

DEVELOPMENT AND GEOGRAPHIC DISTRIBUTION OF THE ROCKFISH,
SEBASTES MACDONALDI (EIGENMANN AND BEESON, 1893),
 FAMILY SCORPAENIDAE, OFF SOUTHERN CALIFORNIA
 AND BAJA CALIFORNIA

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ABSTRACT

The larval and juvenile stages of the scorpaenid fish, *Sebastes macdonaldi*, are described and illustrated. The sequence of ossification of bones and cranial spines in larvae is described in detail. *S. macdonaldi* appears to have the most southerly distribution of any species of *Sebastes* in the eastern north Pacific. The geographic distribution and seasonal abundance of *S. macdonaldi* larvae are discussed and compared with published information on the adults.

The genus *Sebastes* is represented by 65 species in the eastern north Pacific (Chen, 1971). Although all members of the genus are ovoviviparous and have a planktonic larval stage, they exhibit a remarkable diversity in morphology, color, and mode of existence. They rank first in total numbers of fish landed annually by the California sport fishing fleet (Young, 1969) and are a major commercial resource (Heimann and Frey, 1968). Despite their obvious importance, information on the complete life histories of all but a few species is fragmentary or nonexistent. At present a complete life history series (embryonic, larval, juvenile, and adult stages) has been described for only a single eastern Pacific species, *S. paucispinis* (Moser, 1967); however, young-stage larvae attained from pregnant females have been illustrated for four species from central California (Morris, 1956), for nine species from the Pacific northwest (DeLacy, Hitz, and Dryfoos, 1964), and for 14 additional rockfishes from southern California and Baja California (Moser, 1967). Recently, Waldron (1968) has described the early larvae of *S. pinniger*.

Ahlstrom (1961, 1965, 1969) has shown that rockfish larvae are the third or fourth most

abundant kind of larvae collected annually in the plankton surveys of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Early juvenile rockfish, like the larvae, are pelagic but evade plankton nets easily and must be collected by other means. For example, some species are attracted to bright lights at night and can be dipnetted at the surface. Also, some species associate with floating objects (Hitz, 1961) and with drifting kelp (Mitchell and Hunter, 1970) and may be collected when these are brought aboard ship. Finally, pelagic juveniles occasionally appear in midwater trawl samples (Berry and Perkins, 1966; Lavenberg and Fitch, 1966). Demersal juveniles are common constituents of otter trawl catches in coastal waters.

Larvae of *S. macdonaldi* have such a distinctive melanophore pattern that a developmental series was established before it could be identified to species. The extreme southerly distribution of these larvae in the CalCOFI pattern provided a clue to their identity, since adults of *S. macdonaldi* have been collected farther south along Baja California than any other species of *Sebastes* (Chen, 1971). A comparison of intra-ovarian larvae from pregnant *S. macdonaldi* with the smallest individuals from plankton collections provided definitive evidence of the identity of the larval series. Juvenile stages critical

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to the completion of the developmental series were obtained principally from midwater and bottom trawls. These developmental stages are described herein, with special emphasis on the developmental osteology of the larvae. Also, the geographic distribution of the larvae in the CalCOFI area is presented and compared with the known distributions of juveniles and adults.

METHODS

Larvae of *S. macdonaldi* from 4 years (1953, 1960, 1965, 1966) of CalCOFI survey cruises were identified and counted. From these and selected other specimens, two developmental

series that encompassed the entire larval period were established. Larvae of the first series were measured with the ocular micrometer of a stereoscopic microscope to produce a table of morphometrics (Table 1) for comparison of body proportions of *S. macdonaldi* larvae with those of *S. paucispinis* and other species. This series also provided a framework for the descriptions of larval morphology and melanophore pattern. Larvae of the second series, cleared with a graded series of KOH-glycerin solutions and stained with Alizarin Red-S, were used to determine the sequence of ossification of bones and fin rays and to prepare a table of meristic characters (Table 2).

TABLE 1.—Measurements (mm) of larvae and pelagic juveniles of *Sebastes macdonaldi*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Snout-anus distance	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth	Pectoral fin length	Pelvic fin length	Snout to origin of anal fin	Snout to origin of pelvic fin
SIO 65-230	4.5	1.8	1.1	0.38	--	0.37	0.60	0.90	0.27	--	--	--
CalCOFI 6602-117.40	4.7	1.8	1.2	0.30	--	0.45	0.53	1.0	0.40	--	--	--
CalCOFI 6604-123.36	5.0	1.8	1.2	0.30	--	0.46	0.60	1.0	0.33	--	--	--
CalCOFI 6604-117.30	5.2	2.1	1.4	0.48	0.72	0.51	0.68	1.2	0.36	--	--	--
CalCOFI 6604-113.55	5.7	2.4	1.6	0.47	0.67	0.57	0.63	1.3	0.52	--	--	--
CalCOFI 6604-113.55	5.9	2.6	1.8	0.48	0.76	0.55	0.60	1.5	0.45	--	--	--
CalCOFI 6604-107.31	6.3	2.8	1.8	0.56	0.76	0.57	0.87	1.6	0.60	0.05	--	1.9
CalCOFI 6604-93.28	6.7	2.9	1.9	0.56	--	0.63	0.86	1.7	0.61	0.04	--	2.1
CalCOFI 6604-127.40	6.8	3.1	1.9	0.55	0.95	0.70	0.95	1.8	0.62	0.15	--	2.2
CalCOFI 6501-117.45	7.0	3.3	2.1	0.75	1.1	0.70	1.1	1.9	0.60	0.12	--	2.3
CalCOFI 5304-117.45	7.6	3.5	2.2	0.79	1.1	0.73	1.1	2.0	0.68	0.20	--	2.3
CalCOFI 6602-110.40	7.7	3.8	2.7	0.82	1.2	0.84	1.2	2.3	0.90	0.33	4.2	2.5
CalCOFI 6605-117.35	7.9	3.8	2.7	0.82	1.3	0.90	1.2	2.5	0.93	0.25	4.2	2.7
CalCOFI F-47-117.35	8.2	4.2	2.9	1.1	1.3	1.0	1.5	2.5	1.1	0.52	4.8	3.0
CalCOFI F-46-130.40	8.5	4.7	3.2	1.2	1.7	1.0	1.6	3.0	1.3	0.80	4.9	3.2
CalCOFI 5303-123.40	9.0	5.0	3.2	1.1	1.7	1.0	1.6	2.8	1.2	0.65	5.4	3.2
CalCOFI 6604-133.40	9.2	5.3	3.4	1.1	1.5	1.1	1.8	3.1	1.4	0.89	5.4	3.6
CalCOFI C-46-117.40	9.5	5.2	3.6	1.3	1.7	1.2	1.7	3.1	1.5	1.1	5.6	3.6
CalCOFI 6605-123.70	9.7	5.4	3.5	1.2	1.7	1.2	1.8	3.2	1.6	1.1	5.8	3.7
CalCOFI F-46-133.35	10.0	6.2	3.7	1.2	1.9	1.3	1.8	3.5	1.8	1.2	6.4	3.8
CalCOFI 6004-130.45	10.3	6.3	3.8	1.4	2.0	1.3	1.8	3.5	1.7	1.2	6.5	4.4
CalCOFI F-46-133.35	11.2	6.8	3.8	1.4	2.2	1.3	1.8	4.0	2.1	1.5	7.0	3.8
CalCOFI 5304-123.40	12.0	7.7	4.5	1.4	2.5	1.5	1.8	4.2	2.4	1.8	7.7	5.2
CalCOFI 6605-127.45	15.0	9.4	5.8	1.7	3.2	1.9	2.1	5.2	3.5	3.1	9.7	5.4
SIO 65-201	15.4	9.3	5.8	1.7	3.0	1.8	2.2	5.5	4.0	2.9	9.6	5.8
CalCOFI 6604-133.30	15.9	10.0	6.5	2.1	--	2.0	1.9	5.2	3.6	2.8	10.1	7.1
*SIO 61-299	22.6	14.0	8.4	2.7	3.6	2.3	2.5	7.5	6.7	4.8	14.7	9.3
*SIO 54-87	27.8	18.6	10.6	3.1	4.5	2.8	3.0	8.9	8.8	6.2	19.3	11.2
*SIO 69-232	29.2	19.1	10.8	2.9	4.8	3.2	2.9	10.0	9.8	6.5	19.9	11.7
*LACM 8821-9	32.7	20.7	11.8	3.2	4.9	3.6	2.9	10.1	9.7	--	20.8	12.2
*LACM 8821-9	34.5	20.9	11.8	3.2	5.2	4.0	3.2	10.5	10.6	7.7	21.4	12.7
*LACM 8821-9	38.8	25.0	12.8	3.2	5.4	4.0	3.5	11.7	11.2	8.3	25.6	14.4
*LACM 8821-9	40.2	26.8	13.0	3.5	6.1	4.2	3.6	12.0	12.2	8.5	27.4	15.2
*LACM 8821-9	44.4	30.2	14.0	3.8	6.4	4.7	3.8	13.2	13.2	9.2	31.2	16.2

* Pelagic juvenile.

