FOOD AND HABITAT OF THREE SWITCH-FEEDING FISHES IN THE KELP FORESTS OFF SANTA BARBARA, CALIFORNIA

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ABSTRACT

Diets and habitat distributions were compared among the blue rockfish, *Sebastes mystinus*, kelp bass, *Paralabrax clathratus*, and olive rockfish, *Sebastes serranoides*, all of which cooccur in areas of reef and giant kelp off Santa Barbara, Calif. The three species make up a feeding guild of large-mouthed predatory fishes that commonly switch among planktonic prey, nektonic prey (fish and squid), and substrate-oriented prey (invertebrates that live on or about reef and plant surfaces). At the semi-isolated study site, blue rockfish, which are somewhat better adapted than the others to ingest and retain small particles, ate relatively more plankton than did individuals of the other species, while olive rockfish ate more fish. Kelp bass had both the broadest diet and habitat distribution. All three species ate more plankton during winter-spring, yet had smaller dietary overlaps then. Olive rockfish ate more fish and less plankton at the heavily foliaged study site than they did over a deeper kelpless reef farther offshore. The three species tend toward deeper and calmer areas of the reef; kelp bass and olive rockfish prefer clear-water areas of dense kelp; kelp bass often concentrate near the outer kelp-bed margin; and both rockfishes prefer areas of high-relief rocky bottom. The morphologically similar kelp bass and olive rockfish may segregate spatially, perhaps reducing mutual interference. As inferred from other studies and our own, areal variation in feeding habits of the three species may reflect their environmental tolerances, range limits, numbers of competitors, food supplies, habitat structures, or predator densities. The closely related rockfishes show least dietary overlap between themselves and most overlap with the more distantly related kelp bass.

Kelp-bed fishes that have similar diets and habitat requirements form feeding guilds. For example, Bray and Ebeling (1975) described how three species of small picker-type microcarnivorous fishes share substrate-oriented prey and plankton in the kelp forests off Santa Barbara, Calif. Also occupying the midwater zone between kelp canopy and reef bottom is a feeding guild of larger, predatory fishes. These include two members of the scorpaeniform family Scorpaenidae, the blue rockfish, *Sebastes mystinus*, and olive rockfish, *S. serranoides*, and one member of the perciform family Serranidae, the kelp bass, *Paralabrax clathratus*. All have fusiform bodies, head spines reduced or absent, large flexible fins, large mouths, and numerous well-developed and closely set gill rakers. Blue rockfish are ovate with blue-gray bodies stippled darkly above the flanks; olive rockfish and kelp bass are more elongate with brownish bodies and characteristic arrays of white blotches along their backs. The three species are similar enough in general appearance to be grouped by most Santa Barbara fishermen simply as bass: blue, Johnny, and calico basses, respectively. They form the nucleus of a shallow-water sport fishery at the edges of the Santa Barbara kelp forests.

Our primary interest was how the three species share food and space over a single, semi-isolated area of reef and kelp (Naples Reef) near Santa Barbara. We emphasized the most common size range of fishes sighted, large juveniles to small adults. Previous studies indicated that the species are generalized carnivores, occurring throughout the water column and eating a wide variety of large and small prey of all major categories (Limbaugh 1955; Young 1963; Gotshall et al. 1965; Quast 1968a-d; Turner et al. 1969). We wanted to see if the three species can switch (change almost entirely) from eating one prey type to another, and under what circumstances they may do so. Using data from other studies, we also investigated food habits of olive rockfish from a deeper, offshore population living in an environment quite unlike that of the kelp bed, and we investigated the spatial distributions of all three species at Naples Reef and in an adjacent island environment.

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METHODS

Food

For interspecific comparisons, collections were made over a single isolated reef, where the three species probably exploit a common forage base. Naples Reef is a large rocky outcrop surrounded on all sides by sand flats and forested by lush stands of giant kelp, *Macrocystis*. It is located about 1.6 km offshore, 24 km west of Santa Barbara (lat. 34°25′N, long. 119°57′W). Covering an area of about 2.2 ha, the reef averages 8-10 m in depth, although its rocky crest projects to within 5 m of the surface. It is separated from similar habitats by sand and cobble flats at 16-20 m (Ebeling and Bray 1976).

We tried to collect fish as randomly as possible. One of us (Ebeling) using a pole spear shot fish as they were encountered, with two exceptions: he ignored small juveniles and often missed large kelp bass (>300 mm SL, standard length), which were consequently underrepresented in the collections. Thus the samples probably reflect the usual size distribution of fish between ca. 100 and 300 mm SL over the reef (Table 1). In this way, 324 specimens were collected between 0900 and 1500 h during all seasons from March 1971 to June 1972. Of these, 80% had food in their stomachs.

We made considerable effort not to bias stomach-content composition. Underwater chumming or disturbing the bottom were never used as ways to attract fish near the collector. Spearing was begun only after it was ascertained that no sport fishing involving chumming with live bait (usually northern anchovy, *Engraulis mordax*) occurred within visual range of the collecting site. An initial practice of securing individual fish in plastic bags or locking their mouths with paper clips was soon discontinued when no individual was seen to regurgitate food. All specimens were placed immediately in an ice chest aboard the diving skiff. In the laboratory, they were measured (nearest millimeter SL), slit open, and their intestines detached and measured (millimeters SL). Other trophic structures (jaw length, gill rakers on first arch, and greatest width between gill rakers) were measured on a few typical specimens of about 225 mm SL. Specimens were then fixed in 10% Formalin[3] and preserved in 50% isopropanol.

To investigate the effect of habitat on the olive rockfish's diet, one of us (Love) collected an additional 110 individuals from One-Mile Reef, an open, rocky reef located 1.6 km offshore of Santa Barbara Harbor, about 20 km east of Naples Reef. Of these, 72 (65.5%) had stomachs containing food (Table 1). Too deep and turbid to support kelp, this reef is made up of a strip of rocky bottom at about 27 m depth, with 1.5-5.0 m high rock piles scattered along its length. From January to October, fish were caught by angling with artificial lures and by gill net. No sport fishing or chumming were seen to occur during collecting. Fish were preserved and processed as before.

Gut fullness was estimated before stomach contents were sorted and identified. Degrees of fullness of stomach and of the first half of the intestine were scored from 1.0 (empty) to 5.0 (full). Stomach contents were sorted taxonomically into 26 food items (Table 2). The volume of each item was measured by liquid displacement. The "nekton" category of items (prey type) included all nonlarval fish and squid prey. The substrate-oriented prey type included all prey (except fish) that live on or about reef and plant surfaces. Such prey are either motile like shrimps, amphipods, and small crabs, or attached like hydroids, bryozoans, and the algae itself. Plant material was identified as either kelp (*Macrocystis*) or other algae, mostly low lying browns and reds. In computing percent volumes and frequencies of occurrence of prey per

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Number, size, and food containment of specimens examined of the three species of kelp-bed fishes (blue rockfish, kelp bass, and olive rockfish) from Naples Reef or One-Mile Reef (olive rockfish only) off Santa Barbara, Calif. See also Figure 1.

Locality and species	Total specimens examined	Total with food	Percent with food	Specimens with food in their stomachs by size groups								
				50-150 mm SL			151-300 mm SL			301-400 mm SL		
				No.	Range	Median	No.	Range	Median	No.	Range	Median
Naples Reef:												
Blue rockfish	122	97	79.5	30	78-149	118.5	67	150-262	193.0	—	—	—
Kelp bass	102	86	84.3	—	—	—	67	167-296	209.0	19	304-400	328.0
Olive rockfish	100	86	86.0	13	82-150	122.5	73	151-274	196.0	—	—	—
One-Mile Reef:												
Olive rockfish	110	72	65.5	—	—	—	72	158-290	222.0	—	—	—

TABLE 2.—Percent total volume and frequency of occurrence of 26 food items in stomachs with food of the three species of kelp-bed fishes in the 151- to 300-mm size group (Table 1, Figure 1) from Naples Reef or One-Mile Reef (olive rockfish only) off Santa Barbara, Calif. Food items are listed by general characteristics and presumed major daytime source. A tr indicates unmeasurable trace; a dash indicates none.

