately large (mean head length 21.2%, range 18.3–27.7%), with a short snout (mean snout length 5.6%, range 3.5–9.5%) and large, slightly oval to round eyes (mean eye diameter 9.3%, range 7.5–11.7%). All proportions except head width gradually increase with development (Table 1). Preanal and head lengths increase most, reaching means of 46.8% (range 42.5–48.5%) and 29.8% (range 25.9–31.8%), respectively, in flexion stage (Fig. 1B) and 50.4% (range 50.0–50.8%) and 33.6% (range 33.3–33.9%), respectively, by mid postflexion stage. Body depth, snout length, and eye diameter all increase less, to 28.3%, 10.8%, and 10.9% BL, respectively, by mid postflexion stage. Pectoral fin length increases to 14.5% BL through mid postflexion stage.

There are no spines on the head or pectoral girdle until late preflexion stage (between about 5.3–5.6 mm), when 2 spines form at the angle and on the lower limb of the posterior preopercular margin, and a small pterotic spine (<1% BL) forms. During flexion stage (by 6.8 mm) a small spine is added on the upper posterior preopercular margin and 2 small spines form on the anterior preopercular margin, at the angle and on its lower limb. A third small spine is added on the upper anterior preopercular margin of most larvae later in flexion stage (by 7.1 mm). Through mid postflexion stage (Fig. 1C) the preopercular spines become longer but no additional spines form. All preopercular spines have smooth margins until about mid flexion stage (7.1 mm), when the spine at the posterior angle begins to become finely serrate along its anterior margin. That spine always is the longest preopercular spine, initially about 6% BL and reaching about 9% BL in postflexion stage. Small parietal spines (<1% BL) form late in preflexion stage (by 5.6 mm), and a postocular spine (<1% BL) is added over each eye in flexion stage (by 6.6 mm). During notochord flexion, the parietal spine becomes larger (5% BL by 6.6 mm), and by about mid flexion stage (about 7.1 mm) the anterior margin of the spine begins to become serrate. The postocular spine may begin to become serrate along its anterior margin as early as mid-flexion stage (by 7.1 mm) in some larvae, and is serrate in postflexion stage. A small posttemporal spine forms in postflexion stage (by 8.8 mm).

Fin-ray formation begins late in preflexion stage (by 5.6 mm) when the central principal caudal-fin rays begin to form. By mid-flexion most or all principal caudal-fin rays are forming, and by mid postflexion stage (8.8 mm) the full complement of 8+7 principal rays and the first four upper and lower procurrent rays are present. The pectoral-fin rays begin forming in flexion stage with the upper 8–10 rays present by 6.8 mm. Addition of rays is ventrad, with 14–15 rays present by mid-flexion stage (7.1 mm) and the full complement of 17 pectoral-fin rays attained by mid postflexion stage (8.8 mm). Dorsal- and anal-fin anlagen begin to form early in flexion stage, but fin rays were not apparent in the flexion-stage larvae and may not form until postflexion stage. The full adult complement of III,9 anal-fin rays is present by mid postflexion stage, but the last 1–2 soft rays of the dorsal fin may still be forming at mid postflexion stage (forming in the 8.8-mm specimen and apparently formed in the 8.9-mm specimen). Pelvic-fin buds form in mid flexion stage and the full complement of I,5 rays is present by mid postflexion stage.

Larvae are lightly pigmented through at least mid-flexion stage (Fig. 1). Pigmentation on the head is limited to the dorsum, with a pair of melanophores over the midbrain area and one anteriorly over the hindbrain in the smallest larvae, increasing to 4–6 and 1–2, respectively, by mid preflexion stage (4.4 mm) and to as many as 8–15 and 1–3 melanophores, respectively, in flexion stage. In postflexion stage dorsal melanophores evenly cover the midbrain area, and by 8.9 mm they extend over the forebrain as well. An internal melanophore or 2 may form on each side at the posterior margin of the midbrain as early as flexion stage (by 7.1 mm) but more commonly there are none. One or 2 melanophores form anteriorly at the lower margin of the maxilla in flexion stage (by 7.1 mm; occasionally present on one side only),