TABLE 2.—Meristics from cleared and stained larvae of *Sebastes macdonaldi*.

Length (mm)	Primary caudal fin rays		Secondary caudal		Branchio- stegeal rays	Pectoral fin rays	Hypural elements	Dentary teeth	Anal fin rays	Dorsal fin rays	Pelvic fin rays		Verte- bral centra	Neural spines	Haemal spines
	Super- rior	Infe- rior	Super- rior	Infe- rior	Left	Right	Left	Right			Left	Right			
6.3	--	--	--	--	2	2	--	--	--	--	--	--	--	--	--
6.7	--	--	--	--	3	3	--	--	--	--	--	--	--	--	--
6.8	--	--	--	--	3	3	--	--	--	--	--	--	--	--	--
7.0	3	3	--	--	4	4	--	--	--	--	--	--	--	2	--
7.1	4	3	--	--	5	5	--	--	--	--	--	--	--	4	--
7.2	3	3	--	--	5	5	--	--	--	--	--	--	--	4	--
7.7	6	6	--	--	6	6	--	--	--	--	--	--	--	5	--
7.9	4	4	--	--	5	5	--	--	--	--	--	--	--	3	--
8.2	8	7	2	2	7	7	--	--	--	--	--	--	--	3	--
8.5	7	7	--	--	6	6	1	1	11-4	11-0	1-3	1-3	18	20	7
8.7	8	7	--	--	7	7	--	--	--	--	1-3	1-3	18	19	6
9.2	8	7	2	3	7	7	--	--	--	IV-0	1-3	1-3	18	19	6
9.4	8	7	4	4	7	7	3	3	--	XIII-8	1-4	1-4	23	21	5
9.7	8	7	3	4	7	7	2	3	--	XIII-13	1-5	1-5	24	23	13
10.0	8	7	5	6	7	7	2	3	--	XIII-13	1-5	1-5	24	23	12
10.3	8	7	5	5	7	7	2	3	5	XIII-13	1-5	1-5	26	24	14
11.3	8	7	4	4	7	7	2	3	4	XIII-13	1-5	1-5	26	24	14
12.0	8	7	8	7	7	7	2	3	5	XIII-13	1-5	1-5	26	24	14
13.0	8	7	10	11	7	7	2	3	2	XIII-13	1-5	1-5	26	25	14
13.9	8	7	10	11	7	7	3	2	11	XIII-12	1-5	1-5	26	25	14

The critical pelagic juvenile stages were found in the fish collections of the Scripps Institution of Oceanography (SIO) and the Los Angeles County Museum of Natural History (LACM). Demersal juveniles were obtained from bottom trawl collections of the Southwest Fisheries Center, La Jolla, and the University of California at Los Angeles (UCLA), in addition to the two sources mentioned above.

Prior to the completion of notochord flexion during caudal fin formation, the body length is defined as the distance from the tip of the snout to the posterior tip of the notochord. After notochord flexion is completed the usual standard length measurement, the distance from the tip of the snout to the posterior margin of the hypural plate, is used. Morphometric changes in rockfish can be conveniently grouped into three phases that correspond to the stages of notochord flexion—one before flexion, one during flexion, and one after flexion is completed. These stages are separated in the morphometric table. Other terms used in this table are defined as follows:

Snout-anus distance = distance along midline of body from tip of snout to vertical from anus

Head length = distance from tip of snout to cleithrum

Snout length = distance from tip of snout to anterior margin of eye

Upper jaw length = distance from tip of snout to vertical from posterior margin of maxillary

Interorbital distance = width of tissue dorsal to eyes

Body depth = body depth at base of pectoral fin

Pectoral fin length = maximum length of rayed portion of fin

Pelvic fin length = maximum length of rayed portion of fin

Snout to origin of anal fin = distance along midline of body from tip of snout to a vertical from anterior end of anal fin

Snout to origin of pelvic fins = distance along midline of body from tip of snout to a vertical from pelvic fin base.

Terms used in the description of larval osteology conform largely to those used in recent studies of the osteology of adult teleosts (e.g., Harrington, 1955; Weitzman, 1962; Topp and Cole, 1968).

DESCRIPTION OF DEVELOPMENT

DISTINGUISHING FEATURES

Early-stage larvae of *S. macdonaldi* are characterized by a low number of melanophores (average of eight) in the series along the ventral midline of the tail. Of the 27 other species illustrated in the literature, only *S. paucispinis* larvae, with an average of nine melanophores in this series, approaches the low number of *S. macdonaldi*. Early larvae of *S. macdonaldi* are also characterized by their small, densely pigmented pectoral fins. Melanophores cover completely the blade of the fin, but are restricted to the inner surface of the fin base. Also characteristic is the series of melanophores which extends from the nape to the pectoral fin base. Such melanophores are not present on any other of the 27 other eastern Pacific species illustrated to date.

A fourth character of limited utility is the absence of melanophores on the dorsal surface of the tail. *S. macdonaldi* is one of the 16 eastern Pacific species illustrated to date which lacks this pigment, and can be immediately separated from the 12 species in which it is present. This character should be used with caution because the dorsal series of melanophores forms later than the ventral series, at about the time of yolk depletion (Moser, 1967; Waldron, 1968). Thus, prolarvae collected prematurely from the ovaries may not have yet developed their dorsal pigment series, and illustrations of this stage are not strictly comparable with those of larvae cultured to the point of yolk depletion.

GENERAL MORPHOLOGY

Larvae of *S. macdonaldi* are similar in general appearance to those of *S. paucispinis* (Moser, 1967). Larvae hatch within the ovaries at a length of 4 to 5 mm, and then are extruded from

the female. Newborn larvae have large heads with well-formed eyes and functional jaws (Figure 1A). The gut is short and bulbous; usually remnants of the yolk and oil globule are visible anteriorly in the region of the liver.

Relative body depth increases markedly during early larval stages and less so during later larval stages (Figures 1, 2). Body depth at the base of the pectoral fins averages 23% of the body length before notochord flexion, 33% during flexion, and 34% after flexion. In pelagic juveniles (Figure 3), relative body depth decreases slightly to about 30% in individuals 35 to 40 mm long. *S. paucispinis* is more slender throughout the larval and early juvenile stages; body depth averages 20% of the body length before notochord flexion, 24% during flexion, 31% following flexion, and 28% in pelagic juveniles.

Relative gut length increases gradually throughout the larval period. Accordingly, snout-anus length averages 42% of the body length before notochord flexion, 52% during flexion, 60% after flexion, 64% in pelagic juveniles. A similar gradual increase occurs in *S. paucispinis* (41, 44, 56, and 63% in the respective stages).

Relative head length increases slightly during the larval period; head length averages 28% of the body length before notochord flexion and 37% during and after flexion, but decreases during transformation and is 32% in the largest pelagic juveniles. Eye diameter averages 33% of the head length throughout the larval period and shows no trend of relative increase or decrease. Relative eye diameter decreases slightly to about 28% in transforming individuals, but increases to about 32% in the largest pelagic juveniles.