	Naples Reef						One-Mile Reef	
	Blue rockfish		Kelp bass		Olive rockfish		Olive rockfish	
Food item	% vol.	% freq.	% vol.	% freq.	% vol.	% freq.	% vol.	% freq.
Primarily planktonic (Sum =)	(56.7)		(12.6)		(10.5)		(41.8)	
Small crustaceans (0.5-5 mm long):								
Ostracods	—	—	—	—	—	—	tr	2.9
Cladocerans	—	—	—	—	—	—	0.4	8.6
Zoea larvae	0.6	20.9	0.3	6.0	0.3	15.1	6.5	35.7
Copepods	0.2	22.4	1.5	7.5	0.3	15.1	15.8	34.3
Megalops larvae	0.6	11.9	0.1	3.0	2.6	24.7	7.0	47.0
Large crustaceans (>10 mm):								
Euphausiids	tr	1.5	—	—	0.1	2.7	1.2	2.9
Pleuroncodes	—	—	—	—	—	—	4.4	4.9
Small-medium sized, transparent (1-10 mm):								
Eggs	0.6	1.5	2.5	1.5	—	—	—	—
Chaetognaths	1.9	10.4	—	—	—	—	0.1	2.9
Tunicates (small salps, larvaceans)	51.5	40.3	7.8	16.4	5.4	6.8	1.0	5.7
Large, transparent (>15 mm):								
Siphonophores, medusae, etc.	0.7	4.5	0.4	1.5	—	—	—	—
Fish larvae (5-15 mm)	0.6	10.4	—	—	1.8	16.4	5.4	16.7
Primarily nektonic (20-80 mm) (Sum =)	(15.7)		(55.3)		(85.0)		(55.2)	
Fish	7.4	13.4	51.0	46.3	84.2	54.8	51.0	28.0
Squid	8.3	3.0	4.3	6.0	0.8	4.1	4.2	5.7
Ectoparasites of other fish:								
Parasitic copepods	—	—	—	—	tr	2.7	0.4	12.9
Primarily substrate oriented (Sum =)	(27.5)		(32.3)		(4.5)		(2.6)	
Free moving animals:								
Crabs	—	—	0.8	3.0	—	—	—	—
Shrimps	—	—	0.7	1.5	—	1.4	—	—
Mysids	0.3	6.0	0.5	9.0	0.8	8.2	1.4	14.3
Isopods	0.2	3.0	0.2	1.5	—	—	—	—
Gammaridean amphipods	1.6	17.9	2.2	13.4	0.8	6.8	tr	1.4
Caprellid amphipods	0.1	1.5	7.5	13.4	tr	1.4	tr	1.4
Hyperiid amphipods	0.1	1.5	—	—	—	—	0.1	2.9
Polychaete worms	0.3	1.5	0.4	7.5	2.9	20.5	1.0	14.3
Hydroids	13.1	16.4	8.7	16.4	—	—	—	—
Kelp, etc.:								
Kelp (including encrusting bryozoans)	10.5	25.4	8.8	16.4	—	—	0.1	1.4
Other algae (including encrusting bryozoans)	1.3	9.0	2.5	14.9	—	—	—	—
Total volume of food consumed (ml)	171.2		141.3		85.8		102.9	
Total number of specimens examined		67		67		73		72

species (Table 2), fish with empty guts and of sizes outside the middle range of 151-300 mm SL (Table 1, Figure 1) were excluded.

To test for communal switch feeding and dietary consistency, we examined variation among individuals. We counted fish that contained mostly one food item or prey type and that 1) were of one species collected on the same day, 2) were of all three species collected on the same day (Table 3), and 3) were of all species collected at any time (Table 4).

To examine seasonal variation in diet, stomach contents of each species were pooled by seasonal periods that correspond roughly to different oceanographic regimes off Santa Barbara. Brown (1974) concluded that in the Santa Barbara Channel, cooling of surface water typically proceeds from December to July, first by surface mixing and small-scale upwelling associated with storms from December to April, then by large-scale upwelling from May through July. This precedes gradual surface warming from late June to December, with strongest thermal stratification and clearest water from August to December. Therefore, we delimited seasonal periods as: 1) December-February, a period of winter storms and the beginning of vertical mixing and surface cooling (initial breeding season of many species); 2) March-May, a period of most intense upwelling of deep cold water (high surface productivity, zooplankton blooms, appearance of young-of-the-year fish, etc.); 3) June-August, a period of decreasing upwelling and the beginning of thermal stratification and surface warming (a transitional period);

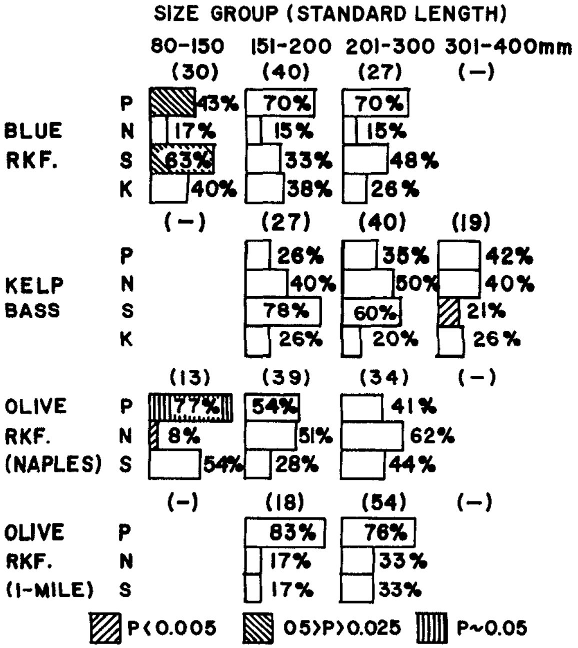

FIGURE 1.—Percentage frequency of prey types (bars and numbers) in stomachs of fish in all size groups of the three species of kelp-bed fishes from Naples Reef (all three species) or One-Mile Reef (olive rockfish only) off Santa Barbara, Calif. Prey types are designated: P, plankton; N, nekton; S, substrate-oriented prey; and K, kelp and other algae (with encrusting bryozoans), and are represented by any constituent food item under the appropriate prey-type heading in Table 2. Numbers in parenthesis are numbers of fish stomachs examined. Hatching shows significantly different frequencies at the indicated probabilities determined by chi-square tests (see text).

and 4) September-November, a period of warm, clear surface water with little vertical mixing. The 26 food items were ranked for each season by volume, using data from all size groups of fishes to maximize sample size (Table 5). Seasonal variation in diet was also tested by frequencies of occurrence of subsets of items comprising major food categories, using data from the 151- to 300-mm SL size group only (Figure 2).

Habitat

Spatial distributions of the three species were determined from underwater movies taken for another project. Observations were made from 2.5-min Super-8-mm underwater movie strips in color (cinetransects) filmed by scuba divers swimming courses started at random either under the kelp canopy or just over the bottom at study sites near Santa Barbara and across the Santa Barbara Channel along Santa Cruz Island (Bray and Ebeling 1975; Ebeling, R. Larson, and W. Alevizon in prep.). An initial set of cinetransects was filmed in 1970 over a variety of habitats and areas at both localities. Then, during the fall seasons of 1971-74, transects were filmed over permanent study sites at Naples Reef and at Santa Cruz Island west of Prisoner's Harbor. Fish were counted by species as the films were projected in the laboratory. Environmental characteristics were measured or scored either on station or during projection.

Breadth and Overlap

Breadth and overlap of resource use were computed from values of p_i, the proportion of item i used by each species, either at Naples Reef (food and space) or off Santa Cruz Island (space only). For food, p_i is the proportionate volume of any of the 26 different food items included in the species total (S); for space it is the proportionate abundance of the species in any of the 297 cinetransects taken over Naples Reef or 331 cinetransects taken along Santa Cruz Island. Resource breadth, $B = 1/\sum_{i=1}^{S} p_i^2$, can be thought of as the theoretical number of equally used food items (or spaces covered by cinetransects) yielding a value of B equal to the observed. For example, if all items are in equal proportions, B equals S, the total items in the spectrum (see Bray and Ebeling 1975). A Hill's (1973) ratio was used to estimate the degree of concentration of each species among cinetransects (the unevenness of distribution of fish numbers): $HR = \exp(H')/B$, where H' is the Shannon-Weaver measure of diversity, $-\sum_{i=1}^{S} p_i \ln p_i$. Since H' is more sensitive to changes in the small to medium values of proportionate abundances than is B, their ratio is a sample-size independent measure of concentration of observations (Peet 1974). Overlap between two species, $I = 1.0 - [0.5(\sum_{i=1}^{s} |p_{ij} - p_{ik}|)]$, where p_{ij} is the proportion of item i used by species j and s is the species total of food items eaten (or cinetransects in which recorded), is scaled from zero (complete discordance of item use) to 1.0 (all items used in equal proportions) (e.g., Whittaker 1960; Cody 1974; Ebeling and Bray 1976).

RESULTS

Morphology, Size Groups, Gut Fullness

Of the three species, the blue rockfish appeared best adapted to eat a diverse array of small prey. It has a shorter jaw (ca. 15% of SL) than the olive rockfish and kelp bass (ca. 17%). It has about the same number of gill rakers on the first arch as the others (34-37); but has significantly smaller interraker widths ($\bar{x} = 1.24 \pm 0.088$ mm, 95% confidence limits, $n = 10$) than the others pooled ($\bar{x} = 1.80 \pm 0.076$, $n = 20$). Blue rockfish have a significantly longer intestine (ratio, intestinal length/SL of $\bar{x} = 1.41 \pm 0.147$, $n = 15$) than either kelp bass ($\bar{x} = 1.11 \pm 0.105$, $n = 18$) or olive rockfish ($\bar{x} = 0.807 \pm 0.098$, $n = 19$).

Tests justified comparing diets of fish within the 151- to 300-mm SL size range, which included 82% of all food-containing individuals (Table 1). Within this range, only the median length of olive rockfish from One-Mile Reef differed significantly from the others (Kruskal-Wallace ranks location test, $P<0.05$ including the One-Mile sample, $P>0.1$ excluding it). Also (Figure 1), diets as expressed by frequencies of occurrence of prey types were not significantly heterogeneous between subgroups: largest chi-square value determined in tests of the resulting 14 contingency tables of dimension two (presence or absence) by two (subgroups within this size range) = 2.31 ($P>0.1$).

However, tests showed less justification for increasing sample size by adding individuals from outside the 151- to 300-mm size range (Figure 1). Diets were often significantly heterogeneous between subgroups when either smaller (blue rockfish, olive rockfish) or larger (kelp bass) sizes were included: 5 of 11 chi-square values determined in tests of the resulting 11 contingency tables of dimension two (presence or absence) by three (subgroups both within and without the 151- to 300-mm range) were significant at $P \approx 0.05$ or less.

Scored stomach fullness in 151- to 300-mm Naples Reef fish was about the same for all three species: $\bar{x} = 2.72$-2.75, an equivalent of about 46% full. Intestinal fullness averaged somewhat greater: $\bar{x} = 2.76$ (olive rockfish) to 3.00 (others). Blue rockfish and olive rockfish in the smaller size categories had fuller stomachs: $\bar{x} = 3.81$-3.10, respectively. Olive rockfish from One-Mile Reef had less food in their stomachs ($\bar{x} = 2.15$) but as much food as the others in their intestines ($\bar{x} = 3.05$). Intestinal contents usually resembled stomach contents.

Food

Diets

Blue rockfish ate mostly swimming, drifting, or attached organisms in midwater under and about the kelp canopy (Table 2, Figure 1). Tunicates, hydroids, kelp, fish, and smaller planktonic prey formed most of the fish's diet throughout the year. Recognizable fish prey included juveniles of pipefish, *Syngnathus;* blue rockfish; and C-O soles, *Pleuronichthys coenosus*; and adults of northern anchovy. Fish larvae made up but a small part of the blue rockfish's diet. Pelagic tunicates—the thaliaceans (salps) *Salpa* and *Doliolum* and the larvacean *Oikopleura*—constituted the largest volume of food consumed. Among the relatively large numbers of small plankters eaten, copepods ranked very low in volume, but relatively high in frequency of occurrence. Hydroids (especially *Sertularia*) ranked high in volume consumed. The blue rockfish were probably not merely ingesting hydroids to obtain the caprellid amphipods that live there (Gotshall et al. 1965), because caprellids were found along with hydroids in only 2 of 20 stomachs. Some 73% of the fish that contained kelp and other algae also contained detached hydroids and encrusting bryozoans (*Membranipora*). So most plant material may have once borne epiphytic prey now detached. And like tunicate tunics, algae per se was apparently passed undigested, so fish probably eat plants for the attached animals (Quast 1968d; Bray and Ebeling 1975).

Kelp bass foraged primarily in midwater, but occasionally ate bottom organisms (Table 2, Figure 1). They ate mostly fish, which ranked first in both total volume and frequency of occurrence. Recognizable fish prey included juveniles of rockfishes, pipefish, kelp greenling, *Hexagrammos decagrammus,* topsmelt, *Atherinops affinis,* anchovy, and jack mackerel, *Trachurus symmetricus,* and adults of anchovy and agonids. Kelp bass ate no fish larvae and relatively less plankton than did the other species. Thaliacean tunicates (*Salpa*) contributed the largest volume of plankton consumed; copepods and other small crustaceans occurred at moderate frequency and in fairly large numbers in a few individuals. Bass ate relatively more substrate-oriented prey, with hydroids (especially *Sertularia*), caprellid amphipods, and kelp ranking highest among such items. Most caprellid amphipods were found in stomachs containing substantial amounts of hydroids and bottom algae, indicating that fish may ingest such turf for the contained animals. About a third of all pieces of kelp bore attached bryozoans (*Membranipora*) or hydroids.

Whether speared from Naples Reef or angled from One-Mile Reef, olive rockfish ate relatively more fish than did the others (Table 2, Figure 1). Recognizable fish prey in Naples Reef individuals included juveniles of blacksmith, *Chromis punctipinnis,* anchovy, pipefish, blue rockfish, other olive rockfish, and adults of topsmelt and anchovy. One-Mile Reef fish had eaten adult anchovies and a young pipefish. Fish larvae made up a relatively large part of the diets of olive rockfish from both localities. One-Mile Reef fish ate more kinds and greater numbers of small zooplankton. Individuals of all sizes ingested and retained such tiny prey as ostracods, cladocerans, and small copepods (e.g., *Coryceus emarginata*). During the winter, copepods and zoea larvae actually outranked fish prey in volumes consumed. Many polychaetes, which occurred commonly in fish from either area, were of the small nereid variety found in the kelp canopy (Quast 1968c) and swarming in the midwater plankton at night (Hobson and Chess 1976). Only olive rockfish contained parasitic copepods among their stomach contents. Although these copepods were identified as *Caligus,* an obligatory ectoparasite, olive rockfish were not observed to clean (i.e., pick such prey from off other host fishes).

Individual Variation

On any given day, individuals of the same species tended to select the same food item. Within particular collections of 2-9 individuals, 67% of a cumulative total of 96 blue rockfish, 60% of 72 kelp bass, and 60.5% of 86 olive rockfish had the same item dominating their stomach contents.

Occasionally, individuals of all three species selected items from the same major prey category, although not necessarily the same item (Table 3). Plankton dominated the stomach contents of most individuals sampled together in a February and in an April collection, while nekton and substrate-oriented prey were favored by those in three May and in one October collections. Yet fish in two November and two January collections showed little communality of diet. And even when they tended to select items from the same prey type, as in the February, April, May, and October collections, they often selected different items. For example, most blue rockfish collected on 22 February 1972 had mostly salps or chaetognaths in their stomachs; kelp bass contained either salps or copepods; and olive rockfish contained larval fish. On the other hand, all blue rockfish and most kelp bass in the 21 January 1972 collection had eaten a single planktonic item, namely salps.

Fish usually selected the same prey type during a particular feeding bout (Table 4). For all species pooled, 76% of the individuals contained more than 95% by volume of items in a single major prey category (prey type), and 39% contained but a single item (20% with relatively small items, 19% with large items). Combinations of prey types varied among the three species: usually plankton and substrate-oriented prey for kelp bass, and plankton and nekton for olive rockfish (Table 4). Of all fish containing kelp, etc. (Figure 1), about 40% also contained relatively large amounts of substrate-oriented prey, about 15% each also contained relatively large amounts of plankton or nekton, and the remainder contained kelp only. About 83% of 81 specimens with recognizable prey in both stomach and intestine had the same prey type dominating the contents of both.

Seasonal Variation

Considering all 26 food items, diets were weakly, though usually significantly concordant among seasons (Table 5). Fish ate relatively greater volumes of plankton during winter-spring periods, and more nekton or substrate-oriented prey during summer-fall. Showing the greatest seasonal variation (least concordance), the blue rockfish's diet included 93% plankton (by volume) in the winter, 75% in the spring, and less than 8% in summer-fall. Tunicates ranked high from December to August, while kelp (with encrusting animals), hydroids, and, later, fish, ranked high from March to November. Similarly, olive rockfish from One-Mile Reef contained 80%, 25%, and <10% plankton (by volume) in the first three seasonal periods, respectively. Small crustaceans ranked high from December to August, while fish and polychaetes ranked high from March to November. Individuals of both species ate larval fish during late winter and spring when such prey are most abundant. Seasonal trends for the others

TABLE 3.—Numbers of the three kelp-bed fishes that contained more than 50% (by volume) of the indicated food items from the Naples Reef collections (identified by date) that contained all three species: blue rockfish (B), kelp bass (K), and olive rockfish (O).

Food item	21 Jan. 1972			24 Jan. 1972			22 Feb. 1972			26 Apr. 1971			5 May 1972			10 May 1972			23 May 1971			7 Oct. 1971			19 Nov. 1971			22 Nov. 1971			1 Dec. 1971		
	B	K	O	B	K	O	B	K	O	B	K	O	B	K	O	B	K	O	B	K	O	B	K	O	B	K	O	B	K	O	B	K	O
Primarily planktonic:																																	
Zoea larvae				2							1																						
Copepods							1	2																				1					
Megalops larvae																				1													
Chaetognaths				6			2																										
Tunicates:																																	
larvaceans										4																							
salps	7	4					2	4		2															5			6					
Polychaete worms (nighttime planktonic?)																								[1]1							[1]1		[1]1
Larval fish									2			[1]1																					
Primarily nektonic (mostly fish)						3		1			1	2			8			3		8	3		1	3	1	2	4			1		1	
Primarily substrate oriented:																																	
Shrimps									[1]1																								
Mysids				1	1												2							1				1					
Gammarid amphipods		1															1																
Caprellid amphipods											1			1																			
Hydroids		1											3						1			5											
Kelp (incl. encrusting bryozoans)		1		3									2	1		2						3	1			4					2		
"Crustacean pieces"																										2							

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[1] Considerable food in the intestine, indicating that the fish may have fed the night before.

TABLE 4.—Numbers of the three species of kelp-bed fishes in the 151- to 300-mm size group (Table 1, Figure 1) from Naples Reef or One-Mile Reef (olive rockfish only) that contained more than 95% (by volume) of items composing prey types (plankton, P; nekton, N; or substrate-oriented prey, SOP) listed in Table 2.

Species	P	N	SOP	P + N	SOP + P	SOP + N
Naples Reef						
Blue rockfish	24	3	18	1	13	1
Kelp bass	11	23	23	1	3	6
Olive rockfish	20	28	5	7	3	4
One-Mile Reef						
Olive rockfish	43	15	—	5	3	—
Totals	98	69	46	14	22	11
% of total (279) food-containing specimens	35.1	24.7	16.5	5.0	7.9	3.9

were less clear. Kelp bass ate tunicates from December to May, but fish, kelp, and hydroids were important prey for much of the year. Olive rockfish from Naples Reef ate mostly fish throughout the year.

To test for seasonal differences in diet, the frequencies of prey types were subjected to chi-square tests of homogeneity calculated from contingency tables of dimension two (presence or absence) by four (seasonal periods). Plankton frequencies were significantly heterogeneous, with highest values during winter-spring periods (Figure 2). As fewer kelp bass and olive rockfish ate plankton during the year, more ate nekton, primarily small fish. More blue rockfish and kelp bass ate more algae (with encrusting animals) later in the year.

Species showed greater overlap in diet during periods when their stomachs were fuller of prey (Table 6). For all species, both stomach fullness and food overlap were greater during summer-fall than during winter-spring (Table 6). Fullness may relate to greater exploitation of nekton during summer-fall (Figure 2). For all species, stomachs

TABLE 5.—Seasonal variation in diets of the three species of kelp-bed fishes in all size groups (Figure 1) from Naples Reef or One-Mile Reef (olive rockfish only) off Santa Barbara, Calif. The first five ranking food items with their percent volume are listed in order for each time period. Sample size is the number of diets (fish) pooled per period; *W* is Kendall's "*W*" rank concordance (Tate and Clelland 1957) among seasons for (*n*) total items.

	December-February		March-May		June-August		September-November		
Species	Item	%	Item	%	Item	%	Item	%	*W*
Naples Reef:									
Blue rockfish	Sample size	26	Sample size	24	Sample size	18	Sample size	29	
20 total	Tunicates	84.2	Tunicates	70.2	Kelp[1]	43.4	Hydroids	55.2	
items	Chaetognaths	8.1	Kelp[1]	13.6	Fish	23.2	Kelp[1]	31.8	0.37
	Kelp[1]	5.8	Hydroids	9.3	Hydroids	18.4	Fish	11.3	
	Copepods	0.7	Copepods	2.1	Tunicates	3.6	Gammarid amphipods	1.5	
	Gammarid amphipods	0.5	Siphonophores, etc.	1.9	Fish larvae	3.6	Megalops larvae	0.07	
Kelp bass	Sample size	25	Sample size	29	Sample size	17	Sample size	15	
19 total	Kelp[1]	32.9	Fish	57.6	Fish	47.4	Fish	63.4	
items	Tunicates	27.2	Tunicates	18.1	Squid	25.7	Hydroids	17.4	0.41*
	Squid	14.2	Caprellid amphipods	8.5	Kelp[1]	22.1	Kelp[1]	16.1	
	Eggs	8.0	Hydroids	6.3	Caprellid amphipods	1.6	Crabs	1.5	
	Fish	7.3	Kelp[1]	4.1	Shrimps	1.4	Tunicates	1.1	
Olive rockfish	Sample size	8	Sample size	39	Sample size	11	Sample size	28	
14 total	Fish	93.8	Fish	82.4	Fish	86.1	Fish	84.5	
items	Fish larvae	2.5	Fish larvae	4.9	Tunicates	4.8	Tunicates	5.4	0.51**
	Polychaete worms	1.9	Megalops larvae	4.0	Fish larvae	4.4	Polychaete worms	4.1	
	"Crustacean pieces"	0.9	Tunicates	3.5	Isopods	2.9	Mysids	2.5	
	Shrimps	0.5	Squid	1.0	Polychaete worms	0.9	Copepods	0.9	
One-Mile Reef:									
Olive rockfish	Sample size	17	Sample size	40	Sample size	10	Sample size	5	
19 total	Copepods	34.5	Fish	39.0	Fish	88.7	Fish	93.2	
items	Zoea larvae	17.6	Fish larvae	19.9	Megalops larvae	6.9	Fish larvae	3.3	0.44**
	Fish	14.9	Polychaete worms	17.9	Zoea larvae	3.6	Mysids	3.0	
	Pleuroncodes	14.7	Squid	5.6	Mysids	0.7	Copepods	0.1	
	Tunicates	13.9	Tunicates	5.1	Parasitic copepods	0.1	Zoea larvae	0.1	

[1] Including encrusting bryozoans
*Significant at $P = 0.05$
**Significant at $P \leq 0.025$.

