Maturity and Fecundity in the Rockfishes, *Sebastes* spp., a Review

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Introduction

Sebastes (rockfishes) is a speciose genus with over 100 species that occupy diverse habitats from the intertidal zone to deep (>1,000 m) water. Within this depth range, they are typically associated with high-relief rocky substrates; however, species display great variation in substrate affinity, ranging from cryptic reef-dwellers to semipelagic schooling species. The eastern North Pacific is the distributional center for *Sebastes*, with over 50 species occurring from California through British Columbia (Eschmeyer and Herald, 1983). About 25 species occur in the western North Pacific (Masuda et al., 1984), four occur in the North Atlantic (Kendall, 1991) and at least one is found in the southern hemisphere off South America and South Africa (Chen, 1971).

Rockfishes are gonochoristic, with internal fertilization. Eggs incubate and embryos hatch in the ovaries, with subsequent extrusion of larvae. They have generally been regarded as classic examples of ovoviviparous fishes; however, recent studies have suggested that developing young use exogenous energy prior to birth (Boehlert and Yoklavich, 1984). Although females of many species of rockfishes release a single brood annually, some species produce multiple broods (MacGregor, 1970). Rockfishes are generally recognized as slow-growing (e.g., Archibald et al., 1981), with a suite of life history characteristics that places them in the K-selected group (Adams, 1980).

Reproductive parameters defining maturity schedules and fecundity are important life history characteristics. Cole (1954) explicitly identified mortality and reproductive variables as determinants of Darwinian fitness and established the paradigm that natural selection acts on a suite of life history characteristics to maximize fitness. Fishes have been used to analyze the accuracy of several life history models (e.g., Bell, 1980; Roff, 1984; Stearns and Koella, 1986). Fish-based data are useful because information on age at maturity, fecundity, and growth are available for a variety of species. The models all follow Cole (1954) in assuming that age at maturity, fecundity, growth, and mortality have coevolved to maximize Darwinian fitness. Observations that significant correlations exist among life history parameters (e.g., Adams, 1980; Pauly, 1980; Roff, 1981,

1984) suggest the assumption is correct.

Our summary of information describes maturity and fecundity as functions of length. Fecundity descriptions should be regarded with caution due to a number of inherent problems. Inconsistent methodology in determination of egg or embryo number may introduce considerable meaningless variation. Additional measurement variation is introduced when estimating fecundity of multiple spawning species (Grimes, 1987). In rockfishes, fecundity measurements also are a function of development stage, as fecundity decreases from pre-fertilizaton to the late embryo stage (Kusakari, In press). Consequently, fecundity estimates should be viewed as approximations, especially in those cases where we have extended the length-fecundity function outside the range of original observations (e.g., estimates of fecundity at maximum length).

The objectives of this review are to assemble the available information on maturity and fecundity in rockfishes, to explore the assembled data for patterns associated with geographic distribution and fish length, and to determine whether patterns are consistent with life history models.

Methods

Data describing length at maturity (length where 50 percent were mature), fecundity, growth, maximum reported length (MRL), and length-weight relationships were assembled from published literature and a limited number of unpublished sources. To identify sources we used our personal bibliographic reference systems, two recent bibliographic summaries (Clay and Kenchington, 1986; Leet and Reilly, 1988), and ab-

ABSTRACT—Literature was reviewed for data describing fecundity, maturity, and growth in the ovoviviparous genus Sebastes *(rockfishes). Assembled data were examined for patterns associated with geographic location and fish length. Rockfishes display great range in length at maturity (9-52 cm total length) and estimated fecundity at maturity (1,700-417,000 eggs or embryos). Within species, length at maturity usually increases at higher latitudes and tends to be greater for females than males. Among species, length at maturity of females is positively and significantly correlated with maximum length and with the ratio of fecundity at maturity to fecundity at maximum length. Fecundity of rockfishes is not notably lower than oviparous fishes such as snappers (Lutjanidae) and cods (Gadidae).*

