

Sexual dimorphism in *Sebastes*

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Synopsis

Sexual dimorphism and factors that may cause it were investigated in 34 species of the genus *Sebastes*. Sexual dimorphism in standard length and morphometric characters are fairly common in rockfish. In many species males are shorter than females. However in males head length, width of orbit, interorbital width, length of upper jaw, longest pectoral fin ray and longest dorsal spine tend to be larger at a specified size than in females. Water-column species tend to be more dimorphic than demersal species. We suggest that the observed differences in dimorphism in standard length may be related to differences in mating and territorial behavior. Dimorphisms in morphometric measurements may be related to compensation in feeding ability for reduced standard length of males, mating and territorial behavior.

Introduction

Sexual dimorphism is a topic of lasting interest to biologists (e.g. Darwin 1871, Lewin 1988). Many vertebrate taxa exhibit sexual dimorphism, and explanations for its cause abound and are sometimes contradictory: e.g. 'Furthermore, biological complexity is such that one can find evidence and devise arguments for proposing that large size leads to decreased survivorship. . . or to increased survivorship. . .' (Murray 1984).

Sexual dimorphism has been demonstrated in species of *Sebastes*. Male *S. umbrosus* have a longer anal fin base, anal fin rays, snout and deeper pre-pelvic body; females have greater pre-anal length (Chen 1971). The urinary bladder of male *S. mystinus* is larger than in females (Helvey 1982). Moser (1967) found sexual differences in the urogenital papilla of *S. paucispinis* and Chen (1986) noted that the dimorphism is a general feature of

Sebastes. Wyllie Echeverria (1986) studied *S. flavidus*, *S. melanops*, *S. mystinus* and *S. serranoides*. Orbit width in all four species was larger in males, and the longest pectoral fin ray was larger in males for all but *S. mystinus*. Chen (1986) found no evidence for sexual dimorphism in meristic counts for *S. semicinctus*.

Adult size of female rockfish is often larger than males (Miller & Geibel 1973, Six & Horton 1977, Boehlert 1980, Fraidenberg 1980, Lenarz 1980, Wilkens 1980, Love & Westphal 1981, Wilkens & Weinberg 1986, Wyllie Echeverria 1986, Lenarz 1987, Nelson & Quinn 1987, Love et al. 1989). However, exceptions exist (see Chen 1971, O'Connell & Funk 1987).

We examine morphometric measurements of 34 species of *Sebastes*, occurring off central and northern California, for evidence of sexual dimorphism. From these data, we have concluded that there are trends in extent of sexual dimorphism among *Se-*

bastes species groups and have used these trends to develop hypotheses on factors effecting dimorphism.

Methods

Specimens were collected by trawl and hook and line off the coasts of California and Oregon. When possible fish were measured while fresh. Otherwise fish were frozen and then thawed before measuring. It is assumed that the effects of method of capture and storage are independent of sex. Standard length (SL) and 23 other measurements were taken (Table 1). Vernier calipers (± 0.01 mm) were used for all measurements except standard, fork and total lengths. Measuring boards (± 1 mm) were used for the latter measurements.

Linear regressions with SL as the independent variable and the other morphometric measurements as dependent variables were done for the sexes separately and combined. Approximately 1% of the observations were deleted as likely errors in measuring or recording. Analyses of covariance were done to test the hypotheses that the relationships between the 23 morphometric variables and SL are independent of sex at the 95% level of confidence. These analyses tested the null hypothesis that one regression explains the relationship between dependent and independent variables against the alternative hypothesis that a separate regression (intercept and slope) for each sex better explains the relationship. Kleinbaum & Kupper (1978) refer to the null hypothesis as 'the two regression lines are coincident'. Examination of the data indicated that the usual assumptions of linearity, normality and independence of residuals were satisfied. Because so many statistical tests were performed ($N = 782$), statistically significant results due to chance alone are to be expected (Type I errors). Assuming a binomial distribution for the test results and no effect of sex, the expected number of Type I errors is 39.1 (782×0.05) with a variance of 37.1 ($782 \times 0.05 \times 0.95$). Using a normal approximation, the expectation is 51 or fewer Type I errors at the 95% confidence level.