TABLE 6.—Seasonal variation in stomach fullness and interspecific dietary overlap in the three species of kelp-bed fishes in all size groups (Figure 1) from Naples Reef off Santa Barbara, Calif. Stomach fullness is mean score, from 1.0 (empty) to 5.0 (full and distended). Food overlap with species in next row down is defined in the text.

	Stomach fullness				Food overlap			
Species	Dec.-Feb.	Mar.-May	June-Aug.	Sept.-Nov.	Dec.-Feb.	Mar.-May	June-Aug.	Sept.-Nov.
Blue rockfish	2.59	2.94	3.75	3.26	0.36	0.28	0.49	0.44
Kelp bass	2.22	2.65	3.12	3.08	0.13	0.64	0.48	0.66
Olive rockfish	2.34	2.93	3.01	2.76	0.08	0.08	0.32	0.12
Blue rockfish								
Unweighted mean	2.38	2.84	3.29	3.03	0.19	0.33	0.43	0.41

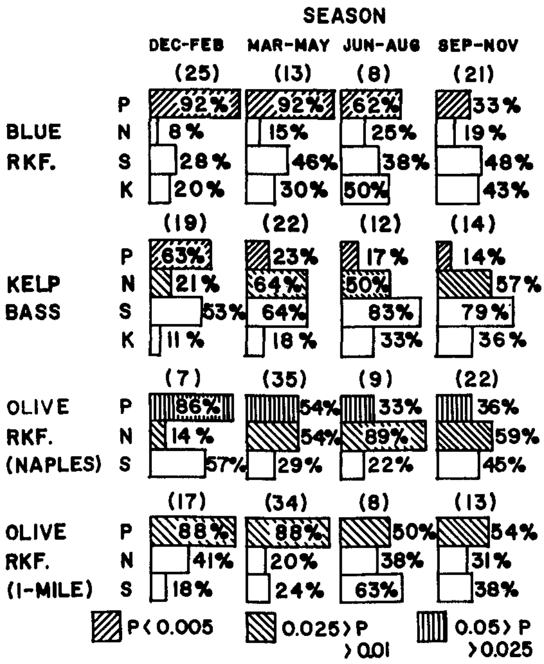

FIGURE 2.—Seasonal variation in percentage frequency of prey types (bars and numbers) in stomachs of fish in the 151- to 300-mm SL size group (Table 1) of the three species of kelp-bed fishes from Naples Reef (all three species) or One-Mile Reef (olive rockfish only) off Santa Barbara, Calif. Prey types (P-K) are designated in Figure 1; seasonal periods are explained in the text; and numbers in parenthesis are numbers of fish stomachs examined. Hatching shows significant seasonal differences at the indicated probabilities determined by chi-square tests (see text).

containing mostly nekton averaged fuller (weighted means pooled among seasons = 3.12-3.48) than stomachs containing mostly other prey (2.14-2.67).

Habitat

The three species occurred throughout the water column. However, most rockfish (juveniles and subadults) were recorded in canopy cinetransects (Table 7), and younger blue rockfish (reddish phase) usually clustered near the bottom close to shelter. In contrast, kelp bass were more abundant in bottom transects (Table 7). Relatively more blue rockfish and kelp bass were recorded in canopy transects over Naples Reef, where bottom and canopy tend to merge along the reef crest.

One of us (Ebeling) has observed small- to medium-sized fish (ca. 100-250 mm SL) feeding together between middepth and kelp canopy during clear-water days over Naples Reef. Blue rockfish often mingle with blacksmith, a specialized daytime planktivore with small mouth and compressed body. Blacksmith are quicker and more maneuverable than blue rockfish, which pick plankton more slowly and seem to have more difficulty repositioning themselves after feeding lunges. Small numbers of kelp bass and olive rockfish occasionally join the plankton pickers and feed at even lower rates. Although all plankton pickers may cooccur in the same field of view, they usually segregate by species. Larger individuals are usually lower in the water column. But even big kelp bass occasionally pick small particles from near the surface.

TABLE 7.—Numbers of the three species of kelp-bed fishes (excluding small juveniles) observed in movie strips (cinetransects) taken at Naples Reef or Santa Cruz Island study sites off Santa Barbara, Calif. Cinetransects are classified as taken either in and about the kelp canopy or reef bottom (see text).

	Naples Reef Cinetransect samples: canopy = 129, bottom = 168			Santa Cruz Island Cinetransect samples: canopy = 146, bottom = 185		
Species	Total fish observed	No. in canopy samples	% in canopy samples	Total fish observed	No. in canopy samples	% in canopy samples
Blue rockfish	3,305	2,953	89.3	919	636	69.2
Kelp bass	861	324	37.6	1,065	318	29.9
Olive rockfish	140	119	85.0	922	843	91.4

All three species were more numerous over greater bottom depths (to about 12 m), where the reef-fish community is generally richer and more abundant (Table 8). Kelp bass and olive rockfish tended toward zones of greater underwater visibility and kelp density, with kelp bass often preferring the outer margin of the kelp bed. Both rockfishes occurred in greater numbers over high-relief rocky bottoms. Olive rockfish (juveniles and subadults) were more numerous higher in the water column.

TABLE 8.—Correlations between numbers of the three species of kelp-bed fishes and environmental variables observed in an initial set of 175 movie strips (cinetransects) taken over a variety of locations and subtidal habitats along ca. 24-km stretches of coastline at the mainland and Santa Cruz Island off Santa Barbara, Calif. Numbers are Kendall's tau coefficients of rank correlation, significant at $P \leqslant 0.05$.

Environmental variable	Blue rockfish	Kelp bass	Olive rockfish
Bottom depth	0.26	0.23	0.15
Height in water column (score)	—	—	0.32
Underwater visibility	—	0.18	0.14
Bottom relief (score)	0.19	—	0.10
Kelp density (score)	—	0.18	0.17
Toward outer margin of kelp (score)	—	0.13	—
Total fish numbers	0.19	0.24	0.23
Total fish species	0.40	0.31	0.20

Resource Breadth and Overlap

Olive rockfish from Naples Reef had the smallest food breadth, less than half as large as breadths of the others (Table 9). The Naples Reef fish, which occurred at relatively low density (Tables 7, 10), ate mostly fish. Blue rockfish and kelp bass, whose diets were much more varied (Table 9), supplemented their fare with plankton and substrate-oriented prey. Olive rockfish from One-Mile Reef extended their diet with plankton.

The kelp bass was the most widespread species both at Naples Reef and at Santa Cruz Island (Table 10). Kelp bass tended to aggregate more at Naples Reef, as indicated by a larger Hill's ratio and smaller spatial breadth. Blue rockfish were also more clumped at Naples Reef. Olive rockfish, which were relatively rare at Naples, were more evenly distributed there.

In diet, the kelp bass overlapped the two rockfishes more broadly than either rockfish overlapped the other (Table 11). The kelp bass and olive rockfish overlapped most in diet and overlapped least in space both at Naples Reef and at Santa Cruz Island.

TABLE 9.—Food breadths of the three species of kelp-bed fishes in the 151- to 300-mm size group (Table 1, Figure 1) from Naples Reef or One-Mile Reef (olive rockfish only) off Santa Barbara, Calif. The text defines the breadth measure *B*, which is based on proportionate item volumes. Sample size is the number of fish examined that had food in their stomachs; *S* is the number of food items eaten; and maximum % volume is of the dominant item (Table 2).

