FOOD HABITS OF JUVENILE ROCKFISHES (*SEBASTES*) IN A CENTRAL CALIFORNIA KELP FOREST

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ABSTRACT

The diets and feeding morphology of juveniles of seven rockfish species (Scorpaenidae: *Sebastes*) were investigated in a kelp forest at Stillwater Cove, Carmel Bay, CA. The seven species could be divided into two groups, those which fed primarily on open water prey in the water column and those which fed on substrate-associated prey. Substrate-associated prey were generally larger than open water prey and were eaten by predators with relatively larger heads and mouths and shorter gill rakers. Comparison of juvenile diets and foraging patterns with those of adults showed that both foraged in similar manners and in the same general habitats. The absence of aggressive interactions within or among species and high intraspecific variability of foraging patterns suggests that little interference or exploitative competition was present.

Most of the literature on rockfishes deals mainly with aspects of either adult or larval biology (DeLacey et al. 1964; Phillips 1964; Miller and Geibel 1973; Westrheim 1975; Larson 1980a, b, c). Little of this literature deals with the juvenile stage. Juvenile rockfishes often use nearshore kelp beds as nursery grounds and, during certain times of the year, are the most abundant members of the kelp-forest fish community (Burge and Schultz 1973). The change from pelagic life to a nearshore, reef-dwelling existence represents a major ecological transition. With so many juvenile rockfish species co-occurring in kelp forests, the potential for competitive interaction is great. Gaining an understanding of these fishes' patterns of resource utilization (e.g., food or space) may be important in assessing the mechanisms that affect their survival.

The purpose of this study was threefold: 1) to investigate the food habits of juvenile rockfishes occurring in a nearshore kelp forest, 2) to determine the extent to which diet differed within and among the various species present, and 3) to compare the relationship between diet and morphology in juvenile and adult forms.

The juveniles of seven rockfish species were studied. The adults of six of these species usually occur nearshore, in association with rock reefs: blue rockfish, *S. mystinus*; black rockfish, *S. melanops*; olive rockfish, *S. serranoides*; copper rockfish, *S. caurinus*; gopher rockfish, *S. carnatus*; and kelp rockfish, *S. atrovirens* (Hallacher 1977; Roberts 1979). Adults of the seventh species, the canary rockfish, *S. pinniger*, occur deeper and usually offshore (Miller and Lea 1972). For purposes of this study, an individual was designated a juvenile upon first appearance in the kelp forest, where fish were usually 25 to 30 mm SL. The fish used in this study generally ranged from 30 to 70 mm SL.

Sebastes mystinus and *S. pinniger* are among the earliest species to recruit, usually appearing as early as April. *Sebastes mystinus* usually occurs in the water column above 6 m while *S. pinniger* occurs on the substrate usually near sand/rock interfaces. *Sebastes caurinus* begins recruiting around late April or May and is found initially among kelp fronds and near the surface. Next to arrive are *S. serranoides* and *S. melanops* which first appear in May and June. Both these species occur mostly in the midwater within the kelp forest. *Sebastes carnatus* usually begins to recruit in late June and July and, like *S. caurinus*, is found initially among kelp fronds at the surface. Both *S. caurinus* and *S. carnatus* move down from the canopy and take positions near the bottom after a couple of months (around June or July for *S. caurinus* and late August or September for *S. carnatus*). The last of these species to recruit is *S. atrovirens*, which begins to appear in late July and August and occurs in the surface kelp canopy.

METHODS AND MATERIALS

Study Site

All observations and samples were taken between

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May 1980 to October 1981 at a rock reef at Arrowhead Point in Stillwater Cove, Carmel Bay, CA (about lat. 36°33.6′N, long. 121°56.3′W). Bottom depths at the study site averaged about 12.5 m below MLLW (mean low low water). The reef was roughly triangular, bounded by sand flats which sloped into deeper water on all but the nearshore side (Fig. 1). The reef substrate was composed of both high and low relief basaltic rock interspersed with areas of coarse, granitic sand and a few patches of worm tubes (*Diopatra* sp.). Stillwater Cove is protected from the prevailing north and northwest swells and winds. However, it is exposed to the most severe southerly storms which commonly occur from October to February.

The rock substrate was covered with an extensive mat of coralline algae and sessile invertebrates. The dominant algal form was the giant kelp, *Macrocystis pyrifera*, which became very thick in the summer months and represented a major structural component of the reef. Except for corallines, understory algae (*Pterogophora californica*, *Cystoseira osmundacea*, and seasonally dense patches of *Desmarestia ligulata*) were relatively sparse and patchy. *Desmarestia* abundance increased in the fall as the surface kelp canopy decreased. Drift algae of several types entered the reef at times and often became a major microhabitat. It usually occurred along the sand/rock interface or in low patches in the interior of the reef.

Field Collections

All fish used for stomach content analysis were collected with a 1 m × 1 m × 1.5 m opening-closing, diver-held net. The net was constructed of 1/8-in stretch-mesh nylon netting on a 1/4-in PVC frame mouth. The mouth of the net was hinged in the middle with tygon tubing. This allowed easy operation by a single diver in close spaces. Collected fish were brought to the surface and the stomachs injected with 10% Formalin[2]. The fish were then preserved whole in 10% Formalin, then washed in freshwater, and stored in 70% ethanol.

The majority of fish collected for gut analysis were taken from June to August of both 1980 and 1981 with some supplemental collections occurring in October and November of 1980. Collections were made during both day and night.

Laboratory Methods

Each fish was blotted dry and weighed to the nearest 0.01 g. The entire visceral mass was removed, and the stomach and intestine were then separated from the remaining viscera. The contents of each stomach were emptied into a small dish and examined under a binocular dissecting scope. Food items were separated by general taxonomic category (e.g., calanoid copepods, zoea larvae, mysid shrimp, etc.). These general categories were used because not all prey items found were in good enough condition to identify to species, thus identifying some items further than others could be misleading. Each category was enumerated by number and percent volume. The percent of the total stomach volume of each prey type was estimated by spreading the contents to a uniform thickness over a background grid and then estimating the area represented by each type. Since contents were spread to an equal thickness, area and volume were considered directly proportional. Digestive state of contents was estimated on a subjective one to five scale (DeWitt and Cailliet 1972). In addition, a subset of each prey type was taken from stomach contents and measured along its longest axis to the nearest 0.005 mm using an ocular micrometer for later estimation of mean sizes of each prey type.

Analytical Methods

A plot of cumulative number of prey types against randomly pooled number of stomachs was constructed for each species in order to assess adequacy of sample sizes. An asymptotic leveling of this type of plot indicates a sufficient sample size. The mean percent by estimated volume (%V) and by number (%N) of each prey type were calculated for each fish species as an average of all values for individual specimens. The mean frequency of occurence (%FO) was also calculated for each prey type in each predator as the number of times the prey type was seen divided by the total of stomachs examined. The importance of each prey type was calculated using the index of relative importance (IRI) described by Pinkas et al. (1971). The IRI used the proportion by amount (%N), volume (%V), and occurrence (%FO) of each prey type (IRI = (%N + %V) × %FO). The diets of the seven species studied were compared using the percent similarity index (PSI) (Whittaker 1952): $\mathrm{PSI} = 1 - 0.5\,\Sigma\, pih - pjh$. Where pi and pj are the proportions by IRI of each prey type (h) in the two predators being compared. In calculating

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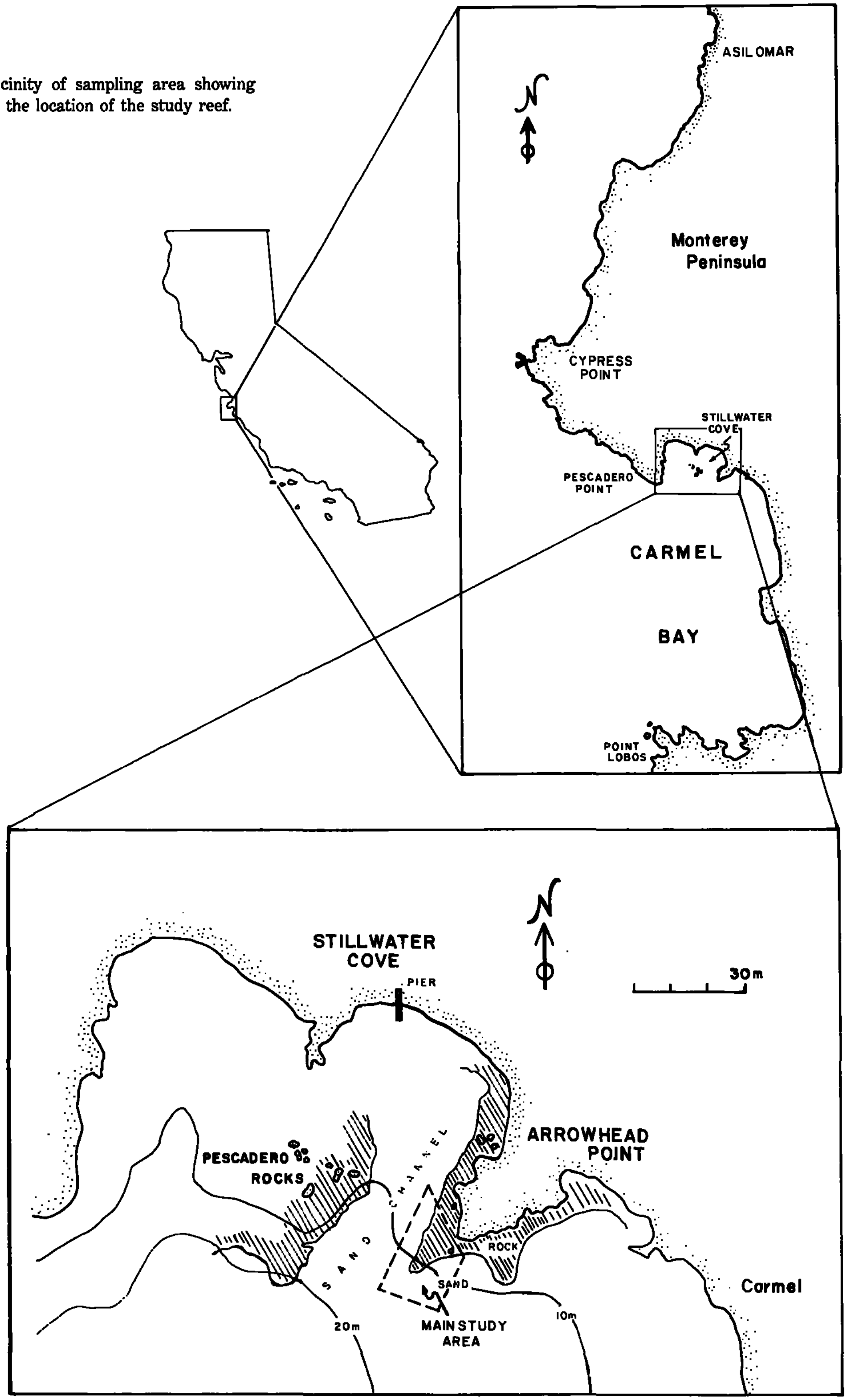
[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

