

Abstract—The widespread and commercially important rougheye rockfish, *Sebastes aleutianus* (Jordan and Evermann, 1898), has been considered a single variable species, with light- and dark-colored forms, found on the outer continental shelf and upper slope of the North Pacific Ocean. Genetic analysis of 124 specimens verified the presence of two species in new specimens collected from Alaska to Oregon, and the two species were analyzed for distinguishing color patterns and morphological characters. Characters distinguishing the two were extended to an analysis of 215 additional formalin-fixed specimens representing their geographic ranges. *Sebastes aleutianus* is pale, often has dark mottling on the dorsum in diffuse bands, and does not have distinct dark spots on the spinous dorsal fin; it ranges from the eastern Aleutian Islands and southeastern Bering Sea to California. *Sebastes melanostictus* (Matsubara, 1934), the blackspotted rockfish, ranges from central Japan, through the Aleutian Islands and Bering Sea, to southern California. It is darker overall and spotting is nearly always present on the spinous dorsal fin. *Sebastes swifti* (Evermann and Goldsborough, 1907) is a synonym of *S. aleutianus*; *S. kawaradae* (Matsubara, 1934) is a synonym of *S. melanostictus*. The subgenus *Zalopyr* is restricted to *S. aleutianus* and *S. melanostictus*. Nomenclatural synonymies, diagnoses, descriptions, and distributions are provided for each species.

Manuscript submitted 20 September 2007.
Manuscript accepted 20 November 2007.
Fish. Bull. 106:111–134 (2008)

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Species of the rougheye rockfish complex: resurrection of *Sebastes melanostictus* (Matsubara, 1934) and a redescription of *Sebastes aleutianus* (Jordan and Evermann, 1898) (Teleostei: Scorpaeniformes)

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Of the more than 110 species of *Sebastes* recognized worldwide, by far the greatest number of species are found in the North Pacific Ocean, where about 100 species are currently considered valid (Kai and Nakabo, 2002; Orr and Blackburn, 2004; Hyde and Vetter, 2007). Although very important commercially, members of the genus have a reputation for being difficult to identify, because they are similar in body shape and share other morphological characters. Live coloration is also an extremely important character used in diagnosis and identification. Molecular characters serve to identify most of these species and generally lend support to traditional morphological identifications and concepts of species limits. In addition, the use of genetic data has uncovered previously unrecognized species-level variation in what had been considered single species, as in the case of the rougheye rockfish complex, now known to comprise the two species *Sebastes aleutianus* (Jordan and Evermann, 1898) and *S. melanostictus* (Matsubara, 1934). The powerful combination of genetic and morphological analyses provides

a means to identify the important characters useful in distinguishing new specimens, as well as archived material that, in some cases, has been preserved for over a century.

Ranging around the rim of the North Pacific Ocean and Bering Sea, from Japan to southern California, the species presently recognized as *Sebastes aleutianus* was originally described by Jordan and Evermann (1898) from four specimens taken in waters around Kodiak Island, Alaska. Evermann and Goldsborough (1907) later described *S. swifti*, a synonym of *Sebastes aleutianus*, from the northeastern Gulf of Alaska.

In the western Pacific, Matsubara (1934) described two species similar to *Sebastes aleutianus*, *S. melanostictus* and *S. kawaradae*. Barsukov (1964, 1970) determined that the names of both of these species were synonyms of *S. aleutianus*, apparently without examining type material. Kanayama and Kitagawa (1982) later examined the types and comparative material used by Matsubara (1934, 1943) as well as new material of *S. aleutianus* from the Bering Sea and Japanese Pacific coast. They also con-

cluded that both *S. melanostictus* and *S. kawaradae* are synonymous with *S. aleutianus*. These decisions were subsequently followed by Sheiko and Fedorov (2000), Love et al. (2002), Mecklenburg et al. (2002), and Nakabo (2002).

The confused history of the nomenclature of *Sebastes aleutianus* has been a result of the perceived wide variation in body coloration and close similarity in morphological features of several other species of *Sebastes*, including *S. borealis* (Barsukov, 1970), short-raker rockfish, and *S. melanostomus* (Eigenmann and Eigenmann, 1890), blackgill rockfish, in the eastern Pacific. Gilbert (1896) misidentified *S. aleutianus*, and probably *S. borealis*, material from the Bering Sea as that of *S. inroniger* (Gilbert, 1890), which was originally described from southern California and is now considered a synonym of *S. melanostomus* (Phillips, 1957; Tsuyuki and Westrheim, 1970). In the same publication as their original description of *S. aleutianus*, Jordan and Evermann (1898) provided a species account of *S. inroniger* that was primarily based on Gilbert's earlier (1896) redescription (Tsuyuki and Westrheim, 1970), again listing its range as including the Bering Sea. Until clarified by Barsukov (1970) and Tsuyuki and Westrheim (1970) with their original descriptions of the new species *S. borealis* Barsukov and its synonym *S. caenaemeticus* Tsuyuki and Westrheim, these reports led to persistent records in the literature of *S. melanostomus* having been taken in the Bering Sea (Jordan and Evermann, 1898; Evermann and Goldsborough, 1907; Jordan et al., 1930; Barsukov, 1964; Allen and Smith, 1988), although it is a species that may range north only to extreme southeastern Alaska (Butler and Love, 2002; Mecklenburg et al., 2002; Love et al., 2002, 2005; Kramer and O'Connell, 2003).

The early work of Tsuyuki and coauthors (Tsuyuki et al., 1965, 1968; Tsuyuki and Westrheim, 1970) and Seeb (1986) on hemoglobin and allozymes of eastern Pacific *S. aleutianus* provided evidence for species-level differences among morphological and color forms—differences that were correlated with genetic variants. Using larger sample sizes and broader geographic ranges, Hawkins et al. (2005) with allozyme data and Gharrett et al. (2005) with DNA markers provided conclusive evidence of species-level differences among individuals in Alaskan waters, and the reality of the presence of two species within *S. aleutianus* was confirmed.

In this revision of the complex presently identified as *Sebastes aleutianus*, we recognize two species: *Sebastes aleutianus*, the rougheye rockfish, restricted to the eastern Pacific; and *Sebastes melanostictus*, the blackspotted rockfish, ranging across the North Pacific from Japan to California. *Sebastes kawaradae* is considered a synonym of *S. melanostictus*, and *S. swifti* is a synonym of *S. aleutianus*. We expand upon the efforts of Gharrett et al. (2006), who distinguished dark and light forms in the Gulf of Alaska, extending our morphological examination across almost the entire range of both species, clarifying the nomenclature, and providing diagnoses and redescrptions of both species.

Methods and materials

Counts, measurements, and statistical analyses followed Orr and Blackburn (2004), except as noted below. The structure of the swimbladder was examined after dissection following the method of Hallacher (1974). Unless indicated otherwise, standard length (SL) is used throughout, always measured from the tip of the snout. Measurements and counts are presented in species descriptions as the range for all material examined followed by the value for the holotype or lectotype in parentheses, when intraspecific variation is indicated.

Collection depths are noted for each cataloged lot in the *Material examined* section (see Appendix) when known. In the analysis of depth distributions, only those lots with a single depth reported were used; when a range of depths was reported for a lot, it was not included. All depths reported are bottom depths unless otherwise stated. Institutional abbreviations follow Eschmeyer (1998). Survey records for "rougheye rockfish" (*Sebastes aleutianus* or *S. melanostictus*) were taken from the Resource Assessment and Conservation Engineering Division, Alaska Fisheries Science Center (AFSC), database, which included catch data from groundfish surveys conducted from the Bering Sea and Aleutian Islands to southern California from 1961 to 2005.

During initial genetic analyses, 124 individuals were identified as *S. aleutianus* or *S. melanostictus* (= *S. sp. cf. aleutianus* of Hawkins et al., 2005) by using allozyme data following Hawkins et al. (2005) and are marked with an asterisk in the *Material examined* section (see Appendix). These specimens were collected primarily in the northern Gulf of Alaska and off Washington; two specimens, however, were collected from the eastern Aleutian Islands and northern California. Based on examination of these genetically identified individuals, significant differences were found in body color, specifically spotting on the spinous dorsal fin or an overall darker color (or both) in *S. melanostictus* (see *Species descriptions* below), that were then used to identify preserved specimens for which tissue was not available for genetic analysis. Allozyme characteristics and body color were used to group individuals for univariate tests, as well as for labeling individuals in graphs of principal components analysis scores. Nomenclature of allozyme protein variants and microsatellite alleles follows conventions of the American Fisheries Society (Shaklee et al., 1990). Statistical analyses were performed with Statgraphics Plus 4.1 (Manugistics, Rockville, MD), Splus 6.2 (Insightful Corp., Seattle, WA), and SPSS 11.5.1 (SPSS Inc., Chicago, IL). Differences were considered significant at $P < 0.05$.

Out of a total of 329 specimens examined morphologically, many had broken spines or other missing characters; thus, the data set was reduced to 137 specimens with complete data, including 40 of those genetically identified, for which both univariate and multivariate analyses could be conducted. A suite of 29 morphometric and 5 meristic characters was analyzed (Table 1). All

Table 1

Proportional morphometrics and meristics of *Sebastes aleutianus* (rougeye rockfish) and *Sebastes melanostictus* (blackspotted rockfish) for specimens in which all characters were used for multivariate analyses. Morphometric data are given in percent SL (standard length) and presented as the range, followed by the mean \pm standard deviation (SD). *P* values are reported for statistically significant differences at α level of 0.05, as evaluated by ANCOVA or Kruskal-Wallis tests when appropriate; ns = not statistically significant at an α level of 0.05.

	<i>Sebastes aleutianus</i>	<i>Sebastes melanostictus</i>	<i>P</i>
	Range (mean \pm SD)	Range (mean \pm SD)	
<i>n</i>	57	80	
Standard length (mm)	77.1–470	101.6–445	
Meristics			
Dorsal-fin rays	12–14 (13.4 \pm 0.5)	13–15 (13.8 \pm 0.5)	<0.0001
Anal-fin rays	6–8 (7 \pm 0.3)	6–8 (7 \pm 0.2)	ns
Pectoral-fin rays (left)	17–19 (18.1 \pm 0.3)	17–19 (18.1 \pm 0.3)	ns
Lateral-line pores (left)	30–34 (31.2 \pm 0.9)	30–36 (32 \pm 1.2)	<0.0001
Gill rakers	29–33 (31.1 \pm 1.0)	30–35 (33 \pm 1.1)	<0.0001
Morphometrics			
Head length	34.6–42.5 (37 \pm 1.6)	34.6–41.4 (37.6 \pm 1.5)	
Orbit length	8.8–13.5 (10.7 \pm 1.1)	8.2–13.3 (10.4 \pm 1.0)	ns
Snout length	5.8–9.7 (7.5 \pm 0.7)	6.6–9.5 (7.9 \pm 0.6)	0.0486
Interorbital width	5.5–8.9 (7.1 \pm 0.7)	5.6–8.8 (7.4 \pm 0.7)	
Suborbital depth	1.6–2.9 (2.3 \pm 0.3)	1.5–3.3 (2.3 \pm 0.4)	0.0019
Upper jaw length	16.9–21.9 (19.2 \pm 0.9)	17.2–21.5 (19.2 \pm 0.7)	
Lower jaw length	20.4–27.2 (23.4 \pm 1.2)	20.7–26.8 (24.5 \pm 1.1)	
Gill raker length	3.4–6.1 (4.8 \pm 0.6)	3.9–6.8 (5.6 \pm 0.5)	<0.0001
Depth at pelvic-fin base	31.6–42.6 (36 \pm 1.9)	31.3–39.7 (34.9 \pm 1.8)	
Depth at anal-fin origin	23.9–31.9 (28 \pm 1.6)	23.5–29.4 (26.2 \pm 1.5)	<0.0001
Depth at anal-fin insertion	11.9–15.3 (13.9 \pm 0.7)	11.3–15.3 (13.3 \pm 1.0)	<0.0001
Dorsal-fin spine I length	4.6–7.2 (5.8 \pm 0.6)	6.1–9.6 (7.9 \pm 0.8)	<0.0001
Dorsal-fin spine IV length	10.6–15 (13.2 \pm 0.9)	12.3–18.9 (14.8 \pm 1.3)	<0.0001
Pectoral-fin base depth	8.4–10.4 (9.4 \pm 0.4)	8.2–10.4 (9.5 \pm 0.4)	ns
Pectoral-fin ray length	25–31 (27.4 \pm 1.3)	22–30 (26.3 \pm 1.4)	0.0013
Pelvic-fin ray length	19.3–25.1 (22.3 \pm 1.1)	19.4–25 (21.5 \pm 1.2)	0.0298
Pelvic-fin spine length	11.1–15.5 (13.5 \pm 1.2)	11.4–16.9 (13.8 \pm 1.2)	<0.0001
Anal-fin spine I length	4.7–9.4 (6.6 \pm 1.0)	4.7–10.1 (7.1 \pm 1.2)	<0.0001
Anal-fin spine II length	11–18.4 (14.4 \pm 1.8)	11.8–20.9 (15.2 \pm 2.2)	<0.0001
Anal-fin spine III length	14.2–19.8 (16.5 \pm 1.3)	12.4–20.9 (16.6 \pm 1.7)	<0.0001
Caudal peduncle depth	7.8–10.7 (9.7 \pm 0.5)	8.2–10.6 (9.2 \pm 0.5)	
Caudal peduncle dorsal length	10.5–15.3 (12.2 \pm 0.9)	11.3–15 (13 \pm 0.8)	
Caudal peduncle ventral length	17.8–21.9 (19.6 \pm 0.9)	17.4–21.7 (20.1 \pm 0.9)	
Preanal length	67.1–77.6 (71.8 \pm 2.5)	63.2–78.5 (70 \pm 2.6)	<0.0001
Predorsal length	31.2–39.5 (34.3 \pm 1.9)	31.6–38.4 (35 \pm 1.4)	
Spinous dorsal-fin-base length	31.9–41.7 (35.5 \pm 2.3)	32.4–40.9 (36.3 \pm 2.0)	ns
Soft dorsal-fin-base length	20.7–25.6 (22.9 \pm 1.2)	17.7–24.7 (21.5 \pm 1.4)	<0.0001
Anal-fin-base length	13.3–18.2 (15.3 \pm 0.9)	12.4–17 (14.2 \pm 1.0)	ns
Pre-pelvic-fin length	37.8–53.1 (44.4 \pm 4.2)	36.6–50.5 (42.4 \pm 2.5)	

morphometric characters were also tested for sexual dimorphism, where gender was treated as a categorical factor and the gender-species interaction was tested. Arcsine-transformed morphometric ratios (with SL or head length [HL] as denominator) were tested to meet the assumptions of normality and equality of variance required for ANCOVA. The following characters exhib-

ited normal distributions and did not differ significantly in variance between species and thus were subjected to ANCOVA: orbit length, snout length, suborbital depth, gill-raker length, body depth at anal-fin origin, body depth at anal-fin insertion, dorsal-fin spine 1 length, dorsal-fin spine 4 length, pectoral-fin base depth, pectoral-fin ray length, pelvic-fin ray length, pelvic-fin

spine length, anal-fin spine 1 length, anal-fin spine 3 length, preanal length, spinous-dorsal-fin base length, soft-dorsal-fin base length, and anal-fin base length. Counts of meristic characters were tested by using the Kruskal-Wallis test.