We attempted to eliminate Type I errors by using

a sign test (Dixon & Massey 1957) for each morphometric variable. Each observation for the sign test was the result of the analysis of covariance from each species. A result was considered positive if female measurements were significantly larger than for males, and negative for the converse. The test was made at the 95% confidence level. Since significantly different regressions often intersected, it was necessary to compare expected morphometric measurements at a specified SL. The comparison was made at the average of the maximum and minimum SL in our samples for both sexes combined. Only measurements that produced significant sign tests were used for examination of trends among species groups. These measurements are referred to as sexually dimorphic characters in the remainder of the paper. This procedure is conservative and may result in our ignoring morpho-

Table 1. Morphometric measurements, measurement codes and source for description of measurement.

Measurement ¹	Measurement code
Standard length (P)	SL
Fork length (P)	FL
Total length (P)	TL
Head length (P)	HL
Body depth at ventral fin (H)	VD
Body depth at anal fin (H)	AD
Width of base of anal fin (P)	AW
Snout length (P)	NL
Width of orbit (P)	OW
Interorbital width (P)	IW
Length of upper jaw (P)	JL
Width of pectoral fin base (P)	PW
Longest pectoral fin ray length (P)	PL
Longest pelvic fin ray length (P)	PR
Length of pelvic spine (P)	PS
Length of first anal spine (H)	AF
Length of second anal spine (H)	AS
Length of third anal spine (H)	AT
Longest anal ray fin length (H)	AL
Longest dorsal spine (H)	DS
Longest dorsal fin ray (H)	DR
Width of caudal peduncle (P)	CW
Distance between anus and anal fin (H)	AA
Longest gill raker on first arch (H)	GL

¹(P) = From Phillips (1957).

(H) = From Holt (1959).

metric measurements that actually are larger in one sex or the other. Rank sum tests (Dixon & Massey 1957) were made at the 95% confidence level to test for differences in proportions of significant sexually dimorphic characters among species groups.

The ratio of male to female SL was used as an index of sexual size dimorphism. We used the average SL of mature fish measured in this study to calculate the ratio. Rank sum tests were made at

the 95% confidence level to test differences in sexual dimorphism in size among groupings of species.

Results

Sample sizes for the morphometric measurements ranged from 11 to 192 and averaged 83. Sample size by sex and detailed results of the regressions and analyses of covariance are available from the au-

Table 2. Results of analyses of covariance testing hypotheses that relationships between morphometric measurements and standard length are independent of sex. M indicates that the measurement is significantly greater for males; F indicates that the measurement is significantly greater for females. Measurement codes are defined in Table 1.

Species	Measurement code																							
	FL	TL	HL	VD	AD	AW	NL	OW	IW	JL	PW	PL	PR	PS	AF	AS	AT	AL	DS	DR	CW	AA	GL	
<i>S. alutus</i>										M													M	
<i>S. auriculatus</i>									F	M														M
<i>S. aurora</i>	F		F																					
<i>S. babcocki</i>			F		M		M		M															
<i>S. carnatus</i>	M	M					M		M			M												
<i>S. caurinus</i>									M	M														
<i>S. chlorostictus</i>				F																				
<i>S. chrysomelas</i>	F																M		M					
<i>S. constellatus</i>					F		M							M										
<i>S. crameri</i>									M		M					M	M	M	M		M	F		
<i>S. diploproa</i>				F				M				M												M
<i>S. elongatus</i>		M	F				M	M		M												F		
<i>S. entomelas</i>									M															M
<i>S. flavidus</i>								M	M	M		M		M		M	M				M			
<i>S. goodei</i>					M			M			M	M	F								F			F
<i>S. hopkinsi</i>														F										
<i>S. jordani</i>	M	M	M	M	M	M	M	M	M	M	M	F	M	F	M			M		M			M	
<i>S. levis</i>	F	F												M							F			
<i>S. maliger</i>										M		M												
<i>S. melanops</i>			M					M	M	F		M			M			F						
<i>S. melanostomus</i>						M						M												F
<i>S. miniatus</i>										M														
<i>S. mystinus</i>				F	F			M		M	F							F	M	F				
<i>S. nebulosus</i>						M								M										
<i>S. ovalis</i>					F			M						F	F									F
<i>S. paucispinis</i>			M			M		M	M	M	M	M		M	M	F	M	M	M	M	M			
<i>S. pinniger</i>		M	M				M	M	M	M	M	M										F		
<i>S. rosaceus</i>																						M		
<i>S. rosenblatti</i>																								
<i>S. ruberrimus</i>									M	M										M				
<i>S. rufus</i>																								F
<i>S. saxicola</i>			M		F	F	M	M		M								F					M	
<i>S. semicinctus</i>		F	M								M							F		F	M			
<i>S. serranoides</i>	F	M		M	M			M	M	M		M		M					M	M		M	M	

