INFLUENCE OF WATER CURRENTS AND ZOOPLANKTON DENSITIES ON DAILY FORAGING MOVEMENTS OF BLACKSMITH, *CHROMIS PUNCTIPINNIS*, A PLANKTIVOROUS REEF FISH

RICHARD N. BRAY[1]

ABSTRACT

The blacksmith, *Chromis punctipinnis*, one of the most abundant fishes in kelp forests off southern California, daily emerges from rock shelters and moves to specific locations where it forages in the midwater on zooplankton. Midwater transects taken over a reef that experiences occasional reversals in water currents indicated that large blacksmith (greater than 150 mm total length) consistently gathered at the incurrent end of the reef. These movements are probably related to the availability of food. Replicate plankton tows taken near the ends of the reef demonstrated that zooplankton densities were greater at the incurrent end. Experiments in which large fish were placed in cages suspended in midwater at both reef ends demonstrated that individuals foraging at the incurrent end consumed more prey. Small blacksmith (less than 125 mm total length) did not undergo foraging movements. Instead, most remained in the shallower portions of the reef, close to cover, even though caging experiments and collections of free-living individuals indicated that these fish would consume more prey if they moved upcurrent. Since small as well as large blacksmith benefit from foraging at the incurrent end, the size-specific differences in foraging movements probably reflect differences in the cost of migrating in terms of time, energy, and predation.

Many fishes on temperate and tropical reefs feed heavily on zooplankton. They eat either by day or by night, and school or shelter when inactive (Hobson 1972, 1973, 1974; Hobson and Chess 1976). Some planktivores limit their movements to the water column above their shelters (e.g., Sale 1971; Hobson 1972, 1973); the distribution and small-scale movements of these parochial species have been the subject of recent quantitative investigations (e.g., Stevenson 1972; Hobson and Chess 1978; de Boer 1978). Other planktivores undergo extensive horizontal movements (Hobson 1972, 1973), and have received less attention. Nonetheless, migrating planktivores are often extremely abundant and probably import substantial amounts of extrinsic energy—drift zooplankton—into reef communities (Stevenson 1972).

The blacksmith, *Chromis punctipinnis*, a planktivorous pomacentrid that may grow to a total length (TL) of 300 mm (Miller and Lea 1972), is one of the most abundant fishes inhabiting the inshore rocky reefs of southern California. In aggregations of up to several hundred indi-

viduals, they feed throughout the day on a variety of zooplankton, including larvaceans, copepods, cladocerans, and various larvae (Hobson and Chess 1976). At dusk, they descend to the reef surface where they shelter in holes and crevices until dawn (Ebeling and Bray 1976; Hobson and Chess 1976). Many tropical congeners of the blacksmith have similar activity patterns (e.g., Hobson 1965, 1972; Collette and Talbot 1972; Emery 1973).

During preliminary observations on rocky reefs near Santa Barbara, Calif., I found that blacksmith often forage and shelter in different areas. Large numbers of blacksmith emerge from shelters at dawn, assemble into a school, and move to a location above a reef, where they disperse into a loose aggregation in the midwater and forage on zooplankton. At least some blacksmith near Santa Catalina Island, Calif., show a similar pattern (Hobson and Chess 1976). In commenting on the location of daytime foraging aggregations, Limbaugh (1955) observed that, "Thick schools of young to half-grown blacksmith often form where a plankton-rich current enters the kelp bed." Such a response to water currents would enable blacksmith to be among the first of many vertebrate and invertebrate planktivores to forage on plankton as it is swept across the reef community. However,

[1] Department of Biological Sciences, University of California, Santa Barbara, Calif.; present address: Department of Biology, California State University, Long Beach, CA 90840.

other factors may also affect the distribution of blacksmith. For example, kelp and high relief rocks may serve as orientation points or shelter for fish in the water column (Limbaugh 1955; Quast 1968a, b, c; Ebeling and Bray 1976; Hobson and Chess 1976).

In this paper, I first examine the distribution of blacksmith in relation to water currents over a reef that is subjected to occasional reversals in current flow to see if they consistently gather at the incurrent end. Since foraging is the major activity of blacksmith while assembled in these midwater aggregations, I then determine if plankton is more abundant at the incurrent end. Finally, by examining caged and free-living individuals, I see whether blacksmith that forage at the incurrent end consume more prey.

METHODS

Study Site

Naples Reef is a large rocky outcrop (275 × 80 m) located 24 km west of Santa Barbara and 1.6 km offshore (Figure 1). The substratum is a series of uplifted sandstone rills and ridges that parallel the coast. Depths across the reef average 8-10 m, although some prominences come to within 5 m of the surface. A sandy bottom 16-20 m deep surrounds the reef, with rocky outcrops inshore and cobbles offshore. The assemblage of plant and animal life on and around the reef is among the richest along the Santa Barbara coast. Giant kelp, *Macrocystis pyrifera*, is always present on the reef, although kelp densities fluctuated considerably throughout the study period. The species composition and abundance of fishes at Naples Reef are listed in Ebeling et al. (1980).

Naples Reef is well suited to study the effects of water currents on the distribution of fish. The reef is almost always swept by measurable longshore currents. Although usually these come from the east, occasionally they come from the west. A shift in the distribution of fish when the currents reverse would provide strong evidence that water currents affect the fish's distribution.

Surveys

In December 1975, I initiated biweekly counts of all fish in the water column at four sites on the reef (Figure 1). At each site, I fixed a line from a
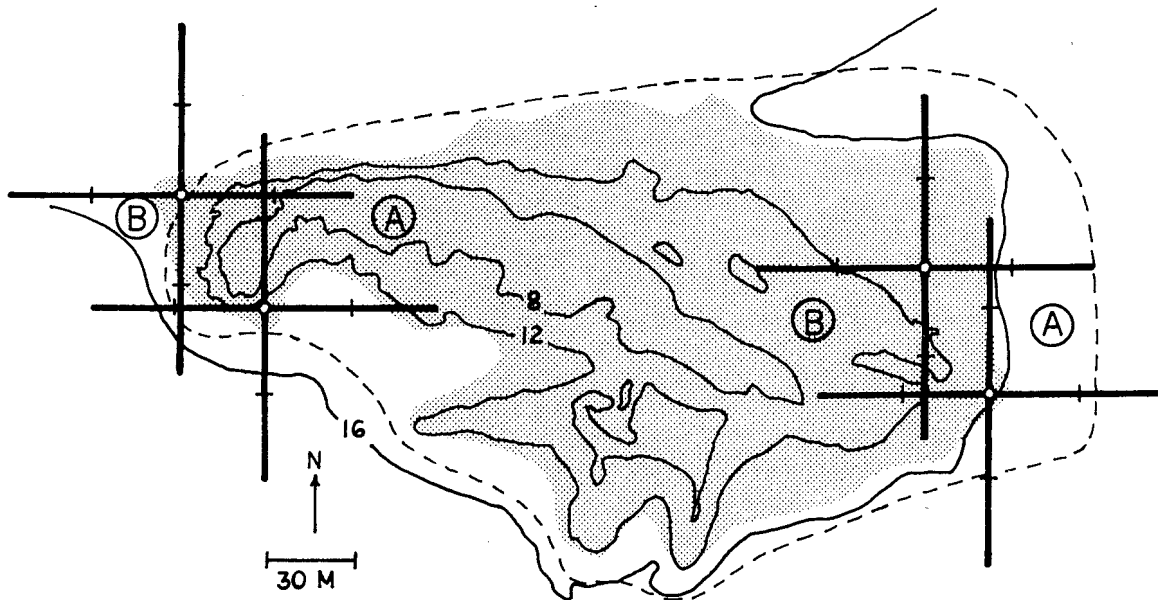

