Sexual dimorphism in four species of rockfish genus *Sebastes* (Scorpaenidae)

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Keywords: Morphology, Sexual selection, Natural selection, Parental care, Discriminant analysis

Synopsis

Sexual dimorphisms, and factors influencing the evolution of these differences, have been investigated for four species of rockfish: *Sebastes melanops, S. flavidus, S. mystinus*, and *S. serranoides*. These four species, which have similar ecology, tend to aggregate by species with males and females staying together throughout the year. In all four species adult females reach larger sizes than males, which probably relates to their role in reproduction. The number of eggs produced increases with size, so that natural selection has favored larger females. It appears males were subjected to different selective pressures than females. It was more advantageous for males to mature quickly, to become reproductive, than to expend energy on growth. Other sexually dimorphic features include larger eyes in males of all four species and longer pectoral fin rays in males of the three piscivorous species: *S. melanops, S. flavidus*, and *S. serranoides*. The larger pectoral fins may permit smaller males to coexist with females by increasing acceleration and, together with the proportionately larger eye, enable the male to compete successfully with the female to capture elusive prey (the latter not necessarily useful for the planktivore *S. mystinus*). Since the size of the eye is equivalent in both sexes of the same age, visual perception should be comparable for both sexes.

Introduction

Natural selection is a mechanism of evolution which can influence physical characteristics of a species, characteristics which reflect selective pressures in the species environment. Sexual selection is a component of natural selection that acts independently upon males or females. Sexual dimorphism can result from either component.

Sexual dimorphisms, which occur in every major group of vertebrates, are commonly manifested in mammals as size differences, in birds as color variations, in reptiles as defensive structures, and in amphibians as sounds. Fishes of both fresh and salt water also exhibit sexual dimorphisms: in swordtails (*Xiphophorus* sp.) and gobies (*Gobius* sp.) as fin variations, in guppies (*Poecilia* sp.) and wrasses (*Labrus* sp.) as color variations, in eels (*Anguilla* sp.) and mullets (*Mugil* sp.) as size differences, and in silurids (*Ompok* sp.) (Rao & Karamchandani 1971) and sculpins (*Myoxocephalus* sp.) as morphological variations in body proportions (Breder & Rosen 1966).

In fishes, secondary sexual dimorphisms are often associated with species that have internal fertilization or protection of the eggs or young by a parent (Breder & Rosen 1966). Despite the widespread relationship between internal fertilization and secondary sexual dimorphism, one of the most speciose groups of live bearers in the northeast

Pacific Ocean, the rockfishes (*Sebastes*) with approximately 70 species occurring in that region, does not show obvious sexual dimorphisms.

Four species of *Sebastes* were studied: *S. melanops*, the black rockfish; *S. flavidus*, the yellowtail rockfish; *S. mystinus*, the blue rockfish; and *S. serranoides*, the olive rockfish. All four species are very similar in body shape and size, with convex interorbital spaces, weak head spines and a dusky olive-to-black coloration, all key characters used in the identification of rockfish (Miller & Lea 1976). Similarities include morphologies and reproductive characteristics while they are separated ecologically by different diets, feeding times, and depth distributions. These four species have been studied more than other rockfish because they comprise a large part of the commercial and sport-fishing landings, and are readily accessible in large aggregations near shore.

In *Sebastes* the contribution to the survival of young is primarily accomplished by the female. Fertilization is internal with possible storage of sperm by the female (Sorokin 1967). During gestation the arterial supply to the gonad serves for the exchange of metabolic wastes (Moser 1967) and the ovarian fluid provides some nutrition for the developing embroys (Boehlert & Yoklavich 1984). Fecundity varies among species, but is always large, increasing with the size of the female (Phillips 1964, Boehlert et al. 1982), with some species possibly having two broods per year (Moser 1967, MacGregor 1970). In *Sebastes*, selection has favored increasing reproductive success by means of large females capable of producing and accommodating large numbers of embryos.