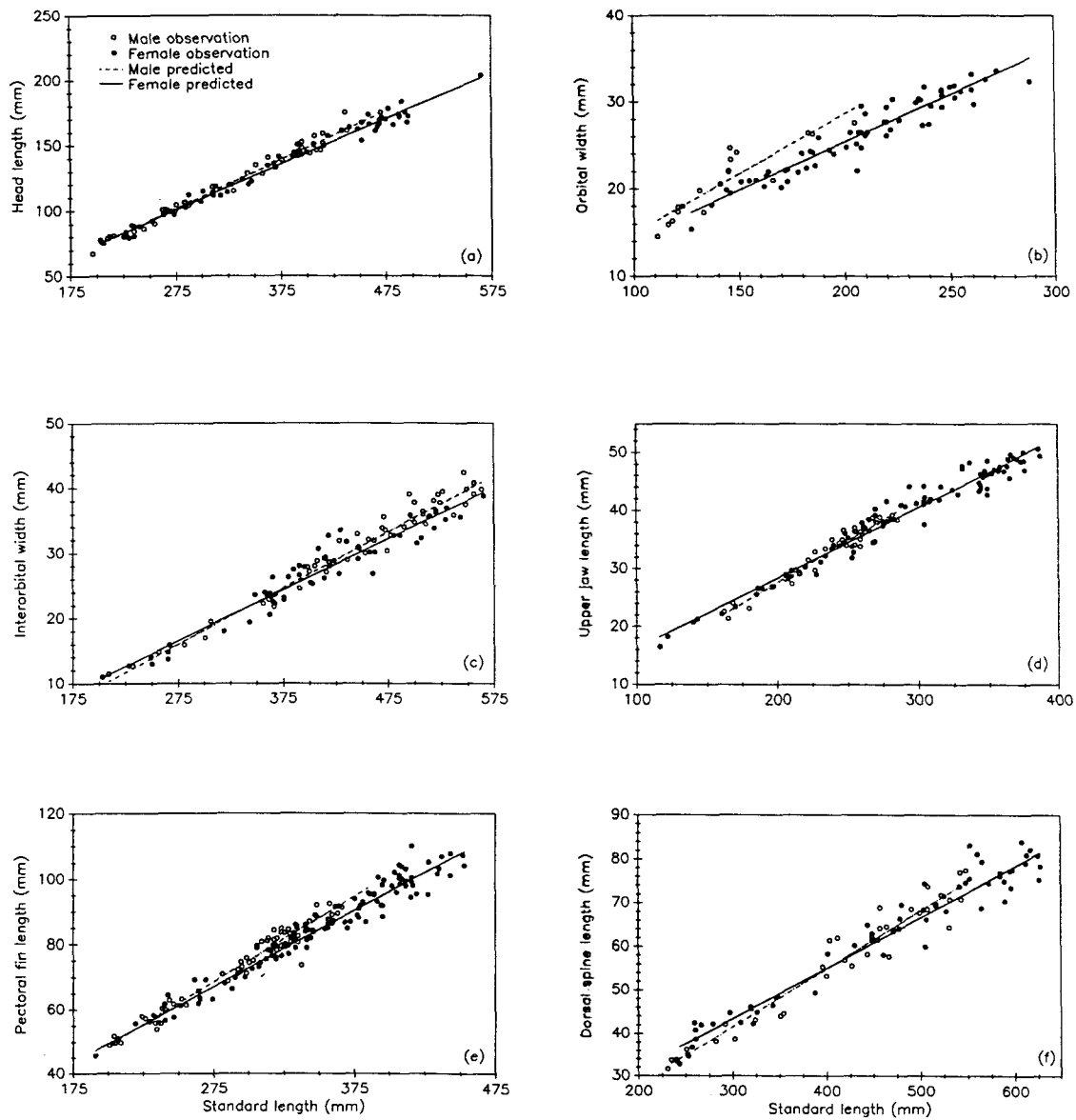


Fig. 1. Examples of relationships between sexually dimorphic characters and standard length for *Sebastes*: (a) head length for *S. pinniger*, (b) orbital width for *S. saxicola*, (c) interorbital width for *S. ruberrimus*, (d) upper jaw length for *S. mystinus*, (e) pectoral fin length for *S. flavidus* and (f) dorsal spine length for *S. paucispinis*.