To aid in distinguishing the two species, a standard principal component analysis (PCA) was conducted on both morphometric and meristic characters. The analyses were conducted on the covariance matrix of log-transformed raw morphometric data and the correlation matrix of raw meristic data. Differences between species were illustrated by plotting principal component (PC) 2 against PC3 of the morphometric analysis, PC1 against PC2 of the meristic analysis, and morphometric PC2 against meristic PC1.

Following the PCAs, a stepwise discriminant function analysis (DFA) was conducted by using morphometric and meristic data to establish the relative significance of those characters in distinguishing between the species. Morphometric data were standardized by dividing by standard length. Only characters meeting assumptions of multivariate normality and that exhibited statistically significant differences were analyzed. The robustness of the DFA was tested by conducting a leave-one-out cross-validation procedure (SPSS Inc., Chicago, IL).

For the data set containing all 329 specimens, only univariate analyses were conducted. The following characters, in addition to all those except orbit length in the reduced dataset, exhibited normal distributions, did not differ significantly in variance between species, and were subjected to ANCOVA: head length, lower-jaw length, body depth at pelvic-fin base, anal-fin spine 2 length, caudal-peduncle depth, caudal-peduncle dorsal length, caudal-peduncle ventral length, predorsal length, and pelvic-fin base to anal-fin origin length. Differences in counts of meristic characters were tested using the nonparametric Kruskal-Wallis test. With the exception of unbranched pectoral-fin rays, meristic data from specimens of all sizes were tested. In juveniles of less than 100 mm, all pectoral-fin rays were simple and counts for these specimens were not included in tests or presented in tables of lower pectoral-fin rays. Meristic data is presented in tables of frequency distributions by region. Four general regions were identified: 1) western Pacific Ocean, for material taken in Japanese and Russian waters; 2) Bering Sea and Aleutian Islands, for material from the eastern Bering Sea and Aleutian Islands to Unimak Pass; 3) Gulf of Alaska, from Unimak Pass to the Alaska-British Columbia border; and 4) the Lower West Coast, from Canada, Washington, Oregon, and California.

Results

Color pattern

Both in life and in preservation, body color differs consistently between *S. aleutianus* and *S. melanostictus*

(Figs. 1–4; see detailed description below). The spinous dorsal fin in *S. melanostictus* is almost invariably discretely spotted. In most specimens, many small spots are scattered across the spinous dorsal fin, often continuing onto the soft dorsal fin; in some individuals, only two or three spots are present on the spinous dorsal fin. The presence or absence of these discrete spots was used in initial statistical analyses as the basis for identifying preserved specimens lacking tissue for genetic analysis. A few dark individuals without spots, or with spots apparently obscured by dark blotching, were aligned morphologically with other spotted individuals, and these dark individuals were also eventually identified as *S. melanostictus*. In contrast, all *S. aleutianus* examined were pale overall and lacked discrete spots, although often having diffuse mottling and blotches extending from the body onto the bases of the spinous and soft dorsal fins.

Morphometric and meristic characters

Specimens of *S. melanostictus* generally had longer dorsal-fin spines (Fig. 5, A and B), other spines, and gill rakers (Fig. 5C), whereas specimens of *S. aleutianus* had a deeper, more robust head and body and longer pelvic- and pectoral-fin rays. Among morphometric characters of specimens with all characters, snout length, suborbital depth, gill raker length, body depth at anal-fin origin, body depth at anal-fin insertion, dorsal-fin spine 1 length, dorsal-fin spine 4 length, pectoral-fin ray length, pelvic-fin ray length, pelvic-fin spine length, anal-fin spine 1 length, anal-fin spine 2 length, anal-fin spine 3 length, preanal length, and soft-dorsal-fin base length differed significantly between *S. aleutianus* and *S. melanostictus* (Table 1). In addition, among specimens of the larger data set, head length, lower jaw length, depth at pelvic-fin base, caudal-peduncle depth, caudal-peduncle dorsal length, and caudal-peduncle ventral length also differed significantly, and anal-fin spine 1 and 3 lengths became nonsignificant (Table 2).

Plots of PCA scores revealed prominent differences between the two species among morphometric characters, as well as slight differences among meristic characters. In the morphometric PCA, all characters were positively loaded on PC1 (the size component; Table 3), which explained 96.8% of the total variation. Among the principal shape components, PC2 explained 1.3% of variation and was heavily loaded on dorsal-fin spine 1 length, gill-raker length, anal-fin spine 1 length, anal-fin spine 2 length, and dorsal-fin spine 4 length (Table 3); PC3 explained 0.3% of variation and was heavily loaded on anal-fin spine 1 length, suborbital depth, gill-raker length, prepelvic length, and orbit length (Table 3). In the plot of PC2 versus PC3, the two clusters representing *S. aleutianus* and *S. melanostictus* overlapped narrowly; 16 (8 *S. aleutianus*, 8 *S. melanostictus*) of 137 individuals examined were in this area of overlap (Fig. 6A). Of 40 genetically identified individuals, three *S. aleutianus* and three *S. melanostictus* were included in the overlap area. One



Figure 1

Sebastes aleutianus (rougheye rockfish), UW 116468, 120.2–138.6 mm, females, northern Gulf of Alaska, 59.6918°N, 148.8569°W, 180 m depth, 28 July 2005. Photo by J. W. Orr.

specimen with an unknown genotype, a possible hybrid, was also included.

Although meristic characters broadly overlapped in ranges, several characters were indicative of a species-level difference between *S. aleutianus* and *S. melanostictus*. Numbers of gill rakers, lateral-line pores, and dorsal-fin rays differed significantly (Tables 1 and 2). No regional or clinal differences were evident in frequency data (Tables 4 and 5). Significant differences were also expressed in the meristic PCA as heavy loadings on PC1 (Table 6), which, however, revealed only a slight separation between broadly overlapping clusters of the two species when scores were plotted for PC1 and PC2 (Fig. 6B).

Plotting the scores of PC1 of the meristic analysis versus PC2 of the morphometric analysis resulted in slightly better resolution between the two species clusters (Fig. 6C). In contrast with the morphometrics-only plot that had 16 individuals in the area of overlap and the meristics-only plot in which the clusters nearly completely overlapped, only nine individuals were found in the area of overlap when the morphometric PC2 was plotted against the meristic PC1. As in the morphometrics-only plot, six of these individuals were genetically identified.



Figure 2

Underwater photo of *Sebastes aleutianus* (rougheye rockfish) taken south of Kodiak Island, Alaska, ca. 56°N, 153°N, July 2005. Photo by D. Hanselman.



Figure 3

Sebastes melanostictus (blackspotted rockfish), UW 48464, 249.5 mm, male, Aleutian Islands, north of Islands of Four Mountains, 53.2207°N, 169.7395°W, 328 m depth, 2 June 2002. Photo by J. W. Orr.

Discriminant function analysis

Although the PCA produced overlapping species clusters of individuals identified and labeled separately from the analysis, the discriminant function analysis verified the *a priori* identification of nearly all individuals. The single linear discriminant function equation produced was highly significant (Wilks's $\lambda=0.197$, $\chi^2=222.772$, 8 df, $P<0.0001$):

$$D = 101.557(d1) + 52.453(snl) + 0.294(gr) + 51.92(grl) + 0.564(dr) - 38.604(p2rl) - 22.601(d2b) - 10.203(pal) - 10.445,$$

where D = the discriminant score of an individual;
 $d1$ = length of dorsal-fin spine 1 divided by SL;
 snl = snout length divided by SL;
 gr = number of gill rakers;
 grl = length of gill rakers divided by SL;

dr = number of dorsal-fin rays;

$p2rl$ = length of pelvic-fin rays divided by SL;

$d2b$ = length of soft-dorsal-fin base; and

pal = preanal length divided by SL.



Figure 4

Underwater photo of *Sebastes melanostictus* (blackspotted rockfish) taken south of Kodiak Island, Alaska, ca. 56°N, 153°N, July 2005. Photo by D. Hanselman.

All but two individuals with negative scores had been previously identified as *S. aleutianus*, whereas all but one individual with positive scores were *S. melanostictus*. The discriminant function equation, therefore, correctly classified 97.8% of individuals. The possible hybrid was classified correctly as *S. aleutianus*. The cross-validation procedure correctly classified 97.1% of individuals. In addition to the three individuals above, one *S. aleutianus* was also misclassified as *S. melanostictus* in cross validation. When using this equation for future species

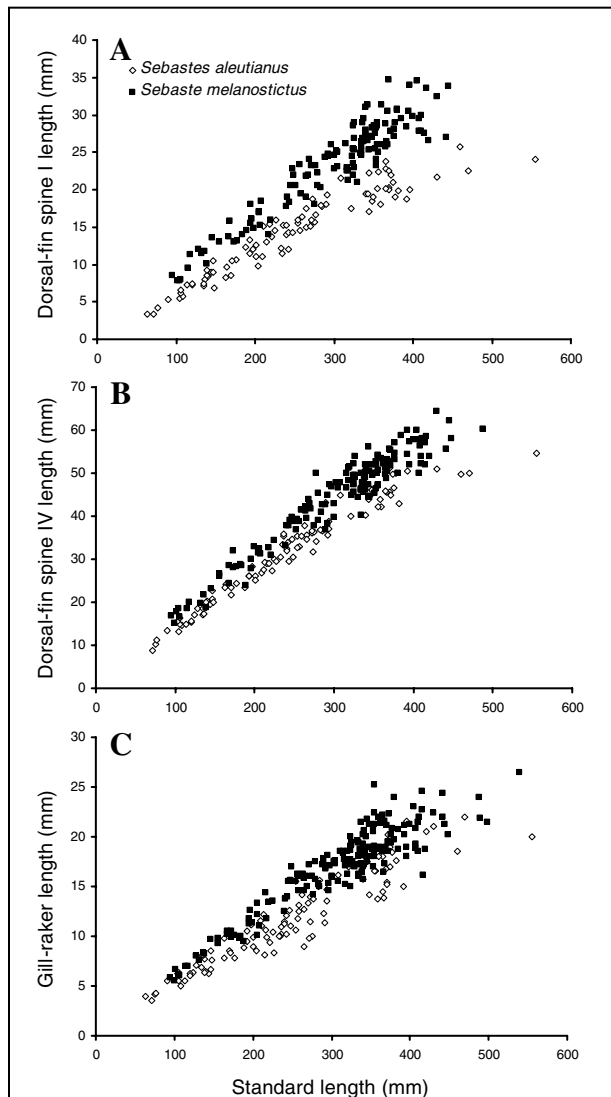


Figure 5

Plots of diagnostic morphometric characters versus standard length of *Sebastes aleutianus* (rougheye rockfish, open diamond) and *S. melanostictus* (blackspotted rockfish, closed square). (A) Dorsal-fin spine I length, (B) dorsal-fin spine IV length, and (C) gill raker length. The first and fourth dorsal-fin spines and gill rakers are longer in most specimens of *S. melanostictus* than in *S. aleutianus*.

separation, one would identify individuals with a score above 0 as *S. melanostictus* and those below 0 as *S. aleutianus*.