FIGURE 1.—Contour map of Naples Reef, southern California. Heavy lines indicate locations of midwater transects: 30 m (to cross mark) and 60 m (to end) from the starting points (circles). Letters indicate incurrent and excurrent locations where zooplankton were sampled: A locations—when current flowed from the east; B locations—when current flowed from the west. Midwater cages were located at the A locations. The shaded portion indicates the rocky substratum, while the surrounding open area represents sand. The dashed line indicates the margin of the kelp bed. Depths are in meters.

permanent anchoring point to a buoy within 1 m of the surface. At middepth (6 m), I attached a transect line and swam four transects at a constant speed, one each to the north, east, south, and west. Without moving my head, I counted all blacksmith within my field of view. Fish were tallied in separate columns on a slate according to their size as estimated by eye: juveniles (<125 mm TL), halfgrown fish (125-150 mm), and adults (>150 mm). These classes refer to sizes and not necessarily to stages of sexual maturity. A complete survey consisted of 16 transects: 4 at each of the four sites on the reef. During the first 26 surveys (9 December 1975-2 November 1976), the length of the transect line was 30 m, so a total of 480 m were traversed each survey. For the remaining 13 surveys (9 November 1976-23 July 1977), the length of the transects was doubled to 60 m each (960 m/survey) to see if large aggregations of blacksmith occurred beyond the areas that were initially sampled. I did not conduct surveys when visibility was <2 m.

I also examined several oceanographic variables at each site on the reef. Water visibility was measured during each transect as the distance at which I could easily discern a fishlike silhouette attached to the line. Water velocities were measured several times at each site by timing the movement of small particles. And surface, midwater, and bottom water temperatures were taken with a small dial thermometer.

Plankton Sampling

Once the movements of blacksmith were determined, I made replicate zooplankton tows at known sheltering sites near the excurrent end of the reef, and known foraging sites at the incurrent end. Incurrent samples were collected at the margin of the kelp bed, over the sand bottom that surrounds the reef. Excurrent samples were taken within the bed, above rocky areas that provide shelter for large numbers of blacksmith at night. The exact location of the sample sites depended on the direction of the water currents (Figure 1). I specifically avoided sampling on days when the current velocity was negligible, when there were obvious eddies, or when the current flow was not along the east-west axis of the reef.

Plankton were collected between 1000 and 1400 h with a 0.5 m diameter 0.333 mm mesh net pushed by a diver. A TSK[2] flowmeter, fitted across the net opening, measured the filtered volume of water. I randomized (by coin flip) my choice of which end to sample first, thereby restricting such variables as collection time, net clogging, diver fatigue, etc., to random error. Each tow was double oblique, going from the surface to a depth of 6 m, then back to the surface. The diver swam a haphazard pattern through the kelp bed and avoided sampling within 1 m of a kelp plant or the bottom. All samples were immediately fixed in 5% buffered Formalin. The time interval between the first and last tows in a collection ranged from 1.5 to 4.5 h.

In the laboratory, samples were split with a Folsum plankton splitter: one-half was used for weighing and the other half was used for counting. For dry weights, samples were filtered (vacuum pressure = 725 mm Hg) onto preweighed GF/C filters, and dried at 60° C to a constant weight. For counting, samples were split two more times, then subsampled with three 10 ml aliquots drawn with a Stemple pipette. The plankton were counted under a dissecting microscope and sorted into broad taxonomic categories. Weights and counts were standardized by conversion to amounts per cubic meter of water sampled.

I analyzed the data in two ways to compare densities of zooplankton between incurrent and excurrent ends of the reef. First, I compared the individual incurrent and excurrent samples within each collection by Mann-Whitney U-tests to look for significant differences in densities between the reef ends. Second, I compared mean densities between incurrent and excurrent samples of each collection, and tested for incurrent-excurrent differences in these means among the eight collections with Wilcoxon's signed-ranks tests; thus, each collection was a paired (incurrent versus excurrent) observation.

Foraging Experiments

To see if blacksmith near the incurrent end consume more prey, I compared gut contents of fish that foraged near the incurrent kelp margin and excurrent shelter sites. I did not compare free-living adults because they were relatively rare near the excurrent end and their major activity might not have been foraging. Instead, I placed individuals in cages located at both ends of the reef. Cages were constructed of a 1 × 1 × 1 m

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

wooden frame covered with galvanized chicken wire, which allowed fairly free passage of water through the enclosure. For experiments using larger fish (>125 mm SL, standard length) the mesh measured 2.5×3.7 cm; mesh size was halved to 1.3×1.9 cm when smaller fish were used. Seine floats were attached to the top of the cages to make them positively buoyant, and the cages were suspended in midwater at a depth of 5 m by a length of rope anchored to the substratum. The cages were located in the same areas on the reef from which plankton were sampled. One cage was placed at the eastern margin of the kelp bed, 60 m east of the reef. The other was placed over the reef top, 50 m from the extreme west end of the reef (Figure 1). When half of the experiments were completed, the cages were translocated.

Blacksmith were captured while in shelters with the anesthetic quinaldine, or while attracted to chum stations (broken sea urchins). Fish were placed in holding tanks on the boat and haphazardly assigned to a cage. One to five fish were captured for each cage. Before each experiment, the cages were scrubbed with a brush to remove encrusting organisms. When fish were placed in the cage, they swam to the bottom; by the next day, they had usually gathered in the middle. At night, the fish nestled in the bottom corners of the cage.

