DAY VERSUS NIGHT ACTIVITY OF REEF FISHES IN
A KELP FOREST OFF SANTA BARBARA, CALIFORNIA

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ABSTRACT

Vertical distributions and feeding activities of residential kelp-bed fishes were compared between day and night in an area of reef and kelp off Santa Barbara, Calif. Abundances and positions of fishes within four vertically oriented zones were observed during 42 paired day and night scuba transects made throughout the year along a line secured to a high-relief rocky reef located about 1.6 km offshore. Feeding activity was determined for surfperches (Embiotocidae) from the proportion of fish collected during the day or night having empty "foreguts," and inferred for other fishes from general observations of individuals. Although almost all of the 25 common fish species recorded were seen both day and night, the number seen and the degree of activity of most of these species decreased considerably at night. Many fishes that fed and moved about in mid-water well above the reef during the day were found in holes and crevices in the reef at night; others that foraged on or just above the bottom during the day showed little change in their position; and still others tended to disperse to adjacent areas of the reef. Daytime aggregations of fishes centered around the crest of the reef and other productive prominences and invariably dispersed at night. Unlike tropical communities of reef fishes, the kelp-bed community included neither a broad replacement for diurnal planktivores in the night shift nor a contingent that moves out over nearby sand flats to forage at night. Kelp-bed fishes showed considerable intraspecific variability in behavior. Thus, the kelp-bed community appears to be more loosely "programmed" even though it follows the same basic pattern of diel activity as the tropical-reef community. The kelp-bed species that belong to primarily tropical families tended to be quite specialized in their nocturnal sheltering behavior. Yet the primarily temperate surfperches, for example, simply became somewhat lethargic and remained exposed at night.

Day-night variations in the activities of reef fishes have received considerable attention recently, especially as these variations may relate to foraging methods (Hobson 1975), and to sharing of limited space (Smith and Tyler 1972). Direct observations of coral reef fishes have shown that, although most species are active mainly during the day, a substantial number are active only during the night (Hobson 1965, 1968, 1974; Starck and Schroeder 1965; Smith and Tyler 1972). In both instances, fish forage mainly during their active periods and school and/or seek shelter during their inactive periods (Hobson 1972). Dawn and dusk are important transitional periods when fishes that had been active seek shelter, when fishes that had been resting begin foraging, and when piscivores become most effective (Hobson 1972; Collette and Talbot 1972; Domm and Domm 1973).

The assemblage of fishes at a particular place on a tropical reef at night may differ markedly from the assemblage gathering at the same place during the day because foraging and sheltering

activities do not always occur in the same area. For example, some surgeonfishes (Acanthuridae) and damselfishes (Pomacentridae), which shelter at night in the shallower portions of coral reefs, migrate offshore at dawn to their feeding grounds in deeper water (Hobson 1972). Nocturnal predators may undergo even more extensive migrations. Some snappers (Lutjanidae) and grunts (Pomadasyidae) are among a considerable number of species that move away from the reef at night to forage over surrounding sand flats (Hobson 1968, 1972). For many planktivores, however, the change in activity simply involves vertical movements from foraging areas in the water column to underlying sheltering sites (Hobson 1973). Thus the important events during the transition period between day and night include vertical as well as horizontal movements of fish.

Less is known about the nocturnal activities of temperate kelp-bed fishes. Some information has been available on a few species: the garibaldi, *Hypsypops rubicundus* (By Clarke 1970); the California sheephead, *Pimelometopon pulchrum* (by Wiley 1974); the kelp perch, *Brachyistius frenatus*; white seaperch, *Phanerodon furcatus*,

and señorita, *Oxyjulis californica* (by Bray and Ebeling 1975); and the horn shark, *Heterodontus francisci*, and swell shark, *Cephaloscyllium ventriosum* (by Nelson and Johnson 1970). More recently, Hobson and Chess (1976) presented more comprehensive comparisons of the day and night feeding activities of fish off Santa Catalina Island: in particular, of the blacksmith, *Chromis punctipinnis*; the walleye surfperch, *Hyperprosopon argenteum*; the kelp rockfish, *Sebastes atrovirens*; the olive rockfish, *S. serranoides*; the queenfish, *Seriphus politus*; and the salema, *Xenistius californiensis*, as well as some of the others mentioned above. Therefore, we initiated a comparative day and night survey of the fishes inhabiting an area of reef and kelp off Santa Barbara, Calif., to see if the fish community undergoes a substantial diel change in its composition, vertical distribution, and activity.