thors. The analyses of covariances resulted in 166 rejections of the hypothesis that the relationship between a morphometric variable and SL is independent of sex (Table 2). This is more than three times the maximum number expected due to Type I

errors. Male measurements were usually larger than female (124 vs. 42, respectively). Sign tests indicated that males often (64 cases) have greater head length, width of orbit, interorbital width, length of upper jaw, longest pectoral fin ray and

longest dorsal spine. These six measurements are called sexually dimorphic characters and are considered in greater detail.

An example of the results is shown for each sexually dimorphic character in Figure 1. The species were randomly selected without replacement for the examples. The dimorphisms are quite noticeable in some cases, but subtle in others. The

male slope is greater than the female in all of the examples. In most examples there is considerable overlap of the dimorphic measurement between sexes for small fish.

Males are smaller than females in 27 of the 34 species (Table 3). The ratio of male to female SL tends to decrease as the number of significant sex-

Table 3. Summary of number of sexually dimorphic characters significantly larger for males than females, ratio of male to female standard length (SL) and classification. Subgenera are as summarized by Seeb (1986).

Species	Number of significant characters	SL ratio	Classification		
			behavior ¹	depth ²	subgenus ³
<i>S. aurora</i>	0	0.98	D	D	S1
<i>S. chlorostictus</i>	0	1.02	D	S	S2
<i>S. hopkinsi</i>	0	0.70	D	S	N
<i>S. levis</i>	0	0.98	D	D	N
<i>S. nebulosus</i>	0	1.05	D	S	P
<i>S. rosaceus</i>	0	1.00	D	S	S2
<i>S. rosenblatti</i>	0	0.98	D	D	S2
<i>S. rufus</i>	0	0.87	W	D	N
<i>S. alutus</i>	1	1.06	W	D	S1
<i>S. chrysomelas</i>	1	1.07	D	S	P
<i>S. constellatus</i>	1	1.10	D	S	S2
<i>S. entomelas</i>	1	0.91	W	D	N
<i>S. melanostomus</i>	1	0.94	W	D	N
<i>S. miniatus</i>	1	0.94	D	S	N
<i>S. ovalis</i>	1	0.80	W	D	N
<i>S. semicinctus</i>	1	0.84	W	D	A
<i>S. auriculatus</i>	2	0.94	D	S	N
<i>S. babcocki</i>	2	0.95	D	D	N
<i>S. carnatus</i>	2	1.02	D	S	P
<i>S. caurinus</i>	2	0.98	D	S	P
<i>S. diploproa</i>	2	0.93	W	D	A
<i>S. goodei</i>	2	0.81	W	D	N
<i>S. maliger</i>	2	0.99	D	S	P
<i>S. crameri</i>	3	0.92	W	D	N
<i>S. elongatus</i>	3	0.87	D	D	N
<i>S. mystinus</i>	3	0.86	W	S	N
<i>S. ruberrimus</i>	3	0.98	D	S	S1
<i>S. saxicola</i>	3	0.69	W	D	A
<i>S. flavidus</i>	4	0.93	W	S	S3
<i>S. jordani</i>	4	0.87	W	D	N
<i>S. melanops</i>	4	0.91	W	S	S3
<i>S. pinniger</i>	5	0.94	W	S	N
<i>S. serranooides</i>	5	0.93	W	S	S3
<i>S. paucispinis</i>	6	0.92	W	D	N

¹W = water-column and D = demersal.

²S = shallow and D = deep.

³A = *Allosebastes*, N = not classified, P = *Pteropodus*, S1 = *Sebastes*, S2 = *Sebastomus* and S3 = *Sebastosomus*.

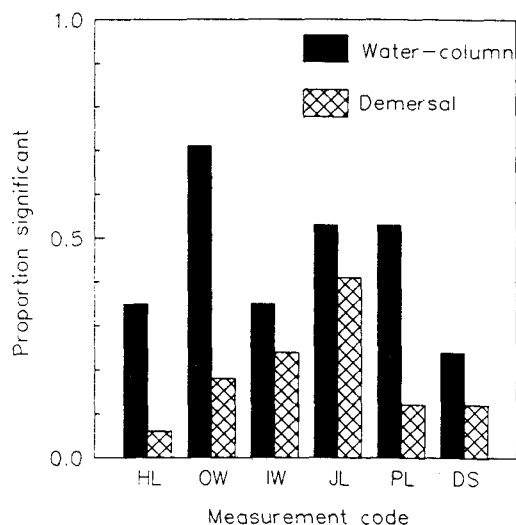


Fig. 2. Proportion of significant differences in sexually dimorphic characters of water-column and demersal species of *Sebastes*. Measurement codes are defined in Table 1.

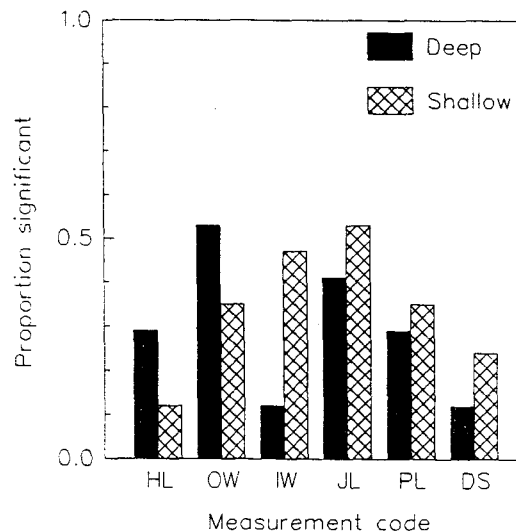


Fig. 3. Proportion of significant differences in sexually dimorphic characters of deep and shallow species of *Sebastes*. Measurement codes are defined in Table 1.

ually dimorphic characters increases, but a rank sum test was not significant.

Species were classified into two ecological dichotomies: water column or demersal and deep or shallow (Table 3). The two classifications are not independent. Most water-column species are deep, and most demersal species are shallow. A species is considered demersal if it seldom leaves the proximity of the bottom. A species is considered a deep species if adults are relatively common deeper than

125 m. These classifications are based on our knowledge of the species, and some judgment is involved. Love et al. (1991) independently classified 26 of the species of our study into ecological categories and divided the species into finer categories than we did. If their categories are combined into ours, the two studies similarly categorize species.

The average SL ratio of male to female is 0.89 for water-column species and 0.97 for demersal. The

Table 4. Average ratios of male to female standard length (SL) and number of significant sexually dimorphic characters per species for rockfish classified into water-column-deep, water-column-shallow, demersal-deep and demersal-shallow categories.

	Deep	Shallow	All species
<i>Water-column</i>			
Number	12	5	17
SL ratio	0.88	0.91	0.89
Number of dimorphic characters	2.08	4.20	2.71
<i>Demersal</i>			
Number	5	12	17
SL ratio	0.95	0.98	0.97
Number of dimorphic characters	1.00	1.17	1.12
<i>Total</i>			
Number	17	17	34
SL ratio	0.90	0.96	0.91
Number of dimorphic characters	1.76	2.06	1.91