Each experiment lasted 7-10 d. Preliminary experiments indicated that at least 5 d were required before caged fish began to feed. Fish were removed from cages in the midafternoon and fixed in buffered Formalin. On three occasions, I speared free-living fish in the vicinity of the incurrent cage at the same time that caged fish were removed, to see if caging affected the fish's diet. Since smaller blacksmith do not undergo large-scale movements and are abundant throughout the reef, I also compared gut contents of free-living juveniles speared at the incurrent and excurrent ends. For all collections, blacksmith at the incurrent end were removed first; those at the excurrent end within an hour later. Thus, positive differences in gut fullness between incurrent and excurrent fish are conservative because excurrent fish were able to forage for a longer period of time.

In the laboratory, fish were measured for standard length, blotted weight, and displaced volume. The gut was removed and divided into stomach and intestine. The contents of each were measured for displaced volume, then examined under a dissecting microscope and identified into broad taxonomic categories. Finally, contents were washed onto a preweighed filter and dried at 60° C to a constant weight.

To standardize for differences in fish sizes, the volumes and weights of the gut contents were expressed as relative measures: 1) volumetric fullness as $(Vg/Vf) \times 10^3$, where Vg is the displaced volume (in milliliters) of the gut contents, and Vf is the displaced volume (in milliliters) of the intact fish; 2) gravimetric fullness as: $(Wg/Wf) \times 10^4$, where Wg and Wf represent weights (in grams) of the gut contents and intact fish. Finally, for each experiment, I scaled volumetric and gravimetric fullness from 1.0 for the largest value, down toward 0, then averaged the two scaled values to obtain an overall estimate of gut fullness. This enabled me to pool data among experiments to increase sample size.

RESULTS

Physical Measurements

I made 39 surveys between December 1975 and July 1977. However, since water visibility directly influenced the volume of water in which I counted fish, I excluded from further analysis those surveys when mean visibility was significantly greater at the incurrent end of the reef (t-tests; $P<0.05$) or when variances in visibility at the incurrent and excurrent ends were heterogeneous (F-tests, $P<0.05$). In the remaining 27 surveys, water flowed over the reef from the east in 23; on 4 occasions (twice in April 1976, once in August 1976, and once in January 1977), the current was reversed and flowed from the west. Mean monthly water visibility ranged from 4.5 m in March to 8.7 m in December. Visibility was slightly greater at the excurrent end of the reef. When the current flowed from the east, visibility averaged 7.1 m at the east end and 7.4 m at the west end; when the current reversed, visibility averaged 6.0 m and 5.1 m at the east and west ends.

Spot checks on the movements of small particles indicated that the net flow of water was roughly unidirectional over most of the reef; this general flow was confirmed on 2 d when pieces of kelp were followed as they drifted the length of the reef (Bailey[3]). Nonetheless, variances in velocity were significantly heterogeneous between reef ends for

[3]Thomas Bailey, Marine Science Institute, University of California, Santa Barbara, CA 93106, pers. commun. June 1977.

individual measurements (F-max test, $P < 0.001$), and for mean velocities among all 27 surveys (variances were: 41.10 incurrent, 16.05 excurrent; $P < 0.05$). These variations were presumably caused by local turbulence produced by kelp and rocky prominences.

Current velocities were consistently greater at the incurrent reef end. When water flowed from the east, mean incurrent and excurrent velocities were 11.0 cm/s and 4.6 cm/s (Wilcoxon's signed-ranks test, $P < 0.001$). When currents were reversed, incurrent and excurrent velocities were 4.9 and 3.6 cm/s ($P > 0.25$); these differences probably would be significant with a larger sample size.

Water temperatures at the surface and midwater averaged 15.6° and 15.3° C, and both ranged from 13° C in April to 20° C in October. Bottom temperatures showed a similar pattern, but averaged approximately 2° C lower. Temperatures taken in 21 surveys when the current flowed from the east did not differ significantly between reef ends at any of the three depths (t-tests for paired samples, $P > 0.25$). I recorded temperatures on only two of the four surveys when currents flowed from the west. Surface and midwater temperatures both averaged around 15° C while bottom temperatures averaged 13° C. I could not detect differences in temperatures between reef ends.

Role of Water Currents

The patterns in water visibility simplified my analysis of the fish counts. I treated each of the 27 surveys as a pair of samples, one from the incurrent and the other from the excurrent reef end. Each member of a pair consisted of a total count of blacksmith from the eight transects taken at one end of the reef (Figure 1). Differences within each pair were then analyzed among surveys with one-tailed nonparametric tests, with the hypothesis that counts of blacksmith are greater at the incurrent reef end. The similarity in water visibility between reef ends automatically standardized the counts for the volume of water that was sampled. Actually, the test of the hypothesis was conservative because visibility (hence the volume of water sampled) was significantly lower at the incurrent end in 6 of 27 surveys. I also calculated for each survey the proportion of blacksmith counted at each end of the reef. Proportions were arc sine transformed for computation of 95% confidence intervals (CI). I checked the preci-

sion of my surveys on two occasions by having another diver swim abreast of me and count blacksmith independently. Our total counts of adult blacksmith were similar: 103 (RNB) versus 112 (partner), and 254 (RNB) versus 273 (partner). Moreover, the surveys seemed to confirm our subjective impressions on the relative abundance of adult blacksmith and other fishes in the midwater.

Blacksmith were the most abundant fish in the midwater and were recorded on every survey. Other abundant fishes in the midwater were kelp bass, *Paralabrax clathratus*, and señorita, *Oxyjulis californica* (Table 1).

Adult blacksmith invariably aggregated at the incurrent end (Table 2). In each of the 27 surveys, more adults were counted at the incurrent than at the excurrent end (Wilcoxon's signed-ranks test, $P < 0.001$). Doubling the length of transects had little effect on the counts of adults at the excurrent end, but resulted in a 3- to 4-fold increase in counts of adults at the incurrent end. This was because large numbers of adults gathered farther upcurrent, beyond the area covered in the short transects. The average proportion of adults at the east end of the reef was 0.99 (95% CI = 0.92-1.0) when it was the incurrent end, and 0.09 (95% CI = 0-0.32) when it was the excurrent end.

Adults respond quickly to changes in current direction. On one occasion around midday, the current reversed during a survey and the adults

TABLE 1.—Relative abundance (percentage of total individuals) and frequency of occurrence (percent of total surveys) of fishes counted in midwater transects at Naples Reef, southern California. Species are listed in order of decreasing abundance.

Species	Percentage of total individuals	Frequency (%)
Chromis punctipinnis	41.58	100.0
Paralabrax clathratus	22.04	100.0
Oxyjulis californica	9.47	81.5
Medialuna californiensis	9.00	92.6
Sebastes mystinus	8.62	55.6
Atherinops affinis	2.70	22.2
Trachurus symmetricus	1.82	25.9
Phanerodon furcatus	1.68	33.3
Sebastes serranoides	0.64	66.7
Brachyistius frenatus	0.59	33.3
Embiotoca jacksoni	0.42	33.3
Phanerodon atripes	0.39	18.5
Seriola dorsalis	0.29	11.1
Rhacochilus toxotes	0.21	18.5
Sebastes atrovirens	0.20	25.9
Embiotoca lateralis	0.20	3.7
Damalichthys vacca	0.05	22.2
Heterostichus rostratus	0.04	14.8
Girella nigricans	0.03	3.7
Mola mola	0.03	11.1
Torpedo californica	0.01	7.4
Sarda chiliensis	0.01	3.7
Total no. of individuals	7,767	
Total no. of surveys	27	

TABLE 2.—Number of blacksmith per survey, average (median), in midwater surveys at the east and west ends of Naples Reef, southern California. Freq. = frequency of occurrence (percent of surveys). Short transects total 480 m; long total 960 m.

Current direction	Length of transects	No. surveys	Adults				Halfgrowns				Juveniles			
			Freq. (%)	East		West	Freq. (%)	East	West		Freq. (%)	East	West	
East to	short	16	100.0	44.2 (32.5)		0.6 (0.1)	31.3	0.9 (0.2)	0.3 (0.2)		12.5	1.9 (1.0)	10.9 (3.4)	
west	long	7	100.0	162.3 (171.0)		0.6 (0.4)	85.7	39.1 (18.0)	5.4 (1.6)		71.4	6.7 (3.0)	123.9 (198.0)	
West to	short	3	100.0	6.0 (8.0)		28.3 (25.0)	66.7	0.0 (0.0)	2.3 (1.0)		0.0	0 (0)	0 (0)	
east	long	1	100.0	3 (3)		84 (84)	100.0	3 (3)	3 (3)		100.0	30 (30)	30 (30)	

TABLE 3.—Abundance of zooplankton at the east and west ends of Naples Reef, southern California. For each collection, differences in abundance between ends of the reef were tested with a Mann-Whitney U-test.

Direction of current flow	Date 1977	Numbers Average no./m³ ± 95% CI				Biomass Average mg/m³ ± 95% CI			
		No. samples	East	No. samples	West	No. samples	East	No. samples	West
East to west	19 Aug.	6	1,302.2 ± 101.3*	5	485.0 ± 260.7	6	34.8 ± 3.1*	5	14.0 ± 4.7
	29 Aug.	10	1,589.2 ± 265.3ns	10	1,467.5 ± 590.4	10	19.8 ± 2.3ns	10	19.7 ± 3.6
	15 Sept.	10	3,301.0 ± 375.9*	10	2,809.4 ± 214.7	10	48.1 ± 4.3**	10	37.2 ± 3.6
	21 Sept.	10	2,585.2 ± 423.9**	10	1,095.8 ± 278.5	10	32.0 ± 3.4**	10	19.8 ± 4.3
	29 Sept.	10	2,849.8 ± 407.2ns	7	2,272.2 ± 582.1	10	67.6 ± 7.7*	7	53.0 ± 6.6
	20 Oct.	10	3,277.5 ± 427.5**	10	1,573.5 ± 289.1	10	43.2 ± 4.8**	10	28.5 ± 2.9
West to east	7 Sept.	10	1,983.2 ± 323.2**	10	3,184.3 ± 253.8	10	41.7 ± 6.3**	10	54.7 ± 3.6
	11 Oct.	10	3,062.2 ± 737.0**	10	5,314.2 ± 539.9	10	44.3 ± 9.3*	10	57.9 ± 7.2

*$P \leqslant 0.05$; **$P \leqslant 0.01$; ns, not significant.

quickly migrated to the opposite end of the reef. I began the survey by counting fish at the west end. The current was flowing from the east and I did not count any adult blacksmith, although visibility averaged 12.2 m. I then started the survey at the east end and counted 81 adults, when the currents shifted and flowed from the west. While swimming the transects, I saw small schools of adults (5-15 individuals) moving toward the west (now incurrent) end. I returned to the boat and followed adults as they swam toward the west end, where I repeated the transects. Even though water visibility dropped to 5.0 m, I counted 43 adults over the area where, 2 h earlier, I had counted none.

The movements of halfgrown blacksmith were less clear. Counts were generally higher at the east end when the current came from the east (Table 2; Wilcoxon's signed-ranks test: short surveys, $P = 0.14$; long surveys, $P = 0.06$; short and long combined, $P = 0.05$). However, the pattern was inconsistent, and counts were actually greater at the west end in 3 of the 11 surveys in which halfgrown fish were sighted. The proportion of halfgrown fish at the east end averaged 0.90 (95% CI = 0.38-1.0). A similar inconsistency occurred when the current flowed from the west. All halfgrown fish counted were at the west end on the two short surveys in which they were seen, but the three individuals counted in the long survey were at the east end.

Juvenile blacksmith did not gather at the incurrent end. When the current flowed from the east, all juveniles were at the west end of the reef in the two short surveys in which they were seen and in the five long surveys (Table 2; Wilcoxon's signed-ranks test; long surveys, $P < 0.05$). The proportion of juveniles at the east end averaged only 0.03 (95% CI = 0-0.18). When the current flowed from the west, juveniles were not seen in the short surveys, and were equally abundant at both ends of the reef on the one long survey. However, these data do not accurately describe the response of juveniles to water currents. Observations along the bottom indicate that, regardless of the current direction, many juveniles occurred throughout the reef in stationary aggregations that form around shallow rocky prominences. The large number of juveniles counted at the west end reflected the location of the transects on the reef: almost 87% of the juveniles counted in the midwater surveys were seen in the two transects at the west end, which were the only transects over the shallowest part of the reef (Figure 1).

Zooplankton Densities

I took eight collections of zooplankton from mid-August to mid-October 1977 (Table 3). In six of the collections, the current flowed from the east; in the other two the current was reversed and flowed from the west.

Even though the counts of plankton were standardized to densities, I attempted to sample the same volume of water in each tow to make it equally likely that relatively rare items would be collected at both ends. In seven of eight collections, volumes of water sampled did not differ significantly between reef ends (t-tests, $P>0.10$); in the last collection a significantly greater volume of water was sampled at the west end of the reef ($P<0.01$). The average length of the tows was 57.1 m, which corresponds to a filtered volume of 11.2 m^3.

Small copepods (<4 mm carapace length) and cladocerans were the most abundant items in the samples, averaging 1,259/m^3 and 836/m^3. Small copepods dominated in 93 samples while cladocerans dominated in the remaining 55 samples. Most of the copepods were calanoids, although cyclopoids were also present. The majority of cladocerans appeared to be *Evadne* sp., but *Penilia* sp. occasionally dominated. Larvaceans ranked third in abundance, averaging 119.6/m^3.

Densities of zooplankton differed markedly between the incurrent and excurrent sample sites at Naples Reef. For each collection, mean number and dry weight of plankton pooled in excurrent samples were lower than those in incurrent samples, regardless of the current direction. Differences in counts were significant in six of the eight individual collections (Table 3), and for all eight collections tested together (Wilcoxon's signed-ranks test, $P<0.005$). Estimates of dry weights followed a similar pattern (Table 3).

The trend of a decreased abundance near the excurrent end was shared among many of the zooplankton groups (Table 4). Cladocerans, larvaceans, and bryozoan larvae were significantly less abundant at the excurrent end in seven of eight collections. Other groups were less abundant near the excurrent end in some collections but not in others. For example, densities of small copepods were significantly lower in excurrent samples in six collections, but were higher in another collection (Table 4). Overall, mean densities of 7 of the 15 plankton groups were significantly lower near the excurrent end. Cladocerans, small copepods, and larvaceans showed the greatest decrease near the excurrent end, while polychaetes and nauplii averaged slightly greater there.

Foraging Experiments

I attempted eight experiments between late July and mid-December 1977; three were deleted because several fish died in the cages. The following analysis is based on the 27 of 31 fish in the remaining five experiments that had food in their guts and showed no signs of injury. The first four experiments used larger individuals (117-214 mm SL); the last experiment used smaller fish (88-117 mm SL). For each experiment, there were only

TABLE 4.—Zooplankton densities near the incurrent and excurrent ends of Naples Reef, southern California. Densities are averaged among means of the eight collection days. Columns to the right indicate number of collections during which plankton densities at the incurrent end were greater, less than, or equal to those near the excurrent end (Mann-Whitney U-tests, two tailed; $P \leqslant 0.05$). Symbols next to incurrent densities indicate P values from a one-tailed Wilcoxon's signed-ranks test for incurrent and excurrent differences in density among all collections combined. Plankton groups are listed in order of decreasing differences in densities between incurrent and excurrent ends of the reef.

Plankton group	Average number per m^3		Number of collections		
	Incurrent	Excurrent	Incurrent < excurrent	Incurrent > excurrent	Incurrent = excurrent
Cladocerans	1,097.2*	575.7	7	0	1
Small copepods	1,402.3ns	1,114.8	6	1	1
Larvaceans	178.7**	60.4	7	0	1
Echinoderm larvae	54.6ns	15.7	3	0	[1]2
Doliolids	41.8**	9.7	5	0	3
Chaetognaths	32.1*	16.9	6	0	2
Medusae	39.8**	25.0	5	0	3
Large copepods	22.8*	9.7	3	1	[1]3
Bryozoan larvae	15.5**	4.3	7	0	[1]0
Fish larvae	3.4ns	1.3	2	1	5
Decapod larvae	3.3ns	2.0	1	0	[1]3
Zoea	5.0ns	4.4	0	0	[1]5
Ostracods	0.3—	0.2	0	0	[1]1
Nauplii	1.0ns	1.2	0	0	[1]2
Polychaetes	0.9ns	1.4	0	0	[1]3

*$P \leqslant 0.05$; **$P \leqslant 0.005$; ns, not significant; — insufficient data;
[1] Not present in all eight collections.

minor size differences between fish in incurrent and excurrent cages (Table 5). Also, when data were pooled among experiments to increase sample size, neither length, weight, nor volume of fish differed significantly between cages (t-tests, $P > 0.75$).

Gut fullness was greater for fish in the incurrent cage (Table 5). Average fullness for 13 incurrent

TABLE 5.—Diets of blacksmith in five cage experiments at the incurrent and near the excurrent ends of Naples Reef, southern California. Only individuals with food in their guts were included in the analyses. Fullness is defined in the text.

Item	Experiment dates, 1977									
	25 July-1 Aug.		3-12 Aug.		15-22 Aug.		9-19 Sept.		11-18 Oct.	
	Incurrent	Excurrent	Incurrent	Excurrent	Incurrent	Excurrent	Incurrent	Excurrent	Incurrent	Excurrent
No. fish: with food, empty	4,0	5,0	3,0	2,1	1,1	1,1	1,1	2,0	4,0	4,0
SL (mm): $\bar{x}$	157.8	165.0	182.7	188.5	175	150	123	121.7	100.5	95.8
Range	145-179	145-187	167-195	161-214				117-129	90-117	88-117
Fullness: $\bar{x}$	0.70	0.30	0.67	0.06	1.0	0.36	1.0	0.47	0.57	0.18
Range	0.37-0.90	0.12-0.54	0.35-1.00	0.04-0.09				0.12-0.82	0.29-1.00	0.05-0.32
Food items	Average number per fish									
Larvaceans	981.3	77.5	148.3		153		452	201.5	482.3	370.3
Large copepods		8.0			67		172	2.5	70.3	2.3
Small copepods	82.3	186.8	12.7		57	20	148	62.0	211.0	156.8
Cladocerans	26.0	20.4						1.0	17.8	29.0
Chaetognaths			6.7					0.5	2.3	0.8
Decapod larvae		0.5						1.0	10.3	0.5
Polychaetes			0.7		10		23	1.5	1.0	3.0
Fish larvae		0.5								
Obelia sp.		3.5		7.5		3				
Total items	1,089.6	289.2	176.4	7.5	287	23	795	270.0	795.0	562.7

TABLE 6.—Diets of free-living and caged blacksmith at the incurrent end of Naples Reef, southern California. Fullness is defined in the text.

Item	Collection date, 1977					
	29 Sept.		18 Oct.		6 Dec.	
	Caged	Free	Caged	Free	Caged	Free
No. fish: with food, empty	3,0	5,0	4,0	5,0	3,1	4,0
SL (mm): Mean	113.7	114.8	100.5	112.2	91.3	100.3
Range	110-118	100-121	90-117	94-127	86-98	91-107
Fullness: Mean	0.34	0.73	0.32	0.69	0.81	0.46
Range	0.30-0.39	0.48-1.00	0.14-0.58	0.41-1.00	0.78-1.00	0.32-0.59
Food items	Average number per fish					
Larvaceans	200.3	1,904.6	482.3	805.4	561.3	865.8
Large copepods	134.0	302.2	70.3	563.6	952.7	267.0
Small copepods	102.0	321.2	211.0	397.6	295.3	615.3
Cladocerans	1.3	150.4	17.8	26.0	14.3	28.8
Chaetognaths	1.3	34.8	2.3	24.6	4.3	13.0
Decapods	2.7	10.2	10.3	27.8	5.3	2.3
Polychaetes	1.7	20.0	1.0	5.8	1.0	2.0
Total items	444.3	2,743.4	795.0	1,850.8	1,834.2	1,794.2

TABLE 7.—Diets of free-living juvenile blacksmith collected near the incurrent and excurrent ends of Naples Reef, southern California. Fullness is defined in the text.