METHODS

Naples Reef is a large rocky outcrop located 24 km west of Santa Barbara (lat. 34°25'N, long. 119°57'W). The reef measures 275 m by 80 m (2.2 hectares) and lies 1.6 km offshore. The substratum consists of a series of sandstone rills and ridges that run parallel to the coast. Depths across the reef average 8 to 10 m, although some prominences project to within 5 m of the surface. The bottom surrounding the reef is 16 to 20 m deep and is comprised of sand with rocky outcrops inshore, or sand and cobbles offshore. The assemblage of plant and animal life on and about the reef is among the richest along the Santa Barbara coast. Giant kelp (*Macrocystis*) is always present on the reef, although kelp densities fluctuated throughout the study period. Temperatures along the top of the reef ranged from 11°C in the spring to 19°C in the fall. Underwater visibility averaged 5 m at the transect line.

A transect line consisting of two 40-m segments was staked along either side, shoreward and seaward, of a high-relief ridge with a crest at 6 m. Day and night counts of fishes along the line were made by scuba divers. For each day-night pair of samples, we counted fish within 2 m on either side of the line. To minimize the effect of nondiel fluctuations on our observations, we always made the night transect member of a pair within 12 h of the day transect. A special effort was made to insure that the night counts of fish were made throughout approximately the same reef area and

overlying volume of water as were the day counts. Powerful 10-cell underwater hand lights, fitted with reflectors to illuminate the data sheets, were used intermittently during the day to inspect holes, and used continuously throughout the night dives.

We evaluated the diel activities of fish species by observing the fishes' vertical distribution and feeding habits. During the transects, fish sightings were tallied in separate columns on our plastic data sheets according to the zone in which each individual was observed (Table 1).

The use of dive lights at night may have attracted or repelled fish depending on the species and/or altered their state of activity. Yet fishes normally inactive at night did not seem to be affected by brief exposures to dive lights. Species normally active at night responded in various ways, from showing hyperactivity to apparent immobilization. Other nighttime observations of reef fishes off California (Nelson and Johnson 1970) and in tropical waters (Hobson 1965; Starck and Davis 1966; Smith and Tyler 1972) also indicate that night-active fishes often respond unpredictably to artificial illumination.

Day and night differences in the feeding habits of many species were inferred either from direct observations of foragers or from changes in the fishes' vertical distribution and activity level (i.e., whether the fish were exposed and responsive to our presence or sheltered and unresponsive). We feel that such observations of fish activity by themselves were sufficient to distinguish feeding from nonfeeding periods for many of the more prominent species. However, such observations proved to be inadequate indicators of foraging activity for surfperches (Embiotocidae), which comprise the most abundant and diverse foraging guild of the fishes on Naples Reef. To test for diel differences in feeding activity of surfperches, therefore, we speared during all hours of day and night approximately 400 adults of the five common demersal species: the black perch, *Embiotoca jacksoni* (median standard length 195 mm, range

TABLE 1.—Zones of vertical orientation in which fish were observed along a transect line

Zone	Extent of zone
IV Mid-water	Greater than 1.0 m above the bottom, in open water and/or near kelp stipes
III Suprabenthic	Within 1.0 m of the bottom
II Bottom	In physical contact with the bottom yet exposed
I Shelter	In holes, crevices, or under ledges