Upper jaw length is variable with respect to head length, probably because of the difficulty in obtaining uniform measurements from specimens with partially opened jaws. There is, however, a general trend of relative increase; jaw length averages 47% of head length before notochord flexion, 49% during flexion, and 52% in postflexion larvae. In large larvae and in pelagic juveniles the end of the maxillary is located beneath the middle of the orbit. With continued elongation of the maxillary in demer-

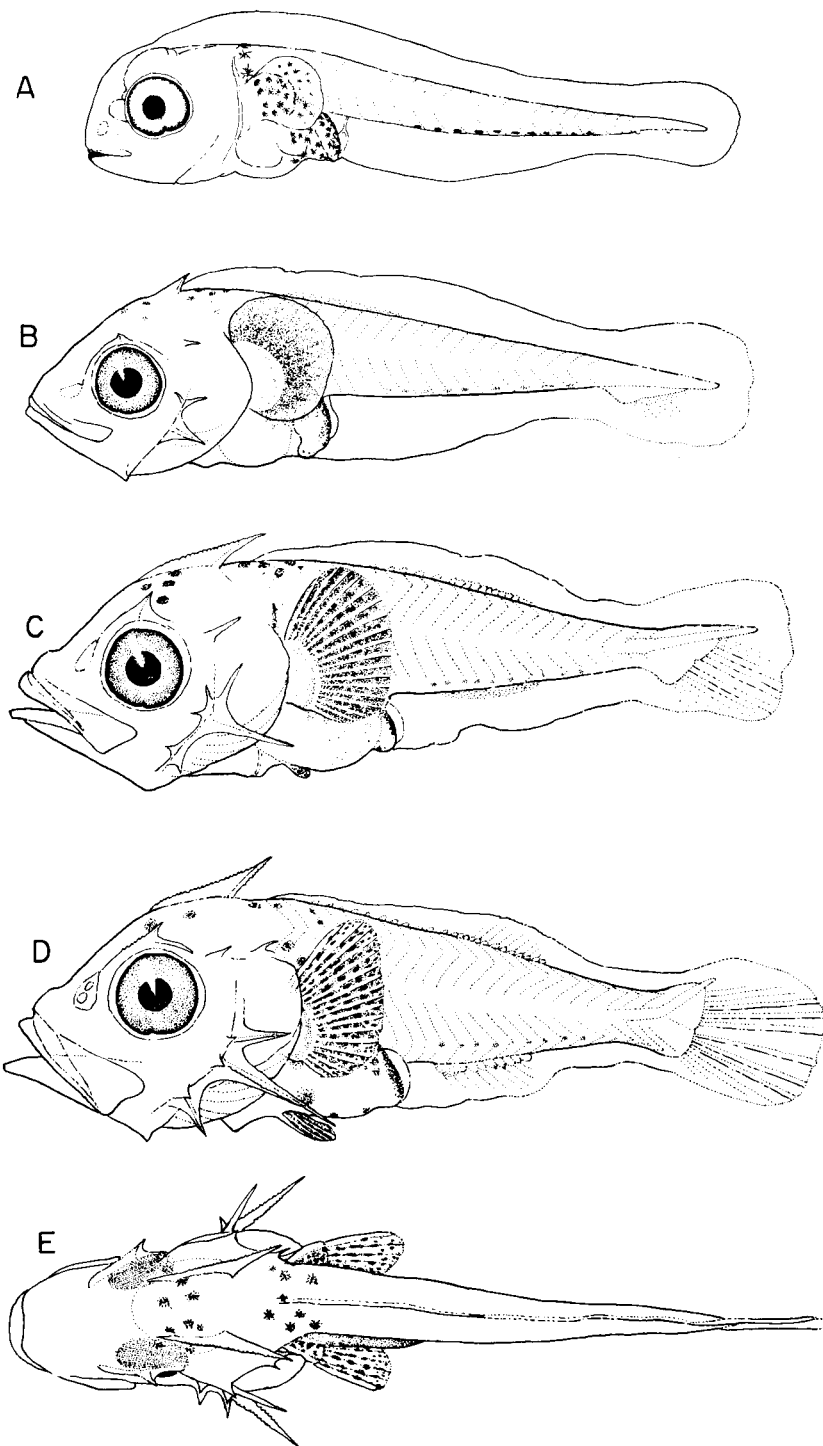


FIGURE 1.—Larvae of *Sebastes macdonaldi* from a pregnant female (A) and from California Cooperative Oceanic Fisheries Investigations (CalCOFI) plankton samples (B-E). A. 4.5 mm; B. 6.3 mm; C. 7.7 mm; D. 9.0 mm; E. dorsal view, 9.0 mm.

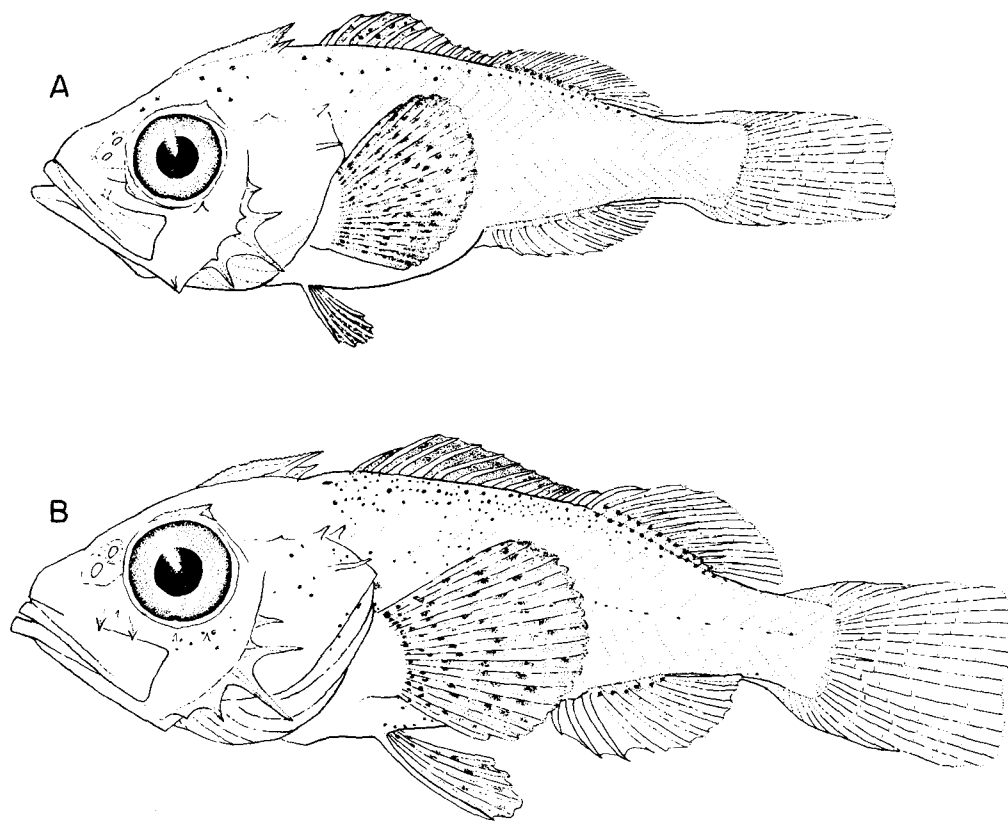


FIGURE 2.—Planktonic larvae of *Sebastes macdonaldi* from CalCOFI plankton samples. A. 11.2 mm; B. 15.9 mm.

sal juveniles (Figure 4) and in adults, its posterior end extends to below the posterior margin of the orbit. The relative length of the snout does not change markedly during the larval period; snout length averages 32% of the head length throughout the larval period. In pelagic juveniles snout length is reduced slightly to an average of 28% of the head length. Likewise, the width of the interorbital region changes little relative to head length in larvae; it averages about 46% of the head length. At the end of the larval period the interorbital distance becomes markedly narrower and averages 27% of the head length in pelagic juveniles. Similar changes in relative growth rate of the head, eyes, jaws, snout, and interorbital region occur in larvae and early juveniles of *S. paucispinis*.

FIN DEVELOPMENT

The pectoral fins begin to form during embryogenesis and, at parturition, the muscular base of each fin is distinct from the fan-shaped future rayed portion. The rayed portion enlarges considerably during early planktonic life and becomes covered solidly with melanophores (Figure 1B). The rays begin to ossify in larvae as small as 6.3 mm (Table 2); ossification begins with the most dorsal rays and then proceeds ventrad sequentially. Larvae 19.2 mm and larger have the full complement of 19 stained pectoral rays. The pectoral fins elongate slowly and gradually and have a short stubby appearance during most of the larval period. The length of the rayed portion of the fin averages 8% of

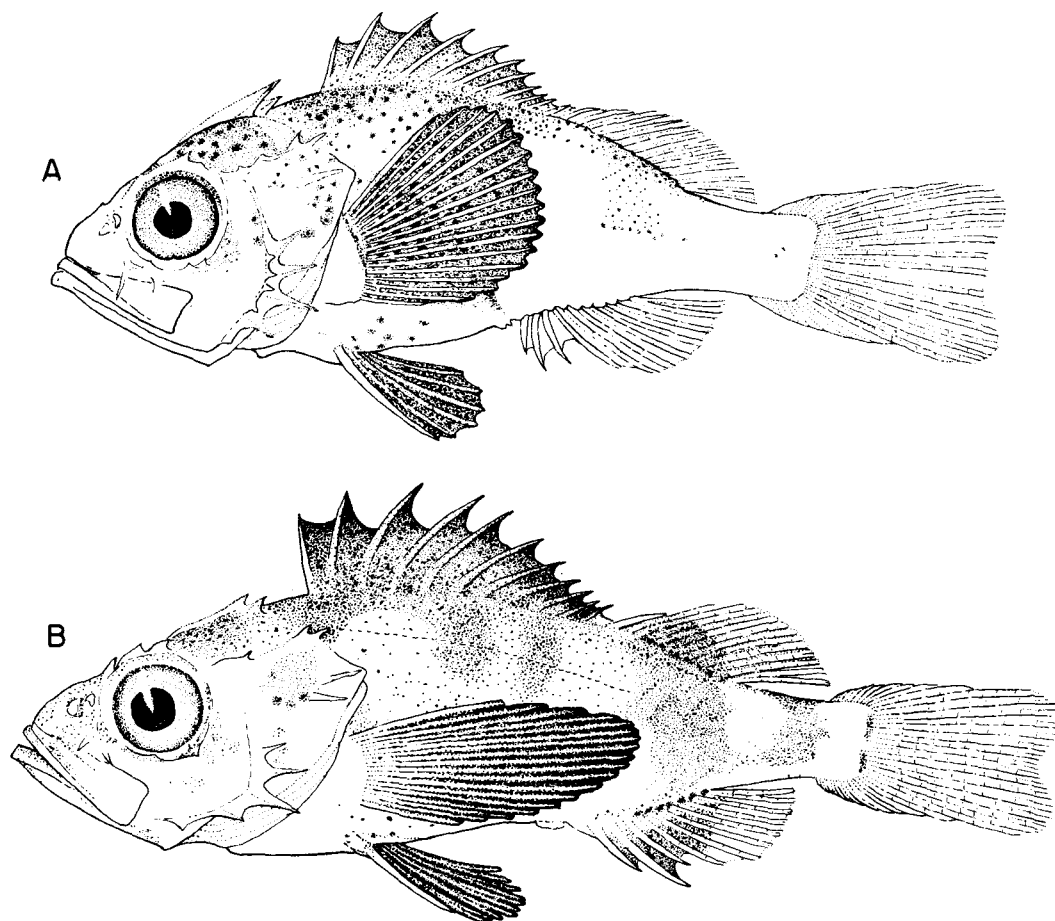


FIGURE 3.—Pelagic juveniles of *Sebastes macdonaldi*. A. A 15.4-mm transforming specimen (SIO 65-201, mid-water trawl) which is just beginning to develop its juvenile melanophore pattern. Note that it is further advanced than the 15.9-specimen in Figure 2. B. A 29.2-mm specimen dipnetted on surface at night (SIO 69-232).

the body length in the stages before notochord flexion, 13% during flexion, and 19% in the stages following flexion. The fin elongates markedly in pelagic juveniles in which its average length is 31% of the body length (Figures 3B, 4A). This sequence of gradual elongation of the pectoral fins throughout the larval and early juvenile period contrasts with that observed in *S. paucispinis* (Moser, 1967). In that species, the maximum length of the pectoral fins, 40% of the body length, is achieved in 13-mm larvae and, thereafter, the pectoral fin length decreases

relative to body length; pectoral fin length is 25% of the body length in newly transformed juveniles of *S. paucispinis*. In both species, the heavily pigmented pectoral fins are the most striking features of larvae and early juveniles.

The pelvic-fin buds appear early, in larvae as small as 6.3 mm, and become covered with melanophores. The rays begin to differentiate in 7-mm larvae. Ossification of the spines is visible initially in a 7.7-mm specimen in the stained series (Table 2). Ossification of the rays proceeds sequentially posteriad from the spines; the

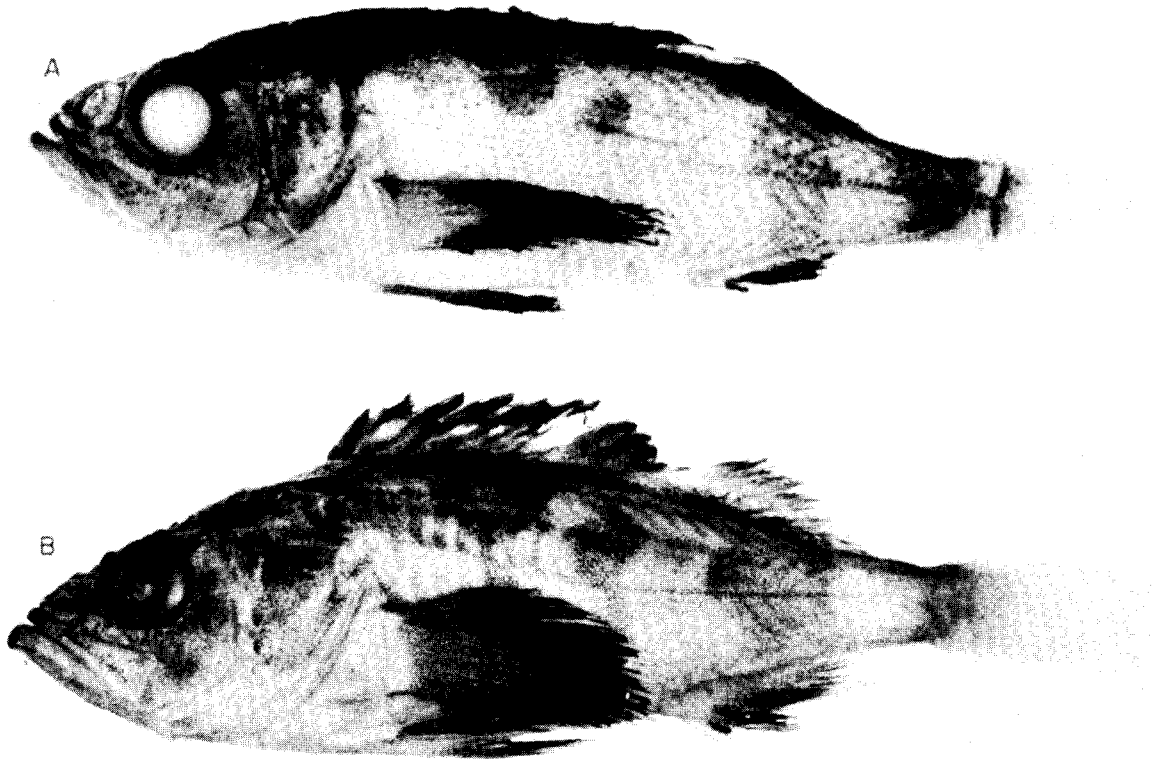


FIGURE 4.—Juveniles of *Sebastes macdonaldi*. A. A 40.2-mm pelagic juvenile (LACM 8821-9) collected by mid-water trawl in the Gulf of California. B. A 62.1-mm demersal juvenile (SIO 65-227) collected by otter trawl near Point Tosco, Baja California.

full complement of five ossified rays is present in each fin in a 9.4-mm stained specimen. Like the pectoral fins, the densely pigmented pelvics elongate gradually throughout the larval period. Pelvic fin length increases from 4% of the body length at the initiation of notochord flexion to 10% at its completion. Following flexion, it increases gradually to a maximum of 18 to 21% of the body length in larvae 15.0 to 16.0 mm long. In pelagic juveniles pelvic fin length is 21 to 22% of the body length.