The only reports of morphological differences between sexes of *Sebastes* are provided by Chen (1971) and Moser (1967). Chen found sexual dimorphism in *Sebastes umbrosus*, with males having a shorter pre-anal length but a greater anal base, upper jaw length, anal ray length, snout length and prepelvic length ($P<0.01$). Moser noted differences in the urogenital papilla of *Sebastodes paucispinis*. In this investigation body measurements taken from four species of rockfish have been analyzed to determine (1) if Chen's findings are more widespread, (2) if there are morphological differences between the sexes of any one species that could be used, in themselves, to characterize the sexes, and (3) if there are differences, what their significance might be.

Working within the definitions of selection that have been made here, an attempt will be made to discern which component – natural or sexual selection – may have exerted the greater influence in any sexually dimorphic feature found in these four species of *Sebastes*. Natural selection will be credited for those features that primarily affect the survival of the entire species, while sexual selection will be limited to those features that affect the reproductive advantage of one individual over another.

Methods

Rockfish were collected throughout 1977 from three localities along the coast of central California: Point Reyes, the Farallon Islands, and Cordell Bank (Fig. 1). These localities lie at the corners of a triangle covering roughly 250 square miles. This relatively limited area was chosen because Miller & Geibel (1973) showed that growth rates in blue rockfish from widely separated geographic areas differed. Fish used in the morphometric study were collected as part of a survey of age and length in the rockfishes of central California (Sen 1984), and constitute a subsample of the fish used in that survey.

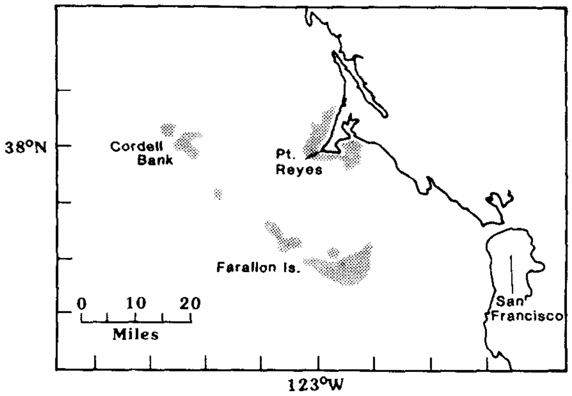

Fig. 1. Rockfish in this study were collected from Pt. Reyes, the Farallon Is. and Cordell Bank where the depth was <40 fathoms.

Specimens were collected from the hook-and-line sportfishing fleet. Fish were filleted on board the fishing boat, and the carcasses were collected and handled in a standardized way to reduce the variability in measurements which occurs between whole fish and carcasses or fresh and frozen fish (Forrester 1967). In the laboratory the otoliths (Sagitta) were collected, the gonad state was determined, and 23 body parts, in addition to standard length, were measured.

Ages of the four species were determined by counting one opaque and one translucent zone of the otolith. Annular growth increments were validated up to 12 years in the black rockfish by Six & Horton (1977), up to 12 years in the yellowtail rockfish by Kimura et al. (1979), and up to 4 years in the olive rockfish by Love & Westphal (1981). Ages of blue rockfish have been determined from scale annuli and comparison between the growth zones of the otoliths and scales showed similiar patterns (Miller & Geibel 1973). All researchers agreed that, for the ages studied, one opaque and one translucent zone are deposited per year. Fish collected in this study also included individuals older than those from previous studies and it was assumed the reliability of the annual marks continued beyond the ages obtained in previous studies.

The average length of the males and females at each age was used to compare growth rates between the sexes. The comparisons were made from all fish sampled (Table 1).

Sex and the stage of gonadal development were determined in the laboratory. Sexes were identified by gonadal inspection: ovaries were characterized by an egg mass encased by the ovarian wall while the testis were characterized by appearing solid in cross-section. Ovaries were classified as: immature, with developing eggs, eggs containing eyed embryos or spent. Testis were classified as: immature, undergoing spermatogenesis, or spent. Gonad states of specimens collected throughout the year were used to determine the reproductive seasonality.

Morphometric measurements were made with vernier calipers (±0.01 mm) on freshly thawed fish carcasses. The 24 body parts measured included: total length, fork length, standard length, head length, length of the base of the anal fin, snout length, interorbital width, width of the orbit, length of the upper jaw, lower jaw projection, width of the pectoral fin base, longest pectoral fin

Table 1. Mean standard length (mm) at age for males (M) and females (F) in four species of rockfish collected during 1977. Numbers (N) of individuals used to calculate length in parentheses.

Age (yr)	*S. melanops*				*S. flavidus*				*S. mystinus*				*S. serranoides*			
	M	(N)	F	(N)	M	(N)	F	(N)	M	(N)	F	(N)	M	(N)	F	(N)
4			283	(4)	235	(4)	227	(8)	189	(3)						
5	288	(3)	294	(7)	259	(8)	259	(13)	229	(9)	234	(4)	258	(3)	283	(1)
6	326	(18)	320	(22)	282	(5)	282	(3)	233	(10)	267	(19)	294	(21)	304	(3)
7	352	(25)	336	(14)	300	(11)	303	(10)	256	(11)	270	(20)	313	(12)	338	(13)
8	377	(21)	383	(10)	309	(15)	326	(18)	265	(11)	294	(15)	321	(13)	339	(13)
9	383	(22)	395	(18)	323	(17)	330	(16)	268	(13)	302	(15)	336	(3)	365	(9)
10	388	(20)	402	(10)	331	(21)	340	(23)	275	(12)	315	(14)	349	(3)	389	(11)
11	405	(14)	423	(4)	339	(35)	357	(26)			323	(11)			417	(7)
12	401	(7)	420	(4)	352	(28)	361	(34)			348	(11)			419	(2)
13	393	(7)	420	(3)	358	(20)	361	(40)			358	(11)				
14					364	(12)	383	(40)			342	(6)				
15					388	(4)	398	(20)			373	(3)				
16							398	(11)			353	(2)				
17							410	(7)			366	(4)				
Total (N)		137		96		180		269		69		136		56		59

ray, longest pelvic spine, and the longest pelvic ray following the procedure described by Phillips (1957); the longest dorsal ray, longest dorsal spine, the lengths of the three anal spines, and the longest anal ray measured from the posterior point of insertion, the longest gill raker on the first arch, body depths at the ventral fin and anal fin, and distance between the anal pore and the anterior insertion of the anal fin following the method of Holt (1959).

Morphometric measurements were subsampled for fish from throughout the size ranges used in the age-length determinations. An attempt was made to measure five fish from each centimeter-interval of total length so that 100–200 fish of each species were represented in the sample. Regressions were used to determine the relationships between 23 body parts regressed against standard length. Analysis of covariance was used to test for significant differences ($P<0.01$)) in the body parts between males and females.

Ontogenetic changes in proportions of the 23 body parts regressed against standard length were also evaluated. By taking the mean standard length at each age from the age-length curve and the regressions the body part size at each age was estimated.

A computer program for discriminant analysis (Nie et al. 1975) was used to determine the probability that sex could be identified, for a particular species, when given only body-part measurements.

Results

In all four species, females were larger than males of the same age after 5–7 years of age (Table 1). The differences were only significant ($P<0.01$) in the blue rockfish, however, a trend can be seen of females getting bigger and living longer than the males even with the small sample size used. This trend agrees with other growth studies for these species (Miller & Geibel 1973, Six & Horton 1977, Love & Westphal 1981).

The linear regressions for the morphometrics showed that a number of body parts differed significantly between the sexes ($P<0.01$) (Table 2). When 23 independent measurements are analyzed for significant differences there is a fairly high probability that, by chance alone, at least one measurement will show significant differences:

$$P = 1-0.99^{23} = 0.21.$$

The probability of two or more significant differences due to chance alone is considerably lower:

$$P = 1-0.99^{23} - \frac{23!}{22!}(0.01)(0.99)^{22} = 0.02.$$

This study showed two to four significantly different body parts per species (Table 2). Body parts which differed by sex in at least one species were: upper jaw length, pelvic spine length, longest anal ray, first anal spine length, longest dorsal ray and orbit width. Two of these body parts were significantly different in at least three of the species (Table 2). The orbit width which was larger relative to standard length in males of all four species, and the longest pectoral fin ray was larger relative to standard length in males of the black, yellowtail and olive rockfishes. Sexual dimorphisms do exist in additional species of *Sebastes* than previously documented (Chen 1971) although the differences are slight (Echeverria 1980).

Ontogenetic studies showed a proportional increase in length or width with respect to growth and these changes often differed for the two sexes. For example, a longer upper jaw and a longer anal spine occurred in males of *Sebastes melanops*. The striking finding was that, in all four species studied, the orbit width and the pectoral fin ray length were related to age so that males and females of the same age had orbits the same width and pectoral fins rays the same length (Table 2). These results indicate that there are some real, although subtle, differences in the growth rates of some body parts.

Discriminant analysis yielded correct assignments of fish to sex of 70% of black rockfish, 75% of yellowtail rockfish, 89% of blue rockfish and 79% of olive rockfish (Table 3). All fish in the analysis were used to estimate the discriminant function; then each fish is assigned a sex based upon the measurements of certain body parts and their respective discriminant values. A sample of fish not used in the analysis were assigned sex based on the relevant body parts. Correct assignments of fish to sex were 74% in black rockfish, 80% in yellowtail rockfish, 92% in blue rockfish

Table 2. Significant ($P<0.01$) sexual dimorphisms in the size of body parts, as related to standard length and to age, in four species of *Sebastes*. In the case of significant differences, the sex with the larger body part is listed.

Body part	*S. melanops*	*S. flavidus*	*S. mystinus*	*S. serranoides*
Anal spine 1				
age				
SL	male			
Pelvic spine				
age		male		
SL		male		
Pectoral fin ray				
age		male		
SL	male	male		male
Anal depth				
age			female	
SL			female	
Anal ray				
age			female	
SL			female	
Dorsal ray				
age			female	
SL			female	
Orbit width				
age				
SL	male	male	male	male
Upper jaw				
age	female			
SL	male			

and 60% in olive rockfish (Table 3). It is clear that there are some statistically significant differences in the body proportions, but, because of the variability in the measurements, and the values of percent agreement, no combination of the measured body parts can be used to adequately predict the sex of these fish.

Rockfishes tend to aggregate by species with the sexes in the same aggregations. Hallacher (1977) studied kelp-bed inhabiting species of rockfishes and found that each species apparently occupied a particular space in the water column with regard to depth and bottom type. In addition to having various spacial localities the species occur in different geographic areas. On the sport-fishing trips sampled in this study, the species were not of equal abundance at the various collection localities (Table 4). When a species occurred both sexes were present. The sampling technique does not allow for a critical examination of the relationship between the sexes in an aggregation. There is no indication that males and females segregate into different areas, however, the sex ratios may exhibit some seasonal variability. It appears that, for the most part, both sexes of a species inhabit the same area, occurring together in aggregations.

Discussion

The study of a species' morphology can provide insight into its natural history, particularly with regard to selective pressures in its environment. In this study, 23 key morphological features of four species of rockfish were examined in an attempt to identify previously undescribed sexual dimorphisms. These morphological data, when combined with known aspects of the life history of these species, provide clues to the evolution of sexual dimorphism in rockfishes.

Sexual size dimorphism is usually attributed to sexual selection, having evolved with respect to

Table 3. Discriminant values used to assign sex from morphometric data in four species of rockfish, the percent predictability from the analysis, and a test sample of other fish.

Body part	Discriminant value
S. melanops	
predictability (N = 136) = 70%	
test cases (N = 31) = 74%	
Standard length	0.0424
Orbit width	0.1303
Upper jaw	0.1117
Pectoral ray	−0.2024
First anal spine	−0.2658
constant	4.1921
male centroid	−0.5215
female centroid	0.3622
S. flavidus	
predictability (N = 113) = 75%	
test cases (N = 24) = 80%	
Standard length	−0.0609
Pectoral fin	−0.1524
Orbit	−0.1674
Pelvic spine	0.1590
constant	3.4183
male centroid	−0.5471
female centroid	0.4471
S. mystinus	
predictability (N = 193) = 89%	
test cases (N = 45) = 92%	
Anal depth	−0.1416
Orbit	0.3884
Dorsal ray	0.0935
Standard length	0.0019
Anal ray	0.0096
constant	6.9223
male centroid	1.5198
female centroid	−1.0573
S. serranoides	
predictability (N = 127) = 79%	
test cases (N = 20) = 60%	
Standard length	0.0601
Pectoral ray	0.1437
Orbit	−0.1377
constant	−4.5387
male centroid	−0.5634
female centroid	0.8628

Table 4. Distribution of the sample for the four species of rockfish used in the age-length study; the area they were fished and the number of males (M) or females (F) sampled.

