THIRTY-FOUR SPECIES OF CALIFORNIA ROCKFISHES: MATURITY AND SEASONALITY OF REPRODUCTION

TINA WYLLIE ECHEVERRIA[1]

ABSTRACT

The viviparous rockfishes (*Sebastes* spp.) differ among species in age and size at maturity, and in the timing of peak spermatogenesis, fertilization, and larval extrusion. Age at 50% maturity ranges from 2 years in *S. jordani* to 9 years in *S. diploproa*. Within species, males usually mature either at the same age and size as females or at a younger age and smaller size. Rockfishes have two major seasons of larval extrusion, winter (November-March) or spring (April-July). The reproductive season for a particular species will fall within one of the major seasons throughout its geographic range. Within the major season, annual variations in the peak month of larval extrusion was observed for individual species. A long reproductive season and variations in the annual timing of that season are evidence of plasticity in the reproductive biology of rockfishes.

Reproductive development at the cellular level was compared with the coincident changes in the gross morphology of the gonads. The resulting description of the developmental sequences of the testes and ovaries enables the determination of maturity stage in the field.

Reproductive parameters such as age and size at maturity have been shown to be adaptive characteristics and are responsive to external pressures. For example, reduced population size due to fishing pressure may be associated with increased growth rate, reduced age at maturity, decreased fecundity, or a change in the gonadal index (Adams 1980; Gunderson 1980). For haddock, *Melanogrammus aeglefinis*, age at maturity was reduced and growth rates increased as the fishery increased (Templeman and Bishop 1979; Beacham 1983). Clupeoids shifted spawning location or time, and reduced age at maturity (Murphy 1977; Blaxter and Hunter 1982). A study of depleted populations of Pacific mackerel, *Scomber japonicus*, suggested a direct relationship between population size and age at maturity (Parrish and MacCall 1978). Pacific halibut, *Hippoglossus stenolepis*, stocks also showed reduced age at maturity and increased growth rates with reduced populations (Schmitt and Skud 1978). Age at maturity may thus be a useful indicator of heavy fishing mortality.

Rockfishes exhibit a variety of life history patterns, but only a few species have been studied in detail (Chen 1971; Miller and Geibel 1973; Patten 1973; Moulton 1977; Larson 1980; Love and Westphal 1981; McClure 1982). Previously, the most comprehensive work on the maturity of rockfishes was by Phillips (1964) and Westrheim (1975). Phillips (1964) sampled market landings from northern and central California over several years. For each of the 10 species he investigated, maturity was reported for the sexes combined, and ages at maturity were derived from back-calculated von Bertalanffy growth curves. Westrheim (1975) summarized 10 years of data gathered on trawl-caught fish off British Columbia and the Gulf of Alaska, for which he reported on size at maturity and reproductive seasonality. Most of the fish in his study are commercially important species for British Columbia and, except for three species, do not occur off California.

There are some difficulties in assessing maturity stages and reproductive seasonality in rockfishes. One problem is the use of external morphology of gonads to determine maturity stages. Some researchers have questioned the accuracy with which immature fish can be distinguished from resting, mature fish during the nonreproductive months (Gunderson et al. 1980; Rosenthal et al. 1982). Also, the potential reproductive season may be protracted and the peak time of reproduction may shift within this season, so that short-term studies may be misleading. Thus, reported variation in length and age at maturity between studies could be the result of uncertainty in maturity-stage determinations.

In this study, I clarify the determination of sexual maturity stages, determine age and size at sexual maturity, and survey the reproductive seasonality for 34 species of rockfishes from the waters off

[1]Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

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northern and central California, from Port San Luis to Crescent City. I outline the reproductive patterns among species and annual variation within species.

MATERIALS AND METHODS

Data for this study were collected between July 1977 and July 1982 from three sources: 1) a coastwide survey for adult rockfish made in July and August 1977 (Gunderson and Lenarz 1980); 2) an ongoing cooperative program, initiated in 1977 by the California Department of Fish and Game and the National Marine Fisheries Service, to sample the commercial (Sen 1984) and sport rockfish landings in northern and central California; and 3) a 1980 expansion of the cooperative program, to include data on gonad condition, prey items, seasonal fluctuation of interstitial fat, and gonad volumes. Additional collections were taken during cooperative survey trips with the National Marine Fisheries Service, Southwest Fisheries Center, and the California Department of Fish and Game. Fish were collected to supplement rarely sampled species and subadults that were not well represented in the three surveys.

Information on maturity was gathered primarily for seven species of commercial and sportfishing importance. Data for 27 additional species are presented, but these were inadequately sampled for statistical treatment of the data (Table 1). For each fish sampled from 1977 to 1982 the species, sex, and total length (mm) was determined in the field and otoliths were collected for age determination. The viscera from each of the 16,444 fish sampled from 1980 to 1982 were removed, preserved in 10% buffered formalin, and sent to the laboratory for analysis. In the laboratory the sex was verified and the maturity stage of the gonads was determined based on the criteria defined in this paper. Total length was measured from the most anterior part of the jaw to the dorsal tip of the caudal fin. When necessary, total lengths were converted to fork length to compare this study with others (Echeverria and Lenarz 1984).

Ages were determined for all fish investigated in this study. Most estimates of age were made from the surface of whole otoliths immersed in 70% ethyl alcohol, under a dissecting microscope at 12×. Standard techniques for counting annuli on whole otoliths were followed (Kimura et al. 1979; Shaw and Archibald 1981). Certain species such as *S. diploproa* required thin sectioning techniques for counting annuli (Beamish 1979). In some species it is difficult to determine what constitutes an annulus (Table 1), and consequently those ages have not been validated. The "break-and-burn" method of age determination (Chilton and Beamish 1982) is useful and more accurate than surface ages when aging fish older than 16 years (Tagart 1984). Ages were not redetermined in this study because the age at maturity occurs before 16 years. Maximum ages, however, may be underestimated.

The gonad conditions described for males are immature, maturing, mature (peak spermatogenesis), spent, and resting. For females, they are immature, maturing, mature (fertilized), ripe (eyed larvae), recently spent, and resting (Lyubimova 1965; Westrheim 1975; Gunderson et al. 1980). Histological sections were examined to define seasonal maturation and the sections were analyzed based on the criteria established by Moser (1967b) for *S. paucispinis* and by Lisovenko (1970) on *S. alutus* for mature fish. The development of germ cells into spermatozoa or mature oocytes was examined to determine the developmental sequence leading to maturity. Cellular development was compared with the external morphology (Westrheim 1975; Gunderson et al. 1980) to understand clearly the developmental sequence and to aid in the interpretation of maturity stages in the field. Gonads were subsampled from fish in all maturity stages. Whole gonads were sectioned and stained with hematoxylin. Histological sections were examined from 519 testes and 708 ovaries from 30 species (Table 1). Egg diameters were routinely measured from histological sections and checked against whole eggs using an ocular micrometer.

To determine age and size at maturity and reproductive seasonality, the approximate age and size when 50% and 100% of the males and females were mature were estimated for each species. For those commercial species for which large samples were available, I checked the accuracy of the rough maturity estimates by applying the method of Gunderson et al. (1980). These authors used the logistic model

$$P_x = \frac{1}{1 + e^{ax+b}}$$

where P_x = proportion mature at size x, and a and b are constants, to estimate the length at 50% maturity for a sample. I applied a transformation of this equation

$$\ln \frac{1}{P_x} - 1 = ax + b$$

to obtain estimates of a and b for size and age by

TABLE 1.—Sample characteristics used to determine age and size at maturity and seasonality for *Sebastes* from central California.

Species of *Sebastes* (common name)	Sampled		Total number		Histology	
	Age (yr)	Size (cm TL)	Immature (*N*)	Mature (*N*)	Males (*N*)	Females (*N*)
alutus (Pacific ocean perch)	5-16	26-54	2	83	2	2
auriculatus (brown rockfish)	1-19	10-52	140	281	16	20
aurora (aurora rockfish)	5-19	20-39	2	92	—	1
babcocki (redbanded rockfish)	3-24	23-66	23	137	1	2
carnatus (gopher rockfish)[1]	2-14	9-37	14	99	3	3
caurinus (copper rockfish)	3-20	19-57	49	276	17	14
chlorostictus (greenspotted rockfish)[2]	3-33	16-57	83	236	17	18
chrysomelas (black and yellow rockfish)[1]	1-12	9-38	19	189	—	—
constellatus (starry rockfish)[2]	2-15	12-44	58	152	6	4
crameri (darkblotched rockfish)	2-24	12-56	42	365	6	27
diploproa (splitnose rockfish)	3-27	13-40	44	266	1	3
elongatus (greenstriped rockfish)	2-21	13-31	33	215	16	12
entomelas (widow rockfish)[3]	3-31	26-58	182	2,285	25	28
flavidus (yellowtail rockfish)[3]	4-32	25-56	548	1,762	30	40
goodei (chilipepper)[3]	2-21	21-59	256	2,312	35	34
helvomaculatus (rosethorn rockfish)[1,2]	5-11	20-28	7	25	1	1
hopkinsi (squarespot rockfish)[1]	2-13	12-30	15	45	—	—
jordani (shortbelly rockfish)[1]	1-12	12-20	47	635	9	9
levis (cowcod)[1,2]	2-22	24-90	17	24	—	—
maliger (quillback rockfish)[1]	6-15	22-44	4	45	3	—
melanops (black rockfish)[3]	2-21	25-61	265	469	29	46
melanostomus (blackgill rockfish)	6-27	25-56	17	109	1	2
miniatus (vermilion rockfish)	5-30	30-67	12	96	7	2
mystinus (blue rockfish)[3]	2-23	21-49	263	1,297	16	48
nebulosus (china rockfish)[1]	1-17	8-44	13	56	4	3
ovalis (speckled rockfish)[1,2]	3-15	23-49	6	101	—	2
paucispinis (bocaccio rockfish)[3]	2-26	32-83	1,402	2,404	170	245
pinniger (canary rockfish)[3]	3-26	22-69	564	641	61	105
rosaceus (rosy rockfish)[2]	3-12	14-32	26	167	30	17
ruberrimus (yelloweye rockfish)[2]	3-30	25-69	46	86	8	6
rubrivinctus (flag rockfish)[1]	4-18	19-45	4	38	3	—
rufus (bank rockfish)[2]	2-24	19-54	25	137	—	—
saxicola (stripetail rockfish)	2-17	14-38	11	102	—	5
serranoides (olive rockfish)[1]	4-19	23-54	47	187	3	9

[1]Denotes species not sampled every month for determination of seasonality.
[2]Denotes difficult to interpret otoliths for age determination.
[3]Denotes species of major importance in the sport or commercial fisheries of California.

standard linear regression. These estimates of a and b were then used to calculate estimates of size or age (x) at 50% maturity (P = 0.5). This was done for all species with a sample of 10 specimens or more for each length or age. Where adequate data existed, P_{50} for a species was calculated by year and area to investigate possible yearly or geographic variation.

Reproductive stages for mature individuals were summarized by month, and the percentages of individuals at each reproductive stage were used to determine principal months of spermatogenesis (approximates mating), fertilization, and larval extrusion for each species. Seasonality was described only approximately for those species that were not present in all months sampled (Table 1).

Reproductive months for mature females were determined and the percentage containing eyed larvae was noted. Data from 1981 through 1985 were tabulated to compare annual variability in the reproductive months and/or the principal month of parturition.

RESULTS

Moser (1967b) described the seasonal changes in gonads of mature *S. paucispinis* and should be consulted for details of morphology. In this study a general description of all maturity stages is included with emphasis on the immature gonad and the transitional stages, which are difficult to interpret. The transitional stages are 1) the determination of the first reproductive year, particularly in species with small maximum size; 2) the prespawned testis during spermatogenesis compared with the spawning and postspawned testis when spermatogenesis is completed and mating is in progress or just completed; 3) the unfertilized egg stage compared with the recently fertilized egg; and 4) the nonreproductive season, compared with the beginning of vitellogenesis or spermatogenesis when the gonads are beginning to mature. A comparison of external morphology with the histological sections indicates that the same sequence of spermatogenesis/vitellogenesis, mating, ovulation, fertilization, and larval extrusion is followed for each species in this study. There were not sufficient samples of all 31 species to discern what developmental variations might exist on the cellular level (Table 1).

Developmental Sequence of Ovaries

The germ cells in ovaries are clustered in oogonial nests, which are present throughout the year in varying numbers. The ovary of an immature rockfish (Gonad Stage 1) consists primarily of oogonial nests with oocytes <0.14 mm in diameter. The ovarian wall is translucent and thin (approximately 0.1 mm thick). Externally the ovary appears translucent with a tiny egg mass (Table 2).

Approaching the first year of maturity (Gonad Stage 2), the ovary is filled with oogonial nests, follicles begin to form around maturing oocytes, and the ovarian wall is translucent and thin. There is no evidence of the resorption and reorganization seen in spent ovaries. Externally the ovary appears pink through the thin wall, and eggs about 0.2 mm in diameter are visible.

As the reproductive season approaches (Gonad Stage 3) eggs are produced by the oogonial nests and vitellogenesis begins, resulting in eggs enlarging from 0.2 to 0.5 mm in diameter. Follicles form around the maturing eggs, a capillary network develops throughout the ovary, and the ovarian wall begins to thicken from 0.3 to 0.5 mm. Externally the ovary appears either white or yellow and firmly packed with eggs in grapelike clusters. The eggs expand during this stage, so that during maturation

TABLE 2.—Reproductive development at the cellular and external morphology level for ovaries of *Sebastes* species.

Gonad stage	Cellular morphology	External morphology
1. Immature	Oogonial nests with oocytes <0.14 mm. Ovarian wall (OW) 0.1 mm thick.	Small and translucent to pink. Ovarian wall (OW) thin.
2. First year maturity	Oocytes <0.2 mm. No evidence of resorption.	Pink with visible eggs. No black pigmentation. OW thin.
3. Vitellogenesis	Mature oocytes 0.2-0.5 mm in diameter within follicles. OW 0.3-0.4 mm thick.	Yellow or white opaque eggs in grapelike clusters. OW thickening.
4. Fertilization	Oocytes 0.9 mm. Yolk globule disintegration, ovulation, fertilization.	Large clear eggs free in ovarian cavity, but enveloped by a network of capillaries.
5. Eyed larvae (parturition)	Larvae developed within chorion with eyes pigmented black or yellow.	Large, soft, gray. Ovary breaks easily, and is filled with eggs and fluid.
6. Spawned	Oocytes 0.08-0.64 mm in diameter. Resorption of blood vessels, atretic oocytes, and residual larvae. Collapsed egg cases. OW 0.5-1.0 mm thick.	Flaccid, reddish-purple, or grayish from residual larvae. OW thick and tough.
7. Resting	Resorption and reorganization. Proliferation of oogonial nests. OW 0.5-0.9 mm thick.	Firm, gray to pink. Tiny black dots indicate residual larvae, OW thick, tough, and loose from eggs.

the ovary swells in size. The eggs remain opaque, and held within a follicle.

Fertilized eggs (Gonad Stage 4) are about 0.9 mm in diameter and have shed their follicles, and the yolk globules have disintegrated. Externally the eggs appear translucent yellow or white and are no longer held in tight grapelike clusters. They are held within an elaborate capillary network, not totally free within the ovary, though they are no longer held within a follicle.

Development of the embryos continues for about a month (Moser 1967a) until they develop pigmented eyes (Gonad Stage 5) and become ready for release. The pigmented eyes are usually black except in *S. ruberrimus* where they are yellow. Externally the ovary is gray (from the pigmented eyes) and very fragile. It breaks easily when handled and usually some larvae are prematurely extruded when the adult is captured.

After normal release of the larvae (Gonad Stage 6), the ovary consists primarily of an elaborate vascular system, larvae that were not extruded, and a few eggs which failed to develop (atretic oocytes). Externally it appears very mushy and reddish gray, with an opaque and flaccid ovarian wall.

Resorption and reorganization of the ovary (Gonad Stage 7) occur until vitellogenesis begins (Gonad Stage 3) again. During the months of reorganization (Figs. 1-7) there is evidence of residual larvae, eggs, and capillaries being resorbed, and a proliferation of oogonial nests producing eggs for the next reproductive season. The ovarian wall is between 0.5 and 0.9 mm thick. Externally the ovary is compact and loosely encased by an opaque wall. During resorption the ovary changes from reddish brown to grayish brown. When vitellogenesis begins again (Gonad Stage 3) the ovary appears yellow or white. There are usually a few pigmented eyes being resorbed through Gonad Stage 3 from the previous year's brood.

The principal external characteristic of an immature ovary entering the first reproductive season is the wall, which is thin (0.1 mm) and translucent. There are also no residual pigmented eyes in the ovary. A spent and maturing ovary from a mature fish usually contains remnants of resorbed larvae (evidenced as black dots) encased by a thick, opaque ovarian wall (0.5 to 0.9 mm).

Developmental Sequence for Testes

It is often difficult to distinguish an immature from a resting testis in rockfish because the presence of sperm in the testis is not necessarily an indication of the fish's maturity. Understanding the developmental sequence of spermatogenesis can help to identify the reproductive stage any time of year (Table 3).

Histological examination shows that the immature testis (Gonad Stage 1) consists of germ cells, primary spermatogonia, and secondary spermatogonia which lend a whitish color at the periphery. Externally the testis is threadlike and translucent, often with a hint of white from the developing spermatogonia.

Spermatogenesis begins at the periphery of the testis and moves centripetally, filling the lumen, the efferent ducts, and finally the sperm duct. A male approaching the first year of maturity (Gonad Stage

TABLE 3.—Reproductive development at the cellular and external morphology level for testes of *Sebastes* species.

Gonad stage	Cellular morphology	External morphology
1. Immature	Germ cells, primary and secondary spermatogonia.	Small, threadlike; transparent to white at periphery.
2. First year maturity	Spermatozoan cysts throughout testis. No residual sperm in tubules or ducts.	Small, ribbonlike, and white. No evidence of sperm in central duct (translucent).
3. Spermatogenesis	Large spermatozoan cysts throughout testis with spermatozoa in lumen.	Milky white and swollen, sperm throughout testis in cross section.
4. Spawning	Sperm duct and lumen filled with spermatozoa. Spermatogenesis ceases at periphery.	Large, soft, white; sperm flows freely when cut. Center of testis white, periphery becoming translucent.
6. Recently spawned	Abundance of germ cells at periphery. Resorption of sperm by tubular boundary cells.	Center is white in cross section, with the periphery becoming firm and darker.
7. Resting	Reorganization of testis. Germ cells line spermatogenic tubules.	Firm, compact, and vaguely triangular. Color dark gray/brown.

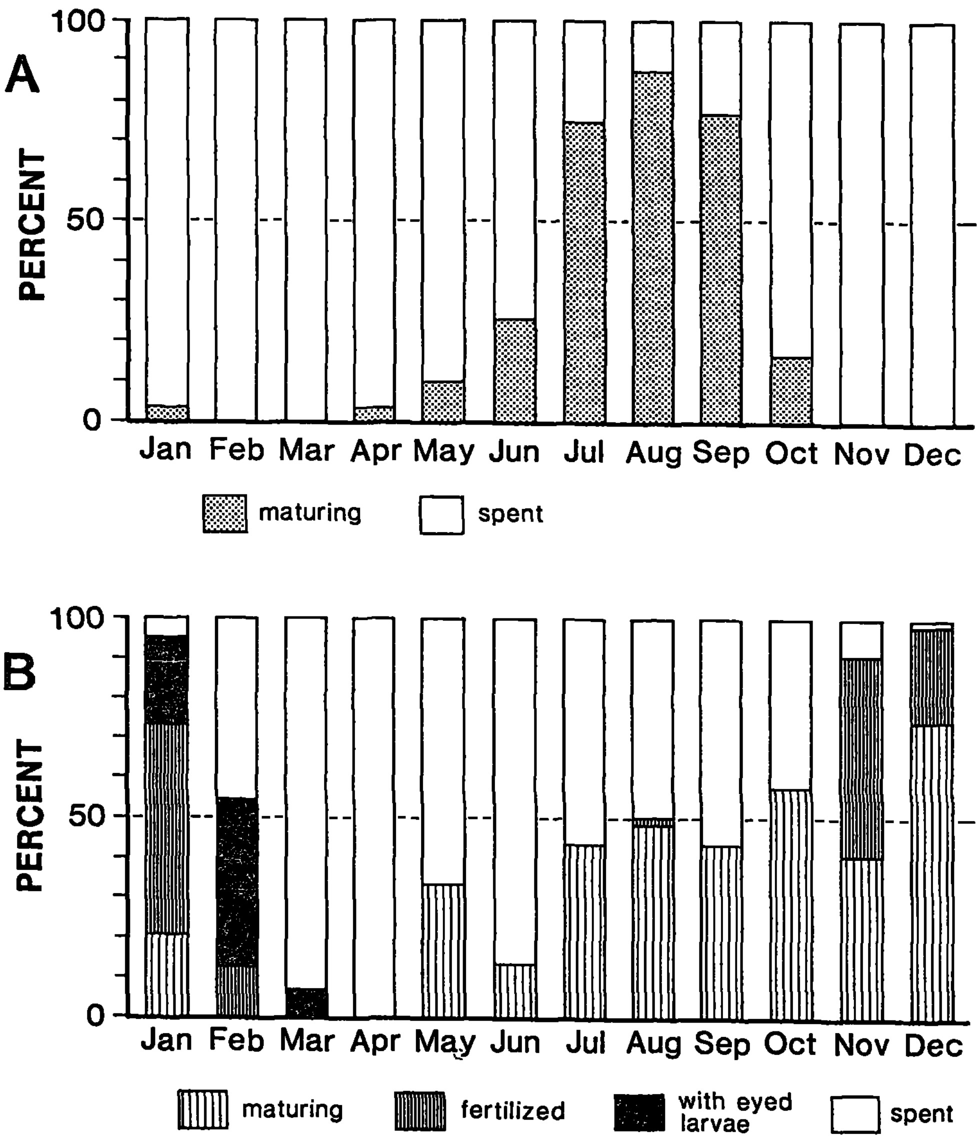

FIGURE 1.—A. Reproductive seasonality of mature males of *Sebastes entomelas* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. entomelas* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

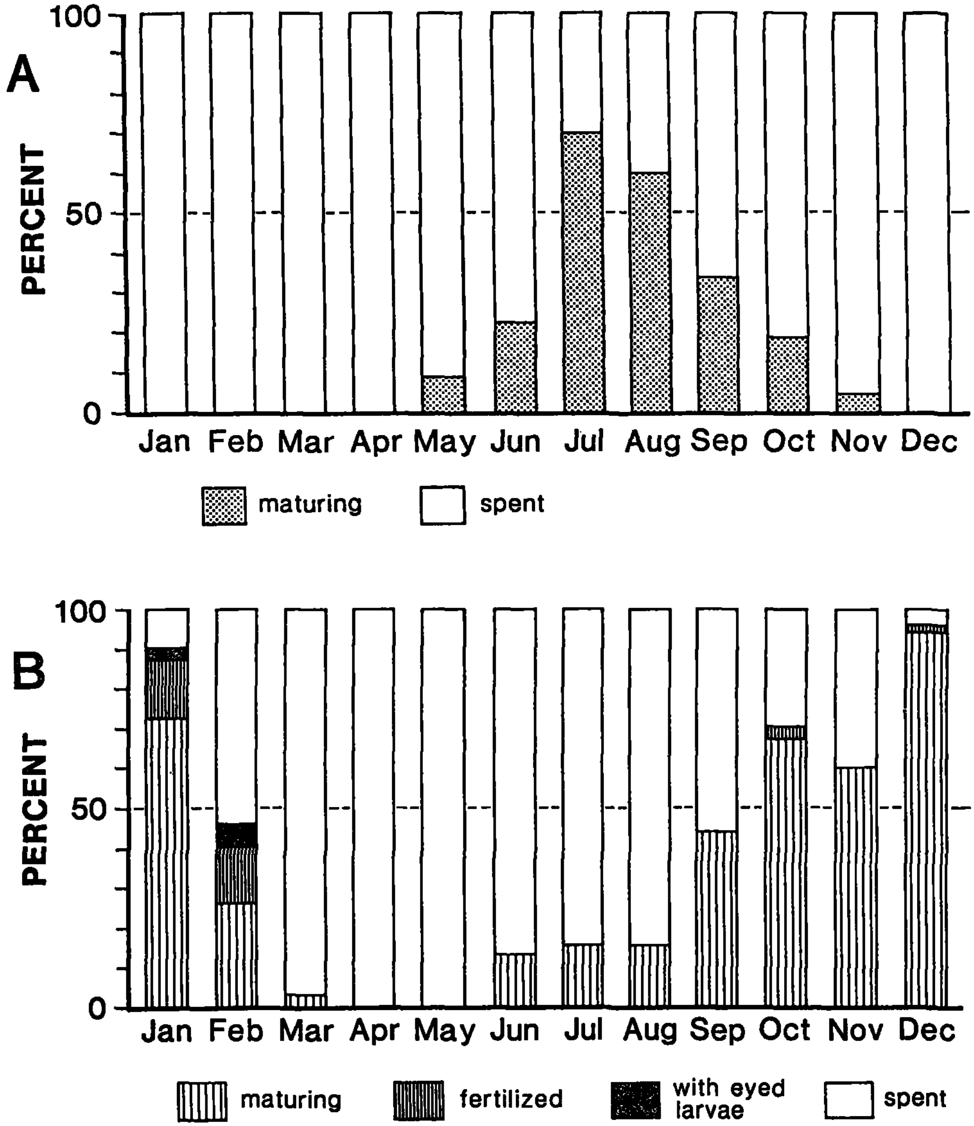

FIGURE 2.—A. Reproductive seasonality of mature males of *Sebastes flavidus* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. flavidus* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

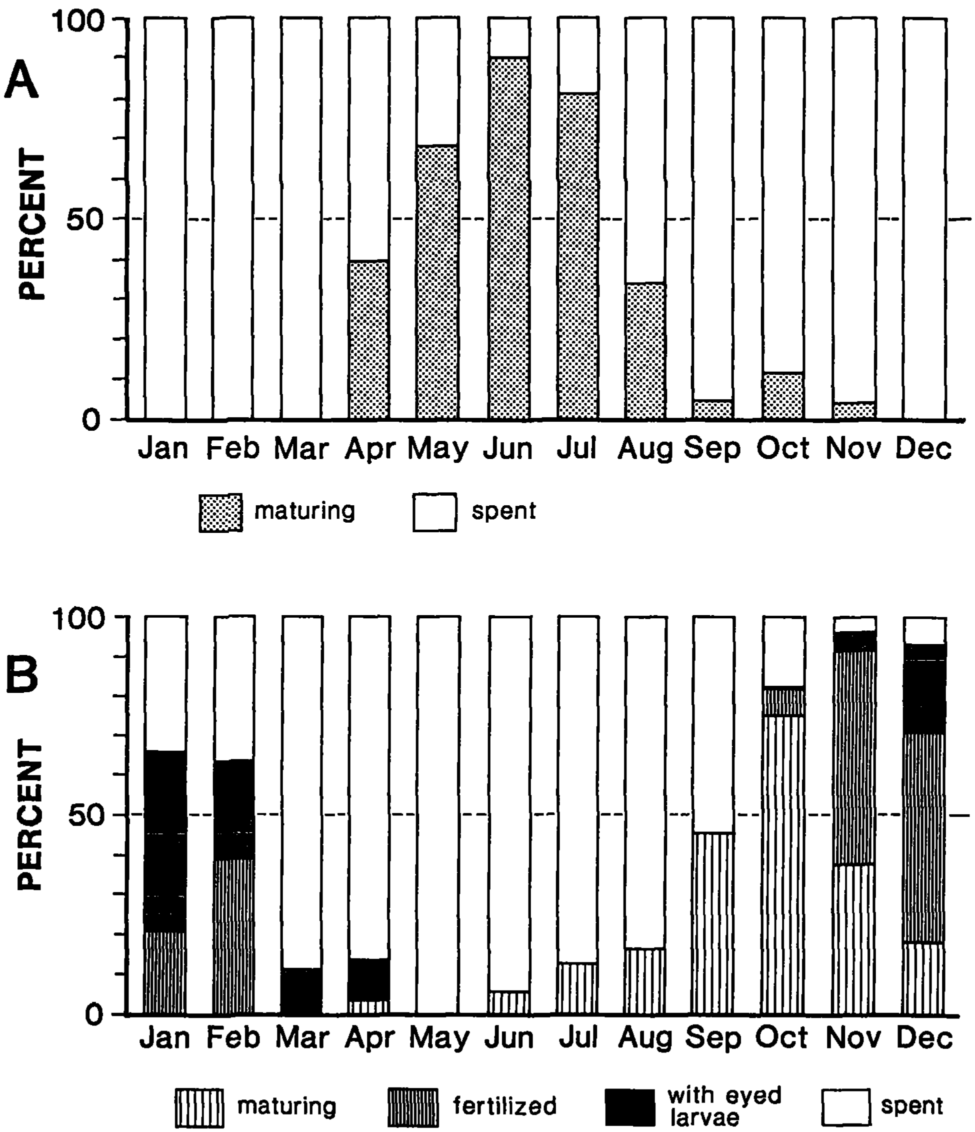

FIGURE 3.—A. Reproductive seasonality of mature males of *Sebastes goodei* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. goodei* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

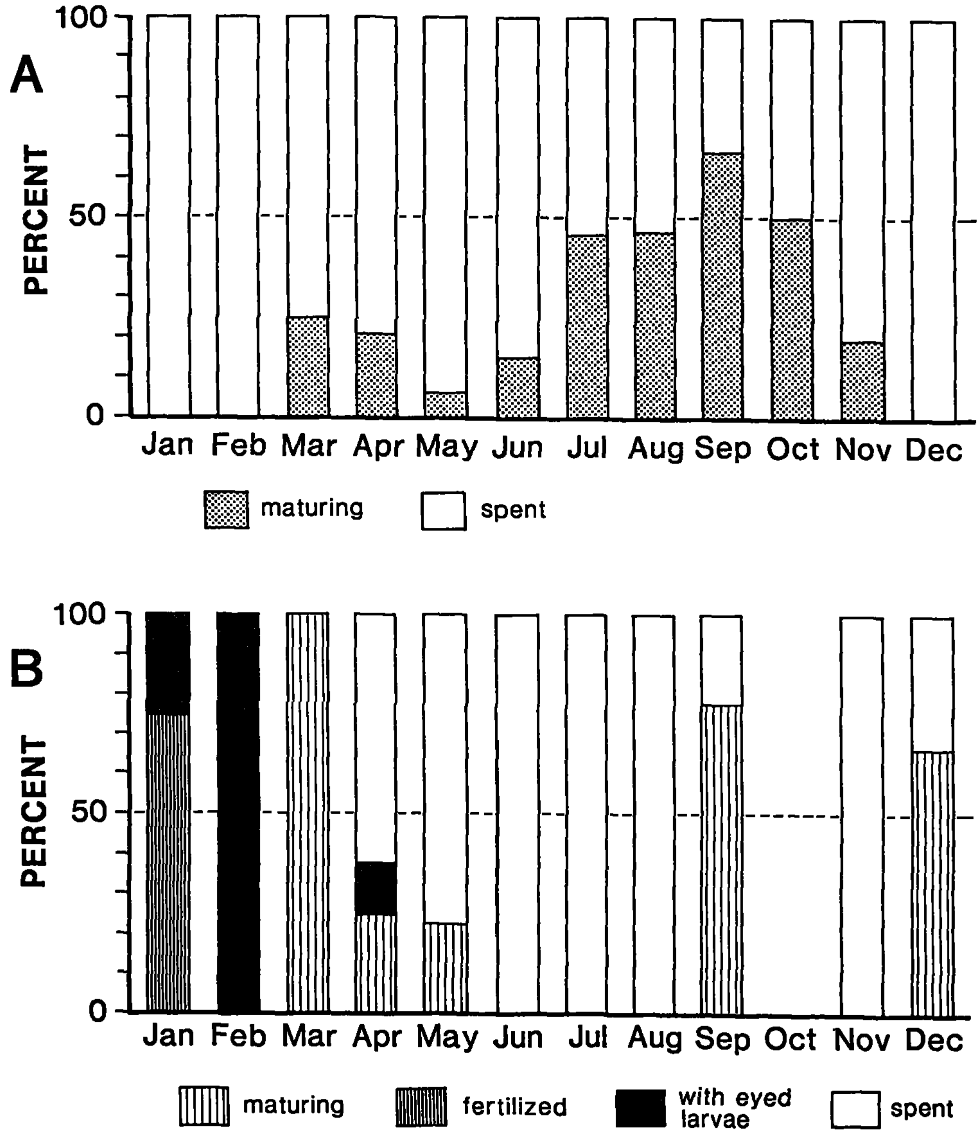

FIGURE 4.—A. Reproductive seasonality of mature males of *Sebastes melanops* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. *B. Reproductive seasonality of mature females of S. melanops* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

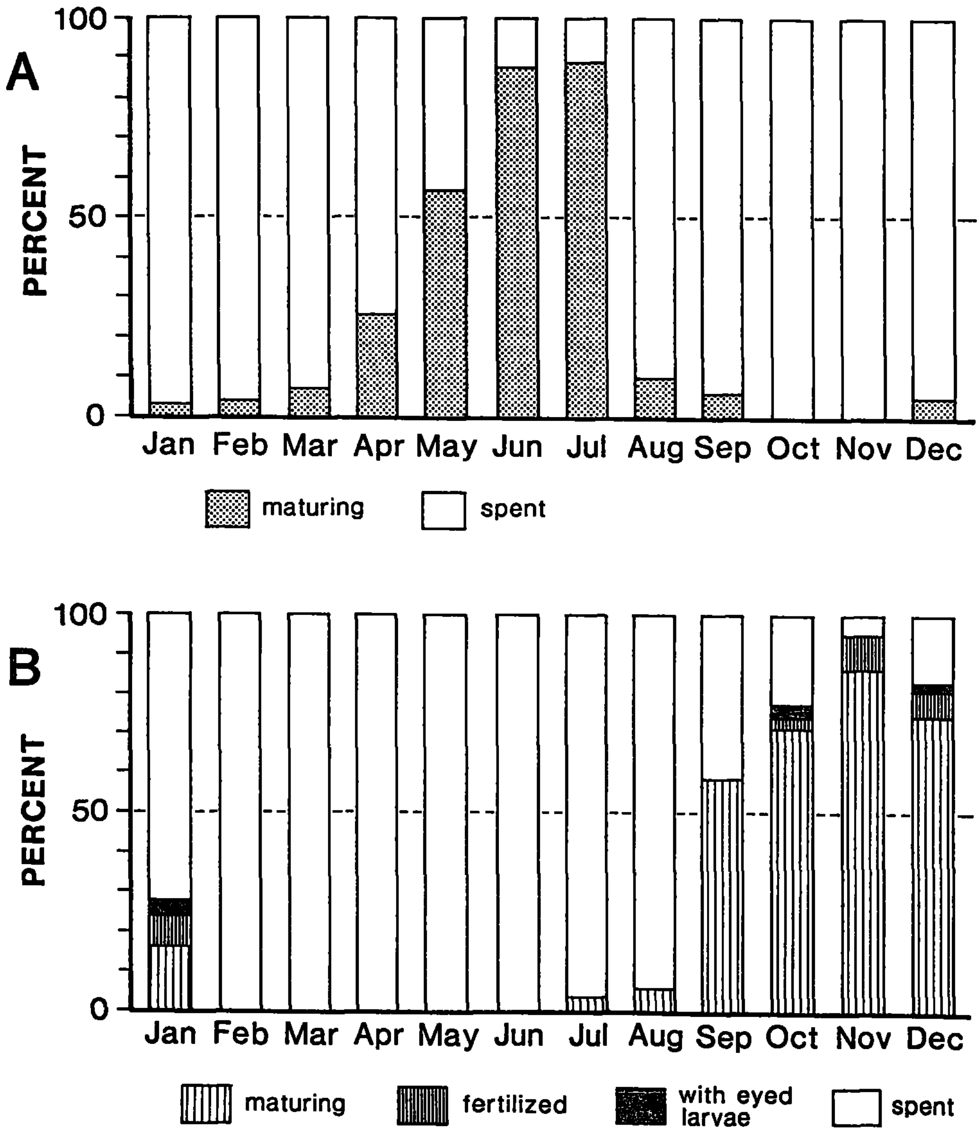

FIGURE 5.—A. Reproductive seasonality of mature males of *Sebastes mystinus* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. mystinus* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

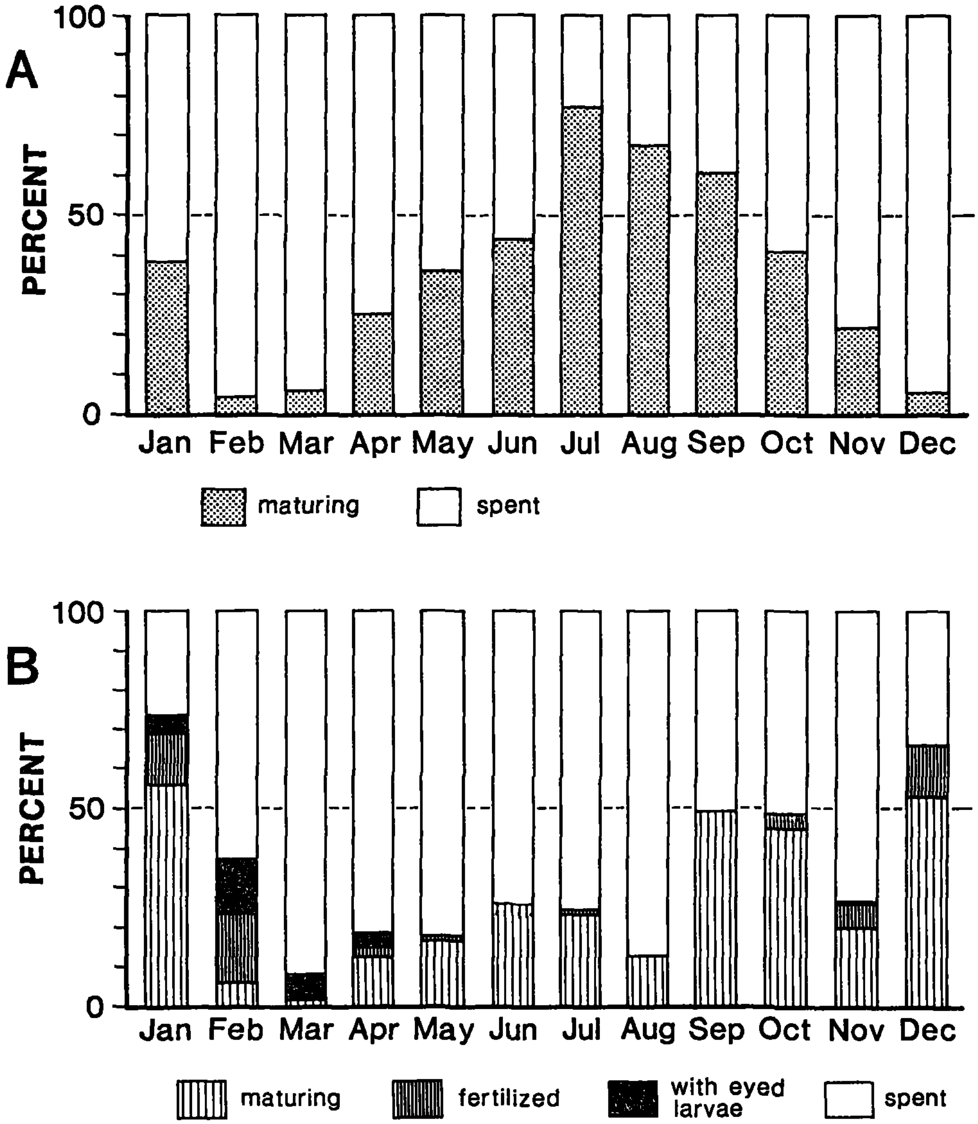

FIGURE 6.—A. Reproductive seasonality of mature males of *Sebastes paucispinis* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. paucipinis* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