Species	Sample size	*S*	*B*	Maximum % volume	Dominant item
Naples Reef:					
Blue rockfish	67	20	3.07	51.5	Tunicates
Kelp bass	67	18	3.44	51.0	Fish
Olive rockfish	73	14	1.40	84.2	Fish
One-Mile Reef:					
Olive rockfish	72	19	3.32	51.0	Fish

TABLE 10.—Spatial breadths of the three species of kelp-bed fishes from Naples Reef or Santa Cruz Island study sites off Santa Barbara, Calif. The text defines the breadth measure *B*, which is based on proportionate abundances of the species in 297 Naples Reef or 331 Santa Cruz Island movie strips (cinetransects). Sample size is the total fish counted (cf. Table 7); *S* is the number of cinetransects in which the species was observed; and *HR* is a measure of concentration (larger values indicate that more individuals are concentrated in fewer of the *S* cinetransects—see text).

Species	Sample size	*S*	*B*	*HR*
Blue rockfish:				
Naples Reef	3,305	185	42.8	1.66
Santa Cruz Island	919	151	51.0	1.61
Kelp bass:				
Naples Reef	861	218	65.4	1.78
Santa Cruz Island	1,065	217	90.2	1.52
Olive rockfish:				
Naples Reef	140	46	32.6	1.21
Santa Cruz Island	922	144	36.0	1.69

The concordance of food and spatial breadths (Tables 9, 10) indicates that the arithmetic mean of food and spatial overlaps may be a realistic measure of total overlap in resource use (Cody 1974; Pianka 1974; Bray and Ebeling 1975). This is because concordance in breadths suggests that diet and spatial distribution may not vary independently; i.e., certain areas may be best for gathering one prey type, while other areas may be best for another. Total overlap does not vary markedly among the three species pairs because food and spatial overlaps are nearly complementary (Table 11). Even so, total overlap between rockfishes is clearly less than that of either rockfish with the kelp bass.

TABLE 11.—Overlap in food and space between members of all pairs of the three species of kelp-bed fishes from Naples Reef or Santa Cruz Island (spatial overlap only) study sites off Santa Barbara, Calif. Thus food overlap, determined from dietary item volumes, and total overlap pertain only to the fish from Naples Reef. Spatial overlap, determined from cinetransect fish counts, is measured separately for Naples and Santa Cruz Island fish.

Paired species	Naples Reef Food (*F*)	Naples Reef Spatial (*Sn*)	Santa Cruz Spatial (*Sn*)	Total overlap (*F*+*Sn*/2)
Blue rockfish × Kelp bass	0.43	0.22	0.26	0.32
Blue rockfish × Olive rockfish	0.17	0.24	0.19	0.20
Kelp bass × Olive rockfish	0.60	0.08	0.16	0.34

DISCUSSION

We first examine possible sources of sampling bias and how they were minimized. Then we argue that within the size range of individuals studied, the three species are indeed able to switch from one prey type to another, and that this ability is not a universal trait of fishes in general. We discuss the circumstances under which the three species may change their diets and why their diets may vary from one place to another. Finally, we discuss coexistence of the three species from an evolutionary viewpoint.

Sampling Bias

Sport fishing activities may bias samples. Fish collected from partyboats often contain anchovies used as chum (Quast 1968d), and the mere presence of regular sport fishing in particular areas may condition or disturb the fish fauna (Quast 1968b, c). Quast inferred that kelp bass move quickly from bare sites into more heavily foliaged, favored habitats as previous inhabitants are removed by fishing. In the present study, however, the influence of sport fishing was minimal because large partyboats visited Naples Reef infrequently from 1970 to 1973 (due to the erratic state of the Santa Barbara sport fishery then), and we made special effort to avoid the few skiff fishermen.

Nonetheless, our samples may be biased in other ways. Quast (1968b) listed such sport-diving activities as shellfish gathering, which disturbs the bottom, and spearfishing among factors that condition fish behavior. Although we designed our sampling regime to minimize most hazards, we admit that spearing may induce wariness, especially in kelp bass. Hence, our method of spearing fishes as they were encountered may have selected certain individuals by virtue of their size or condition.

Perhaps even more importantly, angling olive rockfish from One-Mile Reef, even with unbaited lures, may have selected hungrier or weakened individuals with empty stomachs. Randall (1967) noted that fish angled in tropical areas often have empty stomachs and some regurgitate their meal during the fight. Our One-Mile Reef specimens did in fact average less stomach fullness than did Naples Reef fish. But since they averaged greater intestinal fullness, they probably had been feeding normally.

Our sampling may reflect some temporal bias. We collected most fish near midday when feeding may slacken. In the tropics, larger generalized carnivores feed mainly at dawn and dusk (e.g., Hobson 1974) or even at night if there is sufficient light (Randall and Brock 1960). In a study of kelp-bed fishes off Santa Catalina Island (ca. 160 km south of Santa Barbara) Hobson and Chess (1976) inferred that juvenile olive rockfish in the 65- to 157-mm SL range feed mostly at night. Quast (1968c) found that only 10-50% of specimens of the three species collected during the day off San Diego contained food. In the present study, however, most specimens contained substantial amounts of food in their stomachs, which were often more packed than their intestines. And individuals were often seen feeding during the day but seldom at night, when they usually sit quietly on the bottom or hide in holes (Ebeling and Bray 1976). Similarly off central California, blue rockfish, at least, are typically active during the day (Gotshall et al. 1965; Miller and Geibel 1973).

Evidence for Switch Feeding

Are the three species indeed switch-feeding predators? They are certainly equipped to switch from large to small prey. All have large mouths for engulfing big items, yet have protrusible jaws and well-developed gill rakers for selecting and keeping small ones.

In general, switch feeders show relatively weak preference for alternative prey and readily take the more abundant or otherwise more available kind (Murdoch et al. 1975). Switching mechanisms may involve avoiding a previous prey or selecting a new one (perhaps by acquiring a search image), spending more time in the area occupied by the new prey, or improving capture technique as the new prey becomes more abundant (Murdoch et al. 1975). Any of these mechanisms should make individual fish specialize. We could not compare diets with prey density, which we did not measure. Indirectly, then, we wanted to see if a relatively large proportion of fish contain mostly one of an array of alternative kinds of prey.

This seems to be the case. A fish usually contained mostly one and not a combination of prey types. Moreover, its stomach and intestinal contents usually matched, implying that it had fed on the particular prey type for a few hours (Windell 1971).

Also, the percentage of fish (76%) containing a single dominant food item is relatively large. It exceeds the estimated percentage (55%) for picker-type microcarnivores—small-bodied fishes with pointed, specialized mouths—which also inhabit the midwaters of the kelp bed (original data from Bray and Ebeling 1975). And it greatly exceeds the small percentage (13%) for demersal microcarnivores—somewhat larger fishes (Embiotocidae) with small mouths and fleshy lips—which usually inhabit the waters just above the reef surface (Ebeling and D. Laur in prep.). With food breadths exceeding 4.0, demersal microcarnivores eat a diverse array of prey, but all of the substrate-oriented type, and seldom one item at a time. Fryer (1959) concluded that in Lake Nyasa (Malawi), Africa, switch feeding is easy for more generalized predatory fishes, but is difficult or impossible for many of the more specialized species.

If switching is a simple functional response (in the sense of Solomon 1949) to more of a particular prey type, fish may, e.g., switch to plankton when it is particularly dense. This implies that all switch feeders may eat mostly plankton on certain occasions and eat alternative prey on others. There did seem to be a tendency for species to eat mostly plankton during winter-spring when plankton volumes are characteristically large in this area (Smith 1971, 1974) or when other food may be relatively scarce. Yet a fish may spend more energy ingesting many plankters or tiny substrate-oriented prey than a few large prey. Quast (1968c:92) found it ". . . difficult to understand how the effort required to pick caprellids from kelp fronds may be rewarding to a fish as large as 200 mm SL."