FIGURE 1.—Map of vicinity of sampling area showing Stillwater Cove and the location of the study reef.



overlap values %IRI values were used as the proportion, *p*.

Morphological Comparison

Several measurements were taken on a subsample of fish of each species covering all sizes encountered in this study. These included standard length, head length, and gape. Mean length of the five gill rakers nearest the angle on the ventral limb of the first gill arch, and the gap between them, were also measured.

The feeding related morphological characteristics chosen for statistical comparison were head length, gape, gill raker length, and gill raker spacing. Gape and gill raker spacing were compared as absolute measurements. Gill raker lengths were standardized to a proportion of head length and head length was standardized as a proportion of standard length for comparison.

Gape was compared using a one-way analysis of covariance (ANCOVA). This analysis regressed the natural log of the gape against the natural log of fish standard length to allow comparison over a range of fish sizes and to achieve linearity (Sokal and Rohlf 1969; Chen 1971). Relative head length, gill raker spacing, and relative gill raker length were compared among species with a Model I, one-way analysis of variance (ANOVA).

Multiple range comparisons were then made between individual species to detect groupings. Regression lines resulting from the ANCOVA were subjected to Newman-Keuls pairwise comparisons. Mean values obtained from ANOVAs were subjected to Student-Newman-Keuls (SNK) multiple range tests. All statistical procedures used followed those presented in Sokal and Rohlf (1969) and Snedecor and Cochran (1980).

Prey Abundance

Qualitative assessment of prey abundances was made from zooplankton tows done in the kelp forest. A standard 0.5 m diameter net with 0.333 μm mesh was used. Tows were done in sets of three, 3 min each: one within 0.5 m of the canopy, one in midwater, and one within 0.5 m of the bottom. These were done during both day and night. Generally, only presence or absence of plankton types was noted, along with relative daytime vs. nightime differences in abundances. Absolute abundances were not estimated. Zooplankton samples were taken once in mid-June 1980 and once in mid-July 1981. A total of 12 samples were collected.

RESULTS

A total of 265 juveniles of the seven species was examined for stomach content analysis: 27 *S. melanops* (53 to 67 mm SL, $\bar{x}$ = 57.9); 51 *S. serranoides* (44 to 63 mm; $\bar{x}$ = 51.8); 63 *S. pinniger* (28 to 56 mm, $\bar{x}$ = 43.7); 23 *S. mystinus* (46 to 72 mm, $\bar{x}$ = 59.1); 38 *S. atrovirens* (38 to 64 mm, $\bar{x}$ = 47.1); 42 *S. caurinus* (35 to 62 mm, $\bar{x}$ = 48.7); and 21 *S. carnatus* (33 to 65 mm, $\bar{x}$ = 44.4). An often cooccuring cogener of *S. carnatus*, *S. chrysomelas*, was not found during this study.

Diet Analysis

The cumulative prey type curves versus number of stomachs examined leveled off asymptotically, indicating that sample sizes for all species were sufficient to characterize their food arrays. All species were found to be zooplanktivores, consuming both open water and substrate-associated prey. Open water prey, which mainly float free in the water column, consisted mostly of juvenile copepods, zoea, and juvenile spionid polychaetes, while substrate-associated prey, which were generally found directly associated (<0.5 m away) with a physical structure (rock, kelp, etc.), consisted mainly of gammarid amphipods, mysid and caridean shrimp, and two species of isopod (Table 1).

A wide variety of prey sizes were encountered (Table 2). Prey found in open water, such as calanoid and harpacticoid copepods, zoea, and larvaceans, were mostly < 1 mm in length, whereas substrate-associated prey, such as amphipods and decapods, were 3 to 4 mm or larger.

Mean number of prey items and prey taxa per individual were highly variable within and among species (Table 3). As would be expected, species which fed on small open water prey had higher numbers of prey per stomach. Conversely, those species which fed on large substrate-associated prey, which were often large enough to fill a stomach with a single prey item, had much lower numbers of prey items per stomach.

Sebastes mystinus fed mainly on the larvacean *Oikopleura* sp., with high occurrence of copepods, zoea, and juvenile polychaetes (Fig. 2). They had the most cosmopolitan diet and the highest intraspecific variability of prey types (a mean of almost six different prey types per individual) (Table 3). Because its diet was composed mainly of small open water prey, this species also had the highest mean number of prey items per individual.

Sebastes serranoides and *S. melanops* had very

TABLE 1.—Taxa of prey identified in the stomachs of juvenile rockfish; names in all-capitals are categories used in stomach content analysis. (?) signifies incomplete or unsure identification. Microhabitat associations: OW = open water prey, S = substrate oriented prey.

Prey type			Open water or substrate association
Algae			
Mostly reproductive *Cystociera osmundacea*			S
Occasional pieces of *Macrocystis* fronds			
Invertebrates			
Molluscs	- *Macoma* sp.		S
Copepods	- CALANOIDS: unidentified juveniles		OW
	HARPACTICOIDS: unidentified juveniles		OW/S
OSTRACODS	- Unidentified		OW
POLYCHAETES	- larval/juvenile Spionidae		OW
Cirripidea	- unidentified BARNACLE LARVAE		OW
ISOPODS	- *Dimonella globera*; *Idothea resicata*		S
Amphipods	- GAMMARIDS:	*Aoroides columbiana*	S
		Ampithoe sp.	
		Batea transversa	
		Najna kitmata (?)	
	CAPRELLIDS:	*Caprella* sp.	S
		Unidentified Protocerid	
	HYPERIIDS:	Unidentified	S
MYSIDS	- *Acanthomysis* sp.; *Neomysis* sp.		S
Decapods	- SHRIMP:	*Heptocarpus* sp.	S
		Hippolyte sp. (?)	
	ZOEA LARVAE:	unidentified decapods and brachyurans	OW
	ANOMURANS:	unidentified JUVENILE HERMIT CRAB	S
Larvaceans	- *Oikopleura* sp.		OW
FISH			
unidentified hard parts			S
unidentified fish eggs			OW

TABLE 2.—Mean (±95% confidence interval) sizes of individuals of the nine major prey types of juvenile rockfishes. Measured items were taken from stomach samples.

Species	N	Size (mm) $\bar{x}$	Size (mm) 95% C.I.
Open water prey			
Oikopleura sp.	50	0.69	0.04
Harpacticoid copepods	50	0.88	0.05
Calanoid copepods	50	0.96	0.03
Juvenile polychaetes	35	1.47	0.71
Zoea larvae	50	1.63	0.11
Substrate-associated prey			
Mysids	35	3.48	1.16
Gammarid amphipods	35	4.01	0.77
Isopods	30	4.29	0.89
Caridean shrimp	30	13.95	1.47

similar diets (Fig. 2, Table 4). Both species ate mainly open water prey: calanoid copepods, harpacticoid copepods, and zoea larvae in order of importance. These species also showed fairly high intraspecific diet variability—5.3 and 4.4 prey taxa per individual for *melanops* and *serranoides*, respectively.

The two species which showed major microhabitat shifts (Carr 1983), *S. caurinus* and *S. carnatus*, also showed large dietary changes. While in the canopy (generally <45 mm in SL), *S. caurinus* ate predominantly calanoid copepods, with harpacticoids and zoea also eaten fairly consistently (Fig. 2). However, after moving out of the canopy and down to the bottom near kelp stipes and rocks, its diet shifted to primarily caridean shrimp, with gammarid amphipods being the second most important prey (Fig. 2). *Sebastes carnatus* showed much the same type of dietary shift accompanying its large habitat shift. While in the canopy, smaller *S. carnatus* ate nearly exclusively calanoid copepods (92% of the diet), while large individuals, which were found on the bottom, fed on caridean and mysid shrimp and isopods (Fig. 2). This marked change in diet can also be seen in Table 4. Within each of these species, the diet similarity between size classes was low. However, similarities between the two species within each size class was quite high.

