FOOD, ACTIVITY, AND HABITAT OF THREE "PICKER-TYPE" MICROCARNIVOROUS FISHES IN THE KELP FORESTS OFF SANTA BARBARA, CALIFORNIA

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ABSTRACT

Diets, daily activity, and habitat preference were compared between the kelp perch, *Brachyistius frenatus*; the señorita, *Oxyjulis californica*; and the white seaperch, *Phanerodon furcatus*, all of which co-occur in areas of reef and kelp off Santa Barbara, Calif. The kelp perch and señorita often clean ectoparasites off larger host fishes, whereas the white seaperch is a more generalized picker-type microcarnivore.

The kelp perch and señorita, which co-occur in the kelp canopy, showed the least amount of total overlap in resource use, expressed as a combination of individual overlaps in food, activity, and habitat. The señorita had the narrowest breadth of diet but the widest breadth of habitat (within the kelp-bed areas). Señoritas and white seaperch ate mostly bryozoans encrusted on plants, whereas kelp perch ate mostly plankton and other tiny motile prey. As species, neither the kelp perch nor the señorita derives substantial amounts of food from cleaning, although some individual señoritas may. Unlike the two "cleaners," the white seaperch also ate substantial numbers of bottom prey. None of the species forage at night, when all are relatively inactive, and when the señorita actually buries itself in patches of rubble and sand on the reef. The two perches showed the greatest overlap in daytime activity, as measured both by bi-hourly counts of feeding bites in the field and of swimming movements in a laboratory tank.

Fishes that exploit the same class of environmental resources in similar ways may be thought of as forming a "guild" of species having similar ecological roles regardless of their taxonomic affinities (Root 1967). In and about the forests of giant kelp off southern California, fishes that can select relatively small prey from mid-water and from kelp or other surfaces form a foraging guild of "pickers" (cf. Hobson 1971). Hubbs and Hubbs (1954) stressed the fact that two common and taxonomically unrelated pickers have remarkably similar mouth structures and dentitions: the kelp perch, *Brachyistius frenatus*, which is in the primarily temperate family of surfperches Embiotocidae, has evolved the same general type of pointed snout, tiny jaws, and protruding canines that characterize the señorita, *Oxyjulis californica*, and most other members of the primarily tropical family of wrasses Labridae.

Hobson (1971) noted that the habit of cleaning ectoparasites off larger fishes is widespread among the picker-type fishes. Señoritas, kelp perch, and young of another embiotocid, the sharpnose seaperch, *Phanerodon atripes*, are the most consistent "cleaner fishes" of the kelp beds (Limbaugh 1961; Hobson 1971). Compared to some small tropical wrasses (Randall 1958), however, these species are less specialized as cleaners: their cleaning activities are sporadic and/or confined to certain individuals, and so their principal forage must be elsewhere (Hobson 1971).

With this in mind, we compared the diets, daily activity patterns, and habitat preferences of the señorita and kelp perch, which are the principal cleaner fishes in the Santa Barbara area, with those of a more generalized picker, the white seaperch, *P. furcatus*. These three species have been studied off San Diego (Limbaugh 1955; Quast 1968a, b; Hobson 1971). Yet little has been published on their habits and distribution off Santa Barbara. Here the Channel Islands and the east-west oriented coastline protect kelp beds from swells, enabling giant kelp to anchor on low-relief and soft bottoms as well as to high-relief reefs. Also, species with centers of distribution located far to the north are more frequently encountered (Quast 1968a; Ebeling et al. 1971).

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METHODS

Kelp perch, white seaperch, and señoritas were observed in the field and laboratory. Over a 2-yr period, scuba divers spent more than a total of 125 h watching and collecting fish both day and night at depths ranging from 1 to 20 m. Study localities included areas of reef and kelp in the Santa Barbara Channel–off the Santa Barbara mainland and off Santa Cruz Island located across the Channel some 42 km to the south.

Food

During 27 scuba dives made between February, 1971 and March, 1973, we collected a total of 115 kelp perch (measuring 43-142 mm, averaging 103 mm standard length), 111 white seaperch (74-203, 139 mm), and 65 señoritas (110-227, 169 mm). Gut contents were found in and identified from 50 kelp perch, 55 white seaperch, and 53 señoritas. All fish were taken with a small, 15-prong pole spear. Later they were slit ventrally, fixed in 10% Formalin,[2] washed, and preserved in 45% isopropanol. During the analysis, fish were identified by numbered tag only so as to minimize any bias that might result from forehand knowledge of time of collection, etc.

For all three species, the simple, tubular gut, which is "stomachless" in the sense of Chao (1973), was excised, measured, and divided from front to back into three sections of equal length, here arbitrarily called the "fore-," "mid-," and "hindgut," respectively. Fullness of each section was scored subjectively from 1 (empty) to 5 (full and distended). Scores were plotted against time of day. Because fish were sampled throughout the year, their times of collection were seasonally adjusted relative to times of sunrise and sunset as listed in solar tables for the particular dates. Adjusted time of collection, rounded to the nearest 2-h interval, was measured on the relative scale with sunrise arbitrarily set at 0600 h and sunset at 1800 h.

Displayed under a dissecting scope, the contents of the foregut were sorted into broad taxonomic categories of food items, which were segregated in a small, partitioned tray. Then the percent volume of each item in the array was estimated by eye. Estimates were made quickly to the nearest percent, and their total over the array often exceeded 100% per fish. Yet at the outset, independent estimates of the same item did not vary substantially among successive trials, and series tended to regress toward a mean value (an observer's overestimation of volume on one trial was often countered by his underestimation of the same volume on the next). Item volumes were later standardized to 100%. In computing species means, fish with empty guts were not counted and all others were weighted equally, regardless of fish size or gut fullness (cf. Zaret and Rand 1971).

The frequency of occurrence of a dietary item was expressed as the percent of fish with nonempty foreguts that contained the item. The rank order of item frequencies was highly correlated with that of volumes. Kendall's tau correlation coefficients for the kelp perch, white seaperch, and señorita were 0.51, 0.85, and 0.70, respectively ($P<0.01$).

Activity

In the field, feeding bites made by individuals of each species were counted in six, 2-h intervals between dawn and dusk. Standardized as bites per minute, these counts were necessarily limited to solitary individuals that could be followed by a scuba diver for periods of about 3 to 5 min. It was impossible, for example, to discern the very rapid movements of señoritas feeding in large aggregates, which often formed during the early morning hours. The species value for each 2-h interval is the mean of 13-37 observations, each of a different fish. All counts were made during the first week of October, 1974.

To supplement field observations, swimming movements of individuals were observed in an outdoor tank. Fish were caught live either by hook and line during the day or by hand net underwater at night and transported in aerated containers to a 1-m-deep, 500-gallon, circular concrete tank at the University of California Santa Barbara Marine Laboratory. The tank was located outdoors under a lath roof and so was exposed to a natural, but subdued, 24-h cycle of light and dark. To eliminate visual disturbance, a black opaque plastic shroud perforated with several small peep holes was erected around the sides of the tank. Two, 10-W incandescent red lights, placed 1.5 m above the waterline, provided continuous dim light, especially useful for nocturnal observations. The temperature of the continuously running, filtered seawater, which varied no more than 3°C during

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

any 24-h experimental trial, probably approximated that encountered naturally by the species in nearby shallow inshore waters.

A grid of 10-cm squares was painted on the tank bottom, so that the activity of a fish could be measured as the number of grid lines it crossed during 5-min sample periods, one for each of twelve 2-h intervals (cf. Bortone 1971). On the bottom of the tank were arranged small patches of concrete blocks, rubble, freshly cut kelp, and sand to simulate a natural reef area as much as possible. After each fish had acclimated for a day, it was observed from a platform directly overhead or through the peep holes in the plastic shroud.

Habitat

Habitat occurrences of the three species were determined from previous observations of 414, 2.5-min Super-8 mm underwater movie strips in color (cinetransects) filmed by scuba divers. Cinetransects were made between 1000 and 1500 h during all seasons of 1969-70 and during the fall of 1971 and 1972 in a variety of kelp-bed habitats off the Santa Barbara mainland and Santa Cruz Island (Ebeling, Larson, and Alevizon in prep.). Each cinetransect recorded most fish in a 5-m wide path through or over a particular habitat type and so was classified into scored categories of bottom relief, kelp density, density of low algae on the bottom, and position in the water column ("canopy" or near the bottom). ("Kelp" herein refers to the giant kelp *Macrocystis*; "algae" refers to smaller plants other than giant kelp; and "canopy" refers to the zone of the upper spreading layer of the kelp bed—in our study, within 3 m of the surface.) Fish were tabulated by species as the film was projected in slow motion, reverse, and stop action. Later the frequency of occurrence of each species among all cinetransects was recorded for every habitat parameter.

Concordance, Breadth, and Overlap

For each species, dietary arrays were compared among four "seasons" that correspond roughly to different hydrographic periods off Santa Barbara (cf. Brown 1974): December-February, March-May, June-August, and September-November. Kendall's W coefficient of concordance (Tate and Clelland 1957) was used to measure differences in rank orders of volumes of food items pooled by season. To estimate dietary variability among individuals, concordance was also calculated for each of five or six samples of four to nine fish that were speared at the same general time and place. Thus we assumed that food items must have been about equally available to all the fish in a particular sample.

Breadth and overlap of resource use were computed from values of p_i, the proportion of item i in the sample (fish), or pooled sample of fish (species). For food breadth, p_i is the proportionate volume of any of the species total (S) of different food items; for activity breadth, it is for any of six 2-h daytime intervals, either the proportionate number of bites per minutes by fish in the field or the proportionate number of grid-line crossing per 5-min period by fish in a tank; and for habitat breadth, it is the proportionate occurrence of a species in any of 12 scored categories of habitat: 5 each of kelp density and bottom relief and 2 of depth. Sample values derive only from those resources or activities for which an entire array of items are observable for individual fish, i.e., from food and swimming activity only. Only the habitat parameters that seemed to be mutually independent were included in the analysis. "Density of low algae on the bottom," which was highly correlated with "bottom relief," was excluded. Yet "kelp density" was included. In the study area off Santa Barbara, kelp density is more or less independent of bottom relief because here kelp can anchor to flat as well as high relief bottoms. Because cinetransects were not evenly distributed among habitat categories—most films were taken in relatively dense kelp and high reef—the proportionate frequencies were standardized by total films taken per category.

The sum of p_i^2 over S items in the array equals the probability that any two units selected at random will be of the same item (see Simpson 1949). Thus, the reciprocal, $B = 1/\sum_{i=1}^{S} p_i^2$, measures breadth or diversity (Levins 1968; MacArthur 1972). Or, B is the theoretical number of equally used resources. For example, if all items are in equal proportions, B equals the total items in the array, S. It follows that the value of S determines the maximum value of B. B was computed for fish (individuals within a species) and for pooled sets of fish (individuals pooled by species) as unscaled values and as scaled values. The unscaled values incorporate two contributions to breadth: that of richness (S), and that of evenness of the distribution of amounts among the S items or classes. Values are scaled as B/S between zero, the most uneven distribution possible among S items, and unity, the most even possible.

Proportionate overlap of resource use may be thought of as a measure of mutual use by two species of the same items. The coefficient used here measures overlap between species j and k (Horn 1966):

$$C_\lambda = \frac{2\left(\sum_{i=1}^{S} P_{ij}P_{ik}\right)}{\sum_{i=1}^{S} P_{ij}^2 + \sum_{i=1}^{S} P_{ik}^2}$$

Among the three possible species pairs, activity overlap calculated from field observations of feeding rate varied in the same manner as activity overlap calculated from laboratory observations of swimming rate. For the subsequent calculation of total overlap in food, activity, and habitat, therefore, we used the arithmetic mean of these two independent estimates to express a single activity component.

Two estimates were made of total overlap. If, e.g., food and habitat are mutually independent, i.e., the same foods are available in the same proportions in different habitats, overlap between any species pair is the product of the separate measures for food and habitat. But if food is completely dependent on habitat, i.e., different habitats contain totally different foods, then overlap is the arithmetic mean of the two measures (Pianka 1974). (In the latter case, food and habitat measure the same resource axis, and the separate measures can be thought of as independent estimates of the same overlap.) In general, the actual relation between resource distributions is somewhere between complete independence and dependence. Thus, total overlap as expressed by the mean of the separate overlaps in food, activity, and habitat is a maximum value, and true overlap is somewhere between this and the product estimate (see Pianka 1974).

Kolmogorov-Smirnov tests of goodness-of-fit showed that the distributions of the variates of food breadth (s, b, b/s) differed significantly from normal (were skewed) for the white seaperch and señorita (P = 0.05-0.01), though not for the kelp perch (P>0.05). Therefore, we computed medians, ranges, and the Kruskal-Wallis measure H of differences in location of the ranked variates to test for differences among the three species (see Sokal and Rohlf 1969).

RESULTS

Food

Seasonal Effect

Food arrays were generally correlated among seasons. The rank concordance of diets was significant for all species (Table 1). The same items, which often made up more than 70% of the total food volume, usually occupied one or another of the first three ranks from one season to the next; seldom did the first three positions for any one season contain items not among the first three for the others. Consequently, all samples were pooled by species, regardless of season, for the remaining analyses.

Individual Variability

Food items were generally uncorrelated among fish of the same species collected at the same time and place. Rank concordance was significant for but one of five collections of kelp perch (W = 0.55, P<0.01), and for no collection of white seaperch or señoritas. This might indicate that members of the same species that co-occur were choosing different items from the same forage base. But such a conclusion may be misleading for white seaperch and señoritas. A single item (plant-encrusting bryozoans) usually dominated their foregut contents, and although the second and third ranked items varied considerably among fish, they made up but a minor part of the total.

Kelp Perch

Tiny plankters, mainly copepods, made up more than half of the food consumed by the kelp perch (Table 2). Of 18 categories of items eaten by kelp perch, small calanoid and cyclopoid copepods led in both abundance and frequency; foreguts of six fish contained copepods only, and one was packed with more than 300 individuals. The distinctive genus *Corycaeus* occasionally dominated the contents. Large calanoids longer than 4 mm, which were found in fish collected during late winter only, were relatively rare. Tiny ostracods were frequently consumed, but only in small numbers.

TABLE 1.—Among-season comparison of diets of the three fishes. The first three ranking food items with their percent volume are listed in order for each period. Sample size is the number of diets (fish) pooled per period; W is Kendall's coefficient of rank correlation.

Species	December-February Item	%	March-May Item	%	June-August Item	%	September-November Item	%	W
Kelp perch	Sample size = 19		Sample size = 0		Sample size = 12		Sample size = 19		
18 total items	Small copepods	50			Gammarid ampnipods	67	Small copepods	42	0.51*
	Plant-encrusting bryozoans	12			Small copepods	14	Gammarid amphipods	26	
	Large copepods	10			Caprellid amphipods	13	Plant-encrusting bryozoans	6	
White seaperch	Sample size = 4		Sample size = 24		Sample size = 9		Sample size = 18		
13 total items	Plant-encrusting bryozoans	92	Plant-encrusting bryozoans	42	Plant-encrusting bryozoans	45	Plant-encrusting bryozoans	51	0.48*
	Bare plants	5	Bare plants	18	Polychaete worms	25	Crushed shells	28	
	Gammarid amphipods	1.5	Gammarid amphipods	11	Gammarid amphipods	6	Gammarid amphipods	12	
Señorita	Sample size = 0		Sample size = 17		Sample size = 17		Sample size = 19		
19 total items			Plant-encrusting bryozoans	35	Plant-encrusting bryozoans	65	Plant-encrusting bryozoans	86	
			Gammarid amphipods	11	Serpulid worms	10	Hydroids	5	0.39*
			Hydroids	9	Parasitic copepods	7	Parasitic copepods	3.5	

*Significant at $P < 0.01$

TABLE 2.—Mean proportionate volume and percent frequency of occurrence of 25 food items in foreguts of 50 kelp perch, 55 white seaperch, and 53 señoritas. Food items are listed by their presumed major source.

Food item	Kelp perch % vol	Kelp perch % freq.	White seaperch % vol	White seaperch % freq.	Señorita % vol	Señorita % freq.
Primarily planktonic	51.6	—	—	—	7.0	—
Cladocerans	0.5	18.8	—	—	—	—
Ostracods	1.1	20.8	—	—	1.1	13.7
Small copepods (<4 mm)	42.0	81.2	—	—	1.5	15.7
Large copepods (>4 mm)	3.3	18.8	—	—	2.7	11.8
Nauplius larvae	0.2	2.1	—	—	—	—
Zoea larvae	4.3	18.8	—	—	1.7	11.8
Fish eggs	0.2	2.1	—	—	—	—
From process of "cleaning"	2.9	—	—	—	5.4	—
Parasitic copepods	1.4	22.9	—	—	3.5	11.8
Gnathiid isopod larvae	1.4	2.1	—	—	0.2	3.9
Fish scales	0.1	6.2	—	—	1.7	7.8
Primarily substrate oriented: kelp, other algae, and bottom	45.0	—	81.8	—	87.1	—
Free moving	36.2	—	18.1	—	9.7	—
Mysids (kelp)	4.1	18.8	—	—	0.4	7.8
Isopods	0.7	10.4	1.9	9.8	1.3	7.8
Gammarid amphipods	25.7	62.5	8.4	49.0	4.2	27.4
Caprellid amphipods	4.7	12.5	3.3	23.5	2.2	5.9
Decapod shrimps	1.0	8.3	3.2	5.8	0.4	5.9
Unident. crustaceans	—	—	—	—	1.2	5.9
Pycnogonids	—	—	1.3	5.8	—	—
Attached	9.0	—	63.7	—	77.4	—
Bare kelp and other algae	1.5	12.5	0.3	1.9	5.6	15.7
Plant-encrusting bryozoans	7.3	10.4	63.4	63.4	65.5	80.4
Hydroids	0.2	2.1	—	—	5.2	17.6
Serpulid worms	—	—	—	—	1.1	2.0
Primarily substrate oriented: bottom only	—	—	17.7	—	0.2	—
Crushed shells and debris	—	—	12.6	27.4	—	—
Polychaete worms	—	—	3.7	5.8	0.2	2.0
Cumaceans	—	—	0.5	3.9	—	—
Brittle stars	—	—	0.9	1.9	—	—

Small crustaceans that normally move freely on and about the kelp surfaces were almost equal to plankton in dietary importance. Gammarid amphipods, which may cluster just as abundantly about the kelp as in and about the tufted mat of plants and animals on the bottom, ranked second in overall abundance and frequency. Surprisingly unimportant were the so-called "kelp mysids," which are very abundant in the canopy and are commonly eaten by other fishes (Clarke 1971).

Forage on attached organisms was less important. Cheilostomate bryozoans, principally *Membranipora* ("plant-encrusting bryozoans"), ranked a distant third in overall volume. *Membranipora* is the dominant bryozoan encrusting kelp, where it often covers large areas of the plant (Woollacott and North 1971), and most of the bryozoans in the gut contents were associated with bits of kelp blades. Kelp perch apparently ate no benthic prey.

Cleaning activity was but a minor food source. Parasitic copepods, gnathiid isopod larvae, and fish scales were the only items likely to have been ingested in the process. The combined items never contributed more than 5% to the foregut food volume in a single fish.

White Seaperch

Virtually all prey of the white seaperch were substrate oriented, probably picked from off the kelp or bottom (Table 2). Plant-encrusting bryozoans predominated, and when present, averaged 85% of the foregut contents of individual fish. Moving prey, primarily amphipods and shrimps, were much less important. Many of the gammarid amphipods were quite small (<2 mm long); in one fish, e.g., all of 70 individuals did not fill the foregut.

Only the white seaperch ingested appreciable amounts of bottom items. Crushed shells and sand particles, which often were cemented into tubes, ranked second in overall abundance and third in frequency. The remains of polychaete worms were found in but 3 of 14 sand-containing guts, which did, however, include substantial numbers of the gammarids that commonly inhabit such burrows in the tufted mat on the bottom. Relatively large amounts of loose sand in the mid- and hindguts indicated that these fish generally do not winnow non-food items in their mouth.

Señorita

Most of its prey was substrate oriented, probably picked from off the kelp (Table 2). Like white seaperch, señoritas contained a predominance of plant-encrusting bryozoans, but unlike perch, had almost no bottom prey in the foregut. A third of all fish examined contained only the bryozoan *Membranipora* encrusted on pieces of kelp, and bits of bare plant material were found frequently among the encrusted pieces; of a total of 18 categories of food items found in señorita guts, no other so dominated the contents of even a single fish. Hydroids, another item attached to plants and other substrates, ranked third in overall importance. Moving prey, primarily amphipods, were less important.

Unlike kelp perch, señoritas did not exploit plankton as a major source of food. Although some items occurred frequently, they contributed but little to the overall volume.

Cleaning activity did not produce substantial forage, although it contributed relatively more to the diet of señoritas than to that of kelp perch. Of 10 adult señoritas, 142-184 mm long, that contained items likely to have been ingested during cleaning (parasitic copepods, gnathiid isopod larvae, and/or fish scales), the diets of seven were dominated by other food items. Ectoparasites and scales in guts of most señoritas were mixed with other food items, suggesting that the fish had both cleaned and foraged during the same day. However, guts of two of the remaining three fish contained nothing but parasitic copepods and scales. One specimen, collected at 1400 h, contained 465 fish scales, about 90% of the total contents, and 45 parasitic copepods. Both items were distributed more or less evenly throughout the length of the gut, indicating that this fish had cleaned during most of the day.

Diel Forage

All three species fed mostly, if not exclusively, during the day. Foreguts of kelp perch apparently were beginning to fill soon after dawn, were generally full by midmorning, and contained variable amounts of food through dusk (Figure 1). Of 54 day and 38 late-night (midnight-dawn) foreguts examined, 89% and 13%, respectively, contained food. Guts of white seaperch seemed to reach maximum fullness during midmorning and late afternoon. Of 64 day and 22 late-night foreguts examined, 88% and 4%, respectively, contained food. Fullness of mid- and hindguts of both species generally substantiated this daily cycle of feeding (Figure 2). Most foreguts were empty by midnight, when midguts still averaged at least half full and hindguts usually more. Then, by dawn most hindguts were empty, while foreguts were beginning to fill, a general pattern shown by fish whether collected during moonlit or dark nights. Señoritas seemed to feed actively through early afternoon, showing maximum gut fullness about

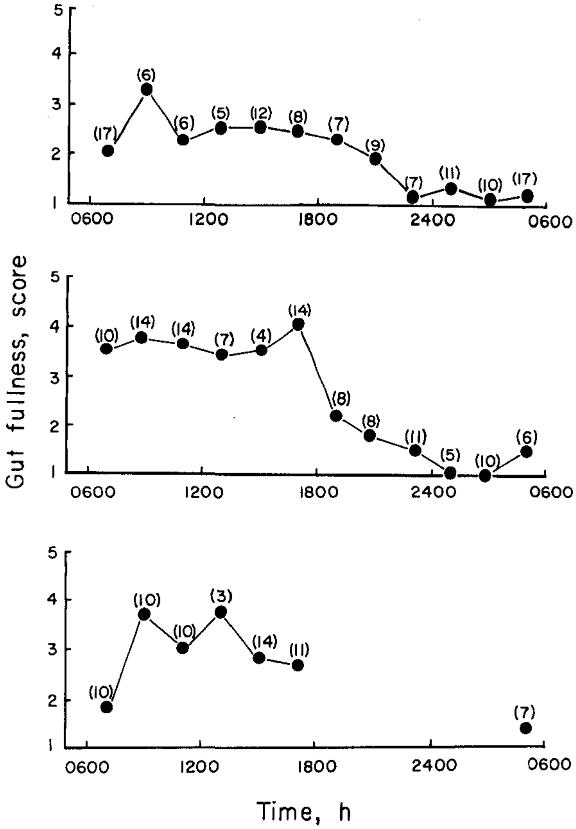

FIGURE 1.–Scored fullness (1, empty - 5, full) of foreguts of: top, kelp perch; middle, white seaperch; and bottom, señorita (which buries itself at night). Each point represents the mean value for (n) individuals collected over a 2-h interval. Time is measured relative to sunrise (0600 h) and sunset (1800 h–see text).

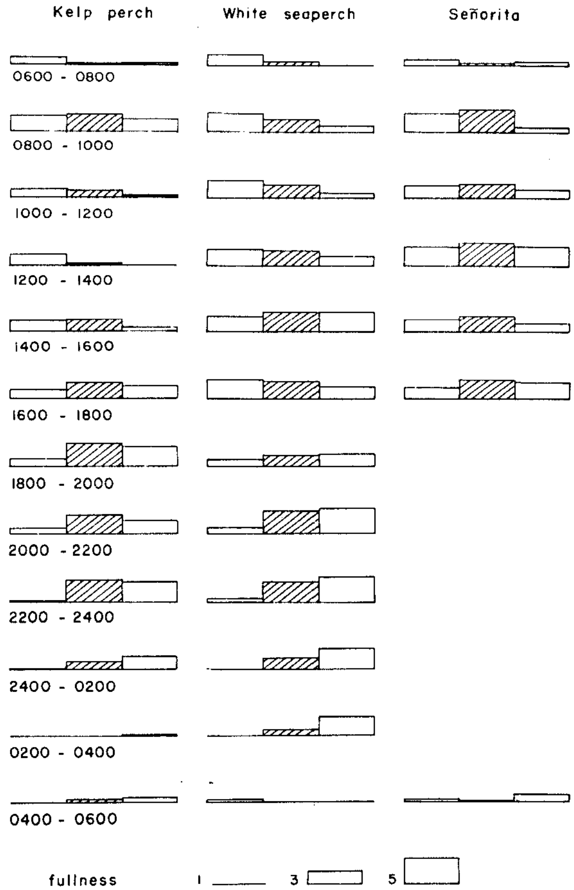

FIGURE 2.–Scored fullness of: foreguts (left open bars), midguts (middle hatched bars), and hindguts (right open bars) for the three fishes over 2-h intervals, beginning at dawn. Heights of the bars, scaled at the bottom of the figure, represent mean scores for the numbers of individuals indicated in Figure 1.

midday. Of 65 diurnal foreguts examined, 78% contained food. At night the fish bury themselves in soft areas of bottom (see next section). However, six of seven guts of fish collected at dawn were completely empty.

The duration of passage of food through the guts of the two perches was estimated from their diel feeding cycles. Assuming that feeding stops at dusk when almost half the foreguts were full or nearly so, and that almost all hindguts have emptied by dawn when almost all were, the retention time is probably no more than 10-12 h.

Activity

Feeding Rate

Field observations of feeding bites indicated that kelp perch fed frequently, at a maximum average rate of 20 bites/min around midday, decreasing to zero toward sunset (Figure 3). White seaperch and solitary señoritas fed much more slowly, at maximum rates of only 3.0 and 1.0 bites/min, respectively. Whereas both perches were seen feeding actively throughout the day, señoritas seemed to feed much less intensely after midafternoon. None of the particular individuals followed during the last two daytime intervals were seen to bite. During this time, however, a few other fish were observed picking away at bits of kelp. But this does not modify our general impression that, during the late afternoon hours, most señoritas feed much less actively than earlier in the day.

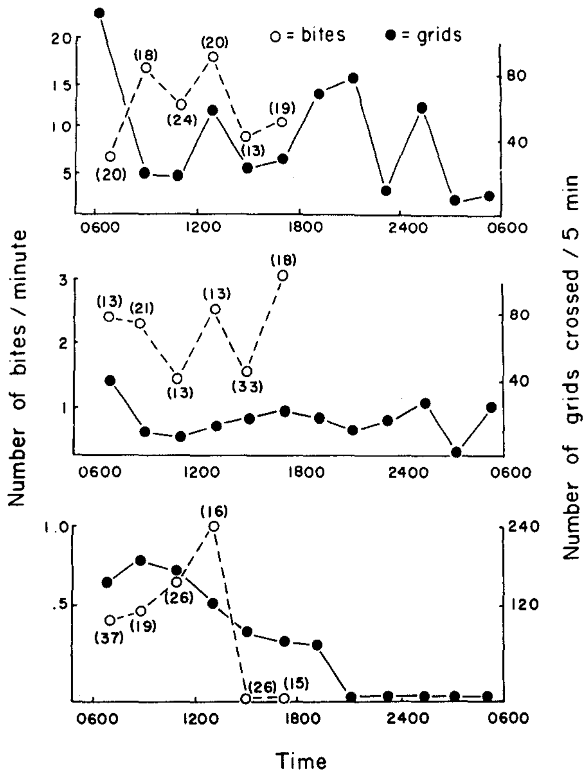

FIGURE 3.—Feeding and swimming activity of: top, kelp perch; middle, white seaperch; and bottom, señorita. Open circles are feeding rates observed in the field and standardized as bites per minute (fish do not feed at night); solid circles are swimming rates observed in a laboratory tank and measured as grid-line crossings per 5-min period. Each point represents the mean value for (n) individuals (feeding rates) or five or six individuals (swimming rates) observed for a 2-h interval.

Swimming Rate

Showing little if any spatial or temporal pattern, the two perches swam sporadically throughout the experimental tank during the day and night (Figure 3). Kelp perch swam in spurts and were slightly more active during the day than at night; white seaperch were most active at dawn; and neither species showed any marked change at dusk. The apparent increase in kelp-perch activity at dawn reflected intense swimming by one individual, whose exclusion from the sum would lower the mean species rate to 38 grid-line crossings per 5-min period, about the same as for white seaperch.

In the field during the day, white seaperch swam more continuously in mid-water and near the bottom than did kelp perch, which tended to hover camouflaged among the kelp canopy and only occasionally darted in and out. At night, white seaperch were occasionally seen drifting slowly in mid-water or over the bottom, while kelp perch tended to hang motionlessly among the kelp stipes or even in open water. Kelp perch, especially, were quiescent at night and easily caught with a small hand net then.

Señoritas swam most actively during the morning, then progressively slower throughout the day before finally burying themselves in the sand for the night (Figure 3). Beginning 20 min before sunset during one 24-h trial, a fish that was observed continuously first swam actively throughout the tank, then more restrictively over the sandy area. Finally after swimming in smaller circles about 4-6 cm off the bottom, it turned on its side and, with a few flicks of its caudal fin, proceeded head first into the sand. This entire episode lasted about 10 min, after which the area became dark. Observations by flashlight showed that the fish had buried itself completely, as had three others that accompanied the fish during the trial. Beginning 5 min after sunrise, the four fish emerged within 12 min. Two first stuck their heads above the sand to expose their pectoral fins, then after a short pause, swam out and milled about in small circles. The second pair emerged in a single movement to join the others in a small school, which soon moved throughout the tank. Of the total of seven fish observed in two trials, all buried themselves but one, which lay motionlessly against some bricks and assumed a mottled color pattern.

In the field, three fish observed on separate occasions over a reef about 10 m deep showed settling and burying behavior like that of the experimental animals, although they did not leave to seek a surrounding area of sand flat. Instead, they left a loose aggregation of fish before dusk to remain near the rocky substrate. They gradually restricted their spheres of activity to a small circular area above depressions filled with coarse sand and rubble. Just before sunset when visibility had decreased to about 3 m, the fish became hypersensitive to a diver's light and would dart away quickly when illuminated. About 15 min after sunset, the fish buried themselves in the depressions, first rolling on their sides and then swimming headfirst into the loose substrate. Gentle excavations caused the fish, which were probably buried within the upper 8 cm, to flee quickly. In more than 150 h of scuba diving at night, we have never seen an exposed señorita either over the reef or the surrounding sand flats.

Habitat

Kelp perch were mostly restricted to the canopy, whereas señoritas were more evenly distributed in the water column (Table 3). The kelp perch, whose frequency of occurrence was highly correlated with kelp density, seemed to require the close presence of kelp and was most abundant in the thick of the canopy far above relatively flat bottom areas. Although most frequently filmed in or near the canopy, señoritas ranged throughout the kelp beds and over relatively naked areas of reef. They were recorded from 48% of all cinetransects, as compared to but 26% for kelp perch.

White seaperch were more bottom-oriented than the others, even though they were occasionally seen schooling in mid-water and singly in the canopy. The occurred most frequently in cinetransects taken over areas of sparse kelp and flat bottom at the margins of reefs and kelp beds, but large numbers have also been seen sporadically in areas of highest reef and densest kelp. The cinetransects were limited to areas of reef and kelp and the immediate environs and did not cover the white seaperch's relatively broad range of habitats. Although the kelp perch and señorita are more or less restricted to the habitats covered by the cinetransects, the white seaperch ranges far afield throughout the marginal sandy areas to bays and submerged artifacts, such as piers and docks. Its frequency of occurrence among cinetransects, 10%, was by far the lowest of the three species.

Resource Breadth

Food

Both as a species and as individuals, the kelp perch had the greatest food breadth (Table 4, B,b). The kelp perch ate more items (S) than the white seaperch, though amounts were about equally even in distribution (B/S). The señorita actually ate the most items, but in variable and often small amounts. Although the median number of items in individual foreguts (s) was the same for all three species, division between one- and multi-item

TABLE 3.—Distributions of the three fishes among scored categories of four habitat parameters. Parameters of kelp density and density of bottom algae are scored from 1 (absent) to 5 (very dense); bottom relief from 1 (flat) to 5 (high relief rock); and position in water column as C, the canopy within about 2-3 m of the surface, or B, the bottom and immediately overlying waters. Frequency is given as the actual percent (given as whole percent) of total cinetransects scored in the particular category, and as the percent standardized (given as 0.1%) by the total films in each category (see text).

		Kelp density					Bottom relief					Density of bottom algae					Position in water column	
Species	Frequency	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	C	B
Kelp perch	Actual	0	10	15	36	42	52	20	32	4	17	44	27	18	13	14	61	6
	Standardized	0	10.4	14.9	34.3	40.3	40.7	16.2	25.7	3.4	13.4	37.7	23.4	15.4	11.4	12.0	90.8	9.2
White seaperch	Actual	18	9	8	5	11	34	11	7	2	3	22	12	6	1	5	16	1
	Standardized	34.8	17.4	15.9	10.1	21.7	57.0	20.2	12.7	5.1	5.1	45.8	26.4	13.9	2.8	11.1	32.5	67.5
Señorita	Actual	37	48	50	52	34	40	40	53	55	35	33	48	49	32	45	54	45
	Standardized	17.0	21.6	22.6	23.3	15.5	18.2	17.9	23.6	24.3	15.9	15.8	23.2	23.5	15.8	21.9	54.4	45.6
No. of cinetransects per category		16	120	127	125	26	44	59	88	69	131	27	127	148	73	35	154	259

TABLE 4.—Food breadths of the three fishes. The text defines the measure B of resource breadth. S is the number of food items; B/S measures the evenness of distribution of proportionate amounts among the S items; medians and ranges (in parentheses) describe the individual (fish) variates; and the Kruskal-Wallis H statistic, distributed as chi-square with 2 df, tests for differences among species in the sample variates.

		Species (pooled) values			Individual (fish) values		
Species	Sample size	S	B	B/S	s	b	b/s
Kelp perch	50	18	4.57	0.25	2.0(1-6)	1.70(1.00-3.14)	0.74(0.34-1.00)
White seaperch	55	13	3.39	0.26	2.0(1-5)	1.00(1.00-2.41)	1.00(0.31-1.00)
Señorita	53	19	2.47	0.13	2.0(1-6)	1.22(1.00-4.84)	1.00(0.41-1.00)
				H	12.82*	13.65*	11.61*

*Significant at $P<0.005$

diets was most even in kelp perch. Distributions of all measures (s, b, b/s) did not differ significantly from normal for the kelp perch, but were strongly skewed for the others. In fact, median dietary evenness (b/s) equalled the maximum possible (1.0) for the others, because most foreguts contained either a single item or, occasionally, two items in equal amounts: 55% of the white seaperch and 47% of the señoritas had but a single item, as compared with only 24% of the kelp perch. Moreover, one-item diets of white seaperch and señoritas were more predictable in composition: 73% (of 30 foreguts) and 88% (of 25), respectively, contained the same item, plant-encrusting bryozoans. Other one-item foreguts of seaperch contained either plants (4 foreguts), shrimps (2), or polychaete worms (2). Other one-item foreguts of señoritas had either small copepods (1), gnathiid isopod larvae presumably from cleaning (1), or serpulid worms (1). The 12 one-item kelp-perch foreguts contained either small copepods (6), gammarid amphipods (4), bryozoans (1), or caprellid amphipods (1).

Activity

Activity breadths measured by feeding rates in the field (Table 5, B) correspond to breadths measured by swimming rates observed experimentally (Table 6, B), even though these two independent measures vary inversely among species. The señorita had the smallest feeding-rate breadth, because bites were observed over the fewest 2-h intervals (Table 5, S). From mid-afternoon on, the particular individuals followed during the test were not seen to bite, even though they swam actively about in the kelp canopy and below. (Recall that a few other individuals were feeding, but the general impression was of curtailment of feeding activity then.) Yet the señorita had the largest swimming-rate breadth because it swam actively and continuously during all six daytime intervals (Table 6, S). Thus both scaled measures (B/S) were relatively large for the señorita: the distribution of counts, whether of bites per minute or swimming movements per 5-min period, was relatively even among all intervals in which the action occurred (S). But it may be misleading to conclude that señoritas were then most consistent in their daytime feeding activity. During the first four daytime intervals when bites were observed for all species, 40-96% of the kelp perch and 46-69% of the white seaperch were recorded as biting. However, only 13-26% of the señoritas were so recorded. Therefore, señoritas show more variability in feeding activity; i.e., individuals may bite very rapidly for a few minutes then stop for extended periods. On the other hand, individual señoritas were the most consistent in their swimming activity. Señoritas led the others in breadth (b) and evenness (b/s), although the inter-species difference in b values was not significant (Table 6).

TABLE 5.–Activity breadths of the three fishes, as measured by their feeding bites per minute in the field. Sample size is the total fish observed in each species; S is the number of 2-h intervals (maximum of 6) in which fish were observed to make the biting motions. See Table 4 for further explanation (note that the nature of feeding-bite breadth precludes samples estimates).

Species	Sample size	S	B	B/S
Kelp perch	114	6	5.29	0.88
White seaperch	111	6	5.60	0.93
Señorita	139	4	3.62	0.91

Habitat

By all measures, the señorita had the greatest breadth of habitat within the area of reef and kelp where all three species co-occur (Table 7). The kelp perch, which was more or less restricted to the canopy, was most specialized in distribution.

Overlap

The white seaperch and señorita overlapped

TABLE 6.–Activity breadths of the three fishes, as measured by their daytime swimming movements in a large outdoor tank. S is the number of 2-h intervals (maximum of 6) in which fish swam across one or more grid lines during a 5-min observation period. See Table 4 for further explanation.

		Species (pooled) values			Individual (fish) values		
Species	Sample size	S	B	B/S	s	b	b/s
Kelp perch	6	6	4.19	0.70	6.0(2-6)	2.47(1.16-4.63)	0.52(0.29-0.77)
White seaperch	5	6	4.59	0.76	6.0	3.47(2.09-4.85)	0.59(0.35-0.81)
Señorita	6	6	5.53	0.92	5.0(2-6)	4.41(1.95-5.82)	0.96(0.87-1.00)
				H	3.52(NS)	2.39(NS)	11.23*

*Significant at $P<0.005$

TABLE 7.—Habitat breadths of the three fishes, measured relative to kelp-density, bottom-relief, and position-in-water-column classifications of the cinetransects (see text and Table 2). Sample size is the number of cinetransects from which the species was recorded; S is the number of habitat categories (maximum of 12) in which fish were photographed. See Table 4 for further explanation (note that the nature of habitat breadth precludes sample estimates).

Species	Sample size	S	B	B/S
Kelp perch	109	11	6.32	0.57
White seaperch	42	12	7.61	0.63
Señorita	201	12	9.84	0.82

most in total resource use, with food the main contributor (Table 8). Yet their large food overlap was caused not by any overall similarity in dietary arrays, but by their sharing one predominating item, the plant-encrusting bryozoans. In fact, rank orders of their food items were not significantly correlated (tau = 0.20, P = 0.16).

The kelp perch had the least amount of total overlap with others. Sharing the kelp-canopy area to a great extent, the kelp perch and señorita overlapped most in habitat even though the señorita had the broader overall spatial distribution within the kelp bed. Also, the two species' small food overlap and different activity patterns tended to minimize their total overlap. Actually, rank orders of their food items were significantly correlated (tau = 0.50, P<0.001), because the two species shared similar proportions of a number of minor items. Yet overlap was small because they did not share the same predominating item. A low amount of overlap in total resource use was shown by the two perches. Although their activity patterns were similar, their diets and habitat preferences differed markedly. In diet, they shared neither a predominating food item nor an array of minor items, and rank orders of their items were uncorrelated (tau = 0.06).

DISCUSSION

The kelp perch and señorita—the two species most often involved in cleaning activity—co-occur to a great extent in the sunlit upper waters and eat few if any benthic prey. Kelp perch typically feed in loose aggregations of a few to over 30 individuals. Constantly changing direction and depth, feeding individuals flit about to pick particles from mid-water or, occasionally, from the surfaces of kelp and from other fishes. In calm, clear water, these aggregations often extend to the more open areas between kelp plants. In strong currents, however, the fishes gather in back of kelp columns where the water is quieter and where food swept off the surfaces of kelp may be consumed. Solitary señoritas occasionally nip at various substrates and large drifting particles, but they feed most intensely when in large schools. These schools move in and about kelp stands, momentarily dispersing for individuals to pick and tear at kelp fronds and encrustations, then re-assembling and moving on to another stand of kelp.

The habit of kelp perch and señoritas of cleaning other mid-water fishes probably is incidental to the co-occurrence of the two species in the kelp canopy. Cleaning is not the principal occupation of either species (Limbaugh 1961, Hobson 1971). Their presence in the canopy better relates to their ability to pick small prey from off and from about the kelp blades. Seldom straying far from the heavy foliage where prey may become densely concentrated (Wing and Clendenning 1971), kelp perch also select plankton from incoming currents. Like other diurnal planktivores (Hobson 1974), the kelp perch has a relatively slender body, deeply forked caudal fin, and a slightly upturned mouth (Hobson 1971). Señoritas, which range more widely in the water column from canopy to near bottom, eat much less plankton. They favor attached food, primarily plant-encrusting bryozoans, either from the drift or torn from living plants.

White seaperch, which usually range nearer the bottom and only clean occasionally (Hobson 1971),

TABLE 8.—Overlap in resource use between members of all pairs of the three fishes. Activity overlap is the mean of two independent estimates: from feeding bites observed in the field, and from swimming movements observed in the laboratory. Habitat overlap is measured relative to kelp-density, bottom-relief, and depth classifications of the cinetransects (see Table 3). Total overlap is somewhere between the minimum and maximum estimates.

Overlap between:	Food F	Activity: Feeding bites T	Activity: Swimming movements M	Activity: Activity $A=(T+M)/2$	Habitat H	Total overlap: Minimum FAH	Total overlap: Maximum $(F+A+H)/3$
Kelp perch and white seaperch	0.25	0.92	0.95	0.94	0.63	0.15	0.16
Kelp perch and señorita	0.21	0.85	0.79	0.82	0.79	0.14	0.61
White seaperch and señorita	0.92	0.72	0.78	0.74	0.74	0.50	0.80

show more generalized behavior and are less specialized for picking than either kelp perch or señoritas. Like señoritas, white seaperch ate mostly plant-encrusting bryozoans, but their foraging behavior is quite different. White seaperch typically feed alone or in very small and loose aggregations. Feeding individuals often hover head down within 1 m of the substrate and, judging from their eye movements, search carefully for food. Even so, the substantial amounts of sand and other debris mingled with the more select items in white seaperch guts indicate that once the fish find their sedentary bottom prey, they engulf it in relatively large and indiscriminate mouthfuls.

Underwater disturbances attract white seaperch and señoritas. For example, the two fishes commonly aggregate and feed where bat ray, *Myliobatis californica*, are stirring up the bottom with their wings. They are also quick to follow and assemble about actively working scuba divers. This seems to be an adaptation to forage opportunistically in the wake and disturbance left by others, a strategy which is commonly used by tropical wrasses (Hobson 1974). In contrast, the kelp perch appears to be much less aware of such disturbances and often seems oblivious of an observer at close range.

Indirect evidence suggests that the plant material ingested with the bryozoans is not a primarily source of food for the fish. Only 10% of the ingested material was bare of bryozoans, indicating that white seaperch and señoritas select the heavily encrusted bits. Also, their relative gut lengths are less than expected for herbivores and many omnivores. Odum (1970) noted that the ratio of gut to fish length is usually less than unity in carnivores, one to three in omnivores, and greater than three in herbivores. Mean ratios from 74 white seaperch and 65 señoritas are only 0.82 + 0.028 (95% confidence interval) and 0.75 ± 0.036, respectively. They do not differ significantly from the mean ratio of 0.76 ± 0.024 from 95 kelp perch, which ingest comparatively little plant material. Likewise, Chao (1973) found no evidence that the cunner, *Tautogolabrus adspersus*, a temperate labrid from off the Atlantic Coast, assimilates the algae it ingests. Small undigested amounts from the intestine of the cunner are usually associated with digested epiphytic animals, including bryozoans. Primarily a shellfish eater, the cunner also has a gut ratio that is less than unity.

Individual diets of kelp perch and señoritas vary considerably from fish to fish, but this is not likely attributable to facultative cleaning. Diets of white seaperch, which do not commonly clean, were no more concordant than those of the other two species. Instead, opportunistic feeding in general may account for most of the variability. Kelp perch may switch from one patch of plankton to another, or feed on the kelp surface as the opportunity arises. Individuals were seen to dart back and forth between open areas and the kelp surface, selecting prey from either source. Although most señoritas eat large amounts of bryozoans, many select small crustaceans, especially amphipods. Hobson (1971) noted that señoritas not only eat mid-water plankton, but are occasionally seen picking about on the bottom. We observed that they are usually among the first to arrive at underwater chumming stations where sea urchins are broken open.

Yet cleaning contributes to the food breadth of kelp perch and señoritas by adding items that can be taken only by that process. And this points out a major problem in measuring food breadth by the "richness" or number-of-items measure, S. The categories of food items cannot be defined objectively, from the fish's point of view at least. For example, the total number of items recorded for the white seaperch would obviously increase if we further diversified the benthic categories (which are not exploited by the cleaners) by—say—distinguishing gastropods from bivalves within the category of "crushed shells." Even though cleaning increases S, its total nutritional importance to the cleaner species may be negligible.

Likewise, it is difficult to conclude whether or not cleaners have specialized diets. The total items eaten by either cleaner exceeded that eaten by the supposedly more generalized white seaperch, and the unscaled food breadth of the kelp perch was greatest of all three species. But the kelp perch and, to a lesser extent, the señorita are in fact limited to smaller items because they have smaller mouths. The 25 subjectively determined food categories included some 15 "small items" (usually <3 mm in diameter) but only 10 "large" (usually >3 mm). Therefore, the diet of the kelp perch appeared to be relatively broad because it includes all of the small items, several of which are exclusively planktonic. On the other hand, the diet of the white seaperch, which rarely visits the canopy, appeared to be more narrow because it includes relatively few of these small prey. Yet having a larger mouth, the white seaperch may eat not only small items, but also an array of items too large to be ingested by the other two.

Other studies indicate that white seaperch forage opportunistically in a relatively broad range of kelp-bed and adjacent habitats. Although plant-encrusting bryozoans were by far their major food in the Santa Barbara areas of kelp and reef, they were of minor importance in fish collected off San Diego. Quast (1968b) reported that 18 fish from a kelp bed contained mostly small crustaceans, worms, and bivalves, while Hobson (1971) noted that 5 fish from shallow areas of surf grass contained small crustaceans, especially caprellid amphipods. DeMartini (1969) concluded that the white seaperch is almost "cosmopolitan" among habitats, including bays and artifacts far from the kelp beds. He observed that, unlike the kelp perch, it has uniformly broad and densely set pharyngeal teeth and commonly eats large, hard-shelled items like barnacles and clams.

Although the kelp perch and señorita have superficially similar feeding mechanisms, they do not overlap broadly in their diets. Off Santa Barbara, in fact, food overlap is least between señorita and kelp perch and greatest between señorita and white seaperch, whose mouth structure and dentition are more generalized. These relations prevail because the kelp perch does not eat substantial amounts of the plant-encrusting bryozoans, the overwhelmingly predominate food item of the other two. Disregarding bryozoans, the remaining (minor) food array of the señorita actually resembles more closely that of the kelp perch than that of the white seaperch. Likewise, off San Diego, kelp perch favor copepods and gammarid amphipods (Quast 1968b), and señoritas favor bryozoans (Quast 1968b; Hobson 1971) but may eat a variety of small crustaceans associated with giant kelp as well (Limbaugh 1955).

Because food overlap between the two cleaners is effectively small, they may co-occur with minimal mutual interference, even though their habitat overlap in the upper kelp bed is relatively broad. Also, their daytime activity patterns differ noticeably. Whereas kelp perch dart sporadically among the kelp blades and seem to feed almost continuously, señoritas move continuously about in open water as well as in dense kelp and seem to feed more sporadically. Also, solitary kelp perch continue their rapid picking about well past mid-afternoon after señoritas were observed to curtail their feeding activity.

It would seem that the señorita and white seaperch are greater potential competitors because they overlap almost completely in both food and habitat within the kelp-bed area. But even so, it is doubtful that availability of their principal food, bryozoans, is a limiting factor in the Santa Barbara area, where encrustations are widespread over the kelp and other substrates. Furthermore, the frequency of occurrence of white seaperch within the kelp bed is quite low compared to that of the señorita. Even though fairly large aggregations are seen occasionally over the reef, the center of abundance of white seaperch may be in more peripheral areas where alternative prey are readily available.

The señorita, which belongs to the large tropical family of wrasses, is more specialized in diel behavior than are the kelp perch and white seaperch. Whereas at night the perches simply slow down and become less responsive, the señorita buries itself in pockets of sand or gravel on the reef. Wrasses in general are strickly diurnal: they seek cover and become quiescent at night, as has been observed for tropical species (Hobson 1965, 1968, 1972, 1974; Stark and Davis 1966; Collette and Talbot 1972; Smith and Tyler 1972) and for other temperate species (Chao 1973; Olla et al. 1975). Various species hide in holes, bury themselves, and/or protect themselves with mucus envelopes (Hobson 1965, etc.). In the tropics, they are among the first fishes to take cover at dusk and the last to emerge at dawn, a practice that may minimize their vulnerability during the crepuscular hours when predation is most intense (Hobson 1968, 1972; Collette and Talbot 1972). In the kelp beds of the temperate zone, there may be relatively few nocturnal piscivores as compared with the tropics. Thus, the señorita may retain the burying habit of its family (which implies a complex genetic basis) simply because there are no pressures actively selecting against this trait (cf. Hobson 1972).

Many tropical "pickers" have elongated snouts and small mouths with projecting teeth for selecting and removing tiny prey from otherwise inaccessible places (Alexander 1967; Hobson 1968, 1974). These are also adaptations for picking ectoparasites from larger fishes, and indeed many of the small and sharp-nosed tropical-reef fishes are part-time or "facultative" cleaners (Hobson 1971, 1974; Losey 1972). Likewise, the tendency of kelp perch and señoritas to clean may vary among situations or individuals (Hobson 1971) and may provide most fish with only a minor dietary supplement.

CONCLUSIONS

In and about kelp beds off Santa Barbara, the kelp perch, the señorita, and to a lesser extent the white seaperch, belong to a foraging guild of picker-type microcarnivorous fishes. Throughout the year, the kelp perch and señorita, which commonly pick ectoparasites from larger fish, spend most of the day in the sun-lit upper waters in and about the kelp canopy. Here they can discern and pick small prey from various surfaces and from the open water. A more generalized picker, the white seaperch, occurs a bit deeper in the water column and, unlike the two cleaner fishes, eats substantial amounts of benthic prey.

Even though the two co-occurring cleaner fishes have superficially similar feeding mechanisms, they seem to minimize mutual interference in resource use by foraging in somewhat different ways. Thus their total overlap in resource use is relatively small because the kelp perch feeds actively all day and does not eat substantial amounts of plant-encrusting bryozoans, the predominate staple of the señorita and white seaperch.

Within the kelp-bed area, the señorita has the widest habitat breadth. It broadly overlaps the white seaperch's range below the canopy and near the bottom. Their sharing of food and habitat would seem to make these species the greater potential competitors. But even so, they may seldom actually interfere with one another because the white seaperch is not limited to the kelp bed and occurs there less frequently than the señorita.

None of the three species forages at night, when all are relatively inactive and the señorita buries itself in soft substrates on the reef.

Neither the kelp perch nor the señorita obtains substantial amounts of food from cleaning, although some individual señoritas may. Of the two species, the señorita is more specialized in its diel behavior and may be somewhat more nutritionally dependent on cleaning.

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