Item	Collection date, 1977					
	29 Sept.		18 Oct.		20 Mar.	
	Incurrent	Excurrent	Incurrent	Excurrent	Incurrent	Excurrent
No. fish: with food, empty	5,0	5,0	5,0	4,0	11,0	11,0
SL (mm): Mean	114.8	111.2	112.2	101.5	118.2	105.7
Range	100-121	85-117	94-127	85-116	101-122	98-114
Fullness: Mean	0.73	0.40	0.69	0.26	0.72	0.51
Range	0.48-1.00	0.04-0.61	0.41-1.00	0.02-0.83	0.62-0.93	0.02-0.81
Food items	Average number per fish					
Larvaceans	1,904.6	1,084.2	805.4	339.5	Not analyzed	
Large copepods	302.2	107.8	563.6	18.0		
Small copepods	321.2	292.8	397.6	313.3		
Cladocerans	150.4	207.2	26.0	34.5		
Chaetognaths	34.8	6.6	24.6	2.8		
Decapod larvae	10.2	4.6	27.8	8.0		
Polychaetes	20.0	8.6	5.8	1.3		
Total items	2,743.4	1,711.8	1,850.8	717.4		

fish, 0.70, was significantly greater than that for the 14 excurrent fish, 0.20 (Mann-Whitney U-test, $P < 0.001$).

Nine categories of food items were identified from gut contents of caged blacksmith (Table 5). Larvaceans and copepods predominated, while other groups were usually rare or absent. All items were typically planktonic except for the sessile stage of the hydrozoan, *Obelia* sp., which quickly colonized cages even though they were scrubbed before each experiment. *Obelia* sp. occurred in gut contents as small branches (< 5 mm long), and each was counted as one individual. Eliminating *Obelia* sp. would decrease gut fullness for excurrent fish even more (Table 5). Dietary variation between cages included differences in relative abundances of larvaceans and copepods, and additions of rare items in the excurrent cages. In the incurrent cage, larvaceans were the most abundant food items in all experiments, but in the excurrent cage, they were most abundant in only two experiments. When present, large copepods (> 4 mm) were found mostly in incurrent-caged fish. Though relatively few in numbers, the size of these copepods (some nearly 10 mm long) probably made them nutritionally important. That excurrent fish ate *Obelia* sp. during three experiments is difficult to explain. Tufts of *Obelia* sp. may have been more abundant in the excurrent cages, because the excurrent cages appeared to foul at a faster rate. Sessile hydroids are not a normal food of blacksmith (Hobson and Chess 1976).

Caging altered the blacksmith diets, but the effects were variable. In two of three collections, free fish had generally consumed more food than caged fish (Table 6). Seven categories of food items were identified in the guts of caged and free fish. As before, larvaceans and copepods were by far the most abundant. Cladocerans were abundant in a few individuals, but chaetognaths, decapod larvae, and polychaetes were uncommon. Free fish ate mostly larvaceans in all of the collections, but caged fish were inconsistent. In one collection, caged fish ate mostly large copepods, but in the other two, they ate mostly larvaceans.

Free-living juveniles at the incurrent end ate more food than those at the excurrent end (Table 7). Pooled among collections, gut fullness differed significantly between reef ends (Mann-Whitney U-test, $P < 0.05$). Nonetheless, dietary composition of all free-living juveniles was similar. Larvaceans always made up the most abundant

item, with copepods and cladocerans also common. Numbers of small copepods were slightly less in excurrent fish, but the difference was not nearly so great as for larvaceans or large copepods. Numbers of cladocerans were greater in excurrent fish.

DISCUSSION

Blacksmith Distribution Patterns

Adults

The midwater surveys indicate that large numbers of adult blacksmith (> 150 mm TL) swim to the incurrent end of Naples Reef. Under the usual current pattern of flow from the east, almost all adults recorded were at the east end; when currents reversed, adults were far more abundant at the west end. During one survey, adults were actually seen migrating to the opposite end as currents reversed. The only times I saw large numbers of adults dispersed throughout the reef occurred when currents were negligible. On another occasion at Toyon Bay, Santa Catalina Island (190 km southwest of Naples Reef), I saw a similar response of blacksmith to a current reversal.

Observations at night indicate that large numbers of blacksmith of all sizes take shelter in holes at the west (usually the excurrent) end of Naples Reef. Indeed, the density of sheltering blacksmith at the west end may exceed that at the east because higher rocky relief and more complex substratum at the west end provide more refuges. An investigation of the sheltering behavior of tagged blacksmith indicated that many individuals tend to return to the same shelter at night (Bray in prep.). Yet when the current flowed from the east, extensive searches throughout the entire reef during the day failed to reveal substantial numbers of adults anywhere but at the east end. During the present midwater surveys, I saw one of these tagged fish in a feeding aggregation at the extreme eastern margin of the kelp, almost 300 m away from the hole where it was tagged. This, and my observation that blacksmith swam the length of the reef when currents reversed, indicates that some adults must swim a considerable distance each day to gather at the incurrent end.

Juveniles

In contrast, juvenile blacksmith (< 125 mm TL)

apparently do not congregate at the incurrent end. Although midwater counts were highest at the excurrent end, bottom observations indicate that juveniles occur abundantly throughout the reef. Some form large stationary aggregations about reef prominences while others are more dispersed, hovering within a few meters of the rocky substratum. Halfgrown fish are most abundant along the reef edge, between aggregations of adults and juveniles. To simplify the transects, I tallied blacksmith as though they were comprised of two major size classes, juveniles and adults; halfgrown fish made up but a small group of intermediate-sized individuals that allowed clearer distinction between these two classes. Actually, fish sizes ranged almost continuously from small juveniles to large adults. The degree of fish movements vary accordingly, from very short forays of newly settled juveniles to extensive migrations of large adults.

Foraging at Incurrent End of the Reef

Adults

In synthesizing day and night observations of fish residing on temperate and tropical Pacific reefs, Hobson (1973) concluded that when fish are active their dominant behavior is feeding, and when they are inactive they seek security either by schooling or by sheltering. Hobson (1972) states, "A suitable feeding location for any given species may or may not be near areas that offer it suitable security during its inactive period. Consequently, the major actions of these fishes characteristic of twilight relate to moving between feeding locations and shelter locations."