Systematics

Sebastes aleutianus (Jordan and Evermann, 1898)

Rougheye rockfish

Figures 1, 2, 5–8; Tables 1, 2, 4, 5

Sebastodes aleutianus Jordan and Evermann, 1898:1795, pl. 16, figs. 1–4 (original description,

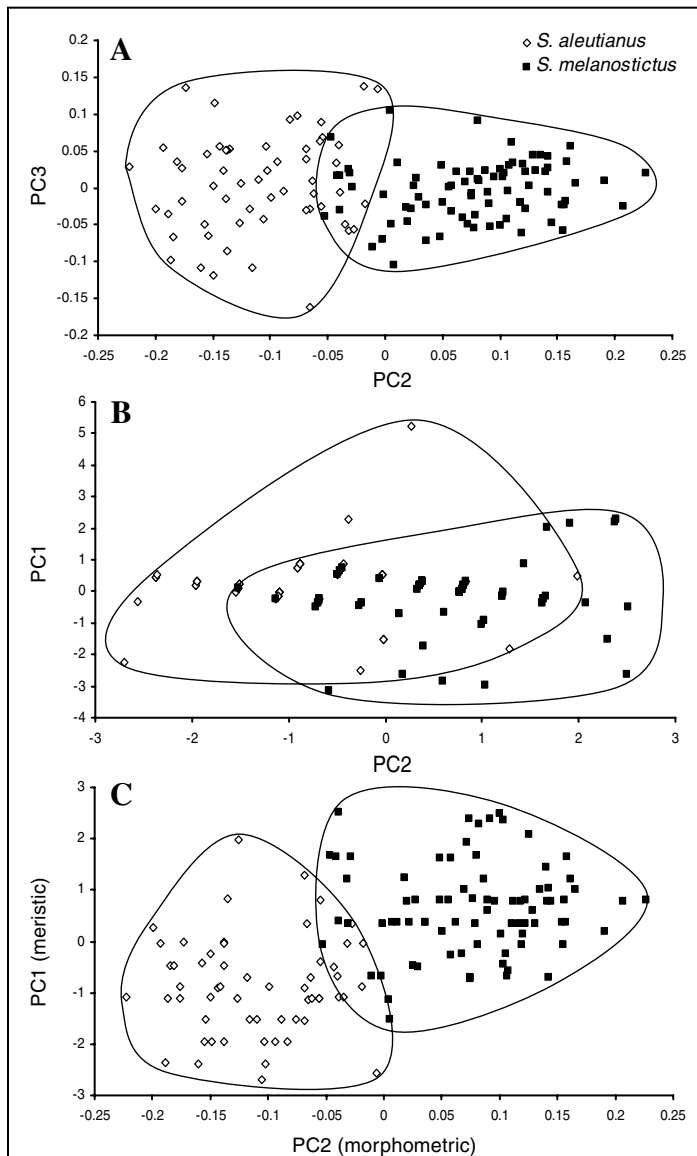


Figure 6

Plots of principal component (PC) scores for morphometric and meristic characters for *Sebastes aleutianus* (rougheye rockfish, open diamond) and *S. melanostictus* (blackspotted rockfish, closed square). (A) Morphometric characters only, (B) meristic characters only, and (C) morphometric (PC2) versus meristic characters (PC1). Differences among specimens along the major axis of dispersion in the morphometric analysis (PC2) were primarily due to longer dorsal-fin spines, anal-fin spines, and gill rakers in *S. melanostictus*. The slight separation among specimens along the major axis in the meristic analysis (PC2) was primarily due to higher counts of gill rakers, lateral-line pores, and dorsal-fin rays in *S. melanostictus*.

four specimens: lectotype herein designated USNM 48800, male, 374.2 mm; paralectotypes, three specimens 370–470 mm, SU 12928, *Albatross* station 3676, Shelikof Strait, Alaska, off Karluk, Kodiak Island, 223 m depth, 20 July 1897).

Table 2

Proportional morphometrics and meristics of *Sebastes aleutianus* (rougeye rockfish) and *Sebastes melanostictus* (blackspotted rockfish) for all specimens examined. Morphometric data are given in percent SL (standard length) and presented as the range, followed by the mean \pm standard deviation (SD). *P* values are reported for statistically significant differences at 0.05 level, as evaluated by ANCOVA or Kruskal-Wallis tests when appropriate; ns = not statistically significant at an α level of 0.05.

	<i>Sebastes aleutianus</i>		<i>Sebastes melanostictus</i>		<i>P</i>
	<i>n</i>	Range (mean \pm SD)	<i>n</i>	Range (mean \pm SD)	
Standard length (mm)	117	63.4–555.2	193	95.5–539	
Meristics					
Dorsal-fin spines	114	12–14 (13.0 \pm 0.2)	182	12–14 (13.0 \pm 0.2)	ns
Dorsal-fin rays	109	12–14 (13.5 \pm 0.5)	184	13–15 (13.7 \pm 0.5)	<0.001
Anal-fin rays	108	6–8 (7.1 \pm 0.3)	182	6–8 (7.1 \pm 0.3)	ns
Pectoral-fin rays	106	17–19 (18.1 \pm 0.3)	170	17–19 (18.1 \pm 0.4)	ns
Unbranched pectoral-fin rays	99	4–9 (7.7 \pm 0.9)	177	5–10 (7.9 \pm 0.7)	ns
Lateral-line pores	105	30–34 (31.4 \pm 1.0)	184	30–36 (32.0 \pm 1.2)	<0.001
Gill rakers	116	29–34 (31.2 \pm 1.0)	191	30–36 (33.0 \pm 1.2)	<0.001
Gill rakers of upper arch	98	8–10 (9.1 \pm 0.5)	165	8–11 (9.6 \pm 0.6)	<0.001
Gill rakers of lower arch	98	21–24 (22.1 \pm 0.8)	165	21–26 (23.4 \pm 0.8)	<0.001
Morphometrics					
Head length	106	33.5–41.4 (36.8 \pm 1.4)	179	34–41.4 (37.6 \pm 1.4)	0.006
Orbit length	93	8.7–13.5 (10.7 \pm 1.1)	145	8.2–13.3 (10.2 \pm 0.9)	
Snout length	93	5.7–9.7 (7.5 \pm 0.7)	143	6.2–9.6 (8 \pm 0.6)	<0.001
Interorbital width	93	5.5–8.9 (7.2 \pm 0.7)	141	5.6–9.2 (7.5 \pm 0.7)	
Suborbital depth	90	1.6–2.9 (2.3 \pm 0.3)	141	1.5–3.3 (2.3 \pm 0.3)	ns
Upper jaw length	89	16.9–21.1 (19.1 \pm 0.7)	141	17.2–21.5 (19.2 \pm 0.8)	
Lower jaw length	91	20.4–27.2 (23.6 \pm 1.2)	138	21.6–27.1 (24.6 \pm 1.0)	<0.001
Gill raker length	106	3.4–6.3 (4.9 \pm 0.6)	178	3.9–7.1 (5.6 \pm 0.6)	<0.001
Depth at pelvic-fin base	89	31.6–42.6 (36.1 \pm 1.9)	143	31.3–40.1 (35.3 \pm 1.9)	0.005
Depth at anal-fin origin	97	23.5–31.9 (27.9 \pm 1.6)	154	22.8–30.5 (26.6 \pm 1.6)	<0.001
Depth at anal-fin insertion	90	11.4–15.6 (13.8 \pm 0.8)	144	11.3–15.6 (13.5 \pm 0.9)	0.003
Dorsal-fin spine I length	91	4.3–7.2 (5.8 \pm 0.6)	135	5.9–9.6 (7.8 \pm 0.7)	<0.001
Dorsal-fin spine IV length	97	9.8–15.5 (13.2 \pm 1.0)	151	12–18.4 (14.8 \pm 1.2)	<0.001
Dorsal-fin ray length	82	13.5–20 (16.6 \pm 1.3)	135	10.4–18.8 (15.5 \pm 1.3)	
Pectoral-fin base depth	88	8.4–10.4 (9.4 \pm 0.4)	142	8.2–10.4 (9.5 \pm 0.4)	ns
Pectoral-fin ray length	90	24.4–31 (27.3 \pm 1.3)	140	22–30 (26.3 \pm 1.4)	<0.001
Pelvic-fin ray length	92	19.3–25.1 (22.1 \pm 1.1)	159	18.8–25 (21.4 \pm 1.2)	<0.001
Pelvic-fin spine length	103	9.5–16.6 (13.4 \pm 1.3)	160	9.6–16.9 (13.7 \pm 1.2)	ns
Anal-fin spine I length	94	4.5–9.7 (6.8 \pm 1.1)	156	4.5–10.1 (7 \pm 1.1)	ns
Anal-fin spine II length	94	11–18.4 (14.5 \pm 1.9)	147	11.8–19.6 (14.9 \pm 1.9)	ns
Anal-fin spine III length	95	13–20.2 (16.6 \pm 1.5)	153	12.2–21.3 (16.5 \pm 1.7)	ns
Anal-fin ray 1 length	63	16–24.2 (19.5 \pm 1.6)	119	15.3–25 (18.9 \pm 1.8)	
Anal-fin ray 2 length	62	17.4–26.4 (21.1 \pm 1.8)	115	16.7–26.9 (19.9 \pm 2.0)	
Last anal-fin ray length	62	6–12.6 (10.4 \pm 1.1)	113	8.3–13.7 (10.4 \pm 0.8)	
Caudal peduncle depth	90	7.8–10.7 (9.6 \pm 0.5)	141	7.9–10.6 (9.2 \pm 0.5)	<0.001
Caudal peduncle dorsal length	87	10.5–13.9 (12 \pm 0.8)	141	11.1–15 (12.9 \pm 0.7)	<0.001
Caudal peduncle ventral length	89	17.7–21.9 (19.5 \pm 0.9)	141	17.4–22.5 (20.1 \pm 1.0)	<0.001
Preanal length	89	67.1–77.6 (71.8 \pm 2.3)	141	63.2–78.5 (70.2 \pm 2.6)	<0.001
Predorsal length	90	30.3–39.3 (34.3 \pm 1.7)	141	31.6–38.4 (34.9 \pm 1.4)	ns
Pelvic-fin base to anal-fin origin length	87	25.9–37 (30.8 \pm 2.6)	139	23.8–38.6 (30.9 \pm 2.9)	ns
Spinous dorsal-fin-base length	91	30.8–41.7 (35.7 \pm 2.3)	141	32.4–41.2 (36.4 \pm 2.0)	ns
Soft dorsal-fin-base length	90	20.2–25.8 (22.8 \pm 1.2)	141	17.3–24.7 (21.4 \pm 1.5)	<0.001
Anal-fin base length	89	13.1–18.2 (15.2 \pm 0.9)	141	12.4–17 (14.2 \pm 1.0)	
Pre-pelvic-fin length	87	37.8–53.1 (44.2 \pm 3.8)	139	36.6–52.6 (42.6 \pm 2.8)	
Caudal-fin length	80	20–28.1 (24 \pm 1.5)	128	19.2–25.2 (22 \pm 1.2)	

Sebastes swifti Evermann and Goldsborough, 1907:285, fig. 36 (original description, two specimens: holotype, USNM 57821, sex unknown, 128.2 mm, *Albatross* station 4234, Yes Bay, Alaska; paratype, USNM 126656, sex unknown, 75.2 mm, *Albatross* station 4246, Kasaan Bay, Alaska, 185–225 m depth, 11 July 1903).

Zalopyr aleutianus: Jordan et al., 1930:365 (new combination).

Sebastes aleutianus: Barsukov, 1970:997 (new combination; comparison with *S. borealis*).

Diagnosis

This species of *Sebastes* is distinguished from all other species except *S. melanostictus* in having eight pairs of head spines and two or more infraorbital spines. It is distinguished from *S. melanostictus* by the following combination of color patterns and morphological and genetic characteristics: body pale, distinct spots absent on the membranes of the spinous dorsal fin; dorsal-fin

spine 1 shorter, 1.5–3.0 times into orbit length, 4.3–7.2% SL (vs. 1.0–1.8 times into orbit length and 5.9–9.6% SL); dorsal-fin spine 4 shorter, 9.8–15.5% SL (vs. 12.0–18.4% SL); gill rakers shorter, 3.4–6.3% SL (vs. 3.9–7.1% SL), and fewer, 29–34 (vs. 30–36) (Table 2). Genetically diagnosed by a combination of the presence of protein variants *ACP*100*, either *IDDH*100* or **500* or both, either *PGM-2*100* or **83* or both, and *XO*100* (Hawkins et al., 2005); homozygosity at microsatellite allele *μSma6*183* (Gharrett et al., 2005, 2006); and mitochondrial haplotype B of Gharrett et al. (2005, 2006).

Description

D XII–XIV (XIII), 12–14 (14); A III, 6–8 (8); P1 17–19 (18), 4–9 (6) simple; lateral-line pores 30–34 (31), scales 42–57; infraorbital spines 2–10 (9); gill rakers 29–34 (8–10 + 21–24) (31:9+22); vertebrae 27 (10+17); pyloric caeca 9–12. Meristic frequency and statistical data are presented in Tables 1, 2, 4, and 5.

Table 3

Factor loadings for principal component (PC) analysis of morphometric characters of *Sebastes aleutianus* (rougheye rockfish) and *Sebastes melanostictus* (blackspotted rockfish), in which all characters were used for multivariate analyses.