The caudal-fin anlage first appears in larvae about 5.0 mm long as a ventral thickening near the tip of the notochord. The cartilaginous hypural elements begin to differentiate when the larvae are about 6.0 mm (Figure 1B) and the maximum number of three superior and two inferior hypurals is present at about 8.0 mm. Ossification of these elements begins in larvae about

8.5 mm long and all hypurals, except the slender dorsal-most element of the superior series, are ossifying in a larva 9.2 mm long. Fusion accompanies further ossification in the superior series; in the largest larva the two larger superior elements have nearly fused into a single plate, while the slender uppermost element remains separate and has just started to ossify. In the inferior series the larger upper element has two centers of ossification which produce a solid calcified plate in the largest larva. The slender lowermost element is also well ossified but remains separate. Thus, larvae of 15-mm length have achieved the adult complement of two superior and two inferior hypurals. The principal caudal rays begin to ossify in 7-mm larvae (Table 2). Ossification proceeds dorsad in the superior series, above the midline of the fin, and ventrad in the inferior series; the adult complement of

8 + 7 principal rays is present in an 8.2-mm larva of the stained series. Also, the initial procurrent rays are ossifying in this specimen. Ossification of these rays proceeds anteriorly in both superior and inferior series. The largest larva (15.9 mm) has 10 superior and 11 inferior ossified rays, but the full complement of 11 to 13 superior and 13 to 15 inferior rays is attained in pelagic juveniles.

The dorsal and anal fins are the last to appear. The bases of the fins appear in larvae 5.3 to 7.0 mm long (Figures 1B, C). Cartilaginous radial elements start to differentiate when the larvae are about 7.0 mm and the full complements of these elements are present in larvae 8.0 to 8.5 mm. Initial ossification of the spinous rays of these fins is visible in an 8.2-mm specimen in which the three anal spines and the anterior seven dorsal spines are stained. A larger, but apparently less advanced specimen, 8.7 mm long has only four stained dorsal spines and shows no stain on the anal spines. A 9.2-mm faintly stained larva has seven spinous and eight soft dorsal rays but shows no stain on the anal rays. The next larva in the stained series, 9.4 mm long, has the adult complement of III-7 anal and XIII-13 dorsal rays. The remaining larvae in the stained series, with the exception of one specimen, also have III-7 anal and XIII-13 dorsal rays.

PIGMENTATION

Newly hatched *S. macdonaldi* larvae have a melanophore pattern similar to that of *S. paucispinis*. The gut is covered with a mantle of melanophores that is solid on the dorsal surface and more sparsely distributed on the lateral and ventral surfaces (Figure 1A). A line of melanistic dashes on the ventral midline of the tail extends posteriorly from the third or fourth post-anal myomere. In a sample of 60 newborn larvae of *S. macdonaldi* the number of melanophores in the ventral midline series ranged from 6 to 14 with a median of 8. Thus, this species has fewer ventral midline melanophores than any eastern Pacific species of *Sebastes* studied to date (see Morris, 1956; DeLacy et al., 1964; Moser, 1967). Head pigmentation in newborn larvae consists

of a series of melanophores that line the anterior region of the lower jaw and one to several melanophores that form a blotch on the nape. The pectoral fins also are pigmented; the inner surface of each fin base is covered solidly with melanophores while the lateral surface is pigmentless. The future rayed portion of the fin has sparsely distributed melanophores on both lateral and inner surfaces.

Melanophores are added throughout the larval period so that large larvae of *S. macdonaldi* are among the most heavily pigmented of all rockfish species (Figures 1, 2, 3). Much of the melanistic pigment is added in the head region. One or two melanophores appear over each optic lobe of the brain in 4- to 5-mm larvae. Similarly one or two melanophores appear above each side of the cerebellum in larvae of the same size. Melanophores are added continuously to the dorsal surface of the brain so that it is covered completely when the larvae reach 8.0 mm. Beginning in larvae about 7.0 mm long, isolated melanophores form anterior to the cleithra and eventually form a small patch that is covered by the opercle. When the larvae reach about 10.0 mm, considerably more pigment is added to the head. Patches of melanophores form around the external nares and along the anterior rim of the upper jaw; gradually the entire dorsal region of the snout becomes covered. Also, a conspicuous melanophore patch appears at the ventroposterior margin of the orbit and on the dorsal surface of the opercle.

Pigmentation on the gut, particularly on the dorsal and lateral surfaces, becomes more extensive during larval development. Beginning in larvae of about 5.0-mm length, melanophores are added in the region dorsal to the pectoral fin base and eventually a continuous band of melanophores extends from the gut to the enlarging melanistic blotch at the nape.

The number of melanophores in the series at the ventral midline of the tail appears to diminish as development proceeds; this may be an apparent reduction since the melanophores become embedded in the developing hypaxial musculature and later become obscured by the developing anal fin. Typically, in larvae larger than 8.0 mm the three posterior melanophores

in the series are visible along the ventral margin of the caudal peduncle while more anterior melanophores of the series are barely visible above the developing anal fin.

The paired fins are strikingly pigmented. Melanophores are added continuously to the rayed portion of the pectoral fin but are scattered until the larvae are about 7.0 mm long (Figure 1C) when they become concentrated on the membranous portions of the fins between the developing rays and give the fins a striated appearance that remains throughout the larval period. The base of the pectoral fin remains heavily pigmented only on the medial surface. Melanophores begin to appear on the pelvic fins in larvae about 7.0 mm long and form a striated pattern like the pectorals when the larvae reach a length of about 8.5 mm.

The median fins develop pigmentation considerably later in the larval period. When larvae reach about 9.0-mm length (Figures 1D, E), the melanophore patch on the nape begins to expand posteriad along the dorsal midline to form an elongated patch at the base of the spinous dorsal fin. A separate elongated patch of melanophores develops at the base of the soft dorsal fin and the two become connected by a narrow bridge of melanophores when the larvae reach about 10.0 mm. Melanophores begin to form on the anterior portion of the spinous dorsal fin when the larvae are about 9.0 mm long. Gradually the pigmented area of the fin enlarges until the entire spinous dorsal is pigmented in larvae longer than 15.0 mm (Figure 2B). Pigment on the soft dorsal fin is limited to a series of melanophores that covers the distal radial elements of the fin base. These melanophores begin to appear in 11-mm larvae and cover nearly all the radial elements when the larvae reach 15.0 mm (Figures 2A, B). A similar series of melanophores develops along the anal fin base when the larvae reach 12.0-mm length. One to several melanophores appear at the posterior margin of the hypural elements. In pelagic juveniles other melanophores are added here to form a vertical line (Figures 3B, 4A).

The beginnings of the juvenile pigment pattern appear in larvae 15.0 to 16.0 mm long when saddles of melanistic pigment start to develop

ventrad from the elongate patches that lie along the dorsal fin base (Figures 2B, 3A). The first of these extends ventroanteriorly from the origin of the dorsal fin to meet with the melanistic blotch on the opercle. A second saddle extends from the middle region of the spinous dorsal fin ventrad to overlie the lateral line, as does a third saddle which extends ventrad from the base of the soft dorsal fin.

These melanistic saddles become further developed in pelagic juveniles. In a 22.6-mm juvenile the pigment saddle at the soft dorsal fin extends almost to the base of the anal fin, and a fourth saddle is present at the caudal peduncle. In a 29.2-mm specimen (Figure 3B) the broad band at the soft dorsal is continuous and extends onto the rays of the dorsal and anal fins. The band at the caudal peduncle also extends to the ventral midline. Also, in this specimen, an additional saddle is present below the posterior end of the spinous dorsal fin, just posterior to the one located below the middle of the fin. In the largest pelagic juveniles (33-44 mm) the most anterior bar at the origin of the dorsal fin is obliterated as it becomes continuous with the solidly pigmented dorsal region of the head (Figure 4A). Melanistic pigment on the fins is augmented in pelagic juveniles. The entire spinous dorsal is dark and has a black margin whereas only the basal regions of the soft dorsal and anal fins are covered with melanophores. The caudal fin lacks melanophores. The pelvic fins remain pigmented as in late-stage larvae; however, a zone without melanophores develops on the basal third of each pectoral fin.

The melanistic pigment pattern of the smallest demersal juveniles (60 mm SL) remains essentially like that of pelagic juveniles (Figure 4). The smallest fresh specimens examined were 150 mm SL. In these the melanistic saddles and bands are separated by dusky areas above the horizontal septa. Below the septa, the background color is crimson, as is the lateral line and the head below the ventral margin of the orbit. The spinous dorsal fin is dusky with a black margin whereas the soft dorsal has a dusky base, a black central zone, and a pale margin. The caudal, anal, pelvic, and pectoral fins have crimson rays alternating with black between the rays.

In large adults the lateral melanistic patches and bands coalesce to form a solid black zone above the horizontal septa with a crimson zone below. At least the posterior half of the lateral line remains bordered by crimson. The spinous and soft dorsal fins become black. The caudal fin is black except for a vertical crimson zone at the base. The anal and ventral fins remain crimson with black between the rays. The pectoral fins become black except for a red zone at the proximal third of each fin.