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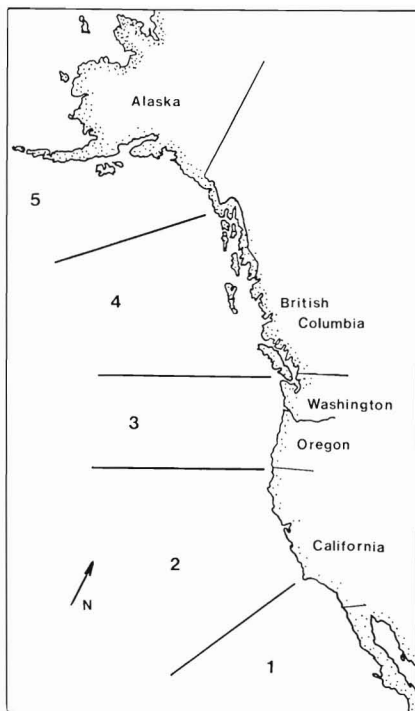
Figure 1.—Geographic areas assigned to rockfish reproductive data from eastern North Pacific species.

stracting journals. Data from the northeast Pacific were assigned to geographic areas (Fig. 1).

Some sources tabulated fecundity-length data for individual fish but provided no fit of data to a model (e.g., Phillips, 1964). In cases where the number of observations appeared adequate, we fit such data to the model $F = a(L^b)$, using a least-squares algorithm. Lengths in the various sources were reported as standard, fork, or total length. We standardized all length measures to total length, based on the regression formulae provided by Echeverria and Lenarz (1985). For those species not included in that source, we used the mean regression coefficients for all species tabulated therein.

We used primary reproductive data (fecundity and length at maturity) and auxiliary data (growth described by the von Bertalanffy model, MRL, length-weight relationships) to generate derived reproductive data including fecundity at maturity (i.e., at length where 50 percent are mature), fecundity at MRL, fecundity per gram weight at maturity, and fecundity per gram weight at MRL.

The effect of latitude on maturity was examined by comparing the reported length at maturity between geographic areas, moving from area 1 northward through area 4 (Fig. 1). To determine whether females tended to mature at smaller or larger lengths than males, we compared the length at maturity for the two sexes in all species, including reports from all geographic areas. Differences were scored between areas or between sexes only if they differed by 2 cm or more. Results were tested for significance with chi-square tests, under the null hypotheses that comparisons scored as different would be evenly distributed between directions (north or south) or sexes.

The effects of fish size (length) on reproduction were examined through two linear regressions. In the first, length at maturity of females was the dependent variable and maximum reported length the independent variable. In the second, we regressed the ratio—fecundity at maturity:fecundity at maximum size—against size at maturity. We also plotted the trajectory of fecundity for each species from the length of 50 percent maturity of females to the maximum reported size for the species, using the fecundity-length parameters selected as typical for each species.

Results

Eastern North Pacific Species

Data describing fecundity and maturity were collected for 45 rockfishes from 27 sources (Table 1). Estimates of length at maturity in more than one geographic area were available in 23 species. Fecundity estimates were usually limited to a single geographic zone. For analyses of reproductive characteristics among species, we used data that typified the fecundity and maturity for each species. If more than one source provided data on a particular parameter, we chose either the one from the geographic area nearest the center of distribution for that species, or the one with the most complete set of data.

With few exceptions, data typifying a species are from a single area.

Length at maturity generally increased at the higher latitudes. Of 32 cases where female maturity could be compared between geographic areas, length at maturity in the northern area was greater in 20 cases, less in 4, and equal in 8 ($P < 0.05$). In 30 cases where males were comparable, the length at maturity was greater in the north 21 times, less 5, and equal 4 ($P < 0.05$). The only two species in which both males and females matured at shorter length in a more northerly area were *Sebastes jordani* and *S. levis*, compared in zones 1 and 2 (Fig. 1).

Females tend to be larger at maturity than males, as this occurred in 29 cases whereas males matured at greater size only 5 times ($P < 0.01$). In 42 cases there was no difference between the sexes. Female length at maturity varied from 9 cm (*Sebastes dalli*) to 52 cm (*S. pinniger* and *S. ruberrimus*). The mean length at maturity was 31 cm for females and 29 cm for males.