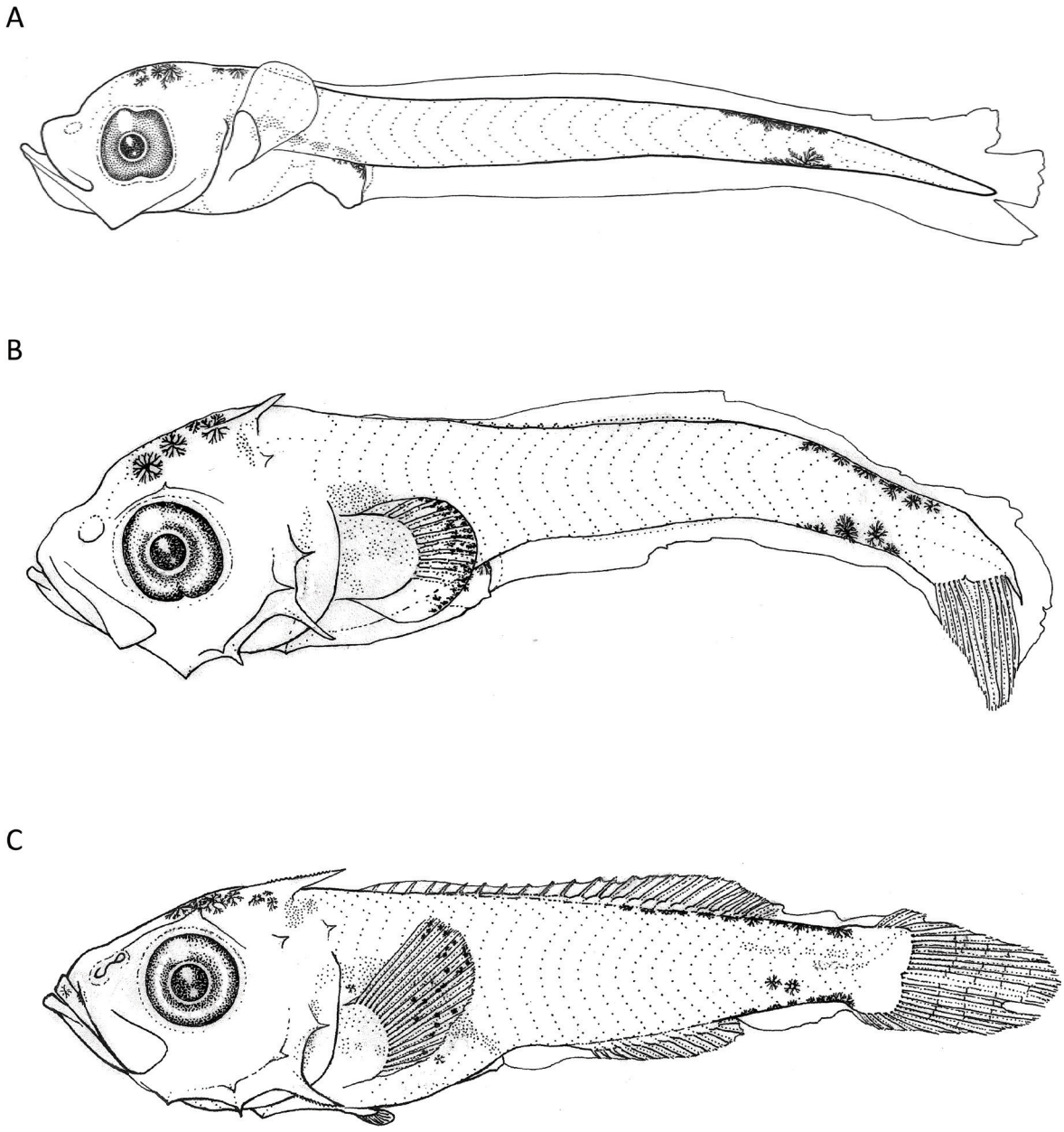

Figure 1

Illustrations of larval whitespotted rockfish (*Sebastes moseri*) collected during the California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys in the California Current region: (**A**) preflexion stage, 4.9 mm body length (BL), (CalCOFI cruise 0901NH, station 93.3 45.0, January 2009, specimen 8-6); (**B**) early flexion stage, 6.8 mm BL (CalCOFI cruise 0602JD, station 93.3 45.0, February 2006, specimen 8-2); (**C**) postflexion stage, 8.8 mm BL (CalCOFI cruise 1301SH, station 93.3 50.0, January 2013, specimen 4-7).

and 1 or 2 melanophores commonly form at the tip of the lower jaw during the latter part of preflexion stage but may be absent in some larvae before mid postflexion stage (Table 2).

The gas bladder and dorsum of the gut are densely pigmented, except somewhat more sparsely on the hindgut. Melanophores extend ventrolaterally from the dorsum, covering as much as the upper 50% of the midgut area in some larvae through flexion stage and all larvae by postflexion stage. Melanophores are sparsely scattered anteriorly down the upper 60–70% of the visceral cavity in most larvae from mid preflexion through about mid flexion stage and in all larvae thereafter. A melanophore may be present at the anteroventral margin of the liver in some larvae but more commonly is absent. There is no other internal or external ventral pigmentation on the abdominal area.

The trunk and tail are unpigmented except for 2 prominent pigment patches far posteriorly on the dorsal and ventral margins of the tail (Fig. 1). The melanophores in each patch tend to be contiguous rather than clearly separated. Early in preflexion stage the dorsal patch consists of 4–6 melanophores along 4–5 myomeres between myomeres 20 and 25, lengthening to 7–12 melanophores along 6–7 myomeres between myomeres 19 and 26 in flexion stage (Suppl. Table 2). Melanophores

Table 1

Measurements, given as percentages of body length, of larval whitespotted rockfish (*Sebastes moseri*) and dwarf-red rockfish (*S. rufinanus*) collected during the California Cooperative Oceanic Fisheries Investigations and Cowcod Conservation Area surveys in the California Current region between 1997 and 2013. The following measurements (in millimeters) were collected for each larva: body depth (BD), body length (BL), eye diameter (ED), head length (HL), head width (HW), pectoral-fin length (P_1L), pelvic-fin length (P_2L), and snout length (SnL). *n*=number of larvae; – = not yet formed; a=not measurable.

Whitespotted rockfish, *Sebastes moseri*

Stage	*n*	BL (mm)	PAL	BD	HL	HW	SnL	ED	P_1L	P_2L
Preflexion	1	2.4	40.0	20.0	20.0	13.3	8.3	11.7	13.3	–
Preflexion	1	2.6	42.3	23.1	27.7	10.8	7.7	11.2	8.5	–
Preflexion	3	2.8	37.9	18.1	20.0	8.6	5.7	10.1	7.6	–
Preflexion	2	2.9	42.8	23.4	26.2	11.0	6.9	10.3	6.9	–
Preflexion	3	3.0	42.3	17.3	20.0	9.1	6.7	9.7	6.0	–
Preflexion	3	3.1	41.9	19.4	22.3	6.9	6.8	9.9	8.4	–
Preflexion	5	3.2	38.3	15.8	21.3	7.1	5.4	9.2	8.8	–
Preflexion	5	3.3	39.2	16.8	19.4	9.0	4.7	9.7	7.7	–
Preflexion	5	3.4	35.5	16.9	19.1	8.2	5.2	8.8	6.0	–
Preflexion	5	3.5	38.6	17.7	19.9	8.7	5.6	9.7	6.4	–
Preflexion	5	3.6	33.6	16.2	17.8	7.9	4.4	8.1	7.3	–
Preflexion	4	3.7	41.1	18.2	22.7	7.2	5.4	8.6	8.1	–
Preflexion	3	3.8	38.6	17.5	18.4	7.7	4.4	9.8	8.4	–
Preflexion	3	3.9	38.8	17.4	22.4	9.1	5.1	10.3	8.0	–
Preflexion	5	4.0	35.6	16.3	19.2	7.8	5.7	8.6	5.7	–
Preflexion	3	4.1	37.7	18.2	21.5	7.8	5.2	8.9	6.0	–
Preflexion	5	4.2	35.8	18.3	21.3	8.5	5.1	9.0	7.6	–
Preflexion	5	4.4	37.0	18.9	22.5	9.4	5.5	9.4	7.5	–
Preflexion	2	4.5	38.4	20.4	21.8	8.9	5.3	8.9	8.7	–
Preflexion	1	4.6	36.5	16.5	18.3	13.0	3.5	7.8	7.8	–
Preflexion	3	4.7	35.7	18.7	20.9	7.7	6.0	8.5	5.7	–
Preflexion	3	4.8	37.2	20.0	23.1	7.8	5.6	10.0	6.7	–
Preflexion	2	4.9	37.6	18.0	23.7	10.6	6.1	10.2	8.2	–
Preflexion	2	5.0	37.6	20.4	22.6	10.0	4.8	9.2	6.4	–
Preflexion	1	5.1	35.3	20.4	22.0	7.8	4.7	7.5	7.1	–
Preflexion	3	5.3	36.9	20.3	21.8	7.2	6.2	8.1	8.2	–
Preflexion	2	5.4	37.0	19.6	23.1	7.4	6.3	9.1	10.0	–
Preflexion	1	5.5	47.3	22.7	24.7	10.5	9.5	10.9	7.3	–
Preflexion	2	6.2	36.8	18.9	24.5	10.3	8.1	8.5	8.5	–
Flexion	1	6.8	43.5	21.2	25.9	11.8	8.8	10.3	7.6	–
Flexion	2	7.1	48.5	25.2	31.8	12.8	9.6	10.7	9.9	bud
Postflexion	1	8.8	50.0	28.2	30.9	13.2	10.0	10.9	14.5	5.2
Postflexion	1	8.9	50.8	28.3	33.3	10.8	10.8	10.8	12.6	a

(continued)

Table 1 (continued)

Dwarf–red rockfish, *Sebastes rufinanus*

Stage	*n*	BL (mm)	PAL	BD	HL	HW	SnL	ED	P_1L
Preflexion	2	2.6	43.8	22.3	24.6	7.7	5.4	12.3	7.3
Preflexion	1	2.7	35.6	15.9	18.5	11.9	5.9	11.9	6.7
Preflexion	3	2.8	a	19.0	a	9.0	a	11.4	7.1
Preflexion	2	2.9	41.4	21.4	23.4	9.7	7.6	11.0	8.6
Preflexion	1	3.0	45.3	22.7	23.3	10.0	7.3	12.0	6.7
Preflexion	2	3.1	39.4	21.0	23.5	9.7	5.8	9.7	7.4
Preflexion	2	3.2	50.0	20.6	29.4	10.6	6.3	11.6	8.1
Preflexion	3	3.3	42.0	16.2	22.2	10.9	6.1	9.7	7.9
Preflexion	2	3.4	34.7	13.5	17.1	10.0	3.5	8.5	5.9
Preflexion	2	3.5	37.7	14.9	26.9	9.1	5.1	8.6	8.6
Preflexion	1	3.6	a	18.9	a	8.9	a	11.1	a
Preflexion	1	3.7	34.6	17.3	21.6	6.5	4.3	8.6	4.3
Preflexion	2	3.8	42.1	22.4	23.2	7.9	5.8	11.1	7.1
Preflexion	2	3.9	37.9	18.8	20.5	8.2	4.4	9.2	5.1
Preflexion	2	4.0	36.8	19.0	21.3	8.5	5.9	9.6	11.0
Preflexion	3	4.3	37.5	17.8	21.1	7.0	6.2	6.0	6.0
Preflexion	3	4.4	37.3	19.5	20.2	7.9	3.7	8.9	8.2
Preflexion	2	4.5	40.9	26.2	26.4	11.3	8.2	10.2	6.2
Preflexion	1	4.6	41.7	20.0	23.0	7.0	5.7	9.6	5.7
Preflexion	2	4.7	38.1	19.1	18.5	8.6	4.3	8.5	6.5
Preflexion	2	4.8	39.2	19.6	19.2	8.8	4.4	9.4	8.5
Preflexion	1	5.0	41.2	16.8	23.2	7.2	7.2	8.4	5.2
Preflexion	1	5.1	39.2	17.3	25.1	7.1	7.8	9.4	7.1
Preflexion	2	5.2	45.4	22.3	26.9	7.3	8.8	10.4	6.5
Preflexion	1	5.3	37.0	18.1	18.9	6.8	4.5	7.5	5.7
Preflexion	2	5.4	42.2	22.6	28.9	11.5	10.0	10.4	7.8
Preflexion	1	5.8	45.5	22.8	26.9	10.3	9.0	9.7	a

continue to be added anteriorly from the dorsal patch during postflexion stage, with 4–6 melanophores remaining on the caudal peduncle and up to 11 extending along each side of the dorsal-fin base to below the first or second dorsal-fin soft ray by 8.9 mm.

Early in preflexion stage the ventral patch consists of 2–5 melanophores along 4–7 myomeres between myomeres 21 and 26. It increases to about 4–9 melanophores along 4–6 myomeres between myomeres 20 and 26 in flexion stage (Suppl. Table 2). This pigment may begin to spread forward along the anal-fin base by mid postflexion: in the 8.9-mm specimen the anterior-most melanophores were at the base of the last anal-fin ray.

Although the melanophores in each series are largely limited to the dorsal and ventral margins, 1–3 in each series may extend dorso- or ventrolaterally in preflexion stage and may be entirely dorso- or ventrolateral, usually near the margins, in flexion and postflexion stages. By mid postflexion stage a shallowly internal midlateral melanophore series begins to form posteriorly in the horizontal septum, at about myomeres 24–26. Internal melanophores also begin to form posteriorly over the vertebral column at about myomeres 23–26 in postflexion stage (by 8.8 mm), and an internal melanophore forms under the anterior end of the urostyle.

Fin pigmentation is limited to the pectoral fin. Pectoral pigment may be present or absent in preflexion stage: the fin base is unpigmented until the flexion stage, but melanophores form near the margin of the fan in some larvae beginning in mid-stage at about 4.9 mm (present in 63% of preflexion stage larvae ≥4.9 mm). A melanophore forms on the inner surface of the pectoral-fin base at its insertion during flexion stage (by 6.8 mm) and may increase to 2 melanophores in postflexion stage (8.8 mm, present in 60% of flexion- and postflexion-stage larvae). Melanophores are present along some to most pectoral-fin rays in all flexion- and postflexion-stage larvae, limited primarily to the distal 10% of the fin in most.

Sebastes rufinanus Lea and Fitch, 1972

The smallest larva available, 2.6 mm, had no yolk or oil globule remaining, and the largest larva, 5.8 mm, was

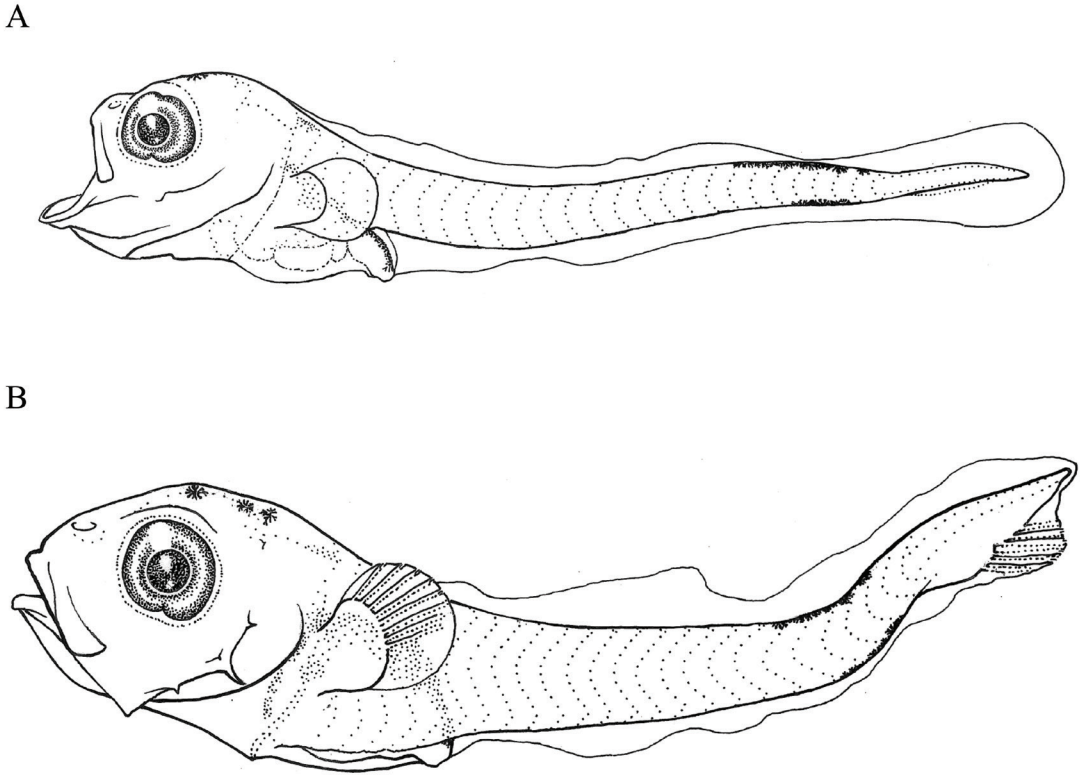

Figure 2

Illustrations of preflexion-stage dwarf-red rockfish (*Sebastes rufinanus*) larvae collected during the California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys in the California Current region: (**A**) 5.3 mm body length (BL) (CalCOFI cruise 1202NH, station 90.0 53.0, February 2012, specimen 25-21); (**B**) 5.8 mm BL (CalCOFI cruise 0701JD, station 86.7 35.0, January 2007, specimen 42-12).

still in preflexion stage although probably near the end of the stage. Larval *S. rufinanus* are moderately slender (mean body depth 19.2%, range 13.5–22.8%) and compressed (mean head width 8.9%, range 6.5–11.9%), with a moderately short preanal length (mean preanal length 40.2%, range 34.6–50%). The head is moderately large (mean head length 22.9%, range 17.1–29.4%) with a short snout (mean snout length 6.0%, range 3.5–10%) and large, slightly oval-to-round eyes (mean eye diameter 9.7%, range 6–12.3%). Pectoral-fin length averages 7.2% (range 4.3–11%) through preflexion stage (Table 1).

There are no spines on the head or pectoral girdle until mid preflexion stage (as early as about 4.8 mm), when a small pterotic spine and the first one or 2 small, posterior preopercular spines may form. Later, during preflexion stage (about 5.2–5.4 mm), 2 small spines form on the upper and lower margins of the anterior preopercular margin. No other head spines form through 5.8 mm.

Larvae are lightly pigmented through preflexion stage (Fig. 2). Pigmentation on the head is largely limited to the dorsum, usually with a pair of melanophores over the midbrain area and one anteriorly over the hindbrain early in the stage (2.6 mm), although it occasionally may be absent in either or both areas in larvae smaller than 4.5 mm (Table 2). During preflexion stage pigmentation gradually increases to as many as 7 melanophores in the midbrain region and 2 in the hindbrain region by late in the stage. An internal melanophore may form anteriorly on each side of the hindbrain in some larvae ≥5.6 mm. A melanophore or 2 may form anteriorly on each side of the lower jaw by about 5.2 mm (present in 43% ≥5.2 mm).

The gas bladder and dorsum of the gut, nearly to the end of the gut, are densely pigmented. Melanophores may extend laterally over the midgut area, but are largely limited to the upper 25% of the area until late in the stage when they begin to cover the upper half. Late in preflexion stage (by about 5.4 mm) melanophores spread anteriorly down the upper 50–90% of the visceral cavity.

There is no other internal or external pigmentation on the abdominal area.

The trunk is unpigmented. Tail pigmentation is limited to 2 prominent patches, one each posteriorly on the dorsal and ventral margins, composed of a series of mostly contiguous melanophores. The dorsal patch of about 4–10 melanophores is located at 4–8 myomeres between myomeres 18 and 23 through 24 and 26. The shorter ventral patch of about 3–7 melanophores is at 3–5 myomeres between about myomeres 20 and 25 through 24 and 26. Melanophores in both patches are largely restricted to their respective body margins and extend only slightly, if at all, dorso- or ventrolaterally, and there are no entirely dorso- or ventrolateral melanophores. Pectoral-fin pigmentation is absent.

Discussion

Early larval *S. moseri* and *S. rufinanus* are typical rockfishes morphologically, but their shared pigmentation pattern, with melanophores on the trunk and tail limited to a pair of posterior patches, appears to be unique relative to other rockfish larvae. This shared morphol-

Table 2

Summary of larval pigmentation in preflexion (pre), flexion (flex), and postflexion (post) whitespotted rockfish (*Sebastes moseri*) and dwarf-red rockfish (*S. rufinanus*) collected during the California Cooperative Oceanic Fisheries Investigations and Cowcod Conservation Area surveys in the California Current region between 1997 and 2013. Values are the percentage of larvae displaying pigment in each location. BL=body length.

Whitespotted rockfish, *Sebastes moseri*

BL (mm)	Stage	Number examined	Lower jaw	Head, dorsal	Nape	Dorsal margin	Ventral margin	Pectoral-fin blade	Pectoral-fin base
2.4	pre	1	0	0	0	100.0	100.0	0	0
2.6	pre	1	0	0	0	100.0	100.0	0	0
2.8	pre	3	0	0	0	100.0	100.0	0	0
2.9	pre	2	0	50.0	0	100.0	100.0	0	0
3.0	pre	3	0	0	0	100.0	100.0	0	0
3.1	pre	3	0	33.3	33.3	100.0	100.0	0	0
3.2	pre	5	0	20.0	0	100.0	100.0	0	0
3.3	pre	10	0	60.0	10.0	100.0	100.0	0	0
3.4	pre	7	0	42.9	14.3	100.0	100.0	0	0
3.5	pre	6	0	100.0	83.3	100.0	100.0	0	0
3.6	pre	7	0	85.7	57.1	100.0	100.0	0	0
3.7	pre	7	0	100.0	85.7	100.0	100.0	0	0
3.8	pre	5	0	100.0	60.0	100.0	100.0	0	0
3.9	pre	7	0	71.4	57.1	100.0	100.0	0	0
4.0	pre	6	0	100.0	66.7	100.0	100.0	0	0
4.1	pre	3	0	100.0	100.0	100.0	100.0	0	0
4.2	pre	8	0	100.0	75.0	100.0	100.0	0	0
4.4	pre	5	0	80.0	60.0	100.0	100.0	0	0
4.5	pre	2	0	100.0	100.0	100.0	100.0	0	0
4.6	pre	1	100.0	100.0	100.0	100.0	100.0	0	0
4.7	pre	3	0	100.0	100.0	100.0	100.0	0	0
4.8	pre	3	0	100.0	100.0	100.0	100.0	0	0
4.9	pre	2	0	100.0	50.0	100.0	100.0	50.0	0
5.0	pre	3	0	100.0	100.0	100.0	100.0	33.3	0
5.1	pre	1	0	100.0	100.0	100.0	100.0	0	0
5.3	pre	3	33.3	100.0	100.0	100.0	100.0	66.7	0
5.4	pre	2	50.0	100.0	100.0	100.0	100.0	0	0
5.5	pre	1	100.0	100.0	100.0	100.0	100.0	100.0	0
6.2	pre	2	100.0	100.0	100.0	100.0	100.0	100.0	0
6.8	flex	1	0	100.0	100.0	100.0	100.0	100.0	100.0
7.1	flex	2	100.0	100.0	100.0	100.0	100.0	100.0	50.0
8.8	post	1	0	100.0	0	100.0	100.0	100.0	0
8.9	post	1	100.0	100.0	0	100.0	100.0	100.0	100.0

(continued)

Table 2 (continued)

Dwarf–red rockfish, *Sebastes rufinanus*

BL (mm)	Stage	Number examined	Lower jaw	Brain	Nape	Dorsal margin	Ventral margin	Caudal spot
2.6	pre	2	0	100.0	0	100.0	100.0	0
2.7	pre	1	0	100.0	100.0	100.0	100.0	0
2.8	pre	3	0	66.7	0	100.0	100.0	0
2.9	pre	2	0	100.0	0	100.0	100.0	0
3.0	pre	1	0	100.0	100.0	100.0	100.0	0
3.1	pre	4	0	75.0	0	100.0	100.0	0
3.2	pre	2	0	100.0	100.0	100.0	100.0	0
3.3	pre	4	0	50.0	25.0	100.0	100.0	0
3.4	pre	5	0	60.0	20.0	100.0	100.0	0
3.5	pre	3	0	33.3	33.3	100.0	100.0	0
3.6	pre	2	0	100.0	50.0	100.0	100.0	50.0
3.7	pre	3	0	100.0	33.3	100.0	100.0	0
3.8	pre	5	0	80.0	80.0	100.0	100.0	0
3.9	pre	6	0	100.0	66.7	100.0	100.0	0
4.0	pre	3	0	66.7	66.7	100.0	100.0	0
4.1	pre	1	0	100.0	100.0	100.0	100.0	0
4.3	pre	3	0	66.7	33.3	100.0	100.0	0
4.4	pre	4	0	75.0	75.0	100.0	100.0	0
4.5	pre	2	0	100.0	100.0	100.0	100.0	0
4.6	pre	2	0	100.0	100.0	100.0	100.0	0
4.7	pre	3	0	100.0	100.0	100.0	100.0	0
4.8	pre	2	0	100.0	100.0	100.0	100.0	0
4.9	pre	1	0	100.0	100.0	100.0	100.0	0
5.0	pre	1	0	100.0	100.0	100.0	100.0	0
5.1	pre	1	0	100.0	100.0	100.0	100.0	0
5.2	pre	2	50.0	100.0	100.0	100.0	100.0	0
5.3	pre	1	0	100.0	100.0	100.0	100.0	0
5.4	pre	2	100.0	100.0	100.0	100.0	100.0	0
5.5	pre	1	0	100.0	100.0	100.0	100.0	0
5.8	pre	1	0	100.0	100.0	100.0	100.0	0

ogy is consistent with their sister species status (Hyde and Vetter, 2007). By contrast, larvae of their nearest relatives, squarespot rockfish (*S. hopkinsi*) and speckled rockfish (*S. ovalis*) (Hyde and Vetter, 2007), have quite different pigmentation patterns, with longer series of melanophores on the dorsal and ventral margins of the tail and pigment forming at the tip of the lower jaw in preflexion stage by about 5 mm (e.g., Moser et al., 1977; Moser and Butler, 1987; Laidig et al., 2008) versus none in most preflexion-stage *S. moseri* and some *S. rufinanus*.

Preflexion-stage larvae of canary rockfish (*S. pinniger*) and the western Pacific species *S. inermis*, like *S. moseri* and *S. rufinanus*, have trunk and tail pigmentation restricted to short dorsal and ventral series of melanophores, but these are more anterior, near mid-tail (e.g., Moser et al., 1977; Nagasawa et al., 2000). Both species also have some ventral pigmentation on the gut, which *S. moseri* and *S. rufinanus* lack. Early preflexion-stage olive rockfish (*S. serranoides*) have dorsal trunk and tail pigment restricted to a short posterior series of melanophores more or less as in *S. moseri* and *S. rufinanus*, but have a much longer ventral melanophore series on the tail, additional head, gut, and pectoral-fin pigmentation not found in *S. moseri* or *S. rufinanus*, and the dorsal melanophore series extends anteriorly to mid-tail or beyond later during the preflexion stage (Moser and Butler, 1987) in contrast to remaining posteriorly as in *S. moseri* and *S. rufinanus* through at least preflexion stage, and into early postflexion stage for *S. moseri*. Thus, larval *S. moseri* and *S. rufinanus* are easily distinguishable from other larval rockfishes, at least through preflexion stage. Although few ethanol-preserved flexion and postflexion stage larval *S. moseri* were available for molecular identification, a few formalin-preserved specimens that appear to be *S. moseri* suggest that melanophores spread farther anteriorly from both posterior patches on the tail later in postflexion stage, so that *S. moseri*, at least, may become increasingly similar to the larvae of several other *Sebastes* species as they grow.

Distinguishing larval *S. moseri* from *S. rufinanus* is more problematic given their close resemblance. The presence of pectoral-fin pigmentation can distinguish some preflexion stage *S. moseri* from *S. rufinanus*, but for the majority of preflexion stage larvae pectoral-fin pigment is absent and therefore not useful. Melanophore distributions on the dorsum or ventrum are useful for distinguishing among the larvae of some *Sebastes* species (e.g., Watson and Robertson, 2004), but that does

not appear to be the case for *S. moseri* and *S. rufinanus*, whose patterns differ very little in either view. The common tendency for pigment to extend onto the lateral body surfaces from the dorsal and ventral pigment patches in *S. moseri* can be a useful character, since that does not happen in preflexion-stage *S. rufinanus*. In an informal test using that character, coupled with the pectoral-fin pigmentation (when present), preflexion-stage *S. moseri* and *S. rufinanus* were correctly identified in 82.6% and 94.0% of cases, respectively.

A potential next step is to analyze our data using the technique developed by Mason et al. (2022) that quantitatively tests the ability to identify morphologically similar larvae to species using machine learning and a Bayesian framework to measure the probability of correctly identifying the larvae. Mason et al. (2022) examined sea basses (genus *Paralabrax*) to determine species' identities of 3 southern California species whose larvae, like *S. moseri* and *S. rufinanus,* have very similar pigmentation and have been considered unreliably distinguishable below the level of genus. However, by documenting pigmentation patterns through larval development, determining true identities through genetic analysis, and then processing the morphological data through their novel methodology, Mason et al. (2022) were able to determine with 99% confidence the species of larvae based only on morphology. Moving forward, it is possible we will be able to correctly identify the *S. moseri*/*rufinanus* complex to species with a similar approach.

Conclusions

A distinctive larval *Sebastes* type, characterized by having trunk and tail pigment limited to a short melanophore patch on each on the dorsal and ventral margins far posteriorly on the tail, has been recognized in plankton collections off the southern half of California and the northern Baja California Peninsula, Mexico, since 1951. Sequencing of a portion of the mitochondrial cytochrome *b* gene of this unidentified larval type demonstrated that it includes both *S. moseri* and *S. rufinanus*, 2 small, deep-living rockfish species that are unfished and not well known.

Larvae of both species are morphologically typical rockfishes and develop much as other *Sebastes* species do, but at least through the end of the preflexion larval stage their shared pigmentation pattern distinguishes them from all other *Sebastes* species whose larvae have been described to date. The most salient feature of this pattern is the pigmentation on the tail, consisting of short melanophore series along the dorsal and ventral margins and uniquely restricted to the last few myomeres. Limited evidence suggests that during the postflexion stage this pigment may spread anteriorly along the margins and the overall pattern may begin to converge with those of several other *Sebastes* species.

Larval *S. moseri* and *S. rufinanus* cannot always be visually distinguished from one another. During preflexion stage a small proportion of larval *S. moseri* develop pigment on the pectoral fins but *S. rufinanus* do not, and the marginal pigment on the tail commonly, but not always, spreads to some extent onto the adjacent dorso- and ventrolateral surfaces in *S. moseri* but not in *S. rufinanus*. Additional specimens, especially in older stages, coupled with the application of a recently developed method that uses machine learning and a Bayesian framework to identify the most relevant characters and estimate the probability of correctly identifying larvae may permit reliable identifications of these larvae in the future.

Acknowledgments

Our thanks to the scientific parties and crews of the multiple vessels involved in collecting the samples used here. We also thank the many lab personnel who sorted the plankton samples and helped with the genetics analyses. Jason Stannard performed the initial genetic analysis that identified the first specimen of *S. moseri*. Andrew Thompson provided valuable assistance with the genetic analyses and helpful comments on the manuscript.

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Published online 4 Sept. 2024.

Cite as: Charter, Sharon R., William Watson, and John R. Hyde. 2024. Early larvae of the whitespotted rockfish (*Sebastes moseri* Eitner, 1999) and the dwarf-red rockfish (*S. rufinanus* Lea and Fitch, 1972) (Pisces: Sebastidae) identified by molecular methods. *In* Early Life History and Biology of Marine Fishes: Research inspired by the work of H Geoffrey Moser (J. M. Leis, W. Watson, B. C. Mundy, and P. Konstantinidis, guest eds.), p. 143–154. NOAA Professional Paper NMFS 24. https://doi.org/10.7755/PP.24.11