GROWTH, REPRODUCTION, AND FOOD HABITS OF OLIVE ROCKFISH, *SEBASTES SERRANOIDES*, OFF CENTRAL CALIFORNIA

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ABSTRACT

We collected data on age-length and length-weight relationships, age at first maturity, spawning season, fecundity, and food habits of olive rockfish, *Sebastes serranoides*, off Diablo Cove, near Avila, California. Fish were aged from otoliths. Von Bertalanffy age-length parameters for females were $L_\infty = 51.9$, $k = 0.18$, and $t_0 = -1.57$; for males $L_\infty = 43.3$, $k = 0.27$, and $t_0 = -1.03$. Females grew at a faster rate than males beginning at the age where most males were mature. Age at first maturity ranged from 3 to 8 years, most fishes maturing by age 6. Olive rockfish spawned once per season, between December and March, with peak spawning in January. Fecundity ranged between 30,000 and 490,000 eggs. Small individuals preyed primarily on plankton, and larger ones concentrated on fishes, squids, and octopuses.

The rockfishes (Scorpaenidae: *Sebastes*) are an important constituent of many marine communities in the eastern North Pacific. Sixty-nine species are known to inhabit these waters (Lea and Fitch 1979) and members of the genus frequent virtually every habitat from intertidal regions to depths of well over 1,000 m.

Though these fishes were of some importance in commercial and sport fisheries in the past, population declines of more popular fishes have led to a steady increase in rockfish demand. Commercial rockfish catches in the Northeast Pacific exceeded 30,000 t in 1978 (Pacific Marine Fisheries Commission 1980) and in California, rockfishes are the most important sport fishes, by number, in party boat catches (Pinkas 1977).

Major, deeper water, commercially important species, such as Pacific ocean perch, *S. alutus* (Westrheim 1973; Gunderson 1977; Wishard et al. 1980); chilipepper, *S. goodei*, and bocaccio, *S. paucispinis* (Phillips 1964; Wilkins 1980; Wishard et al. 1980); and yellowtail rockfish, *S. flavidus* (Phillips 1964; Carlson and Haight 1972; Wishard et al. 1980) have received most attention from researchers. By contrast, with the exception of blue rockfish, *S. mystinus* (summarized in Miller and Geibel 1973), there are few papers on inshore rockfishes.

The olive rockfish, *Sebastes serranoides*, composes a major portion of the sport fish catch, both from party boats and private vessels, along southern and central California (Miller and Gotshall 1965; Wine and Hoban[2]; Maxwell and Schultze[3]). It lives in areas of reef and kelp, from Del Norte County, Calif., to San Benito Island, Baja California, Mexico, and is most abundant in depths of 5-100 m.

Olive rockfish are active, fast-swimming, streamlined predators, usually found in the water column, but occasionally hovering over or resting upon rocky substrates (Quast 1968a; Hobson and Chess 1976; Love and Ebeling 1978). Juvenile olive rockfish are primarily midwater feeders, preying upon zooplankton and small fishes, though some substrate feeding (on isopods, caprellid amphipods, etc.) has been noted (Quast 1968b; Hobson and Chess 1976; Love and Ebeling 1978). No data were available on the food habits of adults. Once they settle out of the plankton, individuals apparently grow to adulthood in a relatively small, circumscribed area (Love 1980) and reefs can be readily depleted of large individuals by overfishing. Off Santa Barbara, Calif., the diminishing sport catch of olive rockfish is now mostly of juvenile and subadult fish, younger than the age of first maturity (Love 1980). Yet, despite

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[2]Wine, V., and T. Hoban. 1976. Southern California independent sportfishing survey annual report July 1, 1975-June 30, 1976. Calif. Dep. Fish Game, 109 p.

[3]Maxwell, W. D., and D. L. Schultze. 1976. Southern California partyboat sampling study. Calif. Dep. Fish Game, Mar. Res. Adm. Rep. No. 76-3, 18 p.; 76-6, 18 p.; 76-9, 13 p.

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the importance and vulnerability of the olive rockfish, little was known about its life history.

METHODS

Specimens were collected between 1972 and 1977, at a group of shallow-water pinnacles, about 11 km west of Avila, Calif. (Figure 1). These pinnacles, at depths of 20-30 m, are situated 100-300 m offshore from Diablo Cove and North Cove, and rise to within 5-10 m of the surface. Brown algae (predominantly *Nereocyctis* sp.) grow on the shallower reefs during summer and fall. Sampling was sporadic until 1975, when, with a few exceptions, monthly collections were made through 1977.

Specimens were collected by hook and line and by pole spear (in about equal proportions), immediately placed on ice aboard the diving vessel, and then frozen for later examination ashore.

All specimens were measured (total and standard lengths—TL, SL) to the nearest millimeter and weighed to the nearest 0.1 g. Individuals larger than about 15 cm TL were sexed and their gonads weighed to the nearest 0.1 g.

Age Determination

Attempts to age rockfish have utilized various calcified structures (scales: Phillips 1964; Miller and Geibel 1973; otoliths: Chen 1971; Patten 1973; Westrheim and Harling[4]; vertebrae, opercles, otoliths, scales, anal pterygiophores, etc.: Six and Horton 1977), each with varying success. Otoliths and scales have been most useful, and in this study fish were aged with saccular otoliths. Sagittae were removed from 616 (320 female and 296 male) specimens. Otoliths were cleaned and stored in water. Often thick and difficult to read, otoliths from *S. serranoides* older than about 7 yr were immersed in clove oil for several months to increase their transparency. A chalky coating covering an occasional otolith was cleared away with a weak hydrochloric acid solution. Care was taken to prevent dissolving annuli at the otolith margins.

Otoliths were placed in a black-bottomed watchglass filled with water (or clove oil) and read under a dissecting microscope at a magnification of 10×. All otoliths were read twice, by the senior author, approximately 2 mo apart. Agreement between reading was highest (100%) in 0-yr fish, declining to 25% in 14-yr-olds (Table 1). If the readings did not agree, the otoliths were read again. The value of two coincident readings was accepted as the best estimate of age. If all three readings were different, the midreading was accepted. A few otoliths were rejected as unreadable due to fluctuations in readings of as much as 4 yr.