Reasons for Switching

In the simple proximate sense, a fish should switch from a dwindling or less accessible type of prey to an increasing or more accessible type (e.g., Murdoch et al. 1975). Yet the factors that ultimately condition fish behavior and control food availability may be many and complex. Quast (1968b) listed predators, hunger, breeding condition, water turbidity, temperature, and neighboring species or conspecific individuals as such factors. Lowe-McConnell (1975) reviewed considerable evidence that generalized predators in tropical freshwaters eat different prey as their environment changes with time, as they occupy different geographic areas and habitats, or simply as they become able to choose among equally abundant food items in a plentiful array. Therefore, we discuss dietary variation with 1) season, 2) geographic areas and faunal mix, 3) habitat, and 4) the presence of large predators.

Unlike wide-ranging, migratory fishes, the three species are limited to the food in their immediate environment. Tagging studies show that even adults have small home ranges. Off central California, juvenile blue rockfish move less than 90 m from their place of settlement unless disturbed by severe winter storms; adults either remain as kelp-bed residents or migrate to deeper water and disperse more widely (Miller and Geibel 1973). Similarly, some 80% of thousands of adult kelp bass tagged off southern California were recovered at or near the release site (Limbaugh 1955; Collyer and Young 1953; Young 1963), and but a small percentage had ventured as far as 8 km (Young 1963). Displaced individuals of *Sebastes flavidus,* a sibling of the olive rockfish, show remarkable homing capabilities (Carlson and Haight 1972).

Feeding habits of kelp-bed residents vary seasonally. All three species eat relatively more plankton on emptier stomachs during the coolwater seasons. Similarly, blue rockfish off central California feed less during winter and more during summer (Gotshall et al. 1965). Unlike Santa Barbara fish, however, their feeding increases during the spring upwelling season when they grow rapidly eating abundant plankton, and decreases during the fall when they grow more slowly eating relatively more substrate-oriented prey and nekton (Miller and Geibel 1973). Like Santa Barbara fish, kelp bass off San Diego feed less during winter, when they are difficult to catch (Limbaugh 1955; Quast 1968c). Quast (1968c) concluded that feeding peaks during fall and late spring may relate to reproductive cycles. Yet in the present study, olive rockfish, which were mostly prereproductive, show the same seasonal feeding cycle as the others. Perhaps here, the seasonal cycle of switching among prey types simply reflects greater availability of larger or more easily accessible prey when fish are most active during warmwater seasons.

Seasonal variation in food overlap corroborates this. Overlap is greatest when stomachs are fullest during summer-fall, and least when stomachs are least full during winter. Zaret and Rand (1971) found that food overlap among sympatric Central American stream fishes was greatest during the food-rich wet season and least during the impoverished dry season when intraspecific competition was presumably greatest. Also, Lowe-McConnell (1975) summarized evidence that diets of species in large African lakes overlap most when food is abundant. Yet we have no direct evidence that smaller overlaps reflect greater competition, because we do not know when, if ever, food is limiting.

Feeding habits vary geographically. Blue rockfish seem to differ markedly in diet, distribution, and behavior between Santa Barbara and San Diego. Quast (1968d) noted that the few blue rockfish sampled from a relatively sparse, marginally distributed population off San Diego (ca. 300 km southeast of Santa Barbara) had eaten little. This prompted him to suggest (1968d:132), "The blue rockfish may be poorly adapted to the environment of this region and the schools may comprise expatriate populations." Off Santa Barbara, a denser population contains a larger size range of better-fed individuals. Similarly, near Monterey (ca. 300 km north of Santa Barbara), kelp beds abound with all growth stages (Miller and Geibel 1973) eating mostly plankton, but including less attached prey and more nekton as adults (Gotshall et al. 1965).

Kelp bass also show differences. Compared with Santa Barbara fish, relatively more medium-sized bass from off San Diego contained clupeiform fishes (mainly anchovies, reflecting the bias due to sampling from partyboats) and motile substrate-oriented prey, such as crabs, shrimps, and amphipods; but fewer contained plankton, algae, nonclupeiform fishes, and hydroids (Quast 1968c). Other, more cursory results (Limbaugh 1955; Young 1963) agree basically with Quast's. However, Turner et al. (1969), who examined kelp bass speared from about oil platforms and other artificial reefs off southern California, found, as we did, large numbers of pelagic tunicates in some individuals. These researchers saw bass eating chains of salps floating near the reefs. Bass would first bite out and ingest the viscera of large salps, then consume the tunics of the gutted prey; they swallowed small salps whole. Quast (1968c) concluded that larger kelp bass eat larger and more motile prey, especially fish, and ingest more kelp. Although we observed a similar trend, we have no evidence that, as Quast suggested, large bass mistake kelp fragmented by boat propellers for fish prey.

These feeding differences in kelp bass cannot be explained by distributional differences. Like San Diego fish (Limbaugh 1955; Quast 1968b, c), all sizes of Santa Barbara fish are frequently encountered from surface to bottom, and prefer areas of dense kelp at the outer margins of the bed. Quast (1968b) concluded, however, that kelp bass also occupy reefs having little or no kelp.

There is less information on geographic variation in feeding habits of olive rockfish. South of Santa Barbara, olive rockfish and kelp bass reportedly cooccur and even intermingle (Quast 1968d; Turner et al. 1969), eat similar foods (Quast 1968d), and so may compete for the same cover and food (Feder et al. 1974). Off Santa Barbara, however, the two may minimize interference by having a relatively small overlap in spatial distribution. Considering the two species' superficial similarities in body form and color pattern, Limbaugh (1955) suggested that olive rockfish may ecologically replace kelp bass north of Santa Barbara, where kelp bass dwindle in numbers (Quast 1968a; Miller and Geibel 1973).

Geographic variation in a fish's feeding habits may reflect its environmental tolerances, range limits, and numbers of competitors, as well as its food supplies. Blue rockfish are more abundant off central California, kelp bass are more abundant off southern California, and olive rockfish occur abundantly in both regions but, unlike the others, are mostly restricted to Californian coastal waters (Limbaugh 1955; Quast 1968a, d; Miller and Geibel 1973). Because the Santa Barbara Channel is near the northern limit of the San Diegan fauna (Hubbs 1960; Quast 1968a), it harbors more central Californian cool-water species (Ebeling et al. 1971; Ebeling, R. Larson, and W. Alevizon in prep.). Hence all three species abound in Santa Barbara kelp forests, and here, for example, the olive rockfish may be better at capturing nekton, thus reducing supplies for the other two. Off San Diego, on the other hand, both rockfishes may occur more sporadically (Quast 1968d) and compete less intensely with the more numerous kelp bass. Generally reduced planktivory off San Diego may either reflect lower average plankton densities there (Smith 1971, 1974), or greater abundances of larger, more preferred prey.

Within the Santa Barbara area, habitat differences may affect prey availability and the species' feeding habits. Like most areas of reef and kelp (Feder et al. 1974; Miller and Geibel 1973), Naples Reef may provide more refuges for larger prey. So here, as suggested generally both from experiments (e.g., Ivlev 1961) and theoretical models (e.g., Schoener 1971; Estabrook and Dunham 1976), predators may concentrate on fewer categories of larger, preferred prey in a greater overall abundance of food. One-Mile Reef, on the other hand, appears less intrinsically productive because it is deeper than Naples Reef and supports no giant kelp. So here larger prey may occur less predictably and olive rockfish must switch to plankton, including the tiniest of items, more frequently. Santa Cruz Island reefs are even more complex and productive than Naples Reef (Alevizon 1975; D. Laur pers. commun.). Thus Santa Cruz supports larger aggregations of olive rockfish, which tend more to segregate from equally large aggregations of blue rockfish.

Finally, food and space need not be the primary factors that limit the sizes of the switch-feeder populations. Severe storms, disease, and predators may eliminate certain numbers of individuals. Menge and Sutherland (1976) reviewed evidence that for complex communities in stable environments, predators may crop prey populations below their environmental carrying capacity. Hence, only top predators must partition resources to avoid competitive exclusion. Thus if adult switch feeders are heavily exploited by sharks, marine mammals, man, etc., or young are decimated by smaller predators, the three species may have little, if any, competitive effect on one another.