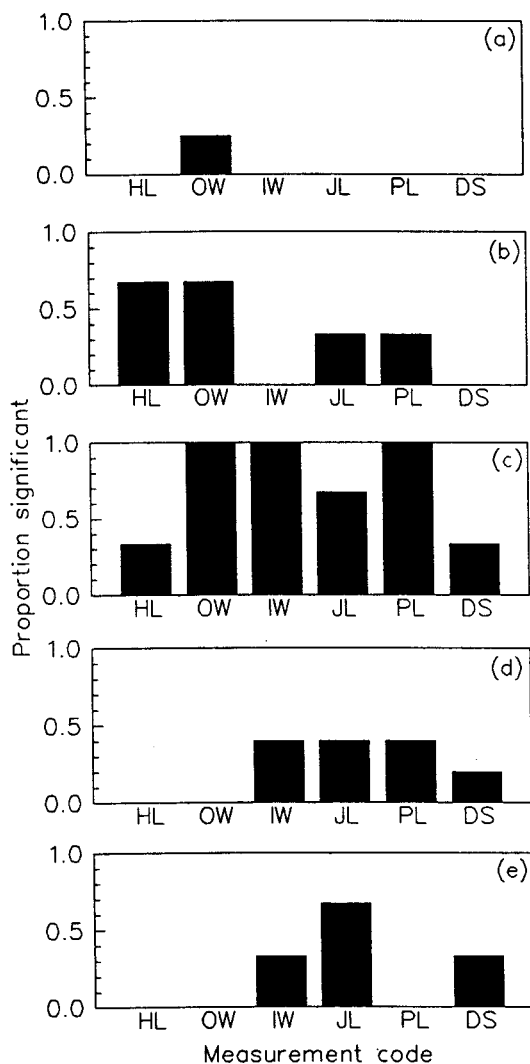


Fig. 4. Proportion of significant differences in sexually dimorphic characters of subgenera of *Sebastes*: (a) *Sebastomus* (b) *Allosebastes*, (c) *Sebastosomus*, (d) *Pteropodus* and (e) *Sebastes*. Measurement codes are defined in Table 1.

difference is significant. The proportion of significant differences in each of the sexually dimorphic characters is consistently greater among the water-column than in the demersal species (Fig. 2). The difference between the two groupings is significant. The differences in proportion are greatest for orbital width and pectoral fin length. The average ratio of male to female sizes is 0.90 for deep species and

0.96 for shallow species. The difference is significant. Shallow species are more often dimorphic for interorbital width than deep species (Fig. 3). However, the proportion of significant differences for the six characters is not significantly different between shallow and deep species.

The variation in the proportion of significant sexually dimorphic characters is significant between demersal and water-column species, but not so between shallow and deep species. While the difference in average size ratio is significant between shallow and deep species, within the water-column and demersal groupings the differences between deep and shallow species are minor (Table 4) and not significant. Thus sexual dimorphism does not appear to be related to the water depth classification.

Species were grouped into classical subgenera as summarized by Seeb (1986) from the literature for some of the species of our study (Table 3). Her biochemical analysis supported the *Sebastomus*, *Sebastosomus* and *Pteropodus* subgenera, but did not support *Allosebastes* and *Sebastes* well. We found the lowest average SL ratio of male to female size for *Allosebastes* (0.82) and the highest ratio for *Sebastes* (1.07). The ratio was 0.92 for *Sebastosomus* and 1.02 for *Sebastomus* and *Pteropodus*. *Sebastomus* had almost no significant sexually dimorphic characters, and *Sebastosomus* had many (Fig. 4).

All but one species (*S. alutus*) in *Sebastomus*, *Pteropodus* and *Sebastes* are demersal, and these three subgenera are not very dimorphic (Table 3 and Fig. 4). All species in *Allosebastes* and *Sebastosomus* are in the water-column group. The two subgenera are relatively dimorphic compared to the other three. *Allosebastes* is more dimorphic in size than *Sebastosomus*, and the converse is true for the proportion of sexually dimorphic characters (Fig. 4). The number of species in each subgenus is too small to test for differences in dimorphism.

Discussion

Wyllie Echeverria (1986) found sexual dimorphisms in the four species that she studied: *S. flavi-*

du, *S. melanops*, *S. mystinus* and *S. serranoides*. The four species are water-column species, and all but *S. mystinus* are in the subgenus *Sebastosomus*. Females of these species reached a larger size than males. Wyllie Echeverria (1986) attributed the dimorphism in size to the fact that larger females produce more eggs. The data available at the time of her study indicated that males mature younger than females. Ostensibly, the younger age of maturity would provide males with more mating opportunities. She argued that increased sperm production resulting from increased size is not as important as increased opportunities to mate.

Many authors have advanced similar arguments for other groups of animals, but there are questions on the validity of the arguments. Shine (1988) showed that in some groups females are larger than males even though fecundity or egg volume is unrelated to size.

Our study, using data on more species than available to Wyllie Echeverria (1986), shows that many species of *Sebastes* are not dimorphic in size. Moreover, males do not always mature at an earlier age than females. Males of only 10 of 31 species studied by both Wyllie Echeverria (1987) and us matured earlier than females. In most species both sexes matured at the same age. Thus the size advantage for egg production is not the only factor related to sexual size dimorphism observed in some species of *Sebastes*. Of the species that exhibited early male maturity, the average ratio of male to female size is 0.94. The average ratio is 0.93 for the other species. The increased spawning opportunity hypothesis for early maturing males does not seem to hold for all species.

There is a considerable difference in the average ratio of male to female size for water-column (0.89) and demersal (0.97) species of rockfish. Demersal species, apparently both sexes for some species, have been observed to defend territories (Hallacher 1977, Haaker 1978, Larson 1980, Shinomiya & Ezaki 1990). Shinomiya & Ezaki (1991) observed male *S. inermis* defending territories during the mating season and that larger males had larger territories. Females did not appear to defend territories.

Aggressive behavior is rarer for water-column

species, and agonistic interactions of any kind seem to occur mainly during the mating season (E. Hobson personal communication). Helvey (1982) observed courtship behavior of *S. mystinus*, a water-column species, during which males were active and females inactive. Helvey (1982) observed what appeared to be aggressive encounters between males when they were associated with a female, but he observed no physical contact between males. The courtship behavior of *S. mystinus* as described by Helvey (1982) was not as elaborate as that of *S. inermis*, a demersal species, as described by Shinomiya & Ezaki (1991).

While observations on territorial and mating behavior of *Sebastes* are limited to a few species, variations have been found. These variations may be related to the differences observed in sexual dimorphism. Territorial behavior has now been observed for several demersal species. In one species males are more territorial than females; in other species sexual differences in territoriality have not been observed. Since larger males have been observed to hold larger territories, the tendency for the ratio of male to female SL to be high for demersal species may be related to an increased tendency for territorial behavior by demersal males. The tendency for the ratio of male to female SL to be low for water-column species may be related to the reduced tendency for territorial behavior by water-column males and a cost due to large size. Recent work on *S. jordani* indicates that old specimens are smaller than middle aged specimens of this unexploited species (D. Pearson personal communication). This result suggests that survival is relatively low for faster growing individuals.

In summary variations of dimorphism in size may be the consequence of trade-offs between the relationship between fecundity and size, the relationship between territory size and fish size and the cost of large size.

Wyllie Echeverria (1986) developed arguments that the relatively large size of pectoral fins and eyes of males of the four species she studied are compensation for reduced size. These relatively large parts could aid males in competing with females for food.

We found that six measurements are relatively large for males. These measurements may be related to feeding ability. The maximum size of dietary items probably is related to length of upper jaw, head length and perhaps interorbital width. The width of the orbit probably is related to the ability to detect food items. Swimming ability, particularly the ability to maneuver for capturing food, is probably related to length of the pectoral fin ray and perhaps the largest dorsal spine. Hobson & Chess (1978) argue that long fin spines found in some planktivores provide a defense against predation when feeding in the water column.

For some species, e.g. *S. entomelas*, *S. ovalis* and *S. rufus*, there is considerable dimorphism in size, but no or only one significant sexually dimorphic character. Conversely *S. ruberrimus* is not dimorphic in size, but male interorbital width, upper jaw length and dorsal spine length are relatively large. Thus it appears that sexually dimorphic characters in rockfish are related to factors other than or in addition to compensation for reduced size of males.

Perhaps the dimorphisms are related to either male mating behavior and/or territorial behavior. Fins are parts of aggressive displays. Relatively large fins and eyes tend to make a fish look larger than it really is. Rockfish have been observed in combat on rare occasions in which the combatants are mouth-locked. Haaker (1978) observed one combatant partially swallowing another. This behavior suggests that large head parts would tend to aid males in territorial behavior for species in which males are territorial. The courtship behavior observed by Helvey (1982) and Shinomiya & Ezaki (1991) suggests that the six relatively large parts could cause subtle advantages in courtship.

In summary the observed differences in dimorphisms in morphometric measurements may be related to compensation in feeding ability for reduced SL of males and territorial and mating behavior.

We believe that further research on sexual dimorphisms of rockfish would be fruitful. While we are confident that the trends we have noted are valid, it would be desirable to increase the sample size of some of the species in our study. It would

also be interesting to verify that the trends we observe extend to other species of rockfish. More behavior studies on nearshore species should lead to a better understanding of the factors related to sexually dimorphic characters.

As we observed in the Introduction, sexual dimorphism is a very interesting subject and explanations for causes appear to be complex. While we do not expect final explanations to be developed soon, we do expect that pursuit of the explanations will lead to a better understanding of factors that affect the life history and population dynamics of rockfish.

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