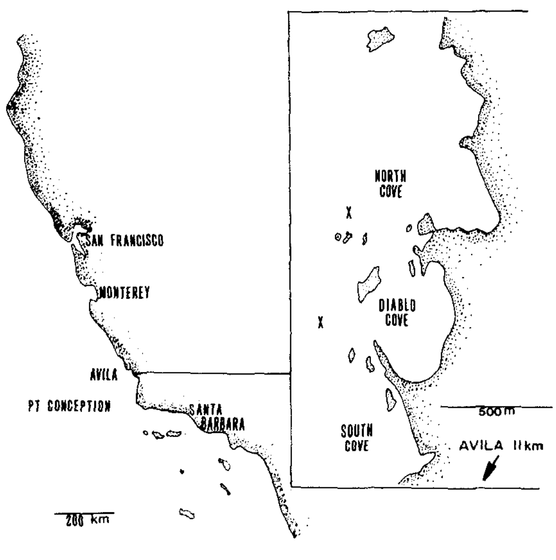

FIGURE 1.—Location of sampling sites (marked with an x) for olive rockfish off Diablo Cove, Calif.

TABLE 1.—Consistency (percent agreement) of duplicate readings from olive rockfish. The readings were made 2 mo apart by the same observer.

No. of zones	Otoliths (no.)	Percent	No. of zones	Otoliths (no.)	Percent
0	45	100	8	60	72
1	12	100	9	45	69
2	55	98	10	37	63
3	72	94	11	15	58
4	66	83	12	10	40
5	72	83	13	8	38
6	74	80	14	12	25
7	73	77			

Maturation and Reproduction

The gonads of mature olive rockfish undergo marked, yearly cyclical changes. Immediately after larvae are released spent ovaries are flaccid and reddish, purple, or gray. A resting period follows as the ovaries firm up, turning pink-red. Ovaries turn bright orange (very rarely cream-colored) and contain opaque eggs, during the mature phase, before fertilization. During the

[4]Westrheim, S. J., and W. R. Harling. 1975. Age-length relationships for 26 scorpaenids in the northeast Pacific Ocean. Can. Fish. Mar. Serv., Res. Dev., Tech. Rep 565, 12 p.

fertilized stage, the eggs are clear and turn gray as larvae develop in the ripe ovaries.

Mature males undergo a simpler cycle. Resting stage testes are small and brown, becoming larger and whitish brown as they develop. Fully developed testes are large, white, and delicate.

With this information, it was possible to determine when fish reproduced and when insemination occurred. Stages of gonad maturation (condition) in 1,056 adult olive rockfish, taken during 1972-77, were determined using the criteria of Westrheim (1975). A gonadosomatic index (gonad weight)/(total body weight) × 100 was computed to quantify changes in gonad size with season.

For fecundity estimates the ovaries of 83 mature fish captured in October and November were placed in modified Gilson's solution (100 ml 60% isopropanol, 880 ml freshwater, 15 ml 80% nitric acid, 18 ml glacial acetic acid, and 20 g mercuric chloride—Bagenal and Braum 1971) to harden the eggs and were periodically shaken to loosen them from ovarian tissue. Eggs were kept in the solution for about 2 mo, after which the fluid was poured off and replaced with water. Before eggs were counted, the ovaries were further broken up and repeatedly washed with water to remove remaining connective tissue. The eggs were placed in a larger beaker and water was then added until 2,000 ml of eggs and water had been obtained. The mixture was stirred magnetically until the eggs were homogeneously distributed throughout the water column, and a 5 ml subsample was drawn with a pipette. Three subsamples were taken.

Eggs in each subsample were counted, using a dissecting microscope, and the mean number per milliliter was calculated for the three subsamples. Fecundity was then estimated by back calculation.

Food Habits

Specimens were collected nearly every month between May 1975 and April 1977 by hook and line and pole spear (in about equal proportions), immediately placed on ice aboard the diving vessel, and frozen soon after for later examination ashore. A total of 591 specimens were collected, of which 374 (63.3%) had some food in their stomachs. We took precautions that only artificial lures were used and chumming or other disturbances were avoided, so that sampling method did not bias the stomach content composition.

Stomach contents were sorted taxonomically into 17 food items and the volume of each category was measured by liquid displacement. Food items were also grouped into three prey types (substrate oriented, nekton, and plankton) based on prey behavior and habitat. Nektonic prey included all nonlarval fish and squid. Substrate-oriented prey included all prey (except fish) that live on or about reef and plant surfaces; these may be motile, such as octopus, or attached, like algae.

To examine seasonal variation in diet within each size class of olive rockfish (except 10.1-20.0 cm which had too few specimens), food data was pooled by seasonal periods roughly corresponding to "upwelling" (March-August) and "oceanic" (September-February) oceanographic regimes off the Avila area (Bakun 1973).

RESULTS AND DISCUSSION

Age and Growth

There was no published work in aging olive rockfish (with the exception of a few fish mentioned in Burge and Schultz[5]), and the use of the otoliths in age studies had not been validated. To determine if the opaque and translucent zones were annular, we observed the development of the opaque zone on the edge of otoliths of fish from Avila, taken during a 5-yr period. The occurrence of a particular zone among most or all individuals during one part of the year would indicate that the zones were suitable for age determination (Williams and Bedford 1974; Dark 1975). Because the opaque zones become narrow and difficult to distinguish in older fish and the timing of zone deposition may be influenced by the species' age or state of maturity (Williams and Bedford 1974; Dark 1975), we limited sampling for otolith validity to 1- to 3-yr-old (immature) olive rockfish.

Data indicated that the opaque zone deposition was seasonal (Figure 2). The percentage of otoliths with opaque edges was low during fall and winter, but rose abruptly during late spring and peaked in summer months. Hence, the production of opaque zones coincides with the upwelling period along central California (Bakun 1973) and probably reflects increased feeding and growth. The percentage of opaque zones during the early spring may be underestimated as the newly deposited opaque material is quite thin. On the other hand,

[5]Burge, R. T., and S. A. Schultz. 1973. The marine environment in the vicinity of Diablo Cove with special reference to abalones and bony fishes. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 19, 433 p.