Sebastes atrovirens was found in the kelp canopy and among kelp throughout all depths during the entire study (Carr 1983). This species fed mainly on gammarid amphipods, with calanoid and harpacticoid copepods and mysid shrimp also being very

TABLE 3.—Mean (±95% confidence interval) number of prey items and prey taxa per stomach and total number of prey types for the seven species of juvenile rockfishes.

		Items		Taxa		S
Species	*N*	$\bar{x}$	95% C.I.	$\bar{x}$	95% C.I.	Total
Open water predators						
Sebastes mystinus	23	142.6	74.9	5.8	0.4	13
S. caurinus (<45 mm)	17	136.4	64.7	3.4	0.7	8
S. carnatus (<45 mm)	12	101.4	79.6	1.9	0.7	5
S. serranoides	50	100.2	33.5	4.4	1.7	9
S. melanops	27	87.0	31.2	5.3	2.3	8
Substrate-oriented predators						
S. pinniger	59	35.5	18.3	4.3	1.6	15
S. atrovirens	33	34.9	20.3	2.2	0.4	8
S. caurinus (>45 mm)	21	2.5	1.3	1.5	0.3	9
S. carnatus (>45 mm)	11	2.3	1.2	1.6	0.7	5

TABLE 4.—Percent similarity (PSI) overlap values of juvenile rockfish diets. Proportions used for calculations are %IRI.

	serranoides	*melanops*	*mystinus*	*caurinus* <45 mm	*carnatus* <45 mm	*pinniger*	*atrovirens*	*caurinus* >45 mm	*carnatus* >45 mm
Sebastes serranoides	—	0.787	0.455	0.874	0.602	0.653	0.389	0.091	0.090
S. melanops		—	0.402	0.732	0.516	0.734	0.318	0.094	0.019
S. mystinus			—	0.384	0.127	0.458	0.239	0.097	0.043
S. caurinus (<45 mm)				—	0.668	0.573	0.427	0.185	0.204
S. carnatus (<45 mm)					—	0.297	0.259	0.043	0.034
S. pinniger						—	0.468	0.174	0.169
S. atrovirens							—	0.218	0.258
S. caurinus (>45 mm)								—	0.634
S. carnatus (>45 mm)									—

important in their diet (Fig. 2). Thus, this species' diet was similar to most other species (Table 4).

Sebastes pinniger had a very diverse diet (highest number of overall prey taxa found; Table 3). Individuals were found mainly over sand areas and the sand/rock interface at the edge of the kelp forest, generally within a few meters of the bottom. This species' diet consisted mainly of copepods and zoea larvae (open water prey), but gammarid amphipods and mysid shrimp (substrate-associated prey) were also important (Fig. 2).

Figure 2 shows that these seven species can be split into two basic categories: open water and substrate-associated predators (this categorization can also be seen in microhabitat differences [Carr 1983]). Open water predators—*S. melanops*, *S. mystinus*, *S. serranoides*, and small *S. caurinus* and *S. carnatus*—are those that ate mainly copepods and zoea larvae. Substrate-oriented predators—*S. atrovirens* and larger *S. caurinus* and *S. carnatus*—are those that ate predominantly amphipods and decapods. *Sebastes pinniger* is intermediate between these categories. Its microhabitat and behavior are that of a substrate-associated predator, but its diet is more similar to the open water predators (Table 4).

Prey Distribution

Midwater organisms such as copepods, zoea larvae, and polychaetes were very abundant in all parts of the water column. Calanoid copepods were the most abundant type during the day at all depths, while both calanoids and harpacticoids were very abundant at night. Amphipods, mysids, caridean shrimp, and isopods were very abundant in and around all substrate types (kelp canopy, stipes, rocks, and drift algae). Isopods and amphipods were most abundant in the canopy and stipes, while amphipods, mysids, and carideans were more often abundant near rock and drift algae and around kelp holdfasts. These invertebrates remained near substrate during the day, moving farther away at night.

Morphological Comparisons

ANOVAs of relative head length, relative gill raker length, and gill raker spacing among species were all significant at the $P < 0.001$ level (Table 5). Generally, the open water and substrate-associated classifications also held true for groupings by morphology.