Length at maturity is related to maximum size attained by a species. Linear regression of female length at maturity on maximum length was highly significant ($P < 0.001$, Fig. 2).

Fecundity as a function of length varied among species (Table 1). The exponent in the power equation ranged from 2.80 (*Sebastes hopkinsi*) to 5.51 (*S. alutus*), with a mean of 4.10. Calculated fecundity at maturity varied from 1,700 in *S. dalli* to 417,000 in *S. paucispinis* (Table 2), with a mean of 124,000. Calculated fecundity at maximum length varied from 35,000 for *S. hopkins* to 5.6 million for *S. miniatus* (Table 2), with a mean of 1.1 million.

Fecundity at maturity as a proportion of fecundity at maximum length varied from 0.01 to 0.25, with a mean of 0.09, and appears to be a positive function of size. A regression of that proportion on length at maturity was significant ($p < 0.05$, Fig. 3).

We used fecundity per gram of body weight (FGB) as an indicator of relative investment in reproduction. At sexual maturity FGB ranged from 70 in *Sebastes alutus* to 325 in *S. elongatus* (Table 2), with a mean of 183. At maximum length

Table 1.—Reproductive and other life history parameters for rockfishes. Areas correspond to those in Figure 1, S[1] (in parentheses following Area) identifies data source from list at bottom of table. All lengths are in total lengths (converted when necessary based on Echeverria and Lenarz (1985). Data include: Maximum reported length (MRL), asymptotic length in the von Bertalanffy equation (L), k in the von Bertalanffy equation (K), the exponent in the length-weight power equation (L-W B), the exponent in the fecundity-length power equation (FEC B), length at 50 percent maturity for females (F MAT) and males (M MAT). Values used to typify species are underlined.