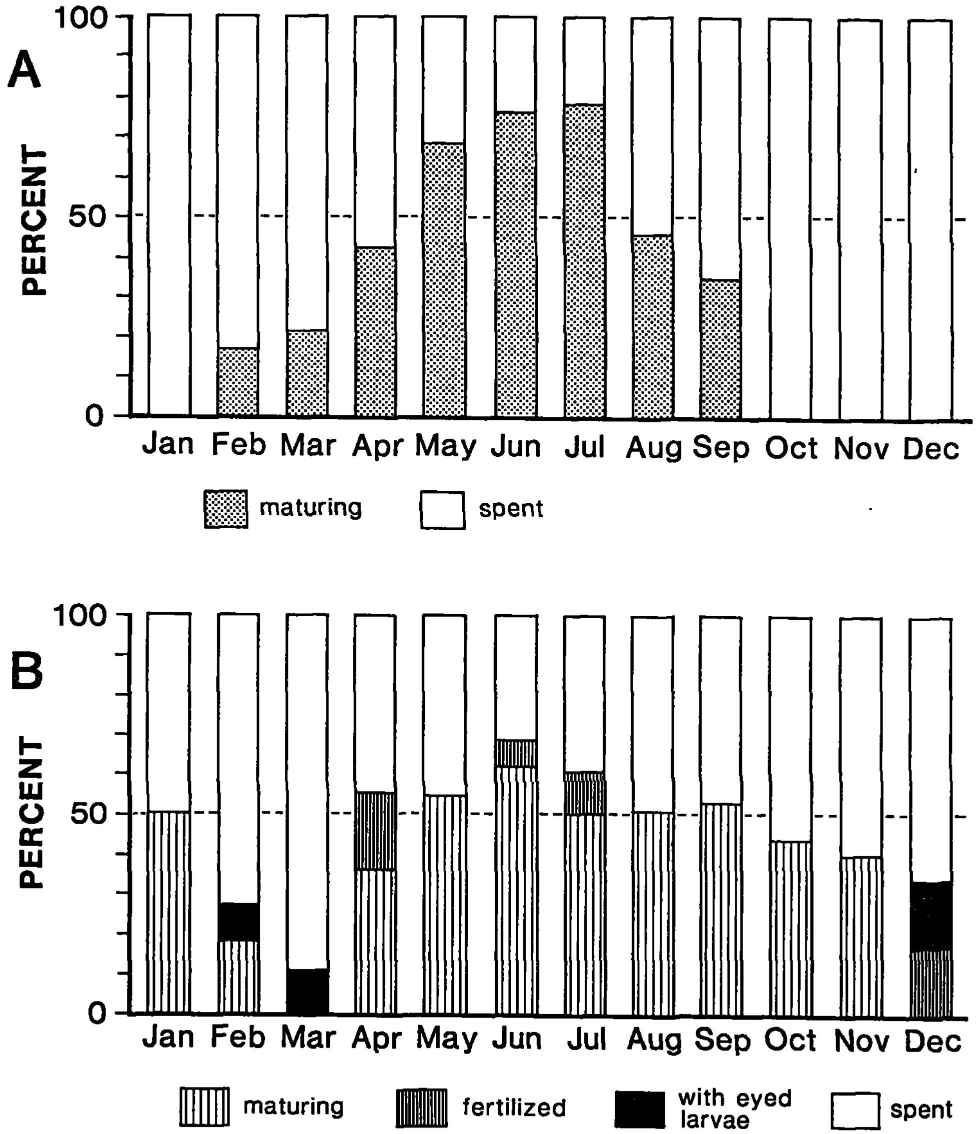

FIGURE 7.—A. Reproductive seasonality of mature males of *Sebastes pinniger* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. pinniger* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

2) has spermatogonial cysts developing throughout the testis. There is no sign of spermatozoa in the sperm duct. Externally, the testes appear slightly swollen and white; in cross section they are translucent in the center because of the absence of sperm in the sperm duct.

In a maturing male (Gonad Stage 3) spermatozoa appear throughout the testis in spermatozoan cysts. The sperm duct often contains remnants of residual sperm from the previous reproductive season. In a cross section the testis is swollen and whitish at the periphery and brownish off-white in the center because of the presence of residual sperm in the sperm duct.

As the reproductive season approaches (Gonad Stage 4) the spermatozoan cysts burst open, releasing spermatozoa into the efferent ducts and the sperm duct. Externally the testis is large, soft, and very white, sperm flows freely when the testis is pressed or cut. During the reproductive season spermatogenesis has ceased and the spermatozoa have moved from the periphery towards the sperm duct so that the periphery becomes hard and discolored. The central area may be swollen with sperm.

At the end of the reproductive season (Gonad Stage 7), the testis undergoes resorption and reorganization, wherein smooth muscle cells, connective tissue, and scattered residual spermatozoa, constituting cellular detritus, are evident in the histological sections. At the periphery, a new generation of germ cells reorganizes along the spermatogenic tubules. Externally the testis is a compact, irregular triangular shape that appears gray or brown.

An understanding of the developmental sequence on the cellular level aids in the interpretation of gonad stage in the field. The four, difficult to interpret, transitional stages can be clarified: 1) The first reproductive year is indicated by a white periphery (sperm) and an absence of sperm in the center of a cross section of testis, a thin ovarian wall and no residual pigmented eyes in ovaries. 2) The center of the prespawned testis is firm and a dark cream color (residual sperm); the periphery is white and swollen with sperm. The postspawned testis usually shows signs of white fluid (sperm) in the sperm duct and is firm and a dark cream color at the periphery. 3) Unfertilized eggs are opaque yellow or white held tightly in grapelike clusters while fertilized eggs are a translucent yellow or white and the outer eggs can be separated from each other. 4) Vitellogenesis is indicated by a deep yellow color and swelling of the eggs so that the ovarian wall fits tightly around the eggs; spermatogenesis is indicated by a softening and swelling of the testis and a whitening at the periphery.

Reproductive Maturity and Seasonality

Maturity was observed over a broad age and size range within species throughout the years sampled. The age and size at first maturity, 50% maturity and 100% maturity were estimated for males and females of each species (Table 4). Males reached 50% maturity either at the same or younger age than females. Size at 50% maturity is generally similar or somewhat smaller for males than for females of the same species. The standard linear regressions were run on the transformed logistic for the seven principal species occurring in this study, resulting in similar estimates of age at 50% maturity for *S. entomelas*, *S. flavidus*, *S. goodei*, *S. melanops*, *S. mystinus*, *S. paucispinis*, and *S. pinniger* (Table 5), and similar, if not exact, sizes at 50% maturity as estimates derived from the raw data. Maturity for species without sufficient data for statistical treatment are estimated from the raw data.

The reproductive season in *Sebastes* can be long with larval extrusion (parturition) seen in females of some species for up to 9 months (Table 6). From all the data collected between 1977 and 1984 a summary of principal month of spermatogenesis, fertilization, and parturition was determined for 32 species (Table 7). A span of 1 to 5 months between peak spermatogenesis and fertilization is seen. The time, when males ripen and mate, is not dependent upon the eggs being fully mature. The time between fertilization and parturition is usually about 1 month (Moser 1967a).

Reproductive seasonality for the principal species sampled is displayed graphically in Figures 1-7. Seasonality histograms are available, upon request, for most species investigated. The general trend in the seasonality of *Sebastes* is a prolonged reproductive period for each maturity stage. This trend is seen in the seven most abundant species sampled (Figs. 1-7). Spermatogenesis (Gonad Stage 3) occurs over 3 to 5 months before the testes are fully ripe (Gonad Stage 4). The timing of mating is estimated from the appearance of testes swollen with sperm. At least part of the male population is ready for mating for a period of 2 to 4 months. In females, generally, fertilized eggs (Gonad Stage 4) are found 1 to 3 months after mating. Eyed larvae (Gonad Stage 5) appear from 1 to 4 months after fertilized eggs were observed and were present in the sampled population for 3 to 6 months, usually with a

TABLE 4.—Estimated age and size at 1st, 50% and 100% maturity for given in cm

Species of *Sebastes*	Male						Female					
	1st		50%		100%		1st		50%		100%	
	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL
alutus	—	—	5	28	7	32	7	26	7	26	7	32
auriculatus	3	26	5	31	10	38	3	26	5	31	10	38
aurora	5	28	—	—	5	28	5	28	—	—	5	28
babcocki	3	27	4	31	5	36	3	32	4	34	6	41
carnatus	4	17	4	17	5	21	4	17	4	17	5	21
caurinus	3	30	4	32	7	40	5	31	6	34	8	41
chlorostictus	4	25	6	27	12	38	5	26	6	28	9	34
chrysomelas	3	14	3	16	5	20	3	14	3	15	5	19
constellatus	6	28	7	30	12	36	5	23	6	27	9	34
crameri	3	25	4	27	7	36	3	24	4	27	6	34
diploproa	7	20	9	22	10	29	6	18	7	19	9	23
elongatus	7	23	7	23	10	27	5	18	7	23	10	27
entomelas[1]	3	31	5	36	8	41	3	29	5	37	8	40
flavidus[1]	4	30	6	35	11	43	4	27	7	36	11	42
goodei[1]	2	26	3	31	7	38	2	29	3	34	6	39
helvomaculatus	7	22	7	22	10	27	5	20	8	23	10	27
hopkinsi	4	15	5	16	5	17	5	17	5	18	7	21

[1]Denotes samples from 1980-82 study only.

peak month of larval extrusion. The external appearance of individual ovaries indicates that larvae are in the eyed stage and ready for release throughout the ovary.

The total number of mature females observed during the reproductive months, and the percentage containing eyed larvae is presented for three commercially important species (Figs. 8-10). For the years 1981-85, variations in the months of parturition and/or the peak month is seen. *Sebastes entomelas* (Fig. 8) showed an annual variation in the months of parturition but not in the peak months (January-February). The peak month for *S. goodei* (Fig. 9) varied from December to February, and in *S. paucispinis* (Fig. 10) from December to March. A variation in which months larval extrusion occurs is seen in all three species. Chi-square tests showed the percentages to be dependent upon year and month. Therefore, there is a relationship between the percent-number of mature females with eyed larvae seen in a particular month, and reproductive year.

DISCUSSION

The reproductive biology of *Sebastes* follows the sequence of spermatogenesis, vitellogenesis, mating, ovulation, fertilization, and larval extrusion (Moser 1967b). As in other viviparous fishes (Turner 1947), sperm can apparently survive within the ovary for many months. In *S. mentella*, ovulation and the activation of sperm coincide with a change in pH (Sorokin 1967). The histological evaluation of the gonads in *Sebastes* of northern California confirms that spermatogenesis is generally completed and mating occurs before the completion of vitellogenesis. The length of time males are fully ripe can be up to 2 months in various species, and the delay between the time males are fully ripe and fertilization (sometimes up to 4 months) indicates that mating does not coincide with fully mature ova (Figs. 1-7). Testes are observed in decreasing degrees of ripeness after spermatogenesis has ceased. This indicates that one mating does not void the testes; males may mate more than once per season. Ovulation in teleosts is regulated by steroids and prostaglandins, which in turn are influenced to some degree by temperature, pheromones, or spatial/temporal cues (Stacey 1984). The presence of sperm in the ovaries of *Sebastes* does not trigger final oocyte maturation and ovulation; therefore, ovulation is probably influenced by environmental conditions. Thus knowing which conditions influence ovulation is necessary to determine some of the factors contributing to a successful reproductive year, as measured by the percent mature females with eyed larvae.

The costs of reproduction for females include the development of a highly vascular network throughout the ovaries, the nourishing of developing embryos (Boehlert and Yoklavich 1984), and the metabolism of waste products from the embryos (Moser 1967a). The ovaries must accommodate the added gonadal weight and volume until larval extrusion.

Sebastes from northern and central California collected 1977-82. Lengths total length (TL).

Species of *Sebastes*	Male						Female					
	1st		50%		100%		1st		50%		100%	
	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL
jordani	1	12	2	14	5	20	2	12	3	14	4	19
levis	4	32	4	32	4	32	4	32	4	32	5	37
maliger	4	22	4	22	7	31	6	26	6	26	7	28
melanops[1]	3	25	6	36	10	43	5	30	7	41	11	48
melanostomus	6	29	7	33	10	39	7	30	8	35	9	36
miniatus	5	35	5	38	8	43	5	37	5	37	9	46
mystinus[1]	4	22	5	27	9	32	5	22	6	29	11	35
nebulosus	3	26	4	27	6	30	3	26	4	27	6	30
ovalis	4	28	4	28	5	30	4	28	4	28	5	29
paucispinis[1]	3	32	3	42	7	55	3	36	4	48	8	60
pinniger[1]	4	28	7	40	9	45	4	27	9	44	13	54
rosaceus	4	16	6	20	8	25	4	15	6	20	8	25
ruberrimus	6	36	7	40	8	46	6	36	7	40	8	46
rubrivinctus	5	29	5	30	6	32	5	29	8	34	10	38
rufus	—	27	3	31	4	36	2	32	3	34	4	41
saxicola	3	15	3	16	4	17	2	17	2	17	3	18
serranoides	4	32	5	33	8	38	4	32	5	35	8	39

TABLE 5.—Standard linear regression used to estimate age (yr) and size (cm) at 50% maturity for males (M) and females (F) in seven species of *Sebastes*. Slope and *y*-intercept were estimated from the equation $\ln \frac{1}{P_x} - 1 = ax + b$. r = correlation coefficient, N = number of ages or sizes used in the regressions; each N represents at least 10 observations per age or size.

Species of *Sebastes*	Sex	Variable	*y*-intercept	Slope	50% maturity	*r*	*N*
entomelas	M	age	4.5598	−1.0006	5	−0.9588	6
		size	10.1042	−0.3162	33	−0.7649	11
	F	age	5.4800	−0.7982	5	−0.9647	5
		size	28.4810	−0.7810	37	−0.9667	4
flavidus	M	age	2.9748	−0.4994	6	−0.9577	10
		size	13.7834	−0.3964	35	−0.9718	14
	F	age	5.3731	−0.7757	7	−0.9541	9
		size	15.7482	−0.4331	36	−0.9723	13
goodei	M	age	1.1620	−0.4093	3	−0.9263	9
		size	7.7618	−0.3044	31	−0.8730	10
	F	age	3.7624	−1.1129	3	−0.9775	6
		size	12.2400	−0.3740	34	−0.9650	15
melanops	M	age	4.3841	−0.8011	6	−0.9769	6
		size	13.7147	−0.3814	36	−0.9411	6
	F	age	5.0627	−0.7149	7	−0.9760	8
		size	11.0749	−0.2720	41	−0.9520	16
mystinus	M	age	1.3482	−0.3669	5	−0.8530	10
		size	4.3885	−0.2049	27	−0.6778	11
	F	age	5.0097	−0.8022	6	−0.9680	9
		size	9.5090	−0.3368	29	−0.9218	17
paucispinis	M	age	1.7138	−0.6677	3	−0.9431	8
		size	10.7040	−0.2564	42	−0.9196	16
	F	age	3.5175	−0.8232	4	−0.9232	7
		size	13.7028	−0.2876	48	−0.9565	20
pinniger	M	age	3.7804	−0.5845	7	−0.9710	9
		size	11.2047	−0.2837	40	−0.9500	16
	F	age	5.1221	−0.5897	9	−0.9800	11
		size	11.5621	−0.5897	44	−0.9460	15

TABLE 6.—Months of parturition for species of *Sebastes* that occur in the northeastern Pacific Ocean. All available data are listed by area (results of this study in parentheses).

Species of *Sebastes*	Gulf of Alaska	British Columbia	Washington	Oregon	North-Central California	Southern California
aleutianus		Apr.[1]		May[2]		
alutus	May[3], Apr.-May[1]	Mar.[3]	Mar.[4]	Jan.-Apr.[2]	(Jan.-Mar.)	
auriculatus				June[5], May[6]	(Dec.-Jan.; May-July), May[7]	
aurora		>June[1]			(Mar.-May)	
babcocki		Apr.[1]		Apr.[2]	(May)	
borealis		Apr.[1]				
brevispinis		>May[1]				
carnatus					(Mar.-May), May[7]	
caurinus			Mar.[8], Apr.[6,9,5]		(Feb.)	
chlorostictus				Apr.[2]	(Apr.-Sept.)	Apr.-July[10], July[11]
chrysomelas					(Feb.-Mar.), Jan.-May[7]	
constellatus					(Apr.-May)	Mar. + May[10,11]
crameri	<June[1]	Feb.[1]		Feb.-Mar.[2]	(Nov.-Mar.), Nov.-Mar.[7]	
diploproa		July[1]	July[6]	Apr.-May[12]	(Jan.-Sept.), Feb.-July[13]	
elongatus		>June[1]		Apr.-May[12]	(May-July)	
ensifer						Feb. + May[10]
entomelas		Apr.[1]		Jan.[2,14]	(Dec.-Apr.), Nov.-Mar.[13]	
eos						Apr.-June[11]
flavidus		Mar.[1]	Jan.-Apr.[4]	Jan.-Mar.[2]	(Jan.-July), Nov.-Mar.[13]	
goodei					(Nov.-June), Nov.-Mar.[13]	Oct.-Mar.[11]
helvomaculatus	>May[1]	>May[1]			(May-June)	
hopkinsi					(Feb.-Mar.)	
jordani				Feb.[2]	(Feb.-Apr.), Nov.-Mar.[13]	
lentiginosus						Mar.[10]
levis					(Dec.-Feb.)	Dec.-Jan.[11]
maliger	May-July[15]	Apr.[1,16], May[5]			(Apr.-July)	
melanops		Jan.[17], <Apr.[1]		Jan.[17]	(Jan.-May)	
melanostomus					(Feb.-Apr.)	
miniatus					(Sept.) Nov.[11], Nov.-Mar.[13]	Nov.[11]
mystinus					(Nov.-Jan.), Nov.-Jan.[18], Jan.-Mar.[19]	
nebulosus					(Jan.-June), Jan.[20]	
nigrocinctus		May[1]				
ovalis					(May)	Jan.-May[11]
paucispinis		<Feb.[1]	Jan.-Apr.[4]	Jan.-Feb.[2]	(Jan.-May), Nov.-Mar.[11]	Oct.-Mar.[11]
pinniger		>Feb.[1]		Dec.-Apr.[2]	(Dec.-Mar.), Nov.-Mar.[11]	
proriger				Apr.-July[2]	(July-Aug.)	
reedi		May[1]		Feb.-May[15]		
rosaceus					(Apr.-July)	Mar. + May[10,11]
ruberrimus	June-Aug.[15]	May[1]	July[6]	Mar.-Apr.[2], Apr.-May[12]	(Apr.-June)	
rubrivinctus		May[1]		Apr.-May[12]	(July)	Mar.-June[10]
rufus					(Dec.-May)	
saxicola		Feb.[1]		Feb.[2]	(Jan.-Mar.), Nov.-Mar.[13]	
serranoides					(Jan.-Mar.)	Jan.[16]
simulator						Feb.-Mar.[10]
umbrosus						Apr.[10]
wilsoni		June[1]				
zacentrus	>May[1]	July[1]		Mar.-July[2], Apr.-May[12]	(May-June)	

[1]Westrheim 1975.
[2]W. H. Barss, Oregon Department of Fish and Wildlife, Marine Science Drive, Newport, OR 97365, pers. commun. 1985.
[3]Lyubimova 1965.
[4]Gunderson et al. 1980.
[5]Washington et al. 1978.
[6]DeLacy et al. 1964.
[7]Larson 1980.
[8]Patten 1973.
[9]Moulton 1977.
[10]Chen 1971.
[11]Moser 1967a.
[12]Hitz 1962.
[13]Phillips 1964.
[14]Barss and Echeverria 1987.
[15]Rosenthal et al. 1981.
[16]Love and Westphal 1981.
[17]Dunn and Hitz 1969.
[18]Wales 1952.
[19]Miller and Geibel 1973.
[20]Burge and Schultz 1973.

TABLE 7.—Reproductive seasonality for *Sebastes* from central California collected 1977-84. Listed by taxonomic order (Barsukov 1981).

Species of *Sebastes*	Principal month(s) of spermato-genesis	fertil-ization	parturi-tion
melanostomus	Nov.	Feb.	Feb.
aurora	Apr.	?	Apr.
ruberrimus	Dec.	Apr.	June
chrysomelas	?	Jan.	Feb.
carnatus	Dec.	?	Mar.
nebulosus	?	Jan.	Jan.
auriculatus	May	May	June
caurinus	Dec.	Jan.	Feb.
maliger	Dec.-Jan.	Apr.	Apr.
elongatus	?	Apr.	May
babcocki	Jan.	?	May
saxicola	?	Dec.	Jan.
diploproa	June	June	July
crameri	?	Dec.	Jan.
alutus	Sept.-Oct.	?	Mar.
pinniger	Oct.	Dec.	Dec.
miniatus	July	?	Sept.
levis	Sept.-Oct.	Oct.	Dec.
rosaceus	May	May	June
constellatus	Dec.	Feb.	Apr.
chlorostictus	Feb.	Apr.	May
goodei	Oct.	Dec.	Jan.
jordani	Nov.	Jan.	Feb.
paucispinis	Oct.	Dec.	Feb.
ovalis	Nov.	?	May
rufus	Nov.	Nov.	Feb.
hopkinsi	Dec.	Feb.	Mar.
entomelas	Oct.	Jan.	Feb.
mystinus	Aug.	Jan.	Jan.
melanops	Oct.	Jan.	Feb.
flavidus	Sept.	Jan.	Feb.
serranoides	Nov.	Jan.	Feb.

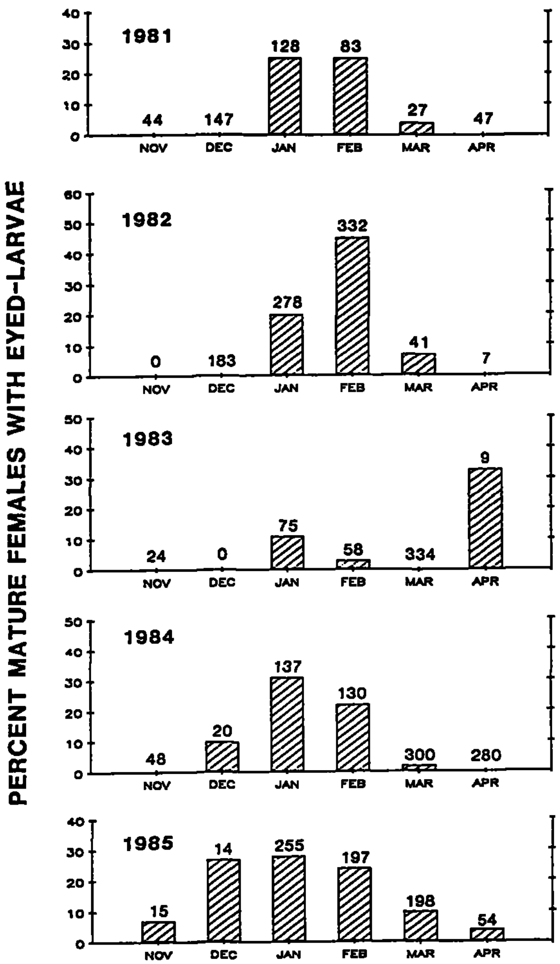

FIGURE 8.—Percent of mature female *Sebastes entomelas* containing eyed larvae for the reproductive months during 1981-85. Total number of mature females observed are indicated over bars.

Females are exposed to changing environmental factors from year to year, so flexibility in the timing of their greatest reproductive involvement may be advantageous. The apparent flexibility of the period between mating and larval extrusion may be a mechanism to optimize reproductive success. A long and variable period of larval extrusion is exhibited by the rockfish group (Figs. 8-10). The evidence of two spawnings per season have been reported for *S. paucispinis* (Moser 1967a), *S. ovalis*, and *S. constellatus* (MacGregor 1970). Multiple broods are indicated by the presence of eyed larvae undergoing resorption in the ovary concurrently with vitelloginic eggs at least 0.4 mm in diameter. During the years and throughout the area of this study, evidence of multiple broods was rare: only one *S. paucispinis* gonad showed evidence of a multiple brood. Moser's (1967b) detailed description of the histology of multiple broods indicates the development and extrusion of a second brood follows within 2 months of the first. In this study, two distinct seasons of larval extrusion, December and June, were noticed in *S. auriculatus* sampled from a limited area (Pt. Reyes-Half Moon Bay) (Table 6) in north-central California. The entire reproductive sequence in *Sebastes* seems to reflect a plasticity for reproduction that may enable the individual to respond adaptively to environmental factors.

The consequences of the reproductive biology in *Sebastes* include the absence of strong spawning pulses, the possibility of multiple mating of males, and flexibility in the timing of fertilization. Apparently mating is not restricted to a short period

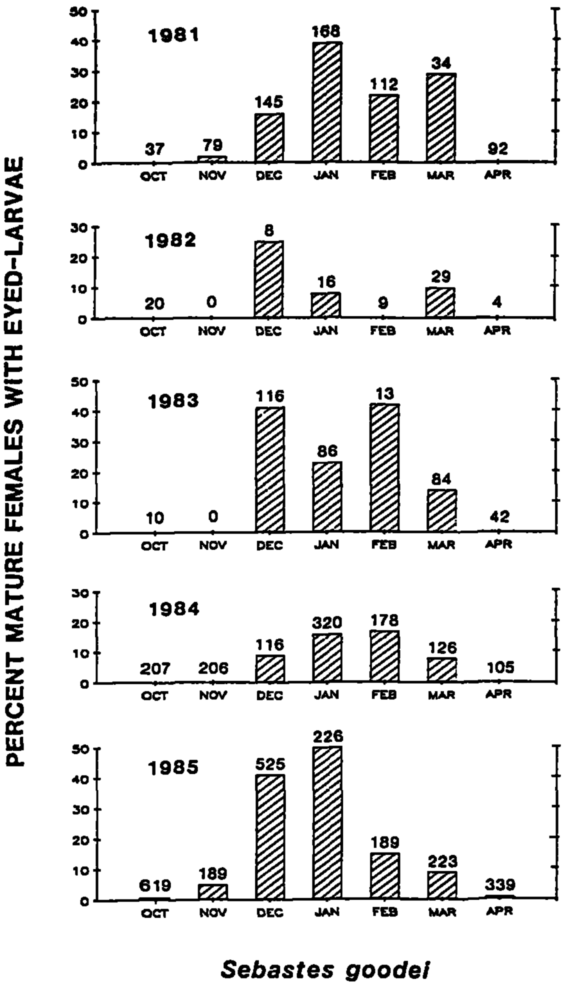

FIGURE 9.—Percent of mature female *Sebastes goodei* containing eyed larvae for the reproductive months during 1981-85. Total number of mature females observed are indicated over bars.

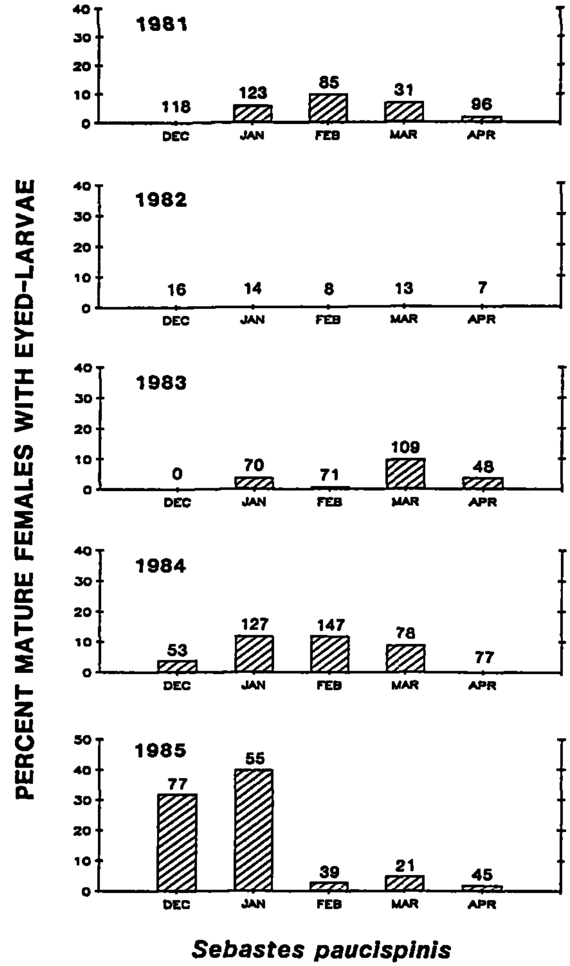

FIGURE 10.—Percent of mature female *Sebastes paucispinis* containing eyed larvae for the reproductive months during 1981-85. Total number of mature females observed are indicated over bars.

of time and elaborate displays to induce ovulation are not necessary. It is not surprising, therefore, to find so little information regarding mating behavior in the most speciose and populous group of fishes in north-central California (Helvey 1982).

Ages and sizes at maturity from this study generally agree with findings in the literature, but sometimes exhibit large discrepancies (Table 8). The variability has possible sources: differences in age determination techniques, length measurements, identification of the immature gonad stage, or sampling at times of the year when it is difficult to distinguish immature from resting fish. Previous studies on maturity often focused on adult populations or were based on samples taken only during summer, when most species are not in reproductive condition (Westrheim 1975; Gunderson et al. 1980; Rosenthal et al. 1981, 1982). The differentiation of an immature gonad stage versus mature "resting" gonads is most difficult and subject to error during the nonreproductive months.

Age and size at 50% maturity by area and year were calculated for *S. flavidus*, *S. goodei*, and *S. paucispinis* (Table 9). Age and size at maturity did not differ geographically but did vary between years. Age varies up to 1 year and size varies up to 3 cm. Apparently, there is some variability in age and size at maturity within a population between years. The normal range of variation of size and age

TABLE 8.—Age and size at 50% maturity for male (M) and female (F) *Sebastes* by area. All lengths are converted to fork length for comparison (Echeverria and Lenarz 1984).

Species of *Sebastes*	Alaska	British Columbia	Washington	Oregon	California	this study
auriculatus						
M			4 yr, 23 cm FL[1]			5 yr, 31 cm FL
F			4 yr, 25 cm FL			5 yr, 31 cm FL
entomelas						
M		37 cm FL[2]		4 yr, 33 cm FL[3]	{4 yr, 29 cm FL[4]	5 yr, 32 cm FL
F		38 cm FL		7 yr, 38 cm FL		5 yr, 36 cm FL
flavidus						
M	{11-15 yr[5]	40 cm FL, 40.5 cm FL[2,6]			5 yr, 31 cm FL[4]	6 yr, 32 cm FL
F	41-45 cm FL	42 cm FL, 45 cm FL				7 yr, 33 cm FL
goodei						
M				26 cm FL[6]	4 yr, 28 cm FL[4]	3 yr, 29 cm FL
F				37 cm FL	4 yr, 30 cm FL	3 yr, 32 cm FL
melanops						
M	10-13 yr, 40-42 cm FL[5]		3 yr, 21 cm FL[7]	5 yr[8]		6 yr, 35 cm FL
F	9-12 yr, 39-42 cm FL		3-4 yr, 33 cm FL	6 yr		7 yr, 40 cm FL
mystinus						
M				3 yr[8]	6-7 yr[9]	5 yr, 26 cm FL
F				4 yr	6 yr	6 yr, 28 cm FL
paucispinis						
M		<57 cm FL[2]	5 yr, 45 cmFL[7]		{4 yr[4]	3 yr, 39 cm FL
F		<62 cm FL	6 yr, 48 cm FL		37 cm FL	4 yr, 45 cm FL
pinniger						
M		41 cm FL[2,6]		12 yr, 39 cm FL[8]	{5-6 yr[4]	7 yr, 39 cm FL
F		48 cm FL		10 yr, 43 cm FL	33 cm FL	9 yr, 43 cm FL

[1]Washington et al. 1978; [2]Westrheim 1975; [3]Barss and Echeverria 1987; [4]Phillips 1964; [5]Rosenthal et al. 1982; [6]Gunderson et al. 1980; [7]Barker 1979; [8]McClure 1982; [9]Miller et al. 1967.

at maturity should be determined before subtle shifts in these parameters are studied.

Later spawning in high latitude populations occurs in some teleosts as a response to temperature and photoperiod (Wootton 1984). The existence of geographical trends for spawning months can be determined for a species if data exist for the same months and years. Parturition occurred somewhat earlier in the southern end of the range of *S. maliger*, *S. ruberrimus*, and *S. entomelas*. *Sebastes maliger* extruded larvae between May and July off Alaska (Rosenthal et al. 1981, 1982) and between April and July off California during 1982. *Sebastes ruberrimus* extruded larvae between June and August off Alaska (Rosenthal et al. 1981, 1982) and between April and July off California during 1982. *Sebastes entomelas* extruded larvae in February off Oregon and in January off California in 1982 (Barss and Echeverria 1987) (Table 6). For species where comparable data exist, parturition is earlier in the southern end of the species range.

TABLE 9.—Age and size of three *Sebastes* species at 50% maturity derived from linear regressions for males (M) and females (F) by area and by year for the area between Crescent City and Morro Bay.

		S. flavidus		*S. goodei*		*S. paucispinis*	
Data base	Sex	yr	cm TL	yr	cm TL	yr	cm TL
North of Point Arena	M	—	—	4	—	3	43
	F	—	—	4	—	4	48
South of Point Arena	M	—	—	4	31	3	43
	F	—	—	4	33	4	47
April 1980-March 1981	M	6	35	4	31	3	43
	F	7	37	4	34	4	48
April 1981-March 1982	M	7	38	5	33	3	42
	F	6	36	4	32	4	47
April 1980-Mach 1982	M	6	35	4	31	3	43
	F	7	36	4	34	4	48

Reproductive seasonality can be classified into one of two broad seasons, early (winter) or late (spring-summer) (Phillips 1964), which seems to hold true throughout a species range (Table 6). The duration of larval extrusion varies from 1 to 9 months and is species-specific. Closely related species have similar seasons of parturition, but the peak month may differ (Table 7).

Data on parturition may be useful when investigating recruitment by estimating annual reproductive success. To predict year-class strength for species of *Sebastes*, it must be possible to identify species in the juvenile stages. Juvenile identifications have been described for 18 species of rockfish that occur off California (Moser and Ahlstrom 1978; Richardson and Laroche 1979; Laroche and Richardson 1980, 1981; Anderson 1983); the difficulties of differentiating between similar species are evident in these studies. Knowledge of the principal month of parturition may be a useful tool when identifying species in the age 0 population. Principal month of parturition would have to be documented for the year that recruitment is investigated.

Life history parameters that are interrelated, such as growth, maturity, and fecundity, can be influenced by external conditions, such as temperature, prey abundance, and predation (Stearns and Crandall 1984). The manner in which they can be affected is species-specific and may change in a predictable manner. Observed changes that coincide with reduced population sizes include increase in growth rates (Templeman and Bishop 1979), decrease in age at maturity (Murphy 1977; Parrish and MacCall 1978; Schmitt and Skud 1978; Templeman and Bishop 1979), and decrease in size at maturity (Alm 1959; Pitt 1975). Stearns and Crandall (1984) proposed that changes in age and/or size at maturity are determined by genetic as well as environmental factors, so that populations will respond in a predictable manner. A shift in either the age or size at maturity in *Sebastes* may be an indication of a change in population densities. In order to detect any population changes, age and size at maturity for species should be determined yearly and within a well-defined geographic area. Fish of the estimated age and size at first maturity should be included—sampling from market fish tends to yield only mature fish. Ages should be determined from the same fish that are sampled for maturity.

Fecundity in poikilotherms is generally related to size; changes in growth rates and size at maturity will affect fecundity. Fecundity often relates more to body size in short-lived species and to available energy in long-lived species (Ware 1980). Fecundity increases with size in at least some species of *Sebastes* (Phillips 1964), but annual reproductive success may be linked to available energy. Gonad volumes of female *S. flavidus* were reported for 1981 (Guillemot et al. 1985) and compared with volumes measured during the El Niño winter of 1983-84 (Lenarz and Wyllie Echeverria 1986); this comparison showed reduced gonad volumes in *S. flavidus* for the 1983 reproductive season. Whether the decreased gonad volume was due to egg size or number was not determined.

Shifts in age and/or size at maturity may occur in species that have a multigenerational, late-maturing population. In his studies of flatfish populations, Roff (1982) predicted that size at maturity would be primarily influenced by size-dependent mortality and that changes in size at maturity would occur in species where growth to a minimal size is more adaptive than early reproduction. Changes in age at maturity will more likely occur in species that mature early. Changes in size, rather than age, at maturity would most likely occur in *Sebastes* subjected to overfishing or long-term environmental stress.

General changes in life history parameters may be predictable according to a species' position on the r-K selection continuum. Increased fishing mortality resulting in decreased populations may affect life history parameters by increasing growth rates, reducing age at first maturity, increasing fecundity at age (Adams 1980; Gunderson 1980), and reducing variability in the gene pool by reducing the number of spawning groups in the more K-selected species (Leaman and Beamish 1984). The reproductive strategy of *Sebastes* reflects more K-type characteristics, which include later maturity, slower growth rates, lower individual fecundity, or some degree of parental care (Garrod and Horwood 1984). The K-type reproductive strategy enables a species to minimize the effects of a poor reproductive year (Roff 1984). A disadvantage for a heavily fished K-type species is the late age at maturity, as exists in *Sebastes*, so that the advantage of many reproductive seasons must be balanced against adult population size to obtain an allowable harvest.

The reproductive strategy of *Sebastes*, with multiple generations reproducing simultaneously and the plasticity of annual timing, results in a buffered system. The populations of exploited stocks of *Sebastes* should be able to recover from a single year of high mortality due either to poor recruitment or to adult mortality. However, overfished populations or long periods of poor recruitment could result in a reduced size at maturity and a corresponding reduced fecundity.

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