In general, open water predators had smaller heads and larger gill rakers. *Sebastes mystinus*, *S.*

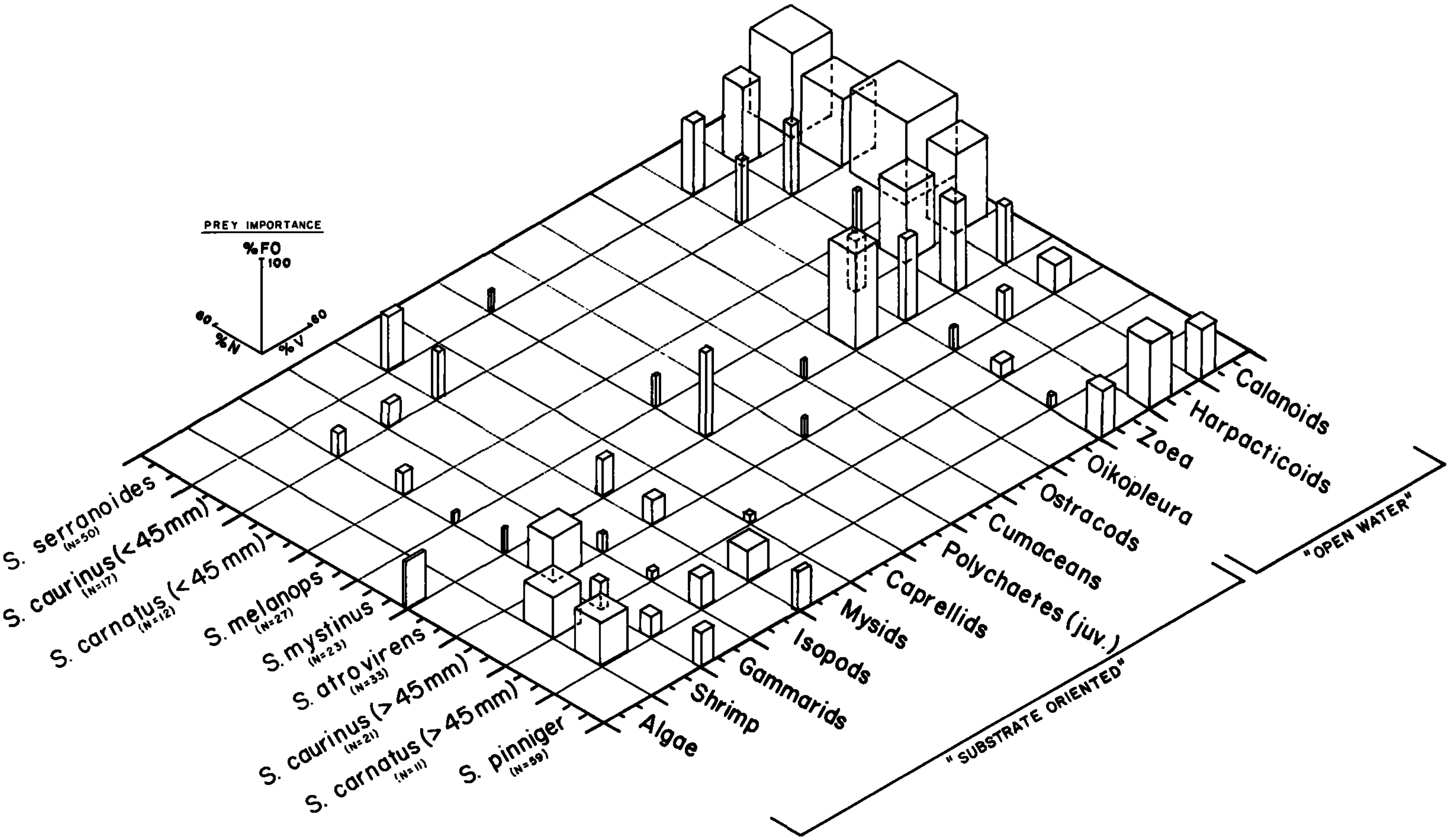


FIGURE 2.—Three dimensional trophic spectrum of juvenile rockfish diets. %N and %V are the horizontal axes with %FO on the vertical axis. Size of each box is equivalent to each prey type's importance.

TABLE 5.—Results of Student-Newman-Keuls multiple range comparisons on head length and gill raker length and spacing of juvenile rockfishes (*Sebastes*). Numbers in parentheses are significance levels of analyses of variance (ANOVA).

Relative head length ($P < 0.0001$)
Groupings at $\alpha = 0.05$ level (mean head lengths)

mystinus	*serranoides*	*melanops*	*atrovirens*	*caurinus*	*pinniger*	*carnatus*
0.3368	0.3620	0.3660	0.3808	0.3882	0.3890	0.3908

Relative gill raker length ($P < 0.001$)
Groupings at $\alpha = 0.05$ level (mean raker lengths)

carnatus	*caurinus*	*atrovirens*	*serranoides*	*pinniger*	*mystinus*	*melanops*
0.1008	0.1070	0.1165	0.1185	0.1222	0.1296	0.1322