Species	Area (S[1])	MRL	L	K	L-W B	FEC B	F MAT	M MAT	Species	Area (S[1])	MRL	L	K	L-W B	FEC B	F MAT	M MAT
aleutianus	4(3,25)	97	57	0.050			47	45	helvomaculatus	4(3)	33					21	23
alutus	2(2)	51					26	28	hopkinsi	1(1)	29	25		2.964	2.799	14	13
alutus	3(18)	51				6.334			hopkinsi	2(2)	29					18	16
alutus	3(16)	51	51	0.091		7.325	36	31									
alutus	4(16)	51	51	0.114		5.513	38	32	jordani	1(5,21)	30	35	0.211	3.152	3.306	16	16
alutus	4(3,22)	51	45	0.126			37	36	jordani	2(2)	30					14	14
alutus	5(15,17)	51			2.913	5.3	30	29									
									levis	1(1)	94			3.093	3.154	43	44
auriculatus	2(2)	52					31	31	levis	2(2)	94					32	32
auriculatus	3(11)	52				3.341											
									maliger	4(7)	61					36	35
aurora	2(2)	38					28	28									
									marinus (Atl.)	(26)	80					41	26
babcocki	2(2)	64					34	31	marinus	(27)	80				4.278	43	
babcocki	4(4)	64					43	39									
									melanops	2(2)	60					41	36
borealis	4(3)	91					47	47	melanops	4(7)	60			3.286		41	42
brevispinis	4(3,22)	71	59	0.085			46	44	melanostomus	1(1)	61			3.042		34	34
									melanostomus	2(2)						35	33
carnatus	2(2)	39					17	17									
									miniatus	1(5)	76				5.686		
caurinus	2(2)	57					34		miniatus	1(1)	76			2.923	5.023	37	35
caurinus	3(12)	57	46	0.160		4.957			miniatus	2(2)	76					37	38
caurinus	3(11,19)	57			3.040	5.300											
									mystinus	2(10)	53			2.808		27	26
chlorostictus	1(1)	50			3.163	4.971	22	22	mystinus	2(2)	53					29	27
chlorostictus	2(2)	50					28	27									
									nebulosus	2(2)	43					27	27
chrysomelas	2(2)	39					15	16									
									ovalis	1(1)	56			3.137		25	24
ciliatus	4(7)	41	52				29	26	ovalis	2(2)	56					28	28
constellatus	1(1)	46	45	0.087	3.160	4.251	22	19	paucispinis	1(5)	91				4.840		
constellatus	2(2)	46					27	30	paucispinis	1(1)	91			3.061	3.270	36	35
									paucispinis	2(6,24)	91	92	0.11			50	47
crameri	1(5)	76				5.059			paucispinis	2(2)	91					48	42
crameri	2(2)	76					27	27									
crameri	3(3,22)	76	40	0.087			39	36	pinniger	1(5)	76				4.021		
									pinniger	2(2)	76					44	40
dalli	1(1)	25			3.215	4.098	9	9	pinniger	3(3,20)	76	70	0.118			52	42
									pinniger	4(6,22)	76	54	0.139			51	40
diploproa	1(5)					4.705											
diploproa	2(2)						19	22	proriger	4(3,22)	51	40	0.166			30	29
diploproa	3(20)	46	39	0.084													
diploproa	4(3)						28	27	reedi	4(3,22)	58	46	0.125			39	38
elongatus	1(1)	38	37	0.098	3.128	3.739	19	18	rosaceus	1(1)	36			3.386	3.650	15	15
elongatus	2(2)	38					23	23	rosaceus	2(2)	36					20	20
elongatus	3(3)	38					24	24									
									rosenblatti	1(1)	48	58	0.053	3.106	4.375	28	30
entomelas	1(5)	53				4.892											
entomelas	1(1)	53			2.943	4.716	35	32	ruberrimus	2(2)	91					40	40
entomelas	2(2)	53					37	36	ruberrimus	4(7,14)	91	67	0.049			52	57
entomelas	3(8,9)	53				5.431	38	33									
entomelas	4(3)	53					41	40	rubrivinctus	2(2)						34	30
flavidus	1(5)	66				4.714			rufus	1(1)	51			3.1468	4.220	36	31
flavidus	1(1)	66			2.822	4.816	36	32	rufus	2(2)	51					34	31
flavidus	2(2)	66					36	35									
flavidus	3(6,23)	66	57	0.163			46	42	saxicola	1(5)	39				3.214		
flavidus	4(3,22)	66	50	0.186			43	41	saxicola	1(1)	39	33	0.064	2.805	3.792	10	10
flavidus	4(7)	66			3.151		43	44	saxicola	2(2)	39					16	17
goodei	1(5)	56				4.384			semicinctus	1(1)	25	18	0.370	2.938	3.916	11	11
goodei	1(1)	56			3.120	3.606	30	28									
goodei	2(2,24)	56	56	0.180			34	31	serranoides	2(2,4)	61	52	0.18	3.063	4.619	34	32
goodei	3(6,24)	56	56	0.180			39	28									
									variegatus	4(3)	32					23	24
helvomaculatus	2(2)	33					23	22									
									zacentrus	4(3,22)	33	36	0.095			25	24

[1]Sources: 1 = Love et al., 1990; 2 = Wyllie Echeverria, 1987; 3 = Westrheim, 1975; 4 = Love and Westphal, 1981; 5 = Phillips, 1964; 6 = Gunderson et al., 1980, 7 = Rosenthal et al., 1982; 8 = Boehlert et al., 1982; 9 = Barss and Wyllie Echeverria, 1987; 10 = Miller and Geibel, 1973; 11 = DeLacy et al., 1964; 12 = Washington et al., 1978; 13 = Paraketsov, 1963; 14 = O'Connell, personal commun.; 15 = Chikuni, 1975; 16 = Gunderson, 1977; 17 = Lisovenko, 1965; 18 = Westrheim, 1958; 19 = Patten 1973; 20 = Boehlert and Kappenman, 1980; 21 = Lenarz, 1980; 22 = Archibald et al., 1981; 23 = Fraidenburg, 1980; 24 = Wilkins, 1980; 25 = Nelson and Quinn, 1987; 26 = Ni and Sandeman, 1984; 27 = Raitt and Hall, 1967
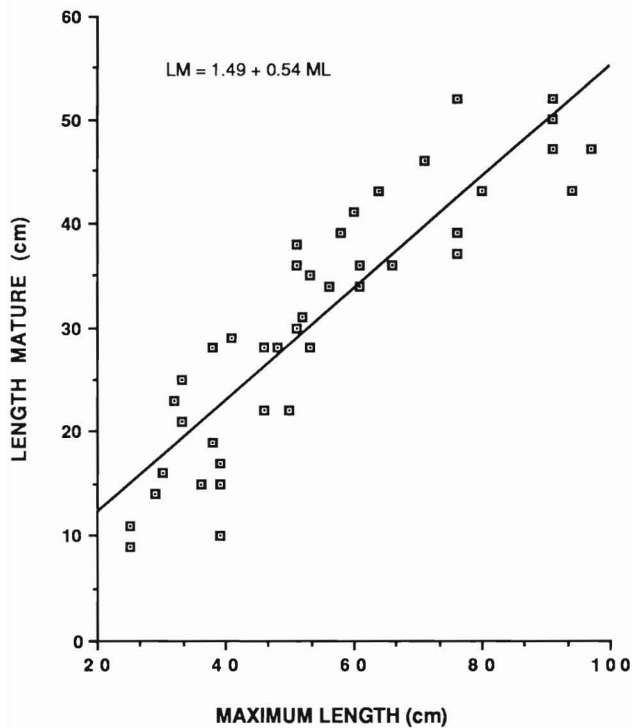
Figure 2.—Linear regression of length at maturity on maximum reported length for 42 *Sebastes* species.
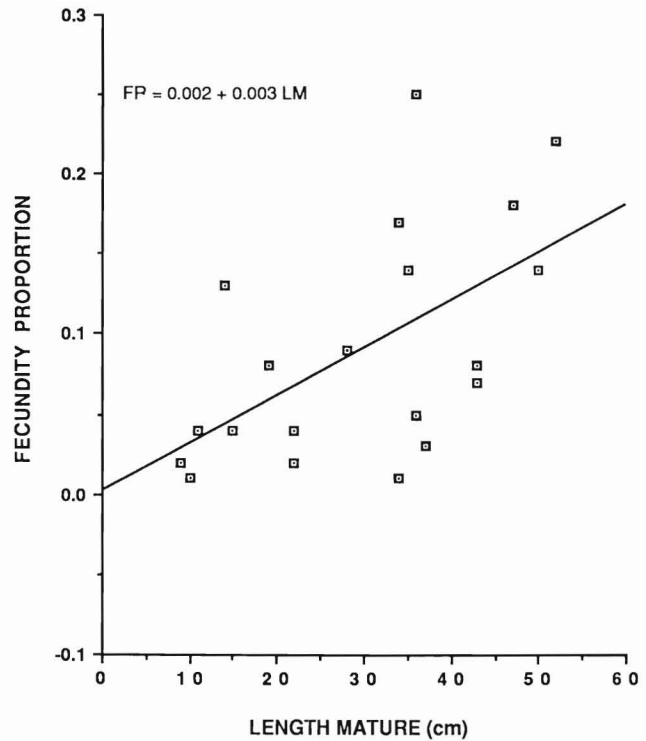

Figure 3.—Linear regression of fecundity at maturity/fecundity at maximum length on length at maturity for 20 *Sebastes* species.

FGB ranged from 163 in *S. alutus* to 826 in *S. miniatus*, with a mean of 416. A regression of FGB on maximum length was not significant.

We plotted fecundity trajectories from fecundity at maturity to fecundity at maximum size (Fig. 4). The trajectories define an envelope of fecundity-at-length values for rockfishes. The species with data points outside the envelope are *Sebastes alutus* and *S. marinus*.

Western North Pacific Species

We located data describing fecundity for six species of western North Pacific rockfishes: *Sebastes inermis*, *S. pachycephalus*, *S. schlegeli*, *S. steindachneri*, *S. taczanowski*, and *S. vulpes* (Table 3). Although we were unable to locate data sets suitable for assessing maturity (i.e., with indications of lengths of immature fish), the minimum length of females reported as mature in fecundity data allowed a very tentative indication of length at maturity, which ranged from 8

cm in *S. pachycephalus* to 34 cm in *S. schlegeli*.

Fecundity of western North Pacific rockfishes was low (Table 3), but typical of small species. When minimum and maximum sizes of fish in those studies

Table 2.—Fecundity-related parameters for rockfish species, including geographic area of data source (Area, from Figure 1), calculated fecundity at length of 50 percent maturity (FMAT, in 1,000's), calculated fecundity at maximum reported length (FMAX, in 1,000's), ratio of fecundity at maturity to maximum fecundity (FRAT), fecundity per gram of body weight at maturity (FGBMAT), fecundity per gram of body at maximum size (FGBMAX), and ratio of FGBMAT to FGBMAX (FGBRAT). Data used to generate parameters are underlined in Table 1.

| Species	Area	FMAT	FMAX	FRAT	FBGMAT	FGBMAX	FGBRAT
alutus	4	40	227	0.18	70	163	0.43
chlorostictus	1	24	1395	0.02	148	651	0.23
constellatus	1	34	772	0.04	198	445	0.44
dalli	1	2	113	0.02	155	383	0.40
elongatus	1	26	344	0.08	325	497	0.65
entomelas	3	134	948	0.14	233	487	0.48
flavidus	1,3	125	1146	0.11	177	593	0.30
goodei	1,2	64	384	0.17	140	178	0.81
hopkinsi	1	7	35	0.13	187	166	1.13
levis	1	241	2842	0.08	212	222	0.95
miniatus	1	151	5602	0.03	182	826	0.22
paucispinis	1,2	417	2954	0.14	324	367	0.88
pinniger	1,3	85	389	0.22			
rosaceus	1	15	354	0.04	291	367	0.79
rosenblatti	1	47	499	0.09	136	271	0.50
rufus	1	111	482	0.25	163	235	0.69
saxicola	1	3	315	0.01	215	825	0.26
semicinctus	1	4	86	0.04	199	494	0.40
serranoides	2	71	1058	0.07	130	324	0.40
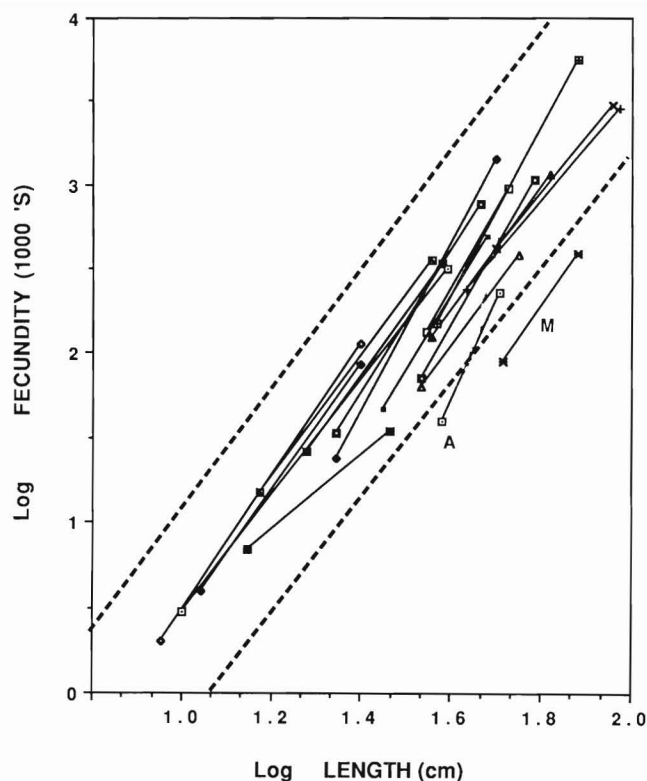
Figure 4.—Fecundity trajectories—the line connecting fecundity at maturity with fecundity at maximum length—plotted against length for 20 *Sebastes* species. The dashed lines represent an fecundity-length envelope for rockfish species fitted by eye. A = *Sebastes alutus*, M = *S. marinus*.