SEQUENCE OF OSSIFICATION

The sequence of calcification of bones in larvae of *S. macdonaldi* is similar to that described for larvae of Myctophidae (Moser and Ahlstrom, 1970). As in myctophids, the maxillaries and cleithra are the first elements to ossify. In fact, the maxillaries, cleithra, and opercles are beginning to ossify in full-term intraovarian larvae. The sequence of ossification of other head, appendicular, and axial elements in a stained series of *S. macdonaldi* is shown in Table 3. For each element, the larval length at initial ossification and the larval length at which the element achieves its adult form are given. Selection of the point at which an element achieves its adult form, admittedly, is somewhat subjective since bone formation is a gradual process that continues throughout the life of the fish. In rockfish, as in most other teleosts, most of the skeletal elements become ossified during the larval period and assume a shape which, except for minor surface irregularities and processes, closely resembles that found in juveniles and adults. The branchial arches and cranial spines ossify gradually and generally have not achieved their adult form before the end of the larval period. For this reason these are listed in separate tables (Tables 4, 5), which give only the sequence of initial ossification.

Although the neurocranium is unossified in unborn larvae, the frontals, pterotics, and parasphenoid form soon after birth, in larvae 5.1 to 5.2 mm. These are followed by the parietals, exoccipital, basioccipital, and supraoccipital, and later the circumorbital bones and the more interior neurocranial elements.

In the upper jaw the maxillaries begin to ossify before birth. These are followed by the main elements of the lower jaw, the dentaries and articulares, which begin to ossify at 5.1 to 5.2 mm. Other elements of the jaws, the premaxillaries and angulars, are beginning to ossify in a 6.3-mm stained larva. All elements of the mandibular arch achieve their adult form early in the larval period, between 7.0 and 8.5 mm. The elements of the palatine series are slower to ossify. The quadrates begin to ossify at about 6.3 mm and the others follow gradually; the last elements to initiate ossification, the palatines and metapterygoids, achieve their adult form in 12.0-mm and 15.9-mm larvae respectively.

The bones of the hyoid arch and opercular series initiate ossification gradually, beginning with the opercle in unborn larvae. The other bones of the opercular series have started to ossify before the larvae reach 6.3 mm, and all have achieved their adult form at 7.9 to 8.2 mm. Elements of the hyoid arch, particularly the ceratohyals and interhyals, are slower to initiate and complete ossification.

In the appendicular skeleton, the cleithra are the first bones to become ossified. They are heavily stained in unborn larvae and are the first skeletal elements to ossify. Following birth, the other bones of the pectoral girdle gradually initiate ossification. Among the last to appear are the four proximal radial elements, which ossify in a dorsal-to-ventral sequence. The coracoids and the single pair of extrascapulars initiate calcification at about 12.0 mm and are formed in the 15.9-mm specimen. The pelvic bones appear initially in a 9.2-mm stained specimen; through gradual ossification the pelvis becomes fused along their medial surfaces.

The paired neural arch elements are the first bones of the axial skeleton to ossify. At first only the most anterior pair is visible in a 7.0-mm larva, but gradually others are added in a posteriad sequence. When the larvae are about 8.0 mm long, the distal ends of each pair begin to fuse in the midline to complete the neural arch. This fusion and the resultant formation of a neural spine on each arch also occurs in an anterior to posterior sequence. The full complement of neural spines, including a shortened one

TABLE 3.—Sequence of ossification in larvae of *Sebastes macdonaldi*. The initial ossification of an element is indicated by "X" and the point of the arrow indicates the larval size at which the element achieves the general shape it will have in the juvenile and adult.

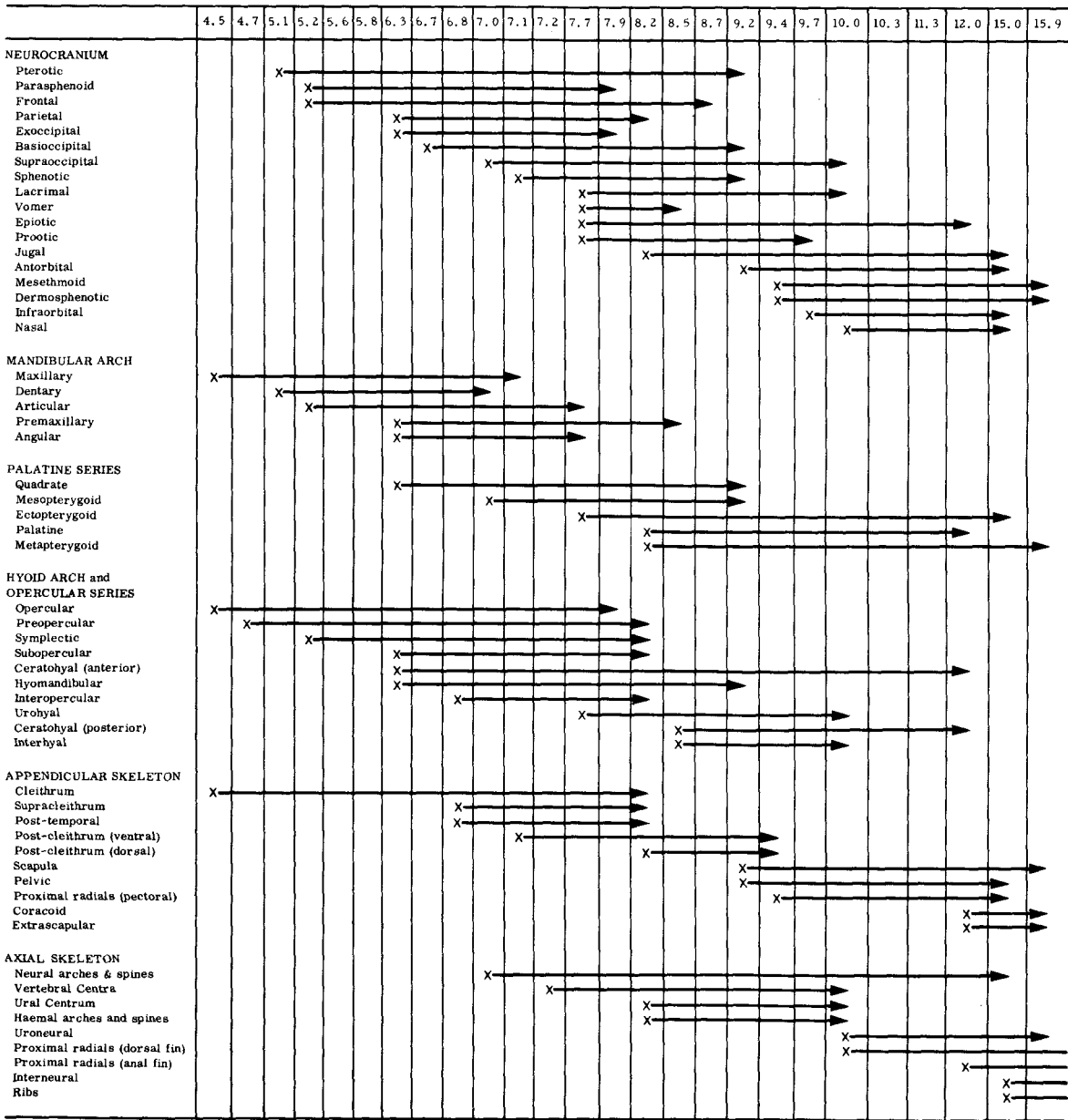


TABLE 4.—Sequence of initial ossification of branchial arch elements in larvae of *Sebastes macdonaldi*.

Element	Larval length at initial ossification (mm)
Pharyngobranchial teeth (3rd arch)	4.7
Ceratobranchial (1st arch)	6.3
Ceratobranchial (2nd arch)	6.3
Ceratobranchial (3rd arch)	6.3
Ceratobranchial (4th arch)	6.7
Ceratobranchial gill rakers (1st arch)	6.7
Ceratobranchial gill rakers (2nd arch)	7.2
Epibranchial (1st arch)	7.2
Epibranchial (2nd arch)	7.2
Ceratobranchial teeth (5th arch)	7.2
Ceratobranchial (5th arch)	7.7
Epibranchial (3rd arch)	7.7
Pharyngobranchial teeth (4th arch)	7.7
Ceratobranchial gill rakers (3rd arch)	7.7
Epibranchial gill rakers (1st arch)	8.2
Epibranchial (4th arch)	8.2
Hypobranchial (1st arch)	8.7
Epibranchial gill rakers (2nd arch)	8.7
Basibranchials	9.2
Hypobranchial (2nd arch)	9.2
Hypobranchial (3rd arch)	9.4

on the ultimate preterminal vertebra, is present in a 15.0-mm stained specimen.

The next elements of the axial skeleton to appear are the vertebral centra. The most anterior centra begin to ossify in larvae about 7.2 mm long. Ossification within each centrum begins at the bases of the neural arch and spreads medially to form a straplike bridge between the bases. A similar structure forms ventrally between the bases of the haemal arch and ultimately the two bridges are joined by lateral ossification, to produce a complete central ring. This process proceeds in a posteriad sequence until the full complement of 25 central rings is attained in larvae of about 10.0 mm. Ossification of the ural centrum begins in an 8.2-mm specimen with the formation of two tandem osseous plates on each lateral surface. These spread rapidly to cover the entire lateral and dorsal surface of the centrum. Ossification of two ventral unossified regions is completed at about 10.0 mm to coincide with the formation of the ultimate preterminal centrum.

Haemal arches begin to ossify at about 8.2-mm length in a manner similar to that of the neural arches. Closure of the haemal processes into arches and the formation of haemal spines proceeds posteriad sequentially; when completed at 10.0 mm, vertebrae 1 to 4 are without haemal

TABLE 5.—Sequence of initial ossification of head spines of larvae of *Sebastes macdonaldi*.

Spine	Element	Size of specimen at initial appearance (mm)
Pterotic	Pterotic	5.1
Preopercular, 3rd, posterior series	Preopercular	5.1
Preopercular, 4th, posterior series	Preopercular	5.2
Parietal	Parietal	6.3
Postocular	Frontal	6.3
Preopercular, 1st, anterior series	Preopercular	6.3
Preopercular, 2nd, anterior series	Preopercular	6.3
Preopercular, 3rd, anterior series	Preopercular	6.3
Preopercular, 2nd, posterior series	Preopercular	6.7
Supracleithral	Posttemporal	7.7
Suborbital, 1st, inferior series	Lacrima	8.2
Suborbital, 1st, superior series	Lacrima	8.2
Preopercular, 1st, posterior series	Preopercular	8.2
Nuchal	Parietal	8.2
Opercular, 1st	Opercle	8.2
Opercular, 2nd	Opercle	8.2
Preopercular, 5th, posterior series	Preopercular	9.4
Suborbital, 3rd, superior series	Jugal	9.4
Cleithral	Supracleithrum	12.0
Nasal	Nasal	15.0
Suborbital, 2nd, inferior series	Lacrima	15.0
Suborbital, 2nd, superior series	Infraorbital	15.0
Preocular	Antorbital	22.6
Supraocular	Frontal	22.6
Tympanic	Frontal	22.6

processes, 5 to 9 have unfused haemal processes, 10 and 11 have haemal arches without spines, and 12 to 25 have arches and spines.

All of the remaining major axial elements begin to ossify in larvae 10.0 mm or longer. The uroneurals appear as a pair of slender elements above the terminal centrum in a 10.0-mm specimen; they remain paired and sliverlike throughout the larval period. The proximal radial elements of the dorsal fin also begin to ossify at 10.0 mm and those of the anal fin at 12.0 mm, both in a posteriad direction; neither series is completed by 15.9 mm. A single interneural appears slightly above and in advance of the first neural spine in a 15.0-mm larva. Also, in this specimen the most anterior few ribs have just begun to ossify.

Several generalizations can be made from the information listed in Table 3. It is obvious that the various skeletal elements begin to ossify over a wide range of larval sizes and that the elements vary greatly in the time required for each to attain its adult form. For example, in the neurocranium, the jugal (third circumorbital) is formed over a span of nearly 7.0-mm length (8.2-15.0 mm) while the vomer begins to ossify

and achieves its adult shape over a span of about 1.0 mm (7.7-8.5 mm). Similar variation is found in the mandibular, palatine, and hyoid arches and in the axial and appendicular skeletons. Another less obvious generalization from Table 3 is that functionally related contiguous elements tend to achieve their adult form at about the same larval stage, regardless of when they underwent initial ossification. For example, the first six bones listed in the table are the major elements of the roof, sides, and floor of the brain case. Although they undergo initial ossification in a gradual sequence, all achieve their adult form in larvae 7.9 to 9.2 mm long. The bones of the opercular series (opercular, preopercular, subopercular, interopercular) begin to ossify in successive stages, but all achieve adult form at about the same stage. The pectoral girdle provides two excellent examples of this tendency in the cleithrum-supracleithrum-posttemporal series and the scapula-proximal radial-coracoid series. Finally, there is no correlation between sequence of ossification and the origin (endochondral or dermal) of a bony element. Thus, of the first six elements of the neurocranium mentioned above, half are endochondral and half are dermal in origin. Here, the early appearance of these elements appears to be related to function and not to the kind of bone formed.

Analysis of the sequence of ossification of branchial elements is difficult since ossification is so gradual that one cannot choose a larval stage at which a given element achieves its basic adult form. Accordingly, only the larval size at which an element begins to ossify is listed in Table 4. As in other teleosts examined by me, the first bony structures to ossify in the larvae are the pharyngobranchial teeth. In *S. macdonaldi*, the tooth patches of the third pair of pharyngobranchial elements appear in the smallest planktonic larvae and enlarge throughout the larval period. In larvae of the Myctophidae it is the tooth patches of the fourth pharyngobranchials which ossify first (Moser and Ahlstrom, 1970). Aside from this, the sequence of ossification is similar in *Sebastes* and Myctophidae. The ceratobranchials are the first elements of the arches to ossify. These are followed by the epibranchials and hypobranchials,

generally in an anterior to posterior sequence, beginning with those of the first arch. The first gill rakers to form are those on the first pairs of ceratobranchials and epibranchials and, gradually, they appear on more posterior arches. Within each arch, ossification proceeds outward from the angle of the arch. The full complement of rakers on the first arch is not achieved during the larval period.

Head spines present a special problem since some of the spines formed during the larval period are not found in adults. The terminology of Phillips (1957) is used in the discussion that follows. The first spines to form on the neurocranium are on the pterotic bones (Table 5). Interestingly, these spines begin to ossify before the bones themselves, and ossification of the bones spreads outward from the base of each spine. The spines are at first acute, but broaden during the larval period to produce a pterotic shelf in the largest larvae. The spine and shelf become reduced in pelagic juveniles and are absent in demersal juveniles and in adults. The two other pairs of spines which develop early in the larval period are the parietals and postoculars. The paired parietal spines develop as the terminal points of a pair of serrated parietal ridges and attain their maximum relative length (20-23% of the head length) in larvae 8.0 to 10.0 mm long. The ridges and their spines become reduced during later larval stages but remain in juveniles and adults. The postoculars develop from lateral shelves of the frontal bones that project over the eyes. Initially the spines are positioned directly above the eyes but gradually shift posteriad to their adult position. Preocular, supraocular, and tympanic spines do not form during the larval period; they are beginning to form in a pelagic juvenile 22.6 mm long and are well formed in the largest pelagic juveniles.

Other prominent cranial spines which develop later in the larval period are the suborbitals, nuchals, and nasals (Table 5). The suborbital spines form in two series: one series of ventrally directed spines develops on the ventral margin of each lacrimal (first circumorbital) bone and another series of laterally directed spines forms directly below the orbit. This lat-

ter series, composed of a single spine on each lacrimal, infraorbital, and jugal element, forms a shelf in late-stage larvae and in juveniles, but usually only the lacrimal spine remains in adults. The inferior series persists in adults and typically contains 3 to 5 spines. A nuchal spine forms directly posterior to each parietal spine in larvae about 8.0 mm long and persists in juveniles and adults. Nasal spines are late to form (15.0 mm) but also persist in adults.

Two spines appear on each preopercle in larvae 5.1 to 5.2 mm long. These are the third and fourth members of a series of five preopercular spines that forms throughout the larval period (Table 5). The third preopercular spines develop three longitudinal serrated ridges and elongate rapidly to become the longest larval spines. They reach a maximum length of 35% of the head length in larvae about 9.0 mm long and then decline in relative length. The five preopercular spines remain in juveniles and adults, but the short spines which develop immediately anterior to the second, third, and fourth preoperculars (Table 5) become obsolescent after the larval period. A pair of spines forms at the posterior margin of each opercle and persists in juveniles and adults.