Gill raker spacing ($P < 0.001$)
Groupings at $\alpha = 0.05$ level (mean spacing)

pinniger	*melanops*	*atrovirens*	*carnatus*	*mystinus*	*caurinus*	*serranoides*
0.226	0.234	0.238	0.248	0.262	0.312	0.316

serranoides, and *S. melanops*, which all have relatively long, slender bodies, had significantly smaller heads than *S. caurinus*, *S. carnatus*, and *S. pinniger* (Table 5). *Sebastes mystinus* and *S. melanops* also had significantly longer gill rakers than *S. caurinus* and *S. carnatus*, with *S. serranoides* having intermediate length rakers. *Sebastes atrovirens* was relatively intermediate in both measurements, but tended to be more like the predators with larger heads and shorter gill rakers. Groupings for gill raker spacing were less distinct. The open water/substrate-associated classifications also broke down with this measurement. *Sebastes pinniger*, *melanops*, and *atrovirens* had more closely spaced rakers, while *S. caurinus* and *serranoides* had the widest spaced rakers. *Sebastes mystinus* had an intermediate value (Table 5). Regression lines obtained from the ANCOVA showed that gape grew isometrically with length in all seven species, but that there were significant differences in the size of gape relative to body size among the species (Table 6). The slopes of the lines of ln (gape) on ln (SL) were all statistically indistinguishable from unity, but the intercepts did show a significant difference ($P < 0.001$, ANCOVA). Much of this significant difference was likely due to *S. caurinus*, which had a much larger mouth than the other species. *Sebastes serranoides* also had a fairly large mouth. All other species had very similar-sized mouths (Table 6).

TABLE 6.—Results of the one way analysis of covariance (ANCOVA) performed on regressions of ln (gape) versus ln (SL) of juvenile rockfishes.

Regression statistics

Species	Slope	Intercept	r
Sebastes			
caurinus	0.6745	−0.4173	0.8259
S. serranoides	0.8332	−1.2024	0.8363
S. pinniger	0.9876	−1.6759	0.9640
S. melanops	0.9761	−1.7070	0.9614
S. mystinus	0.9555	−1.7470	0.9224
S. carnatus	1.0482	−1.8439	0.9652
S. atrovirens	1.0561	−2.0053	0.9661

ANCOVA statistics

	MSnum	df	MSdenom	df	F	P
Slope	0.01	7	0.0057	155	1.76	NS
Intercept	0.16	6	0.039	161	40.68	$P < 0.001$

DISCUSSION

Many species of fish change diet as they grow (Ross 1978; MacPherson 1981). This may be because of changes in habitat, thus changing available food sources, or it may simply be a functional response to changes in fish size and/or metabolic needs. Although there are dietary differences between the juveniles and adults of the species studied here, their foraging patterns and habitats are very much the same.

Species who were water column feeders as juveniles remain water column feeders as adults. Juvenile *S. serranoides* ate primarily copepods and zoea larvae (Hobson and Chess 1976; this study). Adults also feed in the water column, eating primarily small fish and euphausiids (Love 1978). Juvenile *S. melanops* fed in the open water (on copepods), as do the adults, which eat small fish, euphausiids, and polychaetes (Hallacher 1978; Roberts 1979). This trend also holds for *S. mystinus*. Juveniles foraged in the water column, mostly on *Oikopleura* and copepods. Adults also aggregate and feed in the open water, but eat mostly tunicates and crustaceans (Hallacher 1977; Roberts 1979).

The ontogenetic similarity in foraging was also seen in substrate-oriented feeders. Juvenile *S. atrovirens* ate mostly large, demersal, gammarid amphipods. However, copepods ranked second in their diet, presumably because of small individuals feeding in the open water below the kelp canopy. Adults of this species feed on amphipods, shrimp, and crabs which can be either demersal or free swimming (Quast 1968; Hobson and Chess 1976; Roberts 1979). Small juvenile *S. caurinus* and *S. carnatus* fed in the open water, while larger juveniles foraged demersally. The adults of these species also feed demersally. *Sebastes carnatus* is known to eat juvenile rockfish, ophiuroids, and crustaceans (Hallacher 1977; Roberts 1979), while adult *S. caurinus* eat mostly brachyurans and shrimp (Prince 1975; Prince and Gotshall 1976). Juveniles also seem to exhibit the same microhabitat preference as adults. *Sebastes serranoides, mystinus,* and *melanops* were found mainly in the midwater, while *S. caurinus, carnatus,* and *atrovirens* were generally seen to associate more closely with some physical substrate (kelp plants, rocks, etc.) (Carr 1983; pers. obs.). Thus, in these species it seems that once an individual has survived its life as a pelagic larva and entered the kelp forest, it assumes the general habitat and foraging characteristics of an adult.

Sebastes pinniger was the only species which showed different foraging patterns between juveniles and adults. Juvenile *S. pinniger* were generally found close to the bottom over sand or in association with the rock/sand interface at the edge of the reef (Carr 1983; pers. obs.) while adults occur higher in the water column in deep water offshore. Juveniles fed demersally on copepods over sand and drift algae very near the kelp forest. Adults feed in the water column on euphausiids and small fish (Phillips 1964). Recently, adults have been found to be more demersal feeders than other offshore rockfish (Brodeur 1982).

In assessing the mechanisms which might lead to the observed diet differences, several factors must be considered, such as prey distribution and abundance, prey availability, predator morphology, prey and predator activity patterns, and predator distribution.

Qualitative analysis of plankton samples, combined with underwater observations, showed that plankton were very abundant. Although the diel behavior patterns of shallow, inshore zooplankton are highly variable with respect to specific habitats, species, seasons, and latitudes, the patterns of plankton distribution observed were quite comparable with reported accounts in kelp forests (Hobson and Chess 1976; Coyer 1979; Hammer 1981).

Predator morphology is an important factor determining prey size in planktivorous fish. Certain features distinguish water column foraging fish, such as long, slender bodies, sharp head profiles, fine dentition on jaws and pharyngeal bones, and long, closely spaced gill rakers (Yasuda 1960; Davis and Birdsong 1973). Of the seven species studied, the water column feeders—*S. mystinus, S. serranoides,* and *S. melanops*—had smaller heads with longer gill rakers.

Water column foragers and substrate-associated foragers could be separated by both morphology and prey size. The water column foragers—*S. mystinus, S. serranoides,* and *S. melanops*—all had relatively long, slender bodies, small heads, and long gill rakers. This agrees with predictions, especially since the adults of these species are also water column foragers. Water column feeders also ate substantially smaller prey than did substrate predators (see Figure 2, Table 2). The substrate-associated feeders—*S. caurinus, S. carnatus,* and *S. atrovirens,* which ate larger prey—all had stouter bodies, larger heads, and shorter, less ornamented gill rakers.

Juveniles of *S. pinniger* were somewhat intermediate in feeding morphology. Their heads were large and stout, indicative of substrate-oriented feeding. However, they had long, thin bodies and long, fairly closely spaced gill rakers, which is indicative of water column foraging, as is displayed by adults. This intermediate situation may be indicative of the fact that *S. pinniger* may go through a second ecological transition from a reef-dwelling, substrate-associated juvenile form back to a more pelagic offshore situation as an adult.

Differing diel patterns can be one way for co-occurring predators to exploit similar resources while keeping interspecific interactions low (Keast and Webb 1966; Schoener 1974; Bray and Ebeling 1975). In zooplanktivores diel patterns of both predators and prey are important (Hobson and Chess 1976; Robertson and Howard 1978). Most juveniles were active only during the day, with the possible exceptions of *S. pinniger* and *S. serranoides* (Singer 1982). This was also reflected in greater stomach fullness of most species in the afternoon and early evening, indicating diurnal feeding patterns (Singer 1982). Plankton abundances were high during both day and night. However, more species were found in the water column at night. Thus, while some of these fish could do well feeding at night, daytime abundances of food seemed sufficient for their needs. Juveniles were indeed found to be most active and to feed most frequently during daylight hours, but intraspecific variability was high (Singer 1982).

Digestion was fairly slow in all species, taking at least 9 to 12 h for a full stomach of food to be half digested (Singer 1982). Together, these indicate that individuals may not need to feed every day and that both within and among species these populations may feed with a high degree of asynchrony (Singer 1982).

Do the observed differences in diets suggest interspecific competition? Central to competition theory is the presumption that individuals or populations use the same or a very similar resource and that this resource is in short supply (Pielou 1975; Pianka 1978). Abundances of all types of plankton used by these fishes are high. The fact that individuals can probably fill their stomachs in a very short time period (Singer 1982) indicates that their needs are easily met. This suggests that competition for food does not play an important role in the foraging patterns of these species. Other factors, such as the lack of observed aggressive interactions within or among the species studied in over 1,100 min of in situ feeding observations, high overlap in time of feeding, generally low similarity of diet, and high intraspecific variability within foraging patterns suggest there is little food competition (Singer 1982).

Similarly, available evidence suggests little competition for space among juveniles (Carr 1983). When juveniles enter the kelp forest system, they immediately occupy habitats characteristic of adults; thus, habitat preference may be under some genetic control. Close spatial co-occurrence with the absence of agonistic interactions suggests that competition for space is minimal in these fish. Also, within the kelp forest studied, juvenile rockfishes are the predominant planktivores, and are thus relatively free of other possible competitors. Other kelp forest planktivores such as *Chromis punctipinnis*, *Oxyjulius californica*, and *Brachyistius frenata* are present, but in very low numbers, and often only for short periods of time.

Thus, the differences in diet seen in this study appear to be the consequences of these species exploiting localized food resources encountered in different microhabitats. Competition for food does not seem to be a strong ecological influence among these juveniles.

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