	PC1	PC2	PC3
Head length	0.1911	-0.0190	-0.1584
Orbit length	0.1538	0.0215	-0.2248
Snout length	0.2020	-0.0121	-0.2133
Interorbital width	0.2261	-0.0922	-0.0498
Suborbital depth	0.2288	-0.2145	0.3787
Upper jaw length	0.1936	-0.0528	-0.0943
Lower jaw length	0.2026	0.0024	-0.1023
Gill raker length	0.1753	0.3399	-0.3728
Depth at pelvic-fin base	0.1960	-0.1374	-0.0036
Depth at anal-fin origin	0.1944	-0.2055	0.0864
Depth at anal-fin insertion	0.1929	-0.1621	0.0306
Dorsal-fin spine I length	0.1982	0.6188	0.1775
Dorsal-fin spine IV length	0.1755	0.2379	-0.0909
Pectoral-fin base width	0.1905	-0.0489	0.0642
Pectoral-fin ray length	0.1741	-0.0983	-0.0211
Pelvic-fin ray length	0.1746	-0.0690	-0.0030
Pelvic-fin spine length	0.1654	0.0766	0.0457
Anal-fin spine I length	0.1417	0.3270	0.4728
Anal-fin spine II length	0.1369	0.2472	0.1530
Anal-fin spine III length	0.1586	0.1029	0.1761
Caudal peduncle depth	0.1913	-0.1736	0.0632
Caudal peduncle dorsal length	0.1975	0.0578	-0.1842
Caudal peduncle ventral length	0.1869	0.0142	-0.1128
Preanal length	0.1881	-0.0926	0.0627
Predorsal length	0.1876	-0.0057	-0.2195
Spinous dorsal-fin-base length	0.1957	-0.0223	-0.2150
Soft dorsal-fin-base length	0.1804	-0.1481	0.0548
Anal-fin-base length	0.1654	-0.1322	0.1176
Pre-pelvic-fin length	0.1874	-0.1256	0.2757

Table 4

Counts of dorsal-fin spines, soft-dorsal-fin rays, anal-fin rays, and total and unbranched pectoral-fin rays in *Sebastes aleutianus* (rougheye rockfish) and *Sebastes melanostictus* (blackspotted rockfish). Lower West Coast = waters off the coast of British Columbia, Washington, Oregon, and California. Western Pacific Ocean = waters off the coast of the Kuril Islands and Japan.

	Dorsal-fin spines				<i>n</i>		Total left pectoral-fin rays				<i>n</i>			
	12	13	14				17	18	19					
<i>Sebastes aleutianus</i>														
Lower West Coast		29	1				30							
Gulf of Alaska	1	63	2			2	55	7						
Bering Sea and Aleutian Is.		18					9	3						
Total	1	110	3		114	2	94	10	106					
<i>Sebastes melanostictus</i>														
Lower West Coast		17	1				16	1						
Gulf of Alaska	1	80	4			2	72	12						
Bering Sea and Aleutian Is.	2	53				4	50	4						
Western Pacific Ocean		24					20							
Total	3	174	5		182	6	158	17	181					
	Dorsal-fin rays					<i>n</i>		Unbranched left pectoral-fin rays						
	12	13	14	15				4	5	6	7	8	9	10
<i>Sebastes aleutianus</i>														
Lower West Coast		11	19					1	3	20	4			
Gulf of Alaska	1	36	30				1	1	5	9	39	4		
Bering Sea and Aleutian Is.		5	13					1	5	4	2			
Total	1	52	62		115		1	1	7	17	63	10	99	
<i>Sebastes melanostictus</i>														
Lower West Coast		5	13											
Gulf of Alaska		32	53					1	5	9		1		
Bering Sea and Aleutian Is.		17	37	1					10	58	13			
Western Pacific Ocean		6	14	4				1	9	38	10			
Total		60	117	5	182				8	10	2			
<i>Sebastes aleutianus</i>														
Lower West Coast		1	29											
Gulf of Alaska		1	59	6										
Bering Sea and Aleutian Is.			10	2										
Total		2	98	8	108									
<i>Sebastes melanostictus</i>														
Lower West Coast			17	1										
Gulf of Alaska		2	75	7										
Bering Sea and Aleutian Is.			53	5										
Western Pacific Ocean			20											
Total		2	165	13	180				2	32	115	25	1 175	

Body robust, depth at pelvic-fin base 31.6–42.6 (38.1) % SL; relatively deep at anal-fin origin 23.5–31.9 (28.0) % SL; profile of dorsal margin of head gently sloping from dorsal-fin origin to snout, dorsal rim of orbit included in lateral margin of frontals. Mouth large, with posterior end of maxilla extending between pupil and posterior rim of orbit to just beyond the posterior rim of the orbit; maxilla length 16.9–21.1 (19.9) % SL; sym-

physeal knob moderately pronounced with blunt tip, lower-jaw length 20.4–27.2 (25.0) % SL; mandibular pores large to moderate in size. Cranial spines strong, often rough. Nasal, preocular, supraocular, postocular, tympanic, coronal, parietal, and supratemporal spines invariably present; all major head spines strong, except for coronal spines, which are weak; supraocular and postocular spines and parietal ridge often rough;

Table 5

Counts of gill rakers, lateral-line pores, and left infraorbital spines in *Sebastes aleutianus* (rougheye rockfish) and *Sebastes melanostictus* (blackspotted rockfish). Lower West Coast = waters off the coast of British Columbia, Washington, Oregon, and California. Western Pacific Ocean = waters off the coast of the Kuril Islands and Japan.

	Gill rakers								<i>n</i>
	29	30	31	32	33	34	35	36	
<i>Sebastes aleutianus</i>									
Lower West Coast	1	8	15	6	3				
Gulf of Alaska	5	8	28	19	6	2			
Bering Sea and Aleutian Is.		5	4	6					
Total	6	16	43	25	9	2			101
<i>Sebastes melanostictus</i>									
Lower West Coast		1	3	3	4	7	1		
Gulf of Alaska		1	9	25	22	26	10		
Bering Sea and Aleutian Is.		1	7	12	24	10	3	2	
Western Pacific Ocean		1		5	6	5	3		
Total		4	19	45	56	48	17	2	191
Gill rakers of the upper arch									
	8	9	10	11	<i>n</i>				
<i>Sebastes aleutianus</i>									
Lower West Coast	4	21	4						
Gulf of Alaska	3	39	13						
Bering Sea and Aleutian Is.	4	10							
Total	11	70	17		98				
<i>Sebastes melanostictus</i>									
Lower West Coast		2	12	1					
Gulf of Alaska	2	32	40	6					
Bering Sea and Aleutian Is.	3	21	23	1					
Western Pacific Ocean		9	9	2					
Total	5	64	84	10	163				
Gill rakers of the lower arch									
	21	22	23	24	25	26	<i>n</i>		
<i>Sebastes aleutianus</i>									
Lower West Coast	7	14	7	1					
Gulf of Alaska	10	31	10	4					
Bering Sea and Aleutian Is.	2	6	6						
Total	19	51	23	5			98		
<i>Sebastes melanostictus</i>									
Lower West Coast		2	5	8					
Gulf of Alaska	1	9	25	40	5				
Bering Sea and Aleutian Is.	1	6	18	18	4	1			
Western Pacific Ocean	1	3	8	7	1				
Total	3	20	56	73	10	1	163		

continued

sphenotic spines often prominent, occasionally moderate or small in size. Interorbital region wide, 5.5–8.9 (8.7) % SL, flat to slightly concave; frontal ridges between orbits moderate to strong; parietal ridges strong,

with area between ridges slightly convex or flat. Preopercular spines 5, directed posteroventrally; opercular spines 2, upper spine directed posteriorly, lower spine directed posteriorly and slightly ventrally. Posttempo-

Table 5 (continued)

	Lateral-line pores								<i>n</i>			
	30	31	32	33	34	35	36					
<i>Sebastes aleutianus</i>												
Lower West Coast	2	17	9	1	1							
Gulf of Alaska	8	32	15	5	2							
Bering Sea and Aleutian Is.	2	3	4	2	2							
Total	12	52	28	8	5					105		
<i>Sebastes melanostictus</i>												
Lower West Coast	1	6	1	6	2							
Gulf of Alaska	7	29	37	13	2	1						
Bering Sea and Aleutian Is.	3	12	24	12	5		1					
Western Pacific Ocean		5	6	3	3	1	2					
Total	11	52	68	34	12	2	3			182		
	Left infraorbital spines											<i>n</i>
	2	3	4	5	6	7	8	9	10	11	12	
<i>Sebastes aleutianus</i>												
Lower West Coast	1	9	8	6	4	3	1					
Gulf of Alaska	2	10	13	10	6	8	3	2	2			
Bering Sea and Aleutian Is.		1	2	6	3	1						
Total	3	20	23	22	13	12	4	2	2			101
<i>Sebastes melanostictus</i>												
Lower West Coast		2	1	5	5		1	1				1
Gulf of Alaska	4	9	9	12	17	5	11	2	3	3		
Bering Sea and Aleutian Is.	5	11	4	11	6	5	2		1	1		
Western Pacific Ocean			1	3	4	1	1	1				
Total	9	22	15	31	32	11	15	4	4	4	1	148
	Left infraorbital 1 spines						<i>n</i>					
	0	1	2	3	4							
<i>Sebastes aleutianus</i>												
Lower West Coast	1	22	8									
Gulf of Alaska	5	28	15	7								
Bering Sea and Aleutian Is.	3	8	2									
Total	9	58	25	7		99						
<i>Sebastes melanostictus</i>												
Lower West Coast	1	2	9	4								
Gulf of Alaska	2	29	29	9	6							
Bering Sea and Aleutian Is.	2	24	15	4								
Western Pacific Ocean		1	9	1								
Total	5	56	62	18	6	147						

continued

ral and supracleithral spines present. Ventral margin of lachrymal typically with two rounded lobes, both anterior and posterior often with a single small posteriorly directed spine, posterior occasionally with as many as 4 or 5 small spines forming a serrate margin; infraorbital spines small, 2–10 (9): 0–3 (3) on first infraorbital, 0–5 (5) on second, and 1–3 (1) on third;

dorsal margin of opercle nearly horizontal; lower margin of gill cover with 1 or 2 small spines, produced by posteroventral tip of interopercle and anteroventral tip of subopercle.

Dorsal-fin origin above anterodorsal portion of gill slit; dorsal fin continuous, gradually increasing in height from spine I (4.3–7.2% SL, 1.5–3.0 times into

Table 5 (continued)

	Left infraorbital 2 spines								n
	0	1	2	3	4	5	6		
<i>Sebastes aleutianus</i>									
Lower West Coast		11	15	4		1			
Gulf of Alaska	1	14	25	10	2	3			
Bering Sea and Aleutian Is.		1	9	2	1				
Total	1	26	49	16	3	4			99
<i>Sebastes melanostictus</i>									
Lower West Coast	1	5	6	2	1		1		
Gulf of Alaska	4	14	31	13	9	3	1		
Bering Sea and Aleutian Is.	3	16	20	4	1		1		
Western Pacific Ocean		1	7	2	1				
Total	8	36	64	21	12	3	3		147
	Left infraorbital 3 spines								n
	0	1	2	3	4	5	6	7	
<i>Sebastes aleutianus</i>									
Lower West Coast		18	12	1					
Gulf of Alaska		26	25	4					
Bering Sea and Aleutian Is.		2	10	1					
Total		46	47	6					99
<i>Sebastes melanostictus</i>									
Lower West Coast		7	8	1					
Gulf of Alaska	3	27	38	6	1				
Bering Sea and Aleutian Is.	1	18	22	2	1			1	
Western Pacific Ocean		3	7	1					
Total	4	55	75	10	2	0	0	1	147

orbit length; Fig. 5A) to spine IV (9.8–15.5% SL; Fig. 5B; tips of dorsal-fin spines broken in lectotype) and decreasing in height to spine XII; spine XIII much longer, forming anterior support of dorsal-fin rays; membranes of spinous dorsal fin moderately incised, less so posteriorly; soft dorsal fin with anterior rays longest, posterior rays gradually shortening. Anal-fin spine II shorter than or equal to III (11.0–18.4 vs. 13.0–20.2% SL; tip of anal-fin spine II broken in lectotype), relatively longer in juveniles, soft rayed portion of anal fin with anterior rays longest, posterior rays gradually shortening, posterior margin perpendicular to body axis or with slight posterior slant, anterior ray tips directly ventral to or forward of posterior tips, anterior tip of anal fin slightly rounded. Pectoral fins with ray 10 or 11 longest, extending to or slightly anterior to vent, fin-ray length 24.4–31.0 (25.5) % SL; fin-base width 8.4–10.4 (9.1) % SL; dorsalmost ray simple, ventral 5–10 simple, others branched in adults; all rays simple in three juveniles less than 90 mm (63.4–77.1 mm), the smallest examined. Pelvic fins extending about 50–90% of distance from pelvic-fin base to anal-fin origin, falling well short of vent, ray length 19.3–25.1 (22.8) % SL, spine length 51.7–76.0 (59.2) % ray length. All fin

Table 6

Factor loadings for principal component (PC) analysis of meristic characters of *Sebastes aleutianus* (rougheye rockfish) and *Sebastes melanostictus* (blackspotted rockfish) in which all characters were used for multivariate analyses.

	PC1	PC2	PC3
Dorsal-fin rays	0.5620	0.2917	-0.0630
Anal-fin rays	0.2956	0.5901	-0.5291
Pectoral-fin rays (left)	0.1390	-0.6710	-0.5828
Lateral-line pores (left)	0.4905	-0.1233	0.6118
Gill rakers	0.5804	-0.3181	-0.0470

spines exhibit allometric growth, and juveniles have relatively longer spines. Caudal fin shallowly emarginate, length 20.0–28.1% SL (fin damaged in lectotype). Vent positioned below dorsal-fin spine 10–11, 7–21 (9.4) % HL from anal-fin origin.