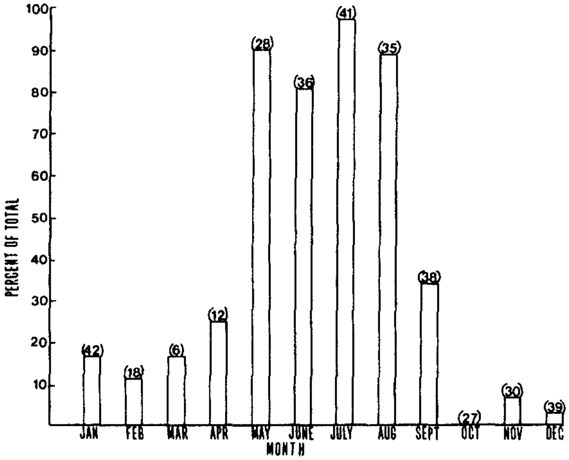

FIGURE 2.—Monthly percentages of 1- to 3-yr-old olive rockfish with opaque margins. Sample size is in parentheses.

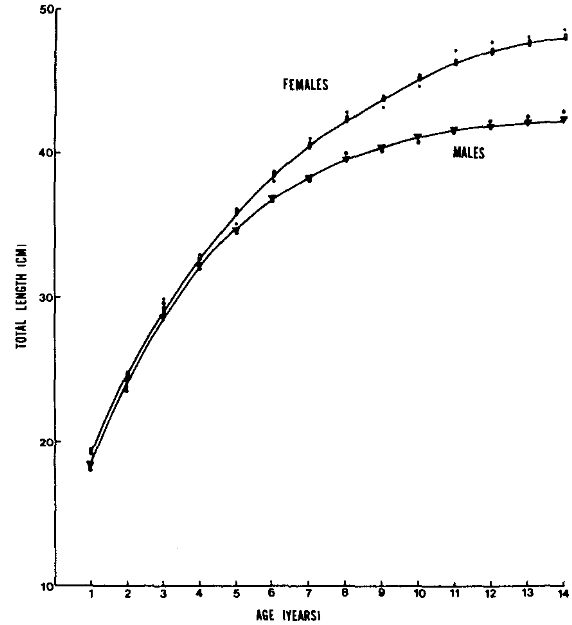

FIGURE 3.—Von Bertalanffy growth curves of female (circles) and male (triangles) olive rockfish. Also included are mean lengths at ages (females—stars, males—dots) computed from direct observation of otolith annuli. Based on 320 females and 296 males taken off Diablo Cove, 1972-77.

the beginnings of the transparent zone during the fall are readily apparent.

Lengths at ages were estimated by direct observation of otolith annuli, back calculation of annuli, and through the von Bertalanffy growth curve model. In this model, the formula

$$L_t = L_\infty [1 - \exp - k(t - t_0)]$$

where L_t = length at time t
L_∞ = theoretical maximum length
k = constant expressing the rate of approach to L_∞
t_0 = theoretical age at which $L_t = 0$

was fitted to the direct observation age-length data.

We transformed the male and female von Bertalanffy growth equations to linear form (Allen 1976) and compared these by analysis of variance. Females were found to grow significantly faster than males ($F = 19.08$, $P < 0.01$), hence we have separated growth data by sex (Table 2).

Mean lengths at ages obtained by direct observations of annuli and as generated by the von Bertalanffy equations are plotted to age 14 (Figure 3). Through direct observation of annuli, we found a few individuals to live to be as much as 25 yr. However, our samples of fishes older than about 14 yr were few, and older fish played little part in growth calculations. Back-calculated lengths (Tables 3, 4) were computed to age 12. Otoliths of fish older than 12 yr were often unusable for back calculations, because these fish laid down heavy layers of opaque material along the axis used to measure annuli, making measurements difficult.

All three measures of growth yielded similar results. Mean lengths at age for females and males were similar through age 4. Females outgrew males beginning at age 5, the age at which over 50% of the males were mature. Both male and female olive rockfish had k values (0.27 and 0.18, respectively) higher than most previously studied rockfish, indicating that the species reached maximum length relatively quickly. The k-values were similar (though slightly higher for both sexes) to those of *S. flavidus* (Fraidenburg 1980; Westrheim and Harling footnote 4), a closely related species.

Because few individuals older than 14 yr were captured, estimates of length at age of older fish produced by the von Bertalanffy equation may be inaccurate. Certainly the L_∞'s are too low, as

TABLE 2.—Parameters of the von Bertalanffy equation for olive rockfish off Diablo Canyon, Calif.

Sex	L_∞	SE	k	SE	t_0	SE
Females	51.90	0.93	0.18	0.01	−1.57	0.23
Males	43.30	.45	.27	.02	−1.03	.19

TABLE 3.—Mean back-calculated total length (centimeters) ± 95% confidence intervals at successive annuli for male olive rockfish captured off Avila during 1972-77.

Age-group	No. of fish	1	2	3	4	5	6	7	8	9	10	11	12
1	3	17.9±5.8											
2	24	18.5±1.0	22.8±0.6										
3	40	19.4±0.4	24.8±0.6	29.7±0.6									
4	34	18.7±0.6	24.9±0.8	29.5±0.6	33.0±0.6								
5	38	19.2±0.2	24.7±0.6	29.6±0.4	33.2±0.4	35.8±0.8							
6	33	19.1±0.8	24.2±0.8	29.0±0.8	32.7±0.6	35.0±0.6	36.7±0.6						
7	33	19.2±0.4	24.7±0.4	30.0±0.4	33.1±0.6	35.4±0.4	36.9±0.4	38.0±0.4					
8	27	18.7±0.6	24.1±0.6	30.4±0.8	33.4±0.6	36.0±0.6	37.2±0.6	38.3±0.6	39.4±0.6				
9	22	18.3±0.6	24.6±0.6	29.6±0.5	32.5±0.6	35.1±0.6	37.0±0.5	38.2±0.5	39.7±0.6	40.4±0.7			
10	14	17.8±0.1	22.8±0.3	28.6±1.2	32.4±1.0	35.9±1.0	36.3±1.2	38.1±0.4	38.0±1.1	39.4±1.1	41.1±1.3		
11	5	17.5±1.4	22.4±1.8	28.2±1.8	32.0±1.5	34.1±1.8	36.1±1.7	37.1±1.9	38.1±1.8	40.2±2.0	39.4±1.9	41.0±1.7	
12	9	18.1±1.5	22.5±1.4	29.0±1.3	32.6±1.7	35.0±1.5	36.5±1.4	37.4±1.4	38.5±0.5	39.3±1.5	41.4±1.5	40.8±1.4	40.9±1.6
Average		18.5	23.8	29.4	32.8	35.3	36.8	37.9	39.0	39.9	40.9	40.9	40.9

TABLE 4.—Mean back-calculated total length (centimeters) ± 95% confidence intervals at successive annuli for female olive rockfish captured off Avila during 1972-77.