Table 3.—Summary of fecundity and derived maturity data for *Sebastes* sp. from the western North Pacific. Estimates include parameters of the fecundity-length power equation ($F = aL^b$): a = FEC A, b = FEC B; length (cm) of smallest fish in fecundity data set (MINL); length of largest fish in fecundity data set (MAXL); fecundity (1,000 eggs) of smallest fish in fecundity data set (MINF); fecundity (1,000 eggs) of largest fish in fecundity data set (MAXF); and number of fish in fecundity data set (N). Sources of data[1] are indicated in parentheses.

Species	FEC A	FEC B	MINL	MAXL	MINF	MAXF	N
inermis (1[1])	0.119	5.56	15.8	23.4	4	62	25
pachycephalus (2)	0.016	3.639	7.8	17.5	1.5	10	43
schlegeli (3)			33.8	60.0	44	780	116
steindachneri (4)			26.9	31.4	112	184	4
taczanowski (4)	0.159	2.858	10.8	32.5	8	111	18
vulpes (4)			25.5	32.6	12	151	7

[1]Sources: 1 = Mio, 1960; 2 = Shiokawa, 1962; 3 = Kusakari, In press; 4 = Sasaki, 1975.

were plotted with their associated fecundity estimates, the fecundity trajectories fell within the envelope defined by eastern North Pacific rockfishes. Futhermore, their lengths at maturity and fecundities are similar to those of eastern North Pacific species that mature at small sizes (e.g., *Sebastes dalli*, *S. saxicola*, *S. semicinctus*)

North Atlantic Species

In the western North Atlantic, there apparently are three *Sebastes* species, *S. marinus*, *S. mentella*, and *S. fasciatus*, although considerable taxonomic confusion has been associated with the latter two. Ni and Sandeman (1984) examined historical data on length at maturity in western North Atlantic populations of the three species. Length at maturity for *S. marinus* was 21-26 cm in males and 38-41 cm in females. The two other species were combined as the beaked redfishes, in which males matured at 16-29 cm and females at 24-43 cm.

Raitt and Hall (1967) reported length at maturity for female *S. marinus* from the eastern North Atlantic as 42 cm and 43 cm for populations near Iceland and the Faroe Islands, respectively. They also reported very similar fecundity estimates for those populations (included in Table 1). The fecundity trajectory from maturity to MRL is to the right of the envelope of fecundity trajectories based on eastern North Pacific species (Fig. 4).

Discussion

Increased maternal investment in progeny through viviparity or ovoviviparity is often assumed to result in decreased fecundity. Comparison of rockfish fecundity with oviparous fish taxa may indicate if total fecundity is indeed lower in rockfishes as a result of their ovoviviparity. Grimes (1987) compiled fecundity estimates for snappers (Lutjanidae), a tropical family generally similar to rockfishes in size and shape. Mean FGB at maximum length for 13 snapper species was 731 (Grimes, 1987); in our compilation of 18 rockfish species, the mean FGB at maximum length was 416. His mean maximum fecundity for the 13 snapper species was 2.2 million at a mean maximum length of 55 cm. For rockfishes the mean maximum length was slightly lower at 52 cm; mean maximum fecundity was 1.1 million, half the value for snappers. However, there was considerable overlap in the ranges of fecundity parameters in rockfishes and snappers. Hislop (1984) summarized fecundity data for four gadoid species from the North Sea and estimated FGB for cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, at 475 and 550, respectively. Those values are very similar to rockfishes, as are estimates of total fecundity at similar lengths. Rockfish fecundity apparently is lower than some comparable oviparous fishes, but the difference is not dramatic.