The supracleithral and cleithral spines develop during the larval period; the supracleithral spines form on the posttemporal elements in larvae about 7.7 mm long and the cleithral spines form on the supercleithra at about 12.0 mm. Both pairs persist into the adult stage.

DISTRIBUTION

S. macdonaldi has the most southerly distribution of any species of *Sebastes* in the eastern north Pacific. Chen (1971) lists its southern range record as Morgan Bank off Baja California (lat 23°24.0'N, long 111°11.5'W) and reports on the capture of a single adult specimen (LACM 8837-4) from Santa Inez Bay in the Gulf of California (lat 26°59.1'N, long 111°48.9'W). A collection of six pelagic juveniles (32.7-44.4 mm SL; LACM 8821-9) by midwater trawl from the Ballenas Channel in the Gulf of California (lat 28°56.5'N, long 113°10.5'W) is reported herein. Although the localities at Morgan Bank and

Santa Inez Bay are separated by a distance of approximately 1,000 km, it is likely that future collections in this region will substantiate Chen's (1971) suggestion that the outer coast and Gulf of California populations are continuous.

The southerly distribution of *S. macdonaldi* is shown by the distribution of the larvae (Table 6, Figure 5). For the 4 years examined, larvae were taken as far north as CalCOFI line 90 and as far south as line 137. Line 90, running southwesterly from Dana Point, Calif., probably delimits the northern extent of reproduction for this species, although an adult has been taken as far north as Pt. Sur, Calif. (Phillips, 1961). Total numbers of larvae and frequency of occurrence of larvae increase to the south of line 90.

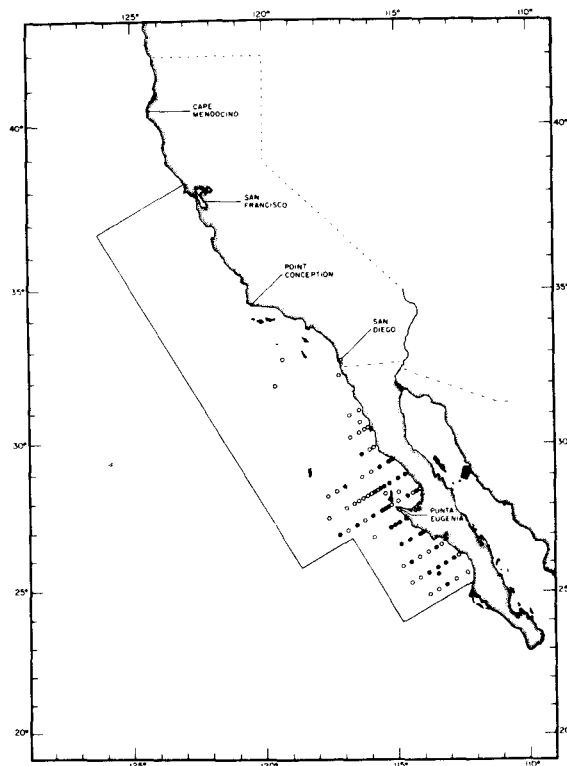


FIGURE 5.—Stations at which larvae of *Sebastes macdonaldi* were collected during 4 years (1953, 1960, 1965, and 1966) of CalCOFI plankton surveys. Solid circles indicate stations where number of *Sebastes macdonaldi* larvae exceeded mean number (4.8) for all positive stations. Area of frequent occupancy is outlined (see Ahlstrom, 1961, for complete grid).

TABLE 6.—Total numbers of *Sebastes macdonaldi* larvae taken on 14 CalCOFI lines for 4 years (1953, 1960, 1965, and 1966) and abundance of larvae of this species compared with the total numbers of *Sebastes* larvae taken in hauls containing *S. macdonaldi*.

CalCOFI line	Latitude ¹	Total number stations occupied	Total stations containing <i>S. macdonaldi</i>	Percentage of positive stations to total stations	Number of <i>S. macdonaldi</i> larvae	Total number of <i>Sebastes</i> larvae in hauls containing <i>S. macdonaldi</i>	Percentage <i>S. macdonaldi</i> larvae of total <i>Sebastes</i> larvae in hauls positive for <i>S. macdonaldi</i>
90	33°28.5'	383	1	0.26	1	31	3
93	32°56.0'	380	1	0.26	1	4	25
97	32°17.5'	325	1	0.31	1	28	4
103	31°07.0'	283	4	1.41	9	226	4
107	30°27.9'	273	8	2.93	12	226	5
110	29°52.0'	306	9	2.94	17	202	8
113	29°24.2'	283	19	6.71	47	285	16
117	28°58.0'	315	47	14.92	289	968	30
120	28°25.0'	365	33	9.04	110	332	33
123	27°26.2'	198	28	14.14	151	613	25
127	26°57.5'	202	33	16.34	143	252	57
130	26°33.5'	243	22	9.05	37	100	37
133	26°08.5'	209	23	11.00	207	224	92
137	25°36.1'	214	15	7.01	39	45	87

¹ Latitude of most shoreward station of each CalCOFI line.

They attain their largest numbers from line 117 to line 127 (Cedros Island to San Hipolito Point) and then decrease to line 137. In contrast, for those hauls containing *S. macdonaldi*, the ratio of this species to the total number of *Sebastes* larvae in these hauls increases continuously southward. *Sebastes* larvae were not taken on lines south of 137, probably because of the infrequent occupancy of these lines. Reproduction of *S. macdonaldi* occurs as far south as Morgan Bank (between lines 147 and 150), since one of the two specimens collected there was a term female with viable larvae.

The seasonal abundance and size of *S. macdonaldi* larvae at all CalCOFI stations during 1953 and 1960 are shown in Table 7. Larvae began to appear in January, increased in numbers in February, and reached a peak in March. Abundance declined progressively from April to June. The mean length of the larvae increased slightly during the 6-month period and the largest larvae were collected from March to June.

The larval stage is ended at about 16 mm; indeed, a 15.4-mm specimen is already beginning to develop the juvenile melanophore pattern and the juvenile arrangement of cranial spines. The pelagic juveniles are rare in plankton collections, probably because of their ability to avoid plankton nets. Also, they may occur deeper than 140 m, the usual maximum depth of CalCOFI plankton tows. Nevertheless, a number of pelagic juveniles, 22.6 to 44.4 mm long, were captured by plankton net, midwater trawl, and dip net. These are listed in Table 1 and discussed in the previous section of the paper. The smallest juvenile collected by bottom trawl was 59.3 mm. This suggests that the transition from pelagic to demersal habitat occurs in the size range of about 45 to 60 mm. Demersal juveniles 60 to 100 mm are captured typically at a depth range of 80 to 100 m. With further growth they appear to seek deeper habitats as there is a trend for larger fish to be collected from greater depths. The largest specimen examined (532

TABLE 7.—Numbers (A), mean length in mm (B), and size range in mm (C) of *Sebastes macdonaldi* larvae taken during 2 years of the California Cooperative Oceanic Fisheries Investigations (CalCOFI).

Year	CalCOFI lines	JANUARY			FEBRUARY			MARCH			APRIL			MAY			JUNE		
		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
1953	97-107	2	4.2	4.2	4	4.2	4.2-4.3	0	0	0	1	4.8	4.8	0	0	0	0	0	0
	110-120	5	4.3	3.8-5.3	19	4.5	3.5-7.1	138	5.0	3.3- 9.5	26	6.2	3.7-10.0	4	4.8	3.8-6.2	0	0	0
	123-137	13	4.4	3.3-3.5	20	4.6	3.9-8.7	143	4.8	3.3-11.2	34	5.3	3.8- 8.8	5	5.4	3.3-9.6	0	0	0
1960	97-107	0	0	0	6	5.1	4.3-6.5	6	5.6	4.7- 8.2	2	4.9	4.9	0	0	0	0	0	0
	110-120	0	0	0	12	4.7	4.4-5.2	81	5.2	3.8- 8.8	25	4.8	4.0- 6.2	4	5.3	4.5-7.3	5	4.3	3.7-5.8
	123-137	1	4.2	4.2	14	4.9	4.0-5.8	184	4.7	3.4-10.8	76	5.3	3.2-10.3	17	5.1	4.1-9.6	1	6.0	6.0

mm SL, SIO 65-126) was taken by hook and line at 256 m.

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