	Point Reyes		Farallon Is.		Cordell Bank	
	M	F	M	F	M	F
S. melanops	137	96	0	0	0	0
S. flavidus	24	49	46	98	119	113
S. mystinus	38	64	31	72	0	0
S. serranoides	2	4	51	53	3	2

reproductive success. This is observed in many mammals where larger males have evolved due to competition for females (Darwin 1871). In the rockfishes studied here, males were smaller than females, which is often the case with invertebrates (Darwin 1871) and many poikilotherms (Shine 1979, Ghiselin 1974), where sexual selection favors males diverting energy from growth into reproduction at an earlier age than females.

Sexual size dimorphism has been shown to occur in many species where there is a different age of maturity for males and females (Wilson 1975). In some species, size dimorphism has been correlated with a later onset of maturity in males (Wiley 1974, Ghiselin 1974). In rockfishes exhibiting size dimorphism the situation appears to be reversed. Where size dimorphism occurs in *Sebastes* males are smaller than females, with different growth rates between males and females tending to occur after the fish are 6 to 8 years old (Westrheim & Harling 1975). For the yellowtail rockfish, *S. flavidus,* sufficient data exist to correlate the differential growth rates with sexual maturity. Using information from the same sample of yellowtail rockfish, Fraidenburg (1980) obtained growth curves and Gunderson et al. (1980) obtained size at sexual maturity. On the average, male yellowtails mature at 407 mm fork length and 8 years of age. Females mature later, when they average 450 mm fork length and 10 years of age. The size of an average 10 year old male is about 430 mm. Growth slows down at maturity so that males grow more slowly after 8 years whereas growth in females does not slow until around 10 years. After the initial change in growth rates an average difference of about 20 mm remains constant, which agrees with results found for yellowtail rockfish examined in this study (Table 1). Growth curves for the other species in this study show that males are smaller than females. This occurs after age 7 in black rockfish (Six & Horton 1977), after age 5 in blue rockfish (Miller & Geibel 1973), and after age 4 in olive rockfish (Love & Westphal 1981). Sexual size dimorphism in black, blue and olive rockfishes probably also correlates to differing ages at which sexual maturity is attained by males and females.

The widespread occurrence of sexual selection and its effect on sexual dimorphism is often related to a species' mating system and the degree of parental investment (Wilson 1975). The evolution of parental care results in an increase in the survival of young (Balon 1984). Perrone & Zaret (1979) proposed that parental care by males occurs when paternity is insured, as in nestspawning fishes where the male guards the nest of eggs after fertilization. Parental care by females usually occurs before fertilization while yolk reserves are built up, or after fertilization if she retains the fertilized eggs.

Larger females and smaller males in *Sebastes* can be understood in terms of differential parental investment. Females, by retaining the fertilized eggs until young are ready to actively feed orally, contribute to the care and protection of the young. Also, the numbers of eggs produced increases with size; therefore, larger females release more young and contribute more to the gene pool. Natural selection favors larger females. In *Sebastes* with internal fertilization and retention of the embryos, the female makes the greatest parental investment, with investment by males limited to contributing sperm.

Sexual size dimorphisms are predicted by Trivers' (1972) theory which suggests, for homeotherms, that males will compete among each other for females if females are more involved with the offspring's survival than males. This results in males being subject to selective pressures directly related to this competition, with larger more aggressive males being favored. Observations of premating by the blue rockfish did not indicate aggressive behavior among males (Helvey 1982), suggesting that sexual size dimorphism in *Sebastes* does not result from male competition for females. There is, however, another possible battleground besides aggressive behavior among males, and that is if the opportunity exists for the sperm to compete. In *S. alutus* there is a possibility that multiple mating occur (Lisovenko 1970). Males may thus be competing by copulating more frequently. With multiple mating and the storage of sperm by females, intraovarian competition between the sperm of different males may contribute to the earlier maturity of males, the advantage of being reproductive earlier relating to sperm production and outweighing any disadvantage related to smaller size (Warner & Harlan 1982). Warner & Harlan suggest sexual selection is responsible for the smaller size of males in the livebearing dwarf surfperch, *Micrometrus minimus*. Similar sexual selection may be responsible for the smaller males found in some species of *Sebastes*.

Sexual dimorphisms exhibited as morphological differences have recently been shown to exist in groups of marine fishes previously not known for dimorphic features (Gordina et al. 1974, Grant et al. 1977). The differences in body form in the species studied here were slight, but statistically significant, and were a result of different growth rates of the body parts.

The disproportionate body parts in male *Sebastes* cannot, based on the available evidence, be firmly attributed to sexual selection. The relatively large eye might be useful in locating females or perceiving visual displays for mating. Fin dimorphisms may be used in sexual displays; however, not enough is known about the behavior of *Sebastes* spp. to relate these differences to sexual behavior. Perhaps they evolved not from sexual interactions but from sexes of different sizes occupying the same habitat, that is, males coexisting with females larger than themselves. How the dimorphisms relate to possible functional advantages will be discussed for the two most common dimorphisms, the orbit width and the length of the pectoral fin ray.

Growth rate of the orbit is equal in males and females (Table 2). Since females grow faster, males have a larger orbit for their size. If the width of the orbit reflects the overall size of the eye, then the eye in males and females of the same age is comparable regardless of the size of the fish. The internal structure of the eye varies widely among species of fishes and is adapted to a particular habitat (Munz 1971). The organization of a fish's eye varies to perceive size, brightness, color, distance, orientation, and motion (Ingle 1971). Predaceous fishes, for instance, have larger eyes which increases visual acuity enabling them to detect motion better (Walls 1967). In the black, yellotwail, blue, and olive rockfishes the eyes of males, although proportionately larger, are probably functionally equivalent to females of the same age. This suggests strong selective pressure favoring visual 'equivalence' between the sexes, presumably related to foraging and avoiding predators.

In higher teleosts, the main functions of pectoral fins are to control orientation during swimming, to maintain a stationary position in the water column (less important in fishes with swim bladders such as *Sebastes*), and to accelerate from a standing start (Gosline 1971). Species of *Sebastes* that aggregate in the water column frequently hover in one location (Hobson & Chess 1976, Hallacher 1977, Moulton 1977). In this situation, the pectoral fin may be used to remain stationary within an aggregation and to assist in thrusts toward prey. Presumably thrust speed would be less important to planktivores (blue rockfish) and, accordingly, may account for pectoral fin ray dimorphism occurring only in the three more piscivorous species (black, yellowtail, and olive rockfishes). The pattern suggests that this characteristic may be a response to the smaller males' need to compete with larger females for elusive prey since they apparently aggregate together (Table 4). In fact, the black rockfish (Moulton 1977), the yellowtail rockfish (Pereyra et al. 1969), the blue rockfish (Miller & Geibel 1973) and juvenile olive rockfish (Hobson & Chess 1976) primarily aggregate by species.

Separation of the sexes for part of the year occur in *S. marinus* (Sorokin 1961) and *S. alutus* (Westrheim 1970, Gunderson 1974). Possible spawning migrations for the black rockfish was indicated by four females in the gravid and recently spawned condition collected offshore in the central north Pacific (Dunn& Hitz 1969). Since the evidence is sparse that the sexes do separate, the species in this study probably co-occur, feeding, seeking shelter, and avoiding predators together.

Since all four species form aggregations; the advantages of associating appear to outweigh disadvantages that may arise due to size disparity between the sexes in the same aggregation. Aggregations are a good defense against predators, providing a confusion of darting bodies that makes it difficult for a predator to home in on a particular prey (Hobson 1978). Being in aggregations also increases the habitat available to a species; hiding places are not necessary because the aggregation serves the purpose (Hamilton 1971). Finally aggregating also helps keep the sexes together during a long mating season. Courtship and insemination in *Sebastes* apparently occurs over a period of at least a month, with extrusion of the young in any one species occurring during at least a 2 month period.

Acknowledgements

I wish to thank Kathy Fourre for her assistance in collecting and measuring the fish, Nancy Wiley for support with the computer analysis, and Margaret Bradbury and Bill Lenarz for their encouragement, guidance and helpful criticisms throughout this study.

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Received 13.9.1984 *Accepted 28.5.1985*