Age-group	No. of fish	1	2	3	4	5	6	7	8	9	10	11	12
1	7	19.2±2.3											
2	24	18.1±0.8	24.0±0.8										
3	32	19.0±0.6	24.5±0.6	30.0±0.8									
4	31	19.4±0.6	24.9±0.8	29.8±0.8	33.7±0.8								
5	39	19.7±0.8	24.8±0.8	30.1±0.8	33.6±0.8	36.0±1.0							
6	35	19.1±0.6	24.4±0.8	28.7±1.0	32.6±1.0	35.2±1.0	37.9±1.0						
7	39	20.5±0.6	26.0±0.8	30.6±0.8	34.1±1.0	36.6±1.1	38.4±0.8	40.7±0.8					
8	32	19.6±0.1	24.8±0.3	31.0±0.5	35.1±0.3	37.1±0.3	39.3±0.4	41.9±0.5	42.6±0.2				
9	23	18.3±0.6	24.5±0.4	30.4±1.0	33.7±0.8	36.2±0.8	38.7±0.8	40.7±0.8	42.8±0.8	42.9±0.8			
10	23	20.3±0.2	26.3±1.3	31.0±1.3	34.6±0.9	36.1±1.3	38.1±1.1	40.1±1.2	41.7±1.4	42.8±1.2	43.9±1.1		
11	10	18.2±1.2	23.7±1.3	28.6±1.4	33.0±1.4	36.1±1.2	38.1±1.6	40.1±1.7	42.1±1.6	41.9±1.6	43.1±1.8	45.2±1.8	
12	4	18.2±1.4	24.0±1.6	28.3±1.8	33.3±1.6	35.4±1.9	38.3±2.0	40.3±2.1	41.9±1.6	41.6±2.1	42.9±1.6	45.1±1.8	45.6±1.9
Average		19.2	24.8	29.9	33.7	36.2	38.5	40.7	42.2	42.4	43.5	45.2	45.6

we did capture females to 61.9 cm and males to 50.2 cm.

No marked Lee's Phenomenon was noted, though it is found in other rockfishes (Chen 1971; Miller and Geibel 1973). A possible explanation is that fish older than age 12 were not used in back calculations, and since some members of the species live to at least 25 yr, the phenomenon may not be apparent until older fish are examined.

Length-Weight Relationships

A total of 312 males and 304 females were weighed and measured. The relationships between total length and weight seemed to fit the relationships $W = aL^b$, where W = weight in grams and L = total length in centimeters, and a and b are constants. The values of a and b were determined using $\log_{10}$ transformation and fitting the values to a straight line by least squares. Females tended to be heavier at a given length (analysis of variance, $F = 15.23$, $P<0.01$) (Figures 4, 5). To test whether this difference was an artifact caused by the larger female gonads, we subtracted gonad weight from body weight, generated the length-weight relationships for each sex and tested these between sexes. Again, females were heavier at length (analysis of variance, $F = 10.18$, $P<0.01$).

Maturation and Reproduction

Insemination and Birthing Season

Larval release occurred from December through March, peaking during January (Figure 6). Spent females were most prevalent during early spring, followed by a June peak in resting fish and a September-October peak in mature individuals. Fertilized fish were found from November through January. Ovary weights remained essentially constant during the spring and summer (Figure 7), averaging perhaps 0.3% of body weight, occasionally as little as 0.1%. Then, during the winter and spawning season, ripe ovaries averaged 13.8% of body weight (maximum 20.7%, minimum 2.3%).

Testes sizes (based on the gonad index) were relatively constant during spring and early summer, though they began to increase in size a month or two earlier than did the ovaries of females (Figure 7). During the constant period, they remained at minimum size, about 0.1% of body

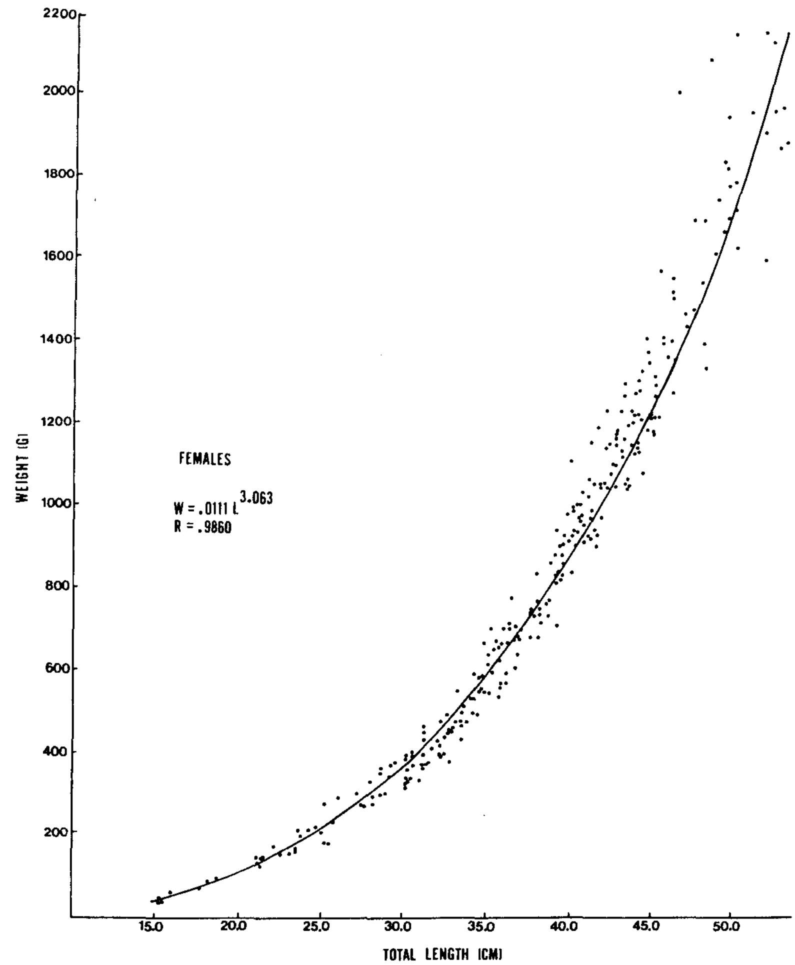

FIGURE 4.—Length-weight relationship based on 304 female olive rockfish sampled off Diablo Cove, 1972-77.

weight. They increased to 0.9-1.0% (maximum 2.2%) of body weight in late fall. It appeared that insemination occurred from October to December, perhaps peaking in November.