Increased length at maturity at higher latitudes is relatively common in eastern North Pacific rockfishes and has also been reported for rockfishes in the eastern North Atlantic (Ni and Sandeman, 1984). Increased size at maturity may be due to an extension in the juvenile period of northerly populations, to faster growth, or a combination of the two. However, few data are available for assessment of geographic variation in growth, and there is no indication of a general pattern. In the eastern North Pacific, *Sebastes pinniger* do not display geographic variation in

growth, whereas *S. diploproa* grow faster in the north (Boehlert and Kappenman, 1980). Love (1978) also reported faster growth by *S. serranoides* to the north. Conversely, Westrheim and Harling (1975) reported a general trend of faster growth in southerly populations in seven out of eight rockfish species. Growth variation may be even more complex—Gunderson (1977) found male *S. alutus* grew faster in a southerly population, whereas females grew faster in the north. Given the lack of clear latitudinal trend in intraspecific growth, increased length at maturity in northern populations is likely due to delayed maturity.

There are several previous reports that female rockfishes mature at larger sizes than males of the same species. Ni and Sandeman (1984) found that females of *Sebastes marinus*, *S. mentella* and *S. fasciatus* all mature at larger sizes than males. Among 17 species of eastern North Pacific rockfishes, Wyllie Echeverria (1987) found that females matured at similar or larger sizes than males, and at older ages. Love et al. (1990) reported that in 7 out of 17 species, females matured at larger sizes than males.

Maturity at larger size in females could result from either later maturity or faster growth. Females have been reported to grow faster than males in *Sebastes marinus* (Kelly and Wolf, 1959), *S. alutus* (Westrheim, 1973), *S. flavidus* (Six and Horton, 1977, Fraidenburg 1980), *S. melanops* (Six and Horton, 1977), *S. pinniger* and *S. diploproa* (Boehlert and Kappenman, 1980), *S. constellatus*, *S. elongatus*, *S. hopkinsi*, *S. ovalis*, *S. rosenblatti*, *S. saxicola*, and *S. semicinctus* (Love et al., 1990). Although Wyllie Echeverria (1987) found older ages at maturity in females of several species, the widespread occurrence of faster growth in female rockfishes suggests that growth differences are a major factor contributing to larger size at maturity in females.

Among life history models, Bell's (1980) model appears generally consistent with a variety of life history patterns observed in fishes and other groups, and is based on an assumption that mortality rate decreases with increasing size. The model predicts that optimal size (or age) at maturity will occur when the rate of increase in fecundity equals the rate of decrease in survival. In other words, if juvenile mortality increases, relative to adult mortality, the optimum size of maturity increases; conversely, if adult mortality increases, relative to juveniles, the size at maturity should decrease. These patterns are consistent with the results of experimental studies (e.g., Barclay and Gregory, 1981), observations of a variety of wild populations (summarized in Stearns, 1977), and natural experiments comparing interpopulation variation of life histories in mosquitofish (*Gambusia*) in Hawaii (Stearns, 1983), guppies in Trinidad (Reznick, 1982) and shad in the eastern North Atlantic (Leggett and Carscadden 1978). Bell's (1980) model also leads to the prediction that females should mature later and/or at larger sizes than males; this was observed in Healey's (1986) analyses of salmon populations and is true for many rockfish species we reviewed.

If the relationship between adult and juvenile mortality determines size at maturity, the observed trend in maturity at smaller size in southern populations of rockfishes suggests that, relative to juveniles, adult mortality is higher in the south than in the north. This is not consistent with the suggestion by Boehlert and Kappenman (1980) that frequent episodes of low survival of larvae (due to offshore transport) has resulted in increased reproductive effort (and as a result, lower growth) in southern populations of *S. diploproa*. If southern populations experience increased larval mortality, Bell's model predicts that they should mature later, rather than earlier, relative to northern populations. Embiotocids, with no pelagic life stages, appear to be similar to rockfishes in having delayed maturity to the north (DeMartini et al., 1983). A possible mechanism might involve geographic differences in size-specific predation rates (Law, 1979).

Acknowledgments

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