Evolutionary Viewpoint

Ultimately, the tendency to choose different prey may be an evolutionary response to coexistence with a close relative. The two rockfishes, which cooccur throughout much of their ranges (Phillips 1957; Quast 1968a), may have coevolved their divergent food habits. Most species of rockfish are spiny types that sit on the bottom and/or live in deep water (Phillips 1957). However, the blue and olive rockfishes are members of a derived group of related species that have smoother, more streamlined bodies and inhabit the entire water column. Extending its distribution from bottom to surface, the common ancestor of this species group could eat plankton and surface nekton as well as benthic prey. Such an ancestor would have the ability to hunt in open water and exploit all three prey types by evolving a more streamlined morphotype. Then, during the process of speciation within the group, the blue and olive rockfishes may have themselves diverged in food habits as might be expected of two cooccuring congeners (e.g., Mayr 1963; MacArthur 1972).

Thus even if their numbers are not limited by predators or other disturbances, the three superficially similar species may coexist by partitioning resources. As a more distantly related serranid, the kelp bass broadly shares the food spectrum with both scorpaeniform rockfishes: the plankton-eating and browsing blue rockfish and the fish-eating olive rockfish. Yet the kelp bass and olive rockfish have the greater dietary overlap and so tend to stay out of each others' way where both are common off Santa Barbara. And if conditions warrant it, kelp bass and olive rockfish can switch to plankton and other tiny prey although they are apparently less well adapted than blue rockfish to do so.

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LITERATURE CITED

ALEVIZON, W. S.
1975. Comparative feeding ecology of a kelp-bed embiotocid (*Embiotoca lateralis*). Copeia 1975:608-615.

BRAY, R. N., AND A. W. EBELING.
1975. Food, activity, and habitat of three "picker-type" microcarnivorous fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 73:815-829.

BROWN, D. W.
1974. Hydrography and midwater fishes of three contiguous oceanic areas off Santa Barbara, California. Los Ang. Cty. Mus. Contrib. Sci. 261:1-30.

CARLSON, H. R., AND R. E. HAIGHT.
1972. Evidence for a home site and homing of adult yellowtail rockfish, *Sebastes flavidus*. J. Fish. Res. Board Can. 29:1011-1014.

CODY, M. L.
1974. Competition and the structure of bird communities. Princeton Univ. Press, Princeton, N.J., 318 p.

COLLYER, R. D., AND P. H. YOUNG.
1953. Progress report on a study of the kelp bass, *Paralabrax clathratus*. Calif. Fish Game 39:191-208.

EBELING, A. W., AND R. N. BRAY.
1976. Day versus night activity of reef fishes in a kelp forest off Santa Barbara, California. Fish. Bull., U.S. 74:703-717.

EBELING, A. W., W. WERNER, F. A. DEWITT, JR., AND G. M. CAILLIET.
1971. Santa Barbara oil spill: Short-term analysis of macroplankton and fish. U.S. Environ. Prot. Agency Water Pollut. Control. Res. Ser. 15080EAL02/71, 68 p.

ESTABROOK, G. F., AND A. E. DUNHAM.
1976. Optimal diet as a function of absolute abundance, relative abundance, and relative value of available prey. Am. Nat. 110:401-413.

FEDER, H. M., C. H. TURNER, AND C. LIMBAUGH.
1974. Observations on fishes associated with kelp beds in southern California. Calif. Dep. Fish Game, Fish Bull. 160, 144 p.

FRYER, G.
1959. The trophic interrelationships and ecology of some littoral communities of Lake Nyasa with especial reference to the fishes, and a discussion of the evolution of a

group of rock-frequenting Cichlidae. Proc. Zool. Soc. Lond. 132:153-281.

GOTSHALL, D. W., J. G. SMITH, AND A. HOLBERT.
1965. Food of the blue rockfish *Sebastodes mystinus*. Calif. Fish Game 51:147-162.

HILL, M. O.
1973. Diversity and evenness: A unifying notation and its consequences. Ecology 54:427-432.

HOBSON, E. S.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., U.S. 72:915-1031.

HOBSON, E. S., AND J. R. CHESS.
1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.

HUBBS, C. L.
1960. The marine vertebrates of the outer coast. Syst. Zool. 9:134-147.

IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. [Translated from Russ.] Yale Univ. Press, New Haven, Conn., 302 p.

LIMBAUGH, C.
1955. Fish life in the kelp beds and the effects of harvesting. Univ. Calif. Inst. Mar. Res., IMR Ref. 55-9, 158 p.

LOWE-MCCONNELL, R. H.
1975. Fish communities in tropical freshwaters. Their distribution, ecology and evolution. Longman Group Ltd., Lond., 337 p.

MACARTHUR, R. H.
1972. Geographical ecology: patterns in the distribution of species. Harper and Row, N.Y., 269 p.

MAYR, E.
1963. Animal species and evolution. Harvard Univ. Press, Camb., Mass., 797 p.

MENGE, B. A., AND J. P. SUTHERLAND.
1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Am. Nat. 110:351-369.

MILLER, D. J., AND J. J. GEIBEL.
1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 158, 137 p.

MURDOCH, W. W., S. AVERY, AND M. E. B. SMYTH.
1975. Switching in predatory fish. Ecology 56:1094-1105.

PEET, R. K.
1974. The measurement of species diversity. Annu. Rev. Ecol. Syst. 5:285-307.

PHILLIPS, J. B.
1957. A review of the rockfishes of California (family Scorpaenidae). Calif. Dep. Fish Game, Fish Bull. 104, 158 p.

PIANKA, E. R.
1974. Niche overlap and diffuse competition. Proc. Natl. Acad. Sci. 71:2141-2145.

QUAST, J. C.
1968a. Fish fauna of the rocky inshore zone. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in southern California, p. 35-55. Calif. Dep. Fish Game, Fish Bull. 139.
1968b. Estimates of the populations and the standing crop of fishes. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in southern California, p. 57-79. Calif. Dep. Fish Game, Fish Bull. 139.
1968c. Observations on the food and biology of the kelp bass, *Paralabrax clathratus* with notes on its sportfishery at San Diego, California. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in southern California, p. 81-108. Calif. Dep. Fish Game, Fish Bull. 139.
1968d. Observations on the food of the kelp-bed fishes. *In* W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in southern California, p. 109-142. Calif. Dep. Fish Game, Fish Bull. 139.

RANDALL, J. E.
1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. (Miami) 5:665-847.

RANDALL, J. E., AND V. E. BROCK.
1960. Observations on the ecology of epinepheline and lutjanid fishes of the Society Islands, with emphasis on food habits. Trans. Am. Fish. Soc. 89:9-16.

SCHOENER, T. W.
1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2:369-404.

SMITH, P. E.
1971. Distributional atlas of zooplankton volumes in the California Current region, 1951 through 1966. Calif. Coop. Oceanic Fish. Invest., Atlas 13, 16 p., 144 charts.
1974. Distribution of zooplankton volumes in the California Current region, 1969. Calif. Coop. Oceanic Fish. Invest., Atlas 20:15-17, charts 118-125.

SOLOMON, M. E.
1949. The natural control of animal populations. J. Anim. Ecol. 18:1-35.

TATE, M. W., AND R. C. CLELLAND.
1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers, Inc., Danville, Ill., 171 p.

TURNER, C. H., E. E. EBERT, AND R. R. GIVEN.
1969. Man-made reef ecology. Calif. Dep. Fish Game, Fish Bull. 146, 221 p.

WHITTAKER, R. H.
1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30:279-338.

WINDELL, J. T.
1971. Food analysis and rate of digestion. *In* W. E. Ricker (editor), Methods for assessment of fish production in fresh waters, 2d ed., p. 215-226. IBP (Int. Biol. Programme) Handb. 3.

YOUNG, P. H.
1963. The kelp bass (*Paralabrax clathratus*) and its fishery, 1947-1958. Calif. Dep. Fish Game, Fish Bull. 122, 67 p.

ZARET, T. M., AND A. S. RAND.
1971. Competition in tropical stream fishes: Support for the competitive exclusion principle. Ecology 52:336-342.