Moser (1967) found "a brood of advanced embryos or larvae and a series of ova undergoing vitellogenesis" in *S. chlorostictus*, *S. constellatus*, *S. eos*, *S. goodei*, *S. levis*, *S. ovalis*, *S. paucispinis*, and *S. rosaceus*, and stated that this offered direct evidence of multiple brood production. Similar findings for some of the above species were reported by MacGregor (1970), and Miller and Geibel (1973) noted that 1 of 648 *S. mystinus* examined showed multiple broods. We found no such evidence in olive rockfish, though females usually retained a few unexpelled eyed larvae, which appeared to be resorbed within a few months.

The evolution of reproductive isolating mechanisms in the genus *Sebastes* may not have included the restriction of random mating by seasonal isolation. It seems likely that the time from insemination to spawning is similar among closely related species. Rockfish species which mate over the same period, probably spawn at the same time during a later season. Olive rockfish and their presumed subgeneric congeners, *S. flavidus*, *S. mystinus*, and *S. melanops*, spawn and probably mate during the same seasons (Phillips 1964; Miller and Geibel 1973) as do other closely related rockfish species groups (e.g., *S. paucispinis*-*S. goodei*—Moser 1967) and other subgenera (*Sebastomus*—Chen 1971).

Instead, habitat isolation among some species (such as *S. chrysomelas*-*S. carnatus*—Larson 1977) may restrict interspecific mating. However, a number of species pairs (notably *S. paucispinis*-*S. goodei*) may aggregate together throughout the year. Even though closely related species mate in the same habitat, during the same season, hybrids

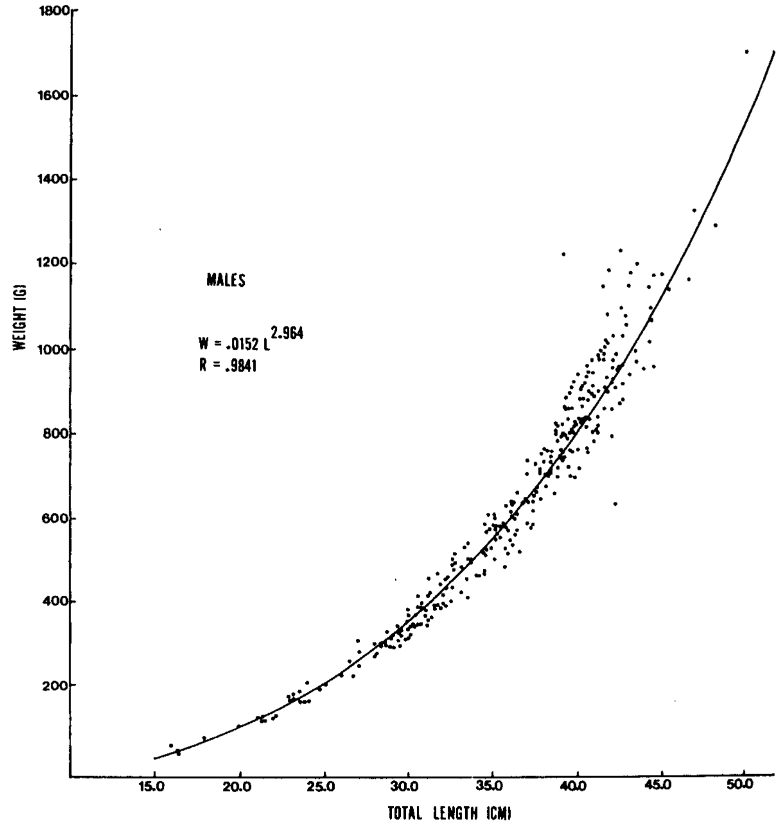

FIGURE 5.—Length-weight relationship based on 312 male olive rockfish sampled off Diablo Cove, 1972-77.

are very rare in California waters (the "hybrids" mentioned by Phillips (1964) are now recognized as distinct species), indicating that other antihybridization mechanisms are involved.

Though it is possible that extensive cross-specific mating occurs, and gametic or zygotic mortality prevents hybridization, it seems more likely that internal fertilization, necessitating close coordinated contact, has lent itself as a mechanism of mechanical and/or behavioral isolation. The copulatory organs of male *S. serranoides* are relatively small, thus a degree of closely coordinated movements is probably necessary to effect mating. Auditory, visual, and chemical cues may all play a part. It is known, for instance, that some rockfish species produce sounds (Hallacher 1974) and these may be used in species recognition. Deeper water species, living in relative darkness, may depend primarily on nonvisual recognition during mating season.

Size and Age at Maturity

It was often difficult to distinguish prereproductive female olive rockfish from mature late resting stage females (as noted by Westrheim 1975 and Gunderson 1977 in *S. alutus*). Females develop small orange ovaries 1 or 2 yr before they reproduce. During much of the year these "maturing" fish were easily distinguished from reproductive individuals by their consistently small, pale orange ovaries. However, during late spring and early summer, the ovaries of both reproductive and maturing fish are small and orange. Because mature and maturing females were not readily differentiated during late spring and early summer, females captured during this period were not included in this analysis.

There was considerable variation in size and age at first maturity (Figures 8, 9). A few fish were mature at 3 yr old (males 28.1-32.5 cm TL, females 31.1-33.6 cm TL). Yet not all males were mature before 7 yr and 39.0 cm TL, nor females before 8 yr and 37.0 cm TL. Over 50% of the females had spawned by 4 yr and 34.0 cm TL, while males were age 5 and 32.0 cm TL before reaching the 50% mark. In general, males first matured at a somewhat smaller size and somewhat later age than females.

Limbaugh (1955) reported that, off southern

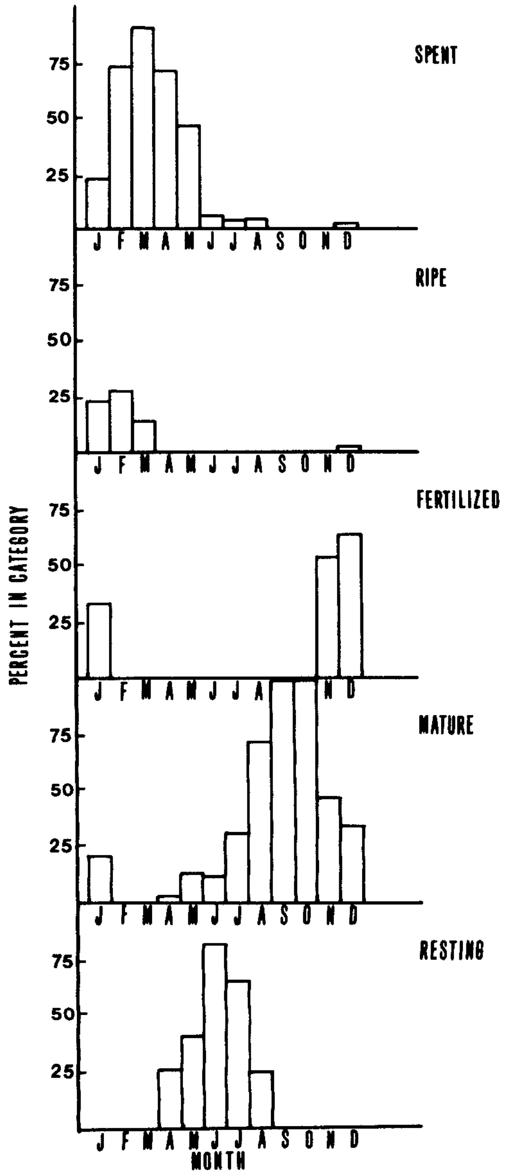

FIGURE 6.—Percent composition by month of five gonad condition stages for female olive rockfish taken off Diablo Cove, 1972-77. Resting refers to that period before egg development, vitellogenesis occurring during the maturing stage, which is terminated by the fertilized stage. Eyed larvae, which define ripe gonads, are extruded and the gonads are called spent.

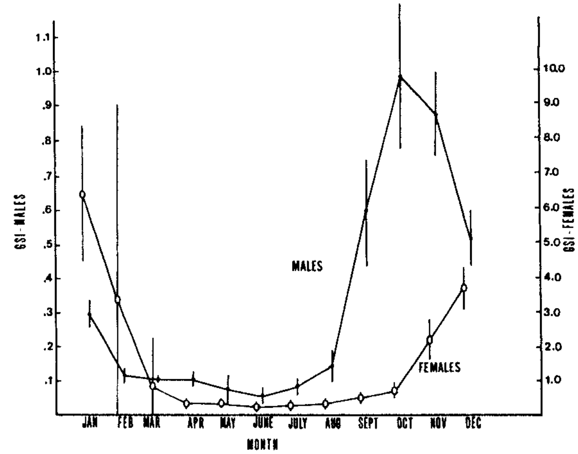

FIGURE 7.—Seasonal changes in the gonosomatic index (GSI—gonad weight as a percent of total body weight) of male and female olive rockfish. Vertical lines indicate 95% confidence intervals of the mean.

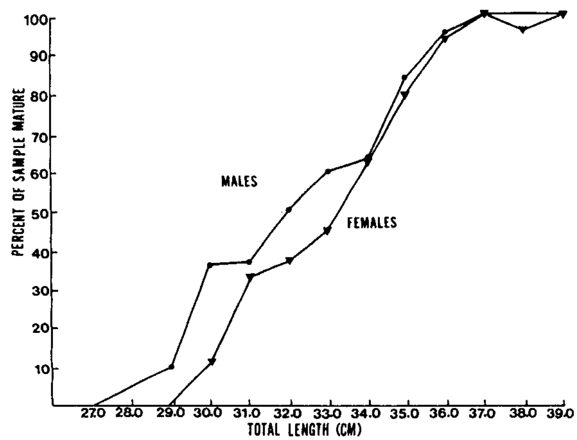

FIGURE 8.—Length-maturity relationship in 331 female and 318 male olive rockfish collected off Diablo Cove, 1972-77.

California, olive rockfish matured at 17-22 cm TL. This is considerably smaller than fishes taken off Diablo Cove. Unpublished data by Love (1978) indicated that olive rockfish off Santa Barbara (in southern California) mature at the same length as fishes farther north. It is possible that Limbaugh mistook prereproductive individuals, whose gonads do swell and color slightly, for mature fish.

Age of first maturity varies widely among rockfish species. At one extreme, *S. emphaeus* matures at 2-4 yr (Moulton 1975); *S. umbrosus*, *S. ensifer* (Chen 1971), and *S. jordani* (Phillips 1964) at 3 yr; while the others, *S. chlorostictus*, *S. rosenblatti*, and *S. constellatus* mature at about 10 yr (Chen 1971) and some stocks of *S. alutus* do not mature until 11 yr or later (Gunderson 1977). Modal period for first reproduction seems to be about 4-7 yr for most species (Phillips 1964; Patten 1973; Miller and Geibel 1973).

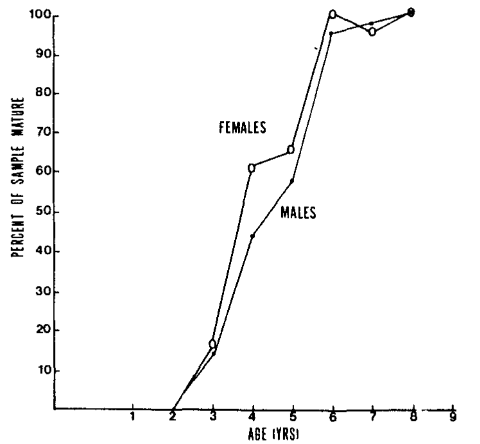

FIGURE 9.—Age-maturity relationship in 317 female and 302 male olive rockfish collected off Diablo Cove, 1972-77.

Fecundity

The nonlinear relation between fecundity and total length (Figure 10) was best described by the function $F = aL^b$, where F = number of eggs in thousands, L = total length in centimeters, and a and b = constants. The value of the parameters a and b were estimated by fitting the linear function $\log F = \log a + b \log L$ by least squares. Estimated fecundity ranged from 30,000 eggs for a 32.6 cm TL individual to about 490,000 for one 46.8 cm long.

Olive rockfish fecundity levels reflected the ranges determined for some other rockfish species, notably *S. flavidus* (Phillips 1964; Gunderson et al. 1980), *S. crameri*, *S. jordani*, and *S. entomelas* (Phillips 1964). They appear to be more fecund per body length than *S. alutus* (Gunderson 1977) and *S. goodei* (Phillips 1964; Gunderson et al. 1980) and less so than *S. elongatus*, *S. diploproa* (Phillips 1964), and *S. mystinus* (Miller and Geibel 1973). In all species studied, smaller individuals tend to carry fewer eggs. There is some evidence (MacGregor 1970) that smaller species also carry fewer eggs per body length.

Fish fecundity measurements, however, are tenuous at best and should only be looked upon as first approximations. Computations made before and after fertilization (Lisovenko 1956) or by differences in subsampling techniques (Gunderson 1977) may cause discrepancies between studies. Moreover the relationship between the number of maturing eggs in an ovary and viable larvae produced is unknown. Unfortunately, it is not practical to count larvae in the ovaries, as some may be lost during capture. Fecundity may also vary due to environmental factors (temperature—Rounsefell 1957 and food availability—Bagenal 1966) or genetic differences (Bagenal 1966).

Juveniles

Rockfish larvae are pelagic for a number of months, after which they settle into waters of various depths. The settling time and habitat of olive rockfish off Diablo Cove was determined from information based on underwater observations and young-of-the-year collected from 1974 to 1977. Though young *S. flavidus* closely resemble *S. serranoides*, and hence might be a source of confusion, they are rare in shallow waters off Diablo Cove (Berge and Schultz footnote 5). Based on spawning season and young-of-the-year sightings, olive rockfish probably spend 3-6 mo as pelagic larvae before settling out. Young-of-the-

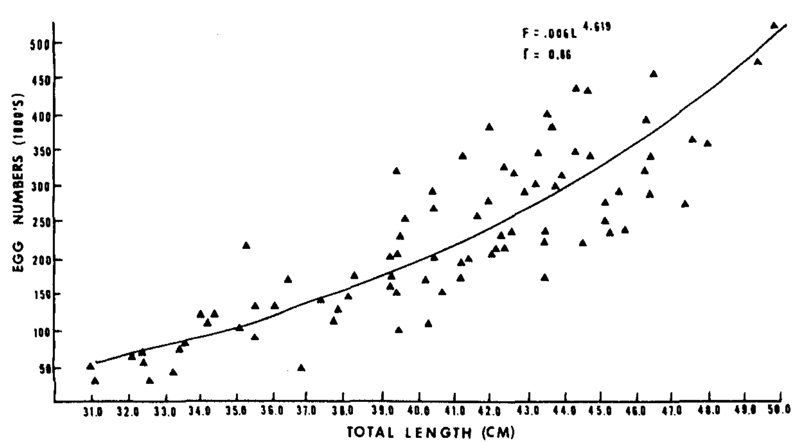

FIGURE 10.—Fecundity-total length relationship for 87 olive rockfish collected off Diablo Cove during October and November 1972-77.

year (of about 2-3 cm TL) first appeared inshore off Avila during March and April. At this stage, they were particularly common under the kelp canopy and over very shallow, protected rocky reefs (occasionally in the lower intertidal zone). Although they were not directly observed there, young-of-the-year probably also occur on reefs somewhat farther offshore (depth 20-50 m), since they were often found in the stomachs of resident rockfish in these habitats.

Food Habits

Olive rockfish were found to be primarily midwater predators of nekton (Table 5). Very important among its prey were small fishes, including blue rockfish; young olive rockfish; pipefish, *Syngnathus* sp.; shiner perch, *Cymatogaster aggregata*; kelp gunnel, *Ulvicola sanctaerosae*; northern anchovy, *Engraulis mordax*; topsmelt, *Atherinops affinis*; and cottids. Another important nektonic prey was the squid *Loligo opalescens*. Among planktonic prey, small crustaceans (particularly crab megalops larvae), tunicates (*Oikopleura* sp., *Doliolium* sp.), euphausids, fish larvae, and polychaetes were commonly eaten. Among substrate-oriented prey, octopus was the most important food item, followed by gammarid amphipods, isopod *Idothea* sp., and other small crustaceans.

As olive rockfish grow, their food habits change. Previous studies (Quast 1968b; Hobson and Chess 1976; Love and Ebeling 1978) have shown juvenile olive rockfish to be primarily midwater feeders, actively swimming after such forms as polychaetes, megalops larvae, mysids, and small fish. In the present study, though planktonic forms were important for individuals of all size classes, nektonic animals, primarily fish and squid, assumed dominance in the diet as the fish grew larger (Table 6). Plankton consumed by smaller individuals included a wide variety of small and large crustaceans, fish larvae, and polychaetes. For larger fish, plankton consumption was essentially limited to large items, such as euphausids, tunicates, and polychaetes. Nekton

TABLE 6.—Percentage occurrence of prey types in stomachs of four size classes (total length) of olive rockfish from Avila, Calif. Probabilities determined by 2 × 2 contingency *G*-test (Sokal and Rohlf 1969).

Size class (cm)	Stomachs with food (no.)	Plankton	Nekton	Substrate oriented
10.1-20.0	25	84.0*	16.0*	20.0
20.1-30.0	75	57.3*	40.0*	29.3
30.1-40.0	158	41.7**	56.5	22.0**
40.1-50.0	116	25.7	56.0	43.1

*$P \leq 0.05$, **$P \leq 0.01$.

TABLE 5.—Percentage total volume and frequency of occurrence of 17 food items in stomachs of olive rockfish off Avila, Calif. Olive rockfish are divided into 10.0 cm TL size groups. Food items are grouped by behavior and habitat.