Lateral body scales often with many (ca. 5–7) accessory scales in posterior field. Maxilla and underside of

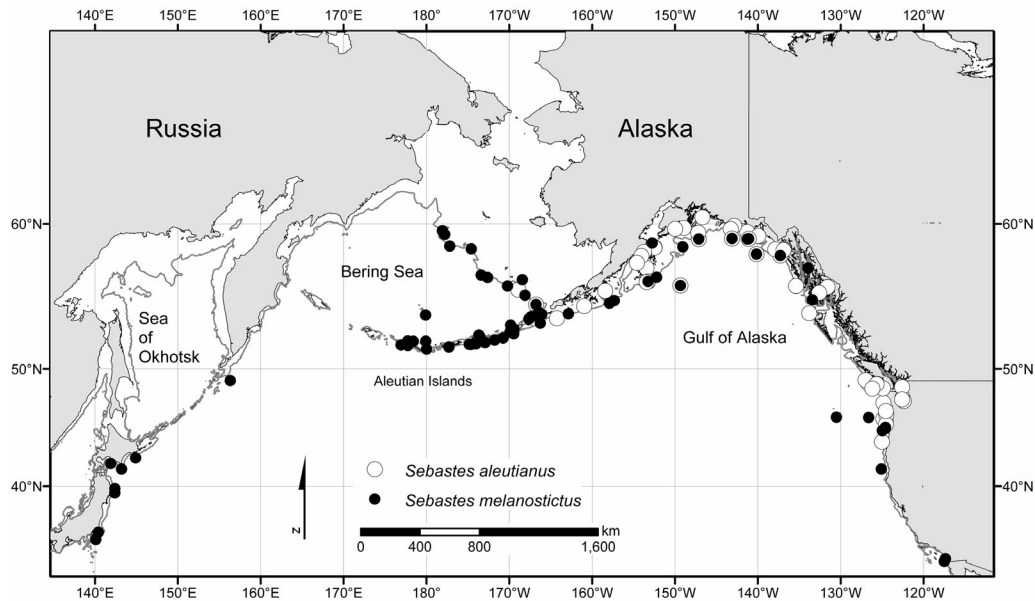


Figure 7

Distribution of *Sebastes aleutianus* (rougeye rockfish, open circle) and *Sebastes melanostictus* (blackspotted rockfish, closed circle) based on material examined. Closed circles superimposed on open circles represent collections of both species at the same locality. Each symbol may represent more than one specimen.

mandible completely scaled; suborbital region scaled; branchiostegal rays scaled.

Gill rakers relatively short, 3.4–6.3 (4.5) % SL (Fig. 5C), and slender on first arch; longest raker in joint between epi- and ceratobranchials; length of preceding rakers on upper arch and succeeding rakers on lower arch progressively shorter; rudiments absent. Extrinsic swimbladder muscle is Type I a–z of Hallacher (1974).

Body color in life pink, red, or reddish orange and darker brownish-red mottling is present in faint bands at and above the lateral line, often extending onto dorsal-fin base. Head light, with irregular shaped dark blotch at posterodorsal corner, other blotches often present on operculum between orbit and lower posterior margin. Orobuccal membranes pink to red, often with dark blotches; jaw membranes light, occasionally dusky. Spinous and soft dorsal fins uniformly pink to red, usually dark along fin margins, occasionally with small diffuse blotches near base of fin. Anal and caudal fins uniformly pink to red, dark along fin margin. Paired fins red, rays often with dark tips. Peritoneum gray to dusky, rarely white or black; stomach, pyloric caeca, and intestines pale. See Figures 1 and 2 and color figures in *S. aleutianus* species accounts of Love (2002; “juvenile” upper left), Kramer and O’Connell (1986, 1988, 1995, 2003; “juvenile”). Juveniles in life similar to adults in general body color, often with more distinct dark red to brown mottling. After preservation, reddish background color fading to light gray, yellowing with age. Dark areas remaining dark brown to black.

No sexual dimorphism is evident in morphometric or meristic characters. Largest specimen examined

555 mm (726 mm total length [TL], 710 mm fork length [FL]; FAKU 119293).

Distribution

The range of *Sebastes aleutianus*, based on material examined, extends from the eastern Aleutian Islands off Unalaska Island and the eastern Bering Sea at Pribilof Canyon at 55.7°N, south to southern Oregon at 43.9°N (Fig. 7). This distribution is nearly identical to that reported in the analyses of Hawkins et al. (2005, as *S. aleutianus*) and Gharrett et al. (2005, 2006, as “Type II”). Our material was collected at depths of 45 m to at least 439 m—a range that overlapped the depth distribution of *S. melanostictus* but which was typically shallower than the depth range of *S. melanostictus* (ANOVA, $F=14.98$, $df=1$, $P=0.002$; Fig. 8). No specimens of *S. aleutianus* are for certain from California, although at least one individual has been captured in northern California and was documented photographically. Catch data from AFSC surveys of the continental shelf and upper continental slope conducted from 1961 to 2001 indicate that neither *S. aleutianus* nor *S. melanostictus* (all identified as *Sebastes aleutianus*) was common in catches off California; only 61 specimens in 36 hauls were recorded for over 3600 tows of survey data (Fig. 9).

Etymology

The specific name *aleutianus* refers to the Aleutian Islands region. At the time of its original description (Jordan and Evermann, 1898), Kodiak Island was consid-

ered part of the geographic area now generally accepted to extend eastward only to Unimak Pass.

Remarks

The four syntypes of *Sebastes aleutianus* were deposited at the USNM and CAS. The single USNM specimen (USNM 48800) was labeled “cotype” and is hereby designated as the lectotype of *Sebastes aleutianus*. Among the syntypes, this was the only specimen illustrated (Jordan and Gilbert, 1899, plate 48). The three specimens at CAS (SU 12928) are designated paralectotypes.

Individuals of *S. aleutianus* were apparently confused by Pallas (1814) as the “summer form” of *S. variabilis* (Pallas, 1814) (Jordan and Evermann, 1898), the dusky rockfish, one of the first species of *Sebastes* described from the Pacific Ocean—the first being its sister-species *S. ciliatus* (Tilesius, 1813), the dark rockfish (Kendall, 2000; Orr and Blackburn, 2004; Hyde and Vetter, 2007). Only a single specimen (MNHN 8670) is extant from the material Pallas examined for his description of *Perca variabilis*, and it has been designated the lectotype of *S. variabilis* (Orr and Blackburn, 2004). The only other specimens identified as *Perca variabilis* by Pallas were housed at ZMB and are missing, presumed to have been destroyed during the Second World War (Paepke and Fricke, 1992).

Evermann and Goldsborough (1907) described *Sebastes swifti* from two juveniles collected in a bay

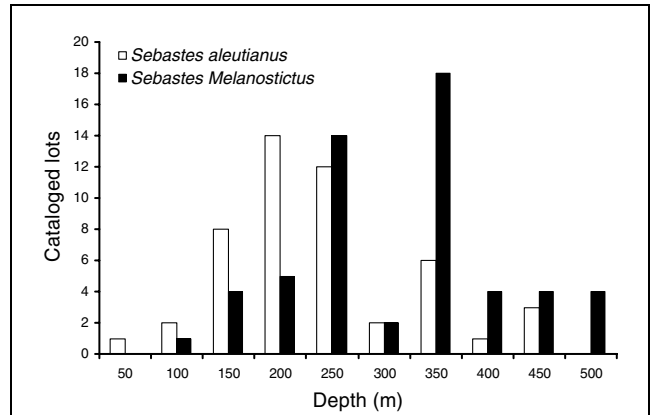


Figure 8

Depth (m) distribution of *Sebastes aleutianus* (rough-eye rockfish, open bar) and *Sebastes melanostictus* (blackspotted rockfish, closed bar) based on material examined. Each bar represents numbers of cataloged museum lots, which may contain one or many specimens. *Sebastes melanostictus* is found at deeper depths than *S. aleutianus* (ANOVA, $F=14.98$, $df=1$, $P=0.002$).

of southeastern Alaska. Although the authors compared them to *S. crameri* (Jordan in Gilbert, 1897), the darkblotched rockfish, both specimens exhibited the diagnostic morphological characters and pale, unspot-

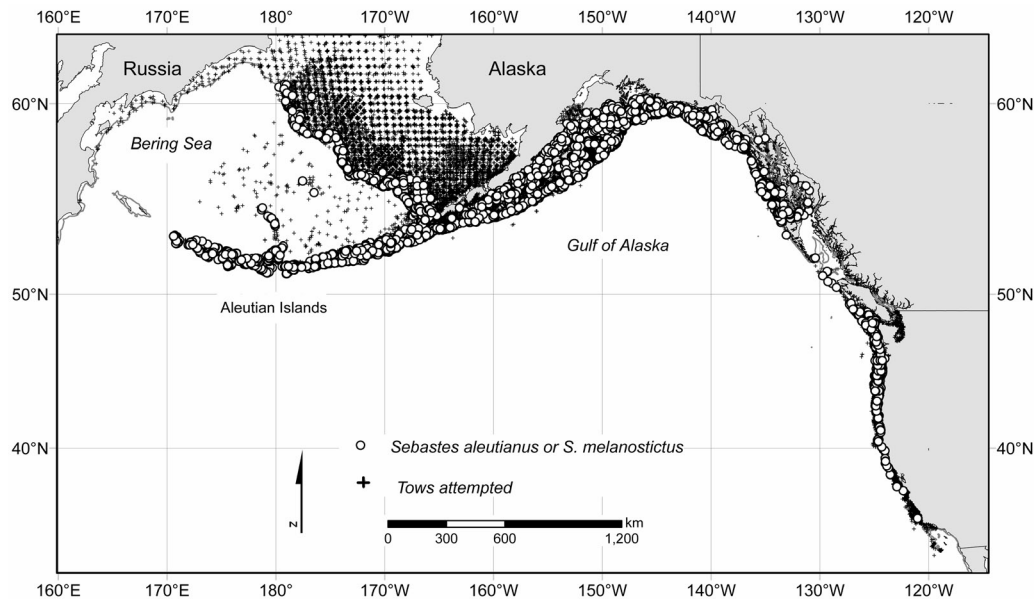


Figure 9

Distribution of the rougheye rockfish complex (open circle) in the eastern Pacific Ocean and Bering Sea based on National Marine Fisheries Service, Alaska Fisheries Science Center, survey data for the years 1961 to 2005. The rougheye rockfish complex includes *Sebastes aleutianus* and *S. melanostictus*, rougheye and blackspotted rockfish, which were recorded in 7758 tows. Although catch records from the northwestern Bering Sea indicated an absence of both species, species of *Sebastes* other than *S. alutus* (Pacific ocean perch) were routinely identified only to genus. Most symbols represent more than one tow and capture.

ted coloration of *S. aleutianus*, falling well within the variation of our material examined.

***Sebastes melanostictus* (Matsubara, 1934)**

Blackspotted rockfish

Figures 3–8; Tables 1, 2, 4, 5

Sebastes melanostictus Matsubara, 1934:206 (original description, one specimen: holotype FAKU 101043, male, 507 mm, “Prov. Kazusa”).

Sebastes kawaradae Matsubara, 1934:207 (original description, one specimen: FAKU 101042, male, 361.7 mm, Japan “off Miyako, near Morioka”).

Sebastes melanostictus: Matsubara, 1943:209 (new combination).

Diagnosis

This species of *Sebastes* is distinguished from all other species, except *S. aleutianus*, in having eight pairs of head spines and two or more infraorbital spines. It is distinguished from *S. aleutianus* by the following combination of color patterns and morphological and genetic characteristics: body and spinous-dorsal fin spotted or, rarely, without spots, dusky overall with diffuse mottling on dorsum; dorsal-fin spine 1 longer, 1.0–1.8 times into orbit length, 5.9–9.6% SL (vs. 1.5–3.0 times into orbit length and 4.3–7.2% SL); dorsal-fin spine 4 longer, 12.0–18.4% SL (vs. 9.8–15.5% SL); gill rakers longer, 3.9–7.1% SL (vs. 3.4–6.3% SL), and more numerous, 30–36 (vs. 29–34) (Table 2). Genetically diagnosed by a combination of the presence of protein variants *ACP*46*, either *IDDH*500* or **750* or both, either *PGM-2*83* or **74* or both, and *XO*109* (Hawkins et al., 2005); homozygosity at microsatellite allele *μSma6*177* (Gharrett et al., 2005, 2006); and mitochondrial haplotype A of Gharrett et al. (2005, 2006).

Description

D XII–XIV (XIII), 12–15 (14); A III, 7–8 (7); P1 17–19 (18), 5–10 (7) simple; lateral-line pores 30–36 (31), scales 40–56; infraorbital spines 2–12 (5); gill rakers 30–36 (8–11 + 21–26) (33: 9+24); vertebrae 26–27 (10 + 16–17) (27, Matsubara, 1934); pyloric caeca 9–12. Meristic frequency and statistical data are presented in Tables 1, 2, 4, and 5.

Body robust, depth at pelvic-fin base 31.3–40.1 (37.5) % SL; relatively slender at anal-fin origin 22.8–30.5 (28.7) % SL, profile of dorsal margin of head gently sloping from dorsal-fin origin to snout, dorsal rim of orbit included in lateral margin of frontals. Mouth large, with posterior end of maxilla extending between pupil and posterior rim of orbit to just beyond the posterior rim of the orbit; maxilla length 17.2–21.5 (20.0) % SL; symphyseal knob moderately pronounced with blunt tip; lower jaw length 21.6–27.1 (25.9) % SL; mandibular pores large to moderate in size. Cranial spines strong, often rough. Nasal, preocular, supraocular, postocular, tympanic, coronal, parietal, and supratemporal spines

invariably present; all major head spines strong, except for the coronal spines, which are weak; supraocular and postocular spines and parietal ridge often rough; sphenotic spines obsolete, occasionally moderate in size. Interorbital region wide, 5.6–9.2 (8.8) % SL, flat to slightly concave; frontal ridges between orbits obsolete to moderate; parietal ridges strong, and area between ridges slightly convex or flat. Preopercular spines 5, directed posteroventrally; opercular spines 2, upper spine directed posteriorly, lower spine directed posteriorly and slightly ventrally. Posttemporal and supracleithral spines present. Ventral margin of lachrymal with two rounded lobes, both anterior and posterior often with a single small posteriorly directed spine, posterior occasionally with as many as 4 or 5 small spines forming a serrate margin. Infraorbital spines small, 2–12 (5): 0–4 (2) spines on first infraorbital, 0–6 (2) on second, and 0–4 (1) on third (7 on third infraorbital of the left side of one anomalous specimen, UW 116497); dorsal margin of opercle nearly horizontal; lower margin of gill cover with two small spines, produced by the posteroventral tip of interopercle and anteroventral tip of subopercle.

Dorsal-fin origin above anterodorsal portion of gill slit; dorsal fin continuous, gradually increasing in height from spine I (5.9–9.6% SL, 1.5–3.0 times into orbit length; Fig. 5A) to spine IV (12.0–18.4% SL; Fig. 5B; tips of dorsal-fin spines broken in holotype) and decreasing in height to spine XII; spine XIII much larger, forming anterior support of dorsal-fin rays; membranes of spinous dorsal fin moderately incised, less so posteriorly; soft dorsal fin with anterior rays longest, posterior rays gradually shortening. Anal-fin spine II slightly shorter than or equal to III (11.8–19.6 vs. 12.2–21.3% SL; tips of anal-fin spines broken in holotype), relatively longer in juveniles, soft rayed portion of anal fin with anterior rays longest, posterior rays gradually shortening, posterior margin perpendicular to body axis or with slight posterior slant, anterior ray tips directly ventral to or forward of posterior tips, anterior tip of anal fin slightly rounded. Pectoral fins with ray 10 or 11 longest, extending to or slightly anterior to vent, fin-ray length 22.0–30.0 (27.9) % SL; fin-base width 8.2–10.4 (10.2) % SL; dorsalmost ray simple, ventral 5–10 simple, others branched. Pelvic fins extending about 50–90% of distance from pelvic-fin base to anal-fin origin, falling well short of vent, ray length 18.8–25.0 (23.1) % SL, spine length 55.1–72.9 (58.6) % ray length. All fin spines exhibiting allometric growth, with juveniles having relatively longer spines. Caudal fin shallowly emarginate, length 19.2–25.2 (22.2) % SL. Vent positioned below dorsal-fin spine 10–11, 7–21 (13.8) % HL from anal-fin origin.

Lateral body scales often with many (ca. 5–7) accessory scales in posterior field. Maxilla and underside of mandible completely scaled; suborbital region scaled; branchiostegal rays scaled.

Gill rakers long, 3.9–7.1 (6.6) % SL, and slender on first arch; longest raker in joint between epi- and ceratobranchials; length of preceding rakers on upper arch and succeeding rakers on lower arch progressively

shorter; rudiments absent. Extrinsic swimbladder muscle Type I a–z of Hallacher (1974).

Body color in life light to dark, often heavily mottled. Light specimens pink to red and with greenish-black spotting below and above the lateral line and on dorsum between lateral line and base of dorsal fins, extending onto spinous and often soft dorsal-fin membranes, occasionally with a yellow wash. Dark specimens with black to greenish wash over red to pink background color, heavily mottled over entire body and spotted at and above the lateral line; heavy dark mottling often obscuring spotting. Body rarely dusky overall but having diffuse mottling, without spotting. Three white blotches often present along base of dorsal fin: anterior blotch at base of dorsal-fin spines 2–4, middle blotch at base of spines 11–12 and anteriormost rays, posterior blotch at base of posteriormost dorsal-fin rays and along anterior portion of caudal peduncle. Head light or dark, with three vague dusky bands often extending from side to side: one across region of nares, a second just posterior to orbits, and a third at posterior half of parietal spines. Head otherwise similar to body coloration, with irregular-shaped dark blotch at posterodorsal corner, other blotches often present on operculum between orbit and lower posterior margin. Iris golden to brassy yellow. Orobuccal membranes blotched or dark on pink to red background; jaw membranes dusky or dark. Spinous and soft dorsal fins variously spotted, on a pink to red or dusky background, usually dark along fin margins. On spinous dorsal fin, spots commonly in two general areas: anteriorly between spines 1–3 and posteriorly between spines 5–11. Anal and caudal fins uniformly pink to red, dark along fin margin. Paired fins red, rays often with dark tips. Peritoneum dusky to dark, rarely light or black; stomach, pyloric caeca, and intestines pale. See Figures 3 and 4 and the color figures identified as *S. aleutianus* or rougheye rockfish of Kanayama and Kitagawa (1982), Amaoka (1984), Kessler (1985), Orr et al. (1998, 2000), Love (2002, lower left and upper right), and Gharrett et al. (2006, bottom dark form). Juveniles in life similar to adults in general body color, often with more profuse spotting. After preservation, reddish background color fading to light gray, yellowing with age. Spotting on dorsal fins and dark areas on body remaining dark brown to black.

No sexual dimorphism in morphometric or meristic characters is evident. Largest specimen examined 539 mm (690 mm TL, 660 mm FL; FAKU 119236).

Distribution and natural history

The range of *Sebastes melanostictus* based on material examined extends from the Pacific coast of Japan, at about 35°N, north through the Kuril Islands, Aleutian Islands, and the Bering Sea to 60.5°N, and south to southern California on Coronado Bank, at 32.6°N (Fig. 7). Our material extends the range of *S. melanostictus*, previously reported by Hawkins et al. (2005, as *S. sp. cf. aleutianus*) and Gharrett et al. (2005, 2006, as “Type I”), to the western Pacific south of the Bering Sea

to central Japan and in the eastern Pacific to southern California.

Collected at depths from 84 to at least 490 m, *S. melanostictus* is more common at deeper depths than *S. aleutianus* among material examined (ANOVA, $F=14.98$, $df=1$, $P=0.002$; Fig. 8). In the Kuril Islands and southeastern Kamchatka, areas where only *S. melanostictus* is known, it is found from 200 to 650 m and is most abundant between 350 and 450 m depth (Orlov, 2005). Two specimens (UW 116884 and UW 116885) were recently captured in midwaters of the Gulf of Alaska at a maximum gear depth of 500–1000 m over 1800–1900 m of bottom depth. Nearly 150 mid-water tows during surveys conducted by AFSC captured *S. aleutianus* or *S. melanostictus* (identified as *S. aleutianus*) at depths of 15–3355 m above the bottom. All were captured north of Washington waters in Alaska and Canada (Fig. 9).

Etymology

The specific name *melanostictus* is derived from the Greek μέλας for “black” and στικτός for “spot” referring to the spotted body coloration.

Remarks

A surprising conclusion of our work is that *S. kawaradae* is synonymous with *S. melanostictus* rather than *S. aleutianus*. As described by Matsubara (1934) and verified in our examination, the body of the holotype of *S. kawaradae* is dusky and lacks the spotting typically present in *S. melanostictus*. Although this color pattern is uncommon in *S. melanostictus*, it is a pattern not found in the material examined and identified as *S. aleutianus* by either genetic or morphological analysis in this revision.

Matsubara (1934) published his original description of both species in the same paper; *S. melanostictus* was followed immediately by *S. kawaradae*, each based only on the holotype. He distinguished the two by several characters, including differences in body color, describing *S. kawaradae* in formalin as dark brown without spots as opposed to *S. melanostictus*, grayish with spots. Other characters included peritoneum silvery rather than black; orbit length longer than either the interorbital width or snout length versus equal to interorbital width or shorter than snout length; infraorbital spines 5 rather than 4; and lateral line pores 34 rather than 31. These characters all fall within the range of our material of *S. melanostictus*.

Later, Matsubara (1943) described additional aspects of the holotype of *S. kawaradae*, including the structure of the infraorbitals and air bladder and counts of vertebrae, and compared the holotype with *S. aleutianus*, from which he distinguished it on the basis of three characters: a higher gill-raker count of 32, narrower interorbital space, and longer second anal-fin spine. Matsubara’s (1943) gill raker count of 24 for *S. aleutianus* was apparently repeated from

Jordan and Evermann (1898), which is an error because the four syntypes of *S. aleutianus* have a range of 30–32 gill rakers. In our material, the gill-raker count of 32 lies within the broad range of overlap in numbers of gill rakers in *S. aleutianus* and *S. melanostictus* (Table 5). Although the length of the second anal-fin spine is longer than in all other *S. aleutianus* of similar size, it is similar in size to the second anal-fin spine of all *S. melanostictus*. Interorbital widths of *S. aleutianus* and *S. melanostictus* differ slightly, and *S. kawaradae* has the wider interorbital of similar size *S. melanostictus*. Based on material examined from throughout the range of the species, all other morphometric and meristic data support the conclusion that *S. kawaradae* is a synonym of *S. melanostictus*.

Examining specimens from the northeastern Gulf of Alaska, Gharrett et al. (2006) distinguished by morphological techniques more than 94% of specimens that had been earlier identified by genetic analyses. They found concordant results between allozyme data (Seeb, 1986; Hawkins et al., 2005) and DNA markers (Gharrett et al., 2005). The results of our work, extending the morphological examination across nearly the entire geographic range of both species, are very similar to theirs with a slightly higher degree of resolution. Detailed diagnostic color differences, as well as a combination of morphological characters, distinguish the two species (the dark “Type I” and light “Type II” of Gharrett et al., 2006). Most importantly, the persisting confusion between the light and dark “Types” is resolved. Most specimens of *S. melanostictus* (“Type I”) display an overall darker coloration than *S. aleutianus* (“Type II”), but this “darker” coloration may range from a dusky or blotched color pattern over the body to a few dark spots on a light background—a pattern that would presumably be called “light” by field biologists. In contrast, *S. aleutianus* is always pale and would invariably be described as light in the field.

The length of the first dorsal-fin spine is of particular importance in distinguishing between the two species. Gharrett et al. (2006) did not measure the first dorsal-fin spine length but found the “longest dorsal-fin spine” to differ significantly between the two species. Among our material, the length of the fourth dorsal-fin spine, which is most often the longest spine, is significantly different but does not differ consistently enough to be useful as a field character. In contrast, especially in field identifications when body color was equivocal, the length of the first dorsal-fin spine was particularly useful. Its heavy weighting in the discriminant function equation underlines its importance.

Evidence of a low-level of hybridization between *S. aleutianus* and *S. melanostictus* has been found from analyses with allozyme data (Hawkins et al., 2005) and DNA markers (Gharrett et al., 2005). Both Hawkins et al. (2005) and Gharrett et al. (2005) found <1% of possible hybrids in their large sample sizes. Although a few specimens have uncertain genotypes in our allozyme

analysis, no individuals were determined conclusively to be hybrids with concepts of hybrid intermediacy, because the range of variation among all morphological characters overlapped to some degree between the two species. However, one individual (UW 116878, 236.0 mm) from the northeastern Gulf of Alaska identified as *S. aleutianus* because of color and general morphological features had the genetic signature of a possible hybrid and was also placed in the overlapping region of the PCA. It was captured with longline gear together with specimens of *S. melanostictus* and other specimens of *S. aleutianus* at an intermediate depth of 300–400 m.

Phenotypically, two species in the eastern North Pacific region are similar and often difficult to distinguish from *S. aleutianus* and *S. melanostictus*. *Sebastes borealis* is the deepest dwelling species of the genus and, like *S. aleutianus* and *S. melanostictus*, is a robust red rockfish. Until the work of Tsuyuki and Westrheim (1970) and Barsukov (1970), it was treated as *S. aleutianus* or *S. melanostomus*. It also may have up to two infraorbital spines and similar cranial spines, although the coronal spine is typically absent. *Sebastes borealis* is uniform reddish-pink, unlike *S. melanostictus*, which invariably has spots on its fins or body and is generally darker in color. At larger sizes, above about 40 cm TL, *S. borealis* can be distinguished by the length of its gill rakers, which are shorter, ca. 5–15% head length, and fewer (27–31) than the longer, ca. 10–20 % HL, and more numerous (29–36) gill rakers of both *S. aleutianus* and *S. melanostictus*.

Sebastes melanostomus is readily distinguished underwater by color (Butler and Love, 2002), exhibiting distinct blotches of red and white, unlike either the uniformly pale *S. aleutianus* or distinctly spotted *S. melanostictus*. When captured and brought to the surface, it is similar to *S. aleutianus* in coloration, having a reddish-pink background coloration and some mottling, especially around the head and on the branchiostegal membranes. It lacks the spotting on the body and fins of *S. melanostictus* and may be distinguished from both species by having only 1 or 2 infraorbital spines and usual absence of the coronal spine.

Four species of western Pacific *Sebastes* are considered to be morphologically similar to *S. aleutianus* and *S. melanostictus*: *Sebastes matsubarae*¹ Hilgendorf (1880), akôdai; *S. baramenuke* (Wakiya, 1917), baramenuke; *S. flammeus* (Jordan and Starks, 1904), sankômenuke; and *S. iracundus* (Jordan and Starks, 1904), ôsaga. All are relatively large and robust reddish rockfishes that live at greater depths than do most other species. As a group they, including *S. melanostictus*, are referred

¹ As noted in editions of Eschmeyer (1998), the name *Sebastes matsubarae* Hilgendorf requires emendation to *Sebastes matsubarae* Hilgendorf because it was named for the male ichthyologist Shin-Nosuke Matsubara (Hilgendorf, 1880: footnote p. 14), a professor of the University of Tokyo and leader of an expedition in the waters around Japan in the mid-1800s, who also served as a translator for F. M. Hilgendorf (Abe, 1986).

to as “menuke” in Japanese, meaning “exploding eye” because of the bulging eyeballs seen in fishes brought to the surface after being captured at depth. Except for *S. matsubarai*, each of these is easily distinguished from both *S. melanostictus* and *S. aleutianus* by the absence of infraorbital spines. In *S. matsubarai*, two spines are present but each is strong and invariably present in the same position: one on the lachrymal and one on the base of the suborbital stay of infraorbital 3. In addition, the lachrymal has two or three strong spines on its ventral margin, in contrast with the two typically rounded or flattened lobes, the second with up to four small spines in *S. melanostictus* and *S. aleutianus*.

Sebastes flammeus and *S. iracundus* are very similar to one another and were considered synonymous by Balanov et al. (2004). However, both Kai et al. (2003) and Hyde and Vetter (2007) found differences in genetic sequences between the two species, providing additional evidence for their validity as separate species. They are morphologically most similar to *S. borealis*, with which they appear to be closely related (Hyde and Vetter, 2007). Both lack infraorbital spines and have reduced cranial spines that lack coronal and nuchal spines.

A recent comprehensive phylogenetic analysis of *Sebastes*, based on molecular data conducted by Hyde and Vetter (2007), revealed notable differences as well as similarities between ideas of relationships based on overall morphological similarity and detailed genetic analyses. Based on maximum parsimony and Bayesian phylogenetic hypotheses, the subgenus *Zalopyr* was placed in a basal position within the tree and encompassed *S. aleutianus* and *S. melanostictus*, as well as the western Pacific species *S. glaucus* Hilgendorf (1880), gray rockfish; *S. steindachneri* Hilgendorf (1880), yanaginomai; *S. minor* Barsukov (1972), akagaya; and *S. owstoni* (Jordan and Thompson, 1914), hatsume. The clade comprising *Sebastes aleutianus* and *S. melanostictus* was placed in a terminal position in relation to the western Pacific species. All other species of *Zalopyr* of Hyde and Vetter (2007) are readily distinguished from *S. aleutianus* and *S. melanostictus* by the absence of infraorbital spines and reduced or obsolete cranial spines. Only *S. aleutianus* and *S. melanostictus* are deeper-water species—both species commonly occurring below 300 m and at least as deep as 500 m; all other species within *Zalopyr* are more shallow-water species recorded to a maximum depth of 300 m.

The purpose of naming elements of phylogenetic trees is to communicate information on evolutionary relationships, primarily the existence of monophyletic groups. The subgenus *Zalopyr* Jordan and Evermann (1898) was originally erected for *Sebastes aleutianus* (the type species of the subgenus) and *S. atrovirens* (Jordan and Gilbert, 1880) (Kendall, 2000). Although *Zalopyr* of Hyde and Vetter (2007) comprised a monophyletic group, the inclusion of any species other than *S. aleutianus* and *S. melanostictus* on the basis of molecular evidence alone is premature, particularly because only the clade including *S. aleutianus* and *S. melanostictus* may be readily diagnosed morphologically. The name *Zalopyr*

should be restricted to the terminal clade of *S. aleutianus* and *S. melanostictus*, a subgenus diagnosed by the combination of two character states: the presence of 2–10 infraorbital spines and 8 pairs of major cranial spines. To avoid naming a paraphyletic group, the species in the more basal portion of the clade should be 1) removed from *Zalopyr* and placed in their own subgenera, 2) the name *Emmelas* Jordan and Evermann (1898) applied to the basalmost member, *S. glaucus*, and 3) the name *Hatumeus* Matsubara (1943), previously used for the monotypic subgenus comprising *S. owstoni*, applied to the western Pacific clade that also includes *S. steindachneri* and *S. minor*.

This phylogenetic hypothesis indicates the derivation of *S. melanostictus* and *S. aleutianus* from a western North Pacific and shallow-water ancestor that dispersed into deeper waters of the eastern North Pacific region. Their divergence from other members of the clade has been estimated to have occurred at over 4.5 million years ago (Hyde and Vetter, 2007) and from one another at about several hundred thousand to just over one million years ago (Gharrett et al., 2005; Hyde and Vetter, 2007).

The zoogeographic pattern exhibited by *Sebastes aleutianus* and *S. melanostictus* is similar to several other species pairs found in waters of Alaska, including *Sebastolobus alascanus* Bean (1890) and *S. altivelis* Gilbert (1896), the long- and shortspine thornyheads; *Lepidopsetta polyxystra* Orr and Matarese (2000) and *L. bilineata* (Ayres, 1855), the northern and southern rock soles; and *Lycodes palearis* Gilbert (1896) and *L. brevipes* Bean (1890), the wattled and shortfin eelpouts (Mecklenburg et al., 2002). In each of these pairs, one species ranges across the North Pacific region from the Kuril Islands in the west to California in the east. The other species is an eastern North Pacific species, ranging more or less into the Bering Sea and ending to the west in the Aleutian Islands at Samalga Pass, the western extent of the ancient and now fragmented Alaska Peninsula. Recent studies across a wide spectrum of organisms, from whales and seabirds to fishes and zooplankton, across the Aleutian Islands have found differences in the nature of oceanographic ecosystems on either side of Samalga Pass: to the east the environment is more like that of the continental shelf, whereas to the west it is more oceanic (Hunt and Stabeno, 2005). Although many of the distribution patterns may be related to geologically recent ecological factors, a deeper vicariant event may have been responsible for affecting species distributions in the region (Logerwell et al., 2005).

Fisheries for rockfish on the U.S. west coast are presently managed by species, geographic region, and habitat (primarily depth) parameters. Although overlapping broadly in distribution, *S. aleutianus* is typically found at shallower depths than *S. melanostictus* (Fig. 8; Hawkins et al., 2005; Gharrett et al., 2005, 2006), and, under present management regimes, *S. melanostictus* may be fished more heavily because the major part of its distribution lies outside the more shallow restricted ar-

eas. Recent preliminary reports from fisheries observers off the Washington and Oregon coasts have indicated a predominance of *S. melanostictus* in catches—catches that because of fisheries restrictions were at depths of 457 m (250 fm) or greater. As more information on the biology of both species is gathered following their future identification in surveys and fisheries, a better understanding of management needs and strategies is certain to emerge.

Acknowledgments

We acknowledge D. Courtney (ABL) for collecting 100 large specimens, and B. Wing (ABL) and K. Maslenikov (UWFC) for processing them. For hosting the senior author in Japan, we especially thank T. Nakabo, as well as Y. Kai (FAKU), M. Yabe, K. Nakaya (HUMZ), K. Matsuura, and G. Shinohara (NSMT). We thank T. Pietsch and K. Maslenikov (UWFC), S. Suzuki (FAKU), O. Tsuruoka, Yuko Kuzume (HUMZ), J. Williams, S. Raredon (USNM), D. Catania (who provided syntype data; CAS), H. J. Walker, C. Klepaldo (SIO) for specimens; D. Stevenson, T. Pietsch, M. Wilkins for reviews; K. Amaoka (HUMZ) for information on the namesake of *S. matsubarai*; L. Britt, D. Hanselman, G. Hoff, Y. Kai, D. Kamikawa, R. Lauth, R. Lea, K. Maslenikov, K. Moots, T. Nakabo, N. Raring, R. Reuter, V. Simon, P. Spencer, D. Stevenson, G. Thiesfeld, C. Wilson, M. Wikins, and K. York for other discussions, photographs, and data.

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Appendix

Material examined

Sebastes aleutianus 131 specimens examined, 63.4-555.2 mm, including the types listed above. **Bering Sea:** UW 113740, 1 (285 mm), 55.7091°N, 168.8126°W, 225 m depth, 21 July 2004, FV *Northwest Explorer*, J.W. Orr; FAKU 119255, 1 (277.3 mm), 54.6887°N, 166.675°W, 330 m depth; FAKU 119293, 1 (555.2 mm), 54.6887°N, 166.675°W, 330 m depth. **Aleutian Islands:** UW 49327, 6 (123.7-272.8 mm), 53.7241°N, 166.8921°W, 188 m depth, 23 May 2000, FV *Dominator*, J.W. Orr; UW 114740, 3 (213-230 mm), 53.7457°N, 166.9795°W, 185 m depth, 23 May 2000, FV *Dominator*, J.W. Orr; UW 114779, 2 (254-259 mm), 58.4864°N, 152.3621°W, 154 m depth, 4 July 2001, FV *Vesteraalen*, J.W. Orr; FAKU 131033, 1 (239.9 mm), 53.79852°N, 166.3926°W, 249 m depth, 25 May 1996, FV *Golden Dawn*, J.W. Orr. **Gulf of Alaska:** KU 28070, 1 (215.8 mm), 59.6317°N, 143.1794°W, 250 m depth, 10 July 1999, FV *Morning Star*, K. Shaw; UW 46609, 2 (176.5-163.9 mm), 59.8329°N, 142.7660°W, 189 m depth, 19 July 1996; UW 45729, 8 (197.2-221.8 mm),

mm), 47.216°N, 124.746°W, 125 m depth, 1 August 1998, FV *Vesteraalen*; UW 114767*, 1 (201 mm), 46.5476°N, 124.4576°W, 125 m depth, 20 July 1998, FV *Vesteraalen*; UW 114768*, 1 (193 mm), 46.54758°N, 124.4576°W, 125 m depth, 10 July 1998, FV *Vesteraalen*, J. W. Orr; UW 44200, 1 (375 mm), 48.35°N, 124.8667°W, 165 m depth, 12 September 1992, FV *Pacific Orion*, J. Firehammer; UW 44201, 1 (345 mm), 4.35°N, 124.8667°W, 293 m, FV *Island Enterprise*, F. Smith. **Oregon:** CAS 40415, 1 (270 mm), 45.4217°N, 124.45°W, 296 m depth, 28 August 1977, RV *Profesor Siedlecki*; UW 114738*, 3 (350–430 mm), 45.9042°N, 124.7654°W, 411 m depth, 19 July 1998, FV *Vesteraalen*; UW 114776*, 3 (170–265 mm), 46.2407°N, 124.4106°W, 242 m depth, 19 July 1998, FV *Vesteraalen*; UW 43415, 1 (377.5 mm), 43.9174°N, 124.9323°W, 387 m depth, 6 July 1998, FV *Vesteraalen*; UW 114037, 1 (165 mm), 44.7809°N, 124.514°W, 175 m depth, 23 July 1995, FV *Vesteraalen*.

Sebastes melanostictus 204 specimens examined, 95.5–539 mm, including the types listed above. **Japan:** FAKU 5760, 1 (365 mm), Japan, Akkeshi, Hokkaido Prefecture; FAKU 5769, 1 (340 mm), Japan, Akkeshi, Hokkaido Prefecture; FAKU 5771, 1 (366.3 mm), Japan, Akkeshi, Hokkaido Prefecture; FAKU 5774, 1 (395 mm), Japan, Akkeshi, Hokkaido Prefecture; FAKU 5775, 1 (325 mm), Japan, Akkeshi, Hokkaido Prefecture; FAKU 81608, 1 (367.7 mm), Japan, off Miyako, Iwate Prefecture; HUMZ 97600, 1 (447.9 mm), Japan, Kushiro Fish Market, 30 miles SE of Cape Erimo; HUMZ 92733, 1 (441.9 mm), Kamaishi fish market, Iwate Prefecture; HUMZ 92746, 1 (419.9 mm), Kamaishi fish market, Iwate Prefecture; HUMZ 103024, 1 (441.6 mm), off Muroran. **Kuril Islands:** HUMZ 134873, 1 (407.3 mm), 49.0167°N, 156.4283°E, 159 m depth, 9 October 1994. **Bering Sea:** UW 46065, 1 (189.5 mm), 56.6981°N, 173.2926°W, 311 m depth, 17 July 2000, FV *Morning Star*, J. W. Orr; UW 111549, 1 (410 mm), 59.3031°N, 177.6877°W, 335 m depth, 14 July 2000, FV *Morning Star*, J. W. Orr; UW 111548, 1 (352.3 mm), 58.5697°N, 177.0833°W, 462 m depth, 16 July 2000, FV *Morning Star*, J. W. Orr; UW 49328, 1 (118 mm), 55.9686°N, 170.1104°W, 313 m depth, 6 June 2002, FV *Morning Star*, J. W. Orr; UW 113851, 3 (155.8–182.7 mm), 56.3865°N, 168.3234°W, 137 m depth, 27 July 2003, FV *Aldebaran*, J. R. Hoff; FAKU 119257, 1 (322.6 mm), 55.3308°N, 167.9962°W, 360 m depth; HUMZ 93691, 1 (368.8 mm), Bering Sea, 59.53°N, 177.97°W, 6 August 1981; HUMZ 93826, 1 (498.1 mm), Bering Sea, 56.54°N, 172.52°W, 18 August 1981; UW 113902, 1 (355 mm), 58.3978°N, 174.4882°W, 340 m depth, 27 June 2004, FV *Northwest Explorer*, D. E. Stevenson. **Aleutian Islands:** UW 48464, 1 (249.5 mm), 53.2207°N, 169.7395°W, 328 m depth, 2 June 2002, FV *Morning Star*, J. W. Orr; UW 49319, 4 (95.5–106.2 mm), 53.8149°N, 167.2937°W, 335 m depth, 26 May 2002, FV *Morning Star*, J. W. Orr; UW 49334, 1 (115 mm), 52.8973°N, 169.5051°W, 240 m depth, 2 June 2002, FV *Morning Star*, J. W. Orr; UW 112634, 1 (101.6 mm), 51.6083°N, 177.18°W, 224 m depth, 4 July 2002, FV *Sea Storm*, J. W. Orr; UW 112317, 1 (410 mm), 52.0601°N, 177.8333°E, 244 m depth, 29 July 1997, FV *Vesteraalen*, J. W. Orr; UW 114733, 4 (195–335 mm), 53.3605°N, 166.162°W, 315 m depth, 23 May 2001, FV *Morning Star*, J. W. Orr; UW 114769, 1 (415 mm), 53.6741°N, 167.5344°W, 309 m depth, 24 May 2000, FV *Dominator*, J. W. Orr; UW 112319, 1 (335 mm), 52.2933°N, 173.3717°W, 360 m depth, 3 June 2000, FV *Dominator*, J. W. Orr; UW 43296, 1 (356 mm), 52.0403°N, 178.5132°E, 389 m depth, 20 July 1994, FV *Pacific Knight*, R. R. Lauth; UW 43456, 1 (326.4 mm), 52.0601°N, 177.8333°E, 244 m depth, 29 July 1997, FV *Vesteraalen*, J. W. Orr; UW 114734, 1 (269 mm), 52.5036°N, 173.5548°W, 238 m depth, 2 June 2000, FV *Dominator*, J.W. Orr; UW 114736, 1 (252 mm), 51.8025°N, 174.7188°W, 315 m depth, 7 July 1997,

FV *Dominator*, R. R. Lauth; UW 114737, 3 (128–271 mm), 52.5987°N, 169.3605°W, 237 m depth, 20 May 2001, FV *Morning Star*, J. W. Orr; UW 114770, 1 (355 mm), 54.1176°N, 166.2599°W, 91 m depth, 22 May 2000, FV *Dominator*, J.W. Orr; UW 45528, 2 (243.8–247.6 mm), 52.7156°N, 169.8153°W, 148 m depth, FV *Golden Dawn*, J. W. Orr; UW 44202, 3 (305–370 mm), 51.7167°N, 178.3°W, 86 m depth, 7 July 1992, FV *Pavlof*, S. Sloane; FAKU 131030, 1 (268 mm), 54.0417°N, 162.7699°W, 193 m depth, 30 May 1996, FV *Golden Dawn*, J. W. Orr; FAKU 131031, 1 (316.0 mm), 54.0417°N, 162.7699°W, 193 m depth, 30 May 1996, FV *Golden Dawn*, J. W. Orr; FAKU 131032, 1 (343.5 mm), 54.0417°N, 162.7699°W, 193 m depth, 30 May 1996, FV *Golden Dawn*, J. W. Orr; FAKU 119236, 1 (539 mm), 51.7667°N, 177.0333°E, 100–885 m depth; FAKU 119245, 1 (373.7 mm), 54°N, 165.9835°W, 340 m depth; FAKU 121032, 1 (407.7 mm), 52.05°N, 179.9833°W, 125–1000 m depth; HUMZ 46218, 1 (264.6 mm), 51.8°N, 174.5167°W, 320 m depth, 16 June 1975; HUMZ 46224, 1 (352.2 mm), 51.8°N, 174.5167°W, 320 m depth, 16 June 1975; HUMZ 67372, 1 (220.3 mm), Bowers Bank, 53.95°N, 180°E; HUMZ 67373, 1 (199 mm), Bowers Bank, 53.95°N, 180°E; HUMZ 67655, 1 (136.5 mm), 51.45°N, 179.88°W; HUMZ 68524, 1 (343.6 mm), 52.1333°N, 171.6667°W, 490 m depth; FAKU 119256, 1 (316.8 mm), 54.6887°N, 166.675°W, 330 m depth; FAKU 119237, 1 (325.8 mm), 51.9333°N, 172.8167°W, 150–1030 m depth; FAKU 119239, 1 (245.1 mm), 51.9333°N, 172.8167°W, 150–1030 m depth; FAKU 119235, 1 (239.7 mm), 51.7667°N, 177.0333°E, 100–885 m depth; FAKU 119238, 1 (318 mm), 51.9333°N, 172.8167°W, 150–1030 m depth; FAKU 131034, 1 (283.8 mm), 53.7985°N, 166.3926°W, 249 m depth, 25 May 1996, FV *Golden Dawn*, J. W. Orr; HUMZ 88965, 1 (205.9 mm), 51.73°N, 177.86°E; HUMZ 88969, 1 (167.2 mm), 51.73°N, 177.86°E, 10 August 1980; HUMZ 89170, 1 (206.2 mm), 52.93°N, 169.33°W, 7 July 1980; UW 116497, 1 (300 mm), 52.499°N, 173.5789°W, 233 m depth, 2 June 2000, FV *Dominator*, J. W. Orr; UW 116488, 1 (265 mm), 52.2796°N, 170.6521°W, 160 m depth, 14 June 2006, FV *Gladiator*, J. W. Orr; UW 116550, 2 (195–200 mm), 51.8444°N, 173.9223°W, 267 m depth, 19 June 2006, FV *Gladiator*, J. W. Orr. **Gulf of Alaska:** UW 15167, 2 (173–241 mm), Alaska, Frederick Sound; UW 116883, 1 (365 mm), 56.279°N, 153.1482°W, 349 m depth, 23 March 2002, RV *Miller Freeman*, C. Wilson; UW 111744*, 9 (254–363 mm), 59.05°N, 143.0167°W, 300–600 m depth, 2001, FV *Ocean Prowler*, D. Courtney; UW 116881*, 10 (265–410 mm), 59.05°N, 143.0167°W, 300–600 m depth, 2001, FV *Ocean Prowler*, D. Courtney; UW 116882*, 9 (290–355 mm), 59.0333°N, 141.0167°W, 300–400 m depth, 2001, FV *Ocean Prowler*, D. Courtney; UW 49325, 1 (372 mm), 59.0182°N, 141.1633°W, 313 m depth, 12 July 1999, FV *Morning Star*, J. W. Orr; UW 45237, 17 (292.5–411 mm), 59.0167°N, 147.033°W, 300–400 m depth, 2001, FV *Ocean Prowler*, D. Courtney; UW 45235*, 6 (303–348.5 mm), 59.05°N, 143.017°W, 300–600 m depth, 2001, FV *Ocean Prowler*, D. Courtney; UW 45236*, 8 (225.1–335 mm), 58.0667°N, 140.067°W, 300–400 m depth, 2001, FV *Ocean Prowler*, D. Courtney; UW 113745, 1 (305 mm), 58.7708°N, 152.6504°W, 206 m depth, 6 July 2003, FV *Gladiator*, J.W. Orr; UW 114763, 1 (132.1 mm), 55.0236°N, 133.34°W, 189 m depth, 31 July 2005, FV *Sea Storm*; FAKU 121176, 1 (395.4 mm), 54.7833°N, 157.8167°W, 250 m depth; FAKU 121177, 1 (488 mm), 54.7833°N, 157.8167°W, 250 m depth; FAKU 121178, 1 (177.1 mm), 54.7833°N, 157.8167°W, 250 m depth; FAKU 121179, 1 (489.4 mm), 54.7833°N, 157.8167°W, 250 m depth; FAKU 121180, 1 (217.7 mm), 54.7833°N, 157.8167°W, 250 m depth; HUMZ 102216, 1 (361.8 mm), 56°N, 149.25°W, 333 m depth, 15 August 1984; HUMZ 102577, 1 (337 mm), 56.55°N, 152.12°W, 152 m depth; HUMZ 102582, 1 (354.3 mm), 56.55°N, 152.12°W, 152 m depth; HUMZ

102583, 1 (351.5 mm), 56.55°N, 152.12°W, 152 m depth; UW 116493*, 1 (290 mm), 58.5212°N, 148.9618°W, 112 m depth, 31 July 2005, FV *Northwest Explorer*, J. W. Orr; UW 46069, 2 (335–353 mm), 54.9668°N, 157.2281°W, 308 m depth, 2 June 1999, FV *Morning Star*, J. W. Orr; UW 113672*, 4 (324.4–415 mm), 59.05°N, 143.0167°W, 300–600 m depth, 2001, FV *Ocean Prowler*, D. Courtney; UW 111745*, 13 (196.6–445 mm), 59.05°N, 143.0167°W, 300–600 m depth, 2001, FV *Ocean Prowler*, D. Courtney; UW 115759, 3 (138.7–184 mm), 53.9637°N, 166.5257°W, 136 m depth, 6 June 2006, FV *Sea Storm*; UW 49336, 1 (246.7 mm), 53.2207°N, 169.7395°W, 328 m depth, 2 June 2002, J. W. Orr; UW 115763, 2 (131.2–140 mm), 57.9752°N, 137.1904°W, 282 m depth, 7 July 1999, J. W. Orr; UW 116885, 1 (430 mm), 58.3523 N, 147.828 W, 498 m gear depth, 1838 m bottom depth, D. E. Stevenson; UW 116884, 1 (455 mm), 58.3492 N, 147.825 W, 1089 m gear depth, 1892 m bottom depth, D. E. Stevenson. **Canada:** CAS 15392, 1 (155.3 mm), off Vancouver I., La Perouse Bank, 46°N, 126.5333°W, 421 m depth, 11 September 1972, RV *G.B. Reed*, T. Iwamoto. **Oregon:** CAS 40414, 3 (205.2–285 mm), 45.1717°N, 124.5117°W, 403 m depth, 5 September 1977, RV *Commando*; UW 43356, 1 (458 mm), 44.8898°N, 124.8867°W, 424 m depth, 19 October 1993, FV *Miller Freeman*, R. R. Lauth; UW 20964, 2 (376.4–385 mm), Brown Bear Seamount, 46.03°N, 130.4167°W, 480 m depth, RV *Pandora II*, D. W. Nelson; SIO 88-187, 1 (207.8 mm), 45.0607°N, 124.5152°W, 379 m depth, 8 December 1988, FV *Miller Freeman*, W. C. Flerx and R. Dotson. **California:** UW 114780*, 1 (430 mm), off Eureka, K.G. Thiesfeld; SIO 75-384, 1 (370 mm), Coronado Bank, 32.5817°N, 117.4°W, 11 April 1975, J. La Grange; SIO 75-386, 3 (385–420 mm), Coronado Bank, 32.581°N, 117.4°W, 421 m depth, 16 April 1975, J. La Grange; SIO 75-432, 1 (385 mm), Coronado Bank, 32.5833°N, 117.41°W, 11 February 1975, J. La Grange; SIO 75-433, 3 (385–405 mm), Coronado Bank, 32.5833°N, 117.41°W, J. La Grange; SIO 75-431, 1 (385 mm), Coronado Bank, 32.5833°N, 117.41°W, 7 February 1975, J. La Grange; SIO 73-434, 1 (377 mm), Coro-

nado Bank, 32.5833°N, 117.41°W, 25 June 1975, J. La Grange; SIO 81-138, 1 (395 mm), 3 mi W of SIO Pier, in SIO Canyon, 32.85°N, 117.27°W, 457 m depth, 17 April 1975, Sullivan and McConnaughy. **Locality unknown:** FAKU-S 2848, 1 (341 mm); FAKU-S 2849, 1 (380.2 mm); FAKU-S 2989, 1 (279.7 mm); FAKU-S 2990, 1 (345 mm); FAKU-S 2991, 1 (333.2 mm); FAKU-S 3150, 1 (300 mm); FAKU-S 3166, 1 (343.1 mm); FAKU-S 3167, 1 (340.3 mm); FAKU 119231, 1 (416.6 mm); HUMZ 93754, 1 (408 mm).

Sebastes melanostomus USNM 77436, 1 (286.3 mm), syntype of *Sebastichthys introniger*, California, Albatross Station 4410, “Long Point, Santa Catalina Island, N. 79 degrees W., 2.8 miles,” 326–357 m depth, 11 April 1904; USNM 77437, 1 (300.2 mm), syntype of *Sebastichthys introniger*, California, Albatross Station 4418, “off Santa Barbara I., SW. Rock Santa Barbara Island, N. 8 deg. E. 6.9 miles,” 435–567 m depth, 12 April 1904.

Sebastes matsubarae USNM 48146, 1 (302 mm), Japan, Kushiri; FAKU 89180, 1 (392.3 mm), Japan; FAKU 89181, 1 (357.3 mm), Japan; FAKU 50100, 1 (291.1 mm), Japan; FAKU 89176, 1 (365.3 mm), Japan; FAKU 89177, 1 (365.5 mm), Japan; FAKU 89178, 1 (398.6 mm), Japan; FAKU 89179, 1 (365.5 mm), Japan.

Sebastes baramenuke 3 FAKU 81605, 1 (409 mm), Japan; FAKU 50097, 1 (279.1 mm), Japan, Miyako Prefecture, 39.7°N, 142.5°E; FAKU 50098, 1 (288.3 mm), Japan, Miyako Prefecture, 39.7°N, 142.5°E.

Sebastes iracundus FAKU 81604, 1 (446.8 mm), Japan.

Sebastes flammeus FAKU 81606, 1 (364.9 mm), Japan; FAKU 81607, 1 (385.6 mm), Japan; FAKU 88906, 1 (555.4 mm), Japan.