The most suitable foraging site for adult blacksmith, in terms of food availability, is likely at the incurrent end of the reef. The paired caging experiments indicated that the amount of zooplankton consumed by adults at the incurrent end was greater than the amount eaten by those over the reef near the excurrent end. Although the caging procedure itself did influence blacksmith foraging, I assume the effect was similar in both cages, so the differences in gut fullness reflected the relative availability of food at the reef ends.

There are at least two possible reasons for the greater food abundance at the incurrent end. First, plankton is probably replenished there at a faster rate. Measurements of current velocities

indicated that water crossing the reef is slowed and deflected by rocky prominences and columns of giant kelp. When feeding in a current, blacksmith often position themselves in areas of slack water behind kelp while currents deliver food (Hobson and Chess 1976). On the other hand, fish in relatively calm water at the excurrent end may have to swim about, possibly farther from kelp or other shelter, to encounter food at a comparable rate. Hobson and Chess (1976) observed that feeding rates of blacksmith were greater in a moderate than a slack current.

Second, the density of zooplankton is greater at the incurrent end. Under the normal pattern of current flow with water coming from the east, zooplankton densities were consistently greater at the east end of the reef. Even more convincing, however, was the effect of current reversal; on these two occasions, zooplankton densities were significantly greater at the west end, with most of the differences attributable to decreased densities of cladocerans, small copepods, and larvaceans. I feel that the plankton samples provided a good measure of the abundance of the blacksmith's potential prey because the most abundant items in the plankton samples (copepods, cladocerans, and larvaceans) were also the major items found in the blacksmith guts. Also, I sampled in areas where blacksmith normally gather in the appropriate current conditions, and I was invariably surrounded by foraging adults while I collected plankton at the incurrent end. Although several investigators have discussed decreased densities of plankton in kelp beds (Limbaugh 1955; Quast 1968b; Miller and Geibel 1973; Feder et al. 1974), to my knowledge, this is the first quantitative documentation.

Juveniles

The incurrent end of the reef would seem to be the most suitable foraging site for juveniles—at least those that forage here consume more prey, as determined by the caging experiments and examinations of free-living individuals. But the surveys showed that juveniles fail to concentrate here, which indicates that other factors override the advantages of incurrent foraging.

Optimization models may be used to interpret foraging movements of planktivorous fishes (Reese 1978). While the benefits of movements usually involve energy gains, costs may include a variety of factors, such as competition, expendi-

tures of time and energy, and the threat of increased predation (e.g., Pyke et al. 1977). The differences in foraging movements between juvenile and adult blacksmith may indicate that although juveniles apparently benefit from foraging at the incurrent end, the cost of migrating to and maintaining station at the incurrent end might outweigh the benefit of greater food intake there. Smaller fish have lower cruising speeds and expend relatively more energy in swimming a given distance (Bainbridge 1958, 1960), so juveniles sheltering at the excurrent end may find it too costly to swim across the reef. Juveniles already at the incurrent end may remain near the bottom, because they find it too costly to maintain station in strong midwater currents. Hobson and Chess (1976) observed that in strong currents, blacksmith abandon open places for the lee of kelp plants. Similarly, when currents are strong over tropical reefs, diurnal planktivores approach the bottom (Hobson and Chess 1978).

Predation pressures may limit the movements of juveniles, which are vulnerable to many more predators than are the adults. Covich (1976:242) presented a simple graphic model that showed how predation can influence distances traveled by foragers if the threat of predation increased farther away from shelter; he stated, "Often the risk of predation to the forager and the distribution of resources are the major interacting variables that regulate consumer movement." In the tropics, juvenile fishes remain closer to reefs than adults, and at dusk when predation is most intense, smaller individuals seek shelter first (Hobson 1972, 1979). Many coral reef fish seek nearby shelter when predators approach (e.g., Hartline et al. 1972), and relocation experiments indicate that damselfishes released away from shelter are quickly eaten (Mariscal 1970; Nolan 1975). Similarly, the threat of predation might discourage juvenile blacksmith from aggregating in midwater at the incurrent end of Naples Reef. *Paralabrax clathratus* ranked second in abundance in my midwater surveys (Table 1), with larger individuals tending toward the incurrent end. Although these predators may exceed 700 mm TL (Miller and Lea 1972), they probably would have difficulty consuming large blacksmith. However, I have observed kelp bass >400 mm TL attacking juveniles, and gut analyses indicate they feed on a variety of small fishes, including juvenile blacksmith (Quast 1968d; Love and Ebeling 1978). Additional predators include

other residential as well as open-water fishes, and marine birds and mammals.

Zooplankton Distribution Patterns

Residents Versus Nonresidents

Comparing differences in plankton densities across a reef has often been used to estimate the importance of plankton to the energetics of reef communities (e.g., Johannes and Gerber 1974). However, others have shown that inshore reefs also contain resident zooplankters with different habitat preferences. Many of these "demersal plankters" form a nocturnal component that either hides in the reef during the day and emerges at night (e.g., Alldredge and King 1977) or resides in deeper water during the day and moves into shallow areas at night (Hobson and Chess 1978, 1979). Thus, as several authors have pointed out (e.g., Alldredge and King 1977), differences in plankton densities across a reef might reflect the habitat preferences or patchiness of resident zooplankton, rather than the consumption of extrinsic zooplankton by fish or other reef residents.

It is doubtful that the incurrent-excurrent differences in plankton densities at Naples Reef resulted from sampling resident, demersal zooplankton. All samples were taken around midday in the water column away from reef or kelp substrata. At this time, most demersal forms hide in or near shelter or in deeper water (Alldredge and King 1977; Hobson and Chess 1976, 1978, 1979). Furthermore, typical reef residents — mysids, cumaceans, polychaetes, and decapods — were insignificant components in the plankton collections, while the groups that were consistently less abundant at the excurrent end — cladocerans and larvaceans — have not been reported as residential forms. However, it would be risky to conclude that the observed decline in zooplankton density across Naples Reef was entirely a consequence of predation by fishes and invertebrates of the kelp-bed community. I did not follow a specific parcel of water as it drifted across the reef; in fact, I sampled the excurrent end of the reef first in five of eight collections. Thus, at least some of the differences in plankton densities between the two ends may have been due to my sampling different patches of plankton. This would explain, e.g., the greater numbers of small copepods at the excurrent end in one collection (Table 4).

Impact of Blacksmith Foraging

Most of the food consumed by blacksmith comes from outside the reef community. Blacksmith diets, of course, depend on the composition of the plankton, but consist largely of larvaceans, cladocerans, and copepods. The same items dominate the diet of blacksmith off Santa Catalina Island (Hobson and Chess 1976). Some copepods may be members of the reef community (as discussed above), but the small calanoids in the blacksmith's diet are more likely a part of the drift plankton; residential forms probably would not occur during the day in the exposed, current-swept midwater areas of the incurrent end of the reef.

Too little is known about the total population and daily food consumption of blacksmith, and about the amount of plankton that passes over the reef, to accurately assess the effect of blacksmith foraging on incoming zooplankton. However, several lines of evidence indicate that blacksmith are major predators. The dominant items in their diets are those that showed the greatest decrease in abundance. Also, individual blacksmith consume a large amount of food each day. The guts of blacksmith are empty at dawn (Hobson and Chess 1976; Bray unpubl. data), so guts of individuals collected at dusk contain food that was consumed that day. The number of plankters in the stomach of 14 blacksmith (124-178 mm SL) that were speared as they sheltered at dusk averaged 1,455 items, 95% of which were larvaceans and small copepods. And these data underestimate the total number consumed. They exclude intestinal items, even though these largely unidentifiable remains weighed an average of 2.2 times the contents of the stomach, and they ignore items evacuated before dusk. Thus, considering that blacksmith composed over 42% of the 7,800 fish tallied, I conclude along with Limbaugh (1955) that they materially affect the plankton that is swept across southern California kelp beds.

ACKNOWLEDGMENTS

LITERATURE CITED

ALLDREDGE, A. L., AND J. M. KING.
   1977. Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Mar. Biol. (Berl.) 41:317-333.
BAINBRIDGE, R.
   1958. The speed of swimming of fish as related to size and to the frequency and amplitude of the tail beat. J. Exp. Biol. 35:109-133.
   1960. Speed and stamina in three fish. J. Exp. Biol. 37:129-153.
COLLETTE, B. B., AND F. H. TALBOT.
   1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. In B. B. Collette and S. A. Earle (editors), Results of the Tektite program: ecology of coral reef fishes, p. 98-124. Nat. Hist. Mus. Los Ang. Cty., Sci. Bull. 14.
COVICH, A. P.
   1976. Analyzing shapes of foraging areas: some ecological and economic theories. Annu. Rev. Ecol. Syst. 7:235-257.
DE BOER, B. A.
   1978. Factors influencing the distribution of the damselfish Chromis cyanea (Poey), Pomacentridae, on a reef at Curacao, Netherlands Antilles. Bull. Mar. Sci. 28:550-565.
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., R. J. LARSON, W. S. ALEVIZON, AND R. N. BRAY.
   1980. Annual variability of reef-fish assemblages in kelp forests off Santa Barbara, California. Fish. Bull., U.S. 78:361-377.
EMERY, A. R.
   1973. Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. Bull. Mar. Sci. 23:649-770.
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.

HARTLINE, A. C., P. H. HARTLINE, A. M. SZMANT, AND A. O. FLECHSIG.
1972. Escape response in a pomacentrid reef fish, *Chromis cyaneus*. *In* B. B. Collette and S. A. Earle (editors), Results of the Tektite program: ecology of coral reef fishes, p. 93-97. Nat. Hist. Mus. Los Ang. Cty., Sci. Bull. 14.

HOBSON, E. S.
1965. Diurnal–nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965:291-302.
1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull., U.S. 70:715-740.
1973. Diel feeding migrations in tropical reef fishes. Helgol. wiss. Meeresunters. 24:361-370.
1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., U.S. 72:915-1031.
1979. Interactions between piscivorous fishes and their prey. *In* H. E. Clepper (editor), Predator-prey systems in fisheries management, p. 231-242. Sport Fishing Inst., Wash., D.C.

HOBSON, E. S., AND J. R. CHESS.
1976. Tropic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fish. Bull., U.S. 74:567-598.
1978. Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. Fish. Bull., U.S. 76:133-153.
1979. Zooplankters that emerge from the lagoon floor at night at Kure and Midway Atolls, Hawaii. Fish. Bull., U.S. 77:275-280.

JOHANNES, R. E., AND R. GERBER.
1974. Import and export of net plankton by an Eniwetok coral reef community. Proc. 2d Int. Symp. Coral Reefs 1:97-104.

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

LOVE, M. S., AND A. W. EBELING.
1978. Food and habitat of three switch-feeding fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 76:257-271.

MARISCAL, R. N.
1970. The nature of the symbiosis between Indo-Pacific anemone fishes and sea anemones. Mar. Biol. (Berl.) 6:58-65.

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.

MILLER, D. J., AND R. N. LEA.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.

NOLAN, R. S.
1975. The ecology of patch reef fishes. Ph.D. Thesis, Univ. California, San Diego, 246 p.

PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV.
1977. Optimal foraging: a selective review of theory and tests. Q. Rev. Biol. 52:137-154.

QUAST, J. C.
1968a. Some physical aspects of the inshore environment, particularly as it affects kelp-bed fishes. *In* W. J. North and C. L. Hubbs (compilers and editors), Utilization of kelp-bed resources in southern California, p. 25-34. Calif. Dep. Fish Game, Fish Bull. 139.
1968b. Fish fauna of the rocky inshore zone. *In* W. J. North and C. L. Hubbs (compilers and editors), Utilization of kelp-bed resources in southern California, p. 35-55. 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 (compilers and editors), Utilization of kelp-bed resources in southern California, p. 81-108. Calif. Dep. Fish Game, Fish Bull. 139.
1968d. Effects of kelp harvesting on the fishes of the kelp beds. *In* W. J. North and C. L. Hubbs (compilers and editors), Utilization of kelp-bed resources in southern California, p. 143-149. Calif. Dep. Fish Game, Fish Bull. 139.

REESE, E. S.
1978. The study of space-related behavior in aquatic animals: special problems and selected examples. *In* E. S. Reese and F. J. Lighter (editors), Contrasts in behavior. Adaptations in the aquatic and terrestrial environments, p. 347-374. Wiley, N.Y.

SALE, P. F.
1971. Extremely limited home range in a coral reef fish, *Dascyllus aruanus* (Pisces: Pomacentridae). Copeia 1971:324-327.

STEVENSON, R. A., JR.
1972. Regulation of feeding behavior of the bicolor damselfish (*Eupomacentrus partitus* Poey) by environmental factors. *In* H. E. Winn and B. L. Olla (editors), Behavior of marine animals. Vol 2: Vertebrates, p. 278-302. Plenum Press, N.Y.