	10.1-20.0 cm		20.1-30.0 cm		30.1-40.0 cm		40.1-50.0 cm		Total	
Food item by prey type	% vol	% freq	% vol	% freq	% vol	% freq	% vol	% freq	% vol	% freq
Primarily planktonic (sum)	(54.2)		(20.9)		(8.8)		(7.9)		(9.3)	
Small crustaceans, 0.5-5 mm:										
Zoea			.7	2.7	tr[1]	1.9			tr	1.3
Copepods	.8	24.0	1.2	4.0	tr	3.2	tr	1.7	tr	4.2
Megalops	4.8	28.0	9.6	33.3	.2	7.0	tr	3.4	.6	12.2
Large crustaceans, >10 mm:										
Euphausids			1.2	2.6	4.2	13.9	2.3	7.8	3.0	8.6
Small-medium sized, transparent										
Tunicates (salps, larvaceans)			.3	1.3	2.6	6.3	5.3	.9	4.0	5.7
Fish larvae	44.5	52.0	.9	6.6	.2	5.0	tr	1.7	.5	7.3
Polychaetes	4.1	16.0	7.0	28.0	1.6	22.8	.3	12.0	1.2	19.5
Primarily nektonic, 20-160 mm (sum)	(44.7)		(72.1)		(81.1)		(64.4)		(71.3)	
Fish	44.7	12.0	66.0	37.3	36.9	52.5	24.5	44.8	31.6	43.2
Squid			6.1	2.6	44.2	7.7	39.9	12.1	39.7	7.6
Primarily substrate oriented (sum)	(1.0)		(6.9)		(10.0)		(27.2)		(19.3)	
Free moving animals:										
Mysids			.9	4.0	tr	.6	tr	.9	tr	1.3
Isopods			.4	4.0	.3	6.0			.1	3.1
Gammaridean amphipods	1.0	20.0	2.2	18.6	.1	3.8	tr	.9	.2	6.8
Caprellid amphipods					tr	.6			tr	.2
Octopus			.7	2.6	9.3	12.0	27.2	37.9	18.6	16.7
Shrimp			.2	2.6					tr	.2
Algae			2.5	2.6	tr	1.9	tr	.9	.2	1.6
Pebbles					.3	1.3	tr	.9	.2	.8
Total volume of food consumed, ml	15.58		101.34		840.82		1,162.65		2,120.39	
Stomachs with food, no.	25		75		158		116		374	
Empty stomachs, %	22.0		33.0		38.3		39.3			

[1]Trace <0.05%.

feeding, though important in all size classes, increased to a peak for fish 30.1-40.0 cm long, then declined somewhat, as larger fish ate more substrate-oriented prey. Predators in the 20.1-30.0 cm size class had the smallest range of food items (Table 7), eating mostly fish. Range increased for larger predators, as their diets were supplemented by squid and octopus.

TABLE 7.—Food breadths (Bray and Ebeling 1975) based on proportionate item volumes for four size classes (total length) of olive rockfish from Avila, Calif. Maximum vol (%) is of the dominant item (Table 5).

Size class (cm)	Stomachs with food (no.)	Food items eaten (no.)	Breadth of diet	Maximum vol (%)	Dominant item
10.1-20.0	25	6	2.49	44.7	Fish
20.1-30.0	75	15	2.20	43.6	Fish
30.1-40.0	158	16	2.92	44.2	Squid
40.1-50.0	116	13	3.40	39.9	Squid

TABLE 8.—Seasonal variation in percentage frequency of occurrence of prey types in stomachs of three size classes (total length) of olive rockfish from Avila, Calif. Seasonal periods are explained in the text. Probabilities determined by 2 × 2 contingency *G*-test (Sokal and Rohlf 1969) on original frequencies.

Size class	Prey type	Seasonal period Mar.-Aug.	Sept.-Feb.
20.1-30.0 cm:			
Stomachs with food, no.		38	37
	Plankton, %	47.4	64.9
	Nekton, %	39.5	51.4
	Substrate oriented, %	31.6	21.6
30.1-40.0 cm:			
Stomachs with food, no.		71	87
	Plankton, %	42.3	46.0
	Nekton, %	70.4*	50.6
	Substrate oriented, %	19.7	23.0
40.1-50.0 cm:			
Stomachs with food, no.		63	53
	Plankton, %	30.2	22.6
	Nekton, %	66.7**	45.3
	Substrate oriented, %	39.7	45.3

*$P \leq 0.05$
**$P \leq 0.01$

Feeding on substrate-oriented forms, primarily gammarid amphipods and isopods, occurred occasionally in fish of the smaller size classes, but was much more frequent in larger fish, where foraging on octopus was important. Octopuses are normally secretive during daylight hours, but are often exposed during the night (D. Behrens[6]). Olive rockfish may feed at night on octopus—an example of a fish not adapted to benthic feeding, preying successfully on a bottom-dwelling form.

Food habits showed some seasonal variation. Nekton feeding significantly increased (in the 30.1-40.0 and 40.1-50.0 cm size classes) during the upwelling period (Table 8). Predation on both squid and young-of-the-year rockfish (which first appear in large numbers during April and May) increased during this period. Though juvenile rockfish were an important food item throughout the year, their importance decreased during fall and winter, probably because these growing juveniles become less vulnerable. Other prey, such as the northern anchovy, were of greater importance during the fall oceanic and winter Davidson Current periods. Tunicates and euphausids were eaten in far greater amounts during the upwelling season, particularly during April and May (an occurrence also noted off Carmel Bay, Calif., by Roberts 1979).

Limbaugh (1955) speculated that olive rockfish may replace kelp bass ecologically in central and northern California, where kelp bass decline in abundance. The two species are similar in appearance—having elongate, fusiform bodies, reduced or (in kelp bass) absent head spines, large mouths, and brownish bodies with light blotches along their back. In central and northern California, olive rockfish do, to a certain degree, assume the lifestyle of kelp bass. Olive rockfish live over high relief bottom and feed primarily on nekton, as do kelp bass. However, with the exception of octopus, olive rockfish rarely prey on the substrate-oriented food items, such as shrimp, algae, and hydroids, favored by kelp bass (Quast 1968b; Love and Ebeling 1978). In central California, olive rockfish and blue rockfish are the major midwater predators over inshore reefs. Though there is considerable overlap, blue rockfish feed primarily on relatively slow moving or drifting prey, such as tunicates, copepods, and chaetognaths (Gotshall et al. 1965; Hallacher 1977) while olive rockfish concentrate on more motile forms. Beginning in northern California, olive rockfish give way to midwater feeding yellowtail rockfish and black rockfish, *S. melanops* (Moulton 1977).

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[6]D. Behrens, Pacific Gas and Electric, Biological Laboratory, P.O. Box 117, Avila, CA 93424, pers. commun. November 1980.

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