86-244 mm); striped seaperch, *E. lateralis* (200, 110-280); rubberlip seaperch, *Rhacochilus toxotes* (279, 165-400); pile perch, *Damalichthys vacca* (210, 97-260); and rainbow seaperch, *Hypsurus caryi* (159, 114-253). Immediately after each dive, individuals were either iced and later frozen, or slit ventrally and fixed in 10% Formalin.[2] The procedure for gut analysis followed the method of Bray and Ebeling (1975), except that the surfperch's gut, which is simple and tubular and lacks a well defined "stomach," was divided into quarters. Fullness of the "foregut," defined as the first quarter of the length of the entire gut, was scored subjectively from 1 (empty) to 5 (full), and plotted against time of collection. Since fish were sampled throughout the year, their times of collection were seasonally adjusted relative to actual times of sunrise and sunset as determined from solar tables.

RESULTS

We identified 25 species of fishes from 21 paired day-night transects made between April 1972 and September 1973. Most of the fishes seen along the transect line were adults. The only abundant juveniles were of the blue rockfish, *Sebastes mystinus*. Hence for blue rockfish only, juveniles and adults were counted separately. We excluded from the analysis all species that could not be consistently observed, such as some of the more cryptic and secretive fishes that blend with their surroundings and hide in kelp and rocks, and species that occur only near the water surface outside our field of vision.

It appeared that our visual counts adequately sampled all of the more conspicuous kelp-bed fishes. The rank order of abundance of fishes recorded in the 21 daytime transects was highly correlated with that of fishes observed in a photographic survey consisting of 125, 2.5-min motion pictures (Ebeling, Larson, and Alevizon unpubl. data) filmed over the same area (Kendall's tau coefficient of rank correlation = 0.65; $P < 0.001$).

The species composition of seasonally pooled samples and the relative abundances of the different species varied surprisingly little during the 17-mo study period. Almost all species were seen throughout the year, and rank orders of species abundances, pooled over day and night samples,

were significantly concordant among seasonal periods that correspond roughly to annual oceanographic periods defined by Brown (1974) (Table 2).

During the day, almost 4,000 fishes representing 11 families of teleosts and 1 family of sharks were counted along the transect line. The two dominant groups—surfperches (Embiotocidae) and rockfishes (*Sebastes*)—were represented by six species each. The most abundant species was *S. mystinus* whose juveniles accounted for 44% of the individuals sighted during the day (Table 3).

Most individuals of all species of fishes (66%) were observed in the mid-water zone higher than 1 m off the bottom (Table 4). The two most abundant species in the mid-water zone, *S. mystinus* and *Chromis punctipinnis* often formed large, mixed aggregations above rocky prominences and around columns of giant kelp. Besides *S. mystinus* and *C. punctipinnis*, more than 80% of the individuals in several other species were observed in the mid-water zone: the kelp bass, *Paralabrax clathratus*; *Oxyjulis californica*; opaleye, *Girella nigricans*; and *S. serranoides* (Table 4). But 10 of the total of 19 species recorded from the mid-water zone were more abundant in other zones.

Some 25% of the total individuals of all species were observed in the suprabenthic zone, within 1 m of the rocky bottom (Table 4). This zone included the most species (21) and was dominated by surfperches: 71% of the individuals observed in the suprabenthic zone were surfperches, as compared with but 12% in the mid-water zone. Nearly half the individuals were *Embiotoca jacksoni* or *E. lateralis*.

Less than 10% of the total individuals recorded during the day were observed either in the bottom zone, contacting the reef in an exposed position, or in the shelter zone, occupying a crevice or hole (Table 4). Most of these were demersal, "ambusher-type" predators, e.g., rockfishes and sculpins (Cottidae), although a few of the midwater species, e.g., *S. mystinus* and *C. punctipinnis*, were also observed in these zones in small numbers.

We recorded substantially fewer individuals at night than during the day (Table 3). Day to night decreases in total numbers were consistently significant among the 21 pairs of day-night samples (Wilcoxon signed-ranks test for paired observations, $P < 0.005$). Also, lists of species, ranked by abundance, differed at night. All 21 rank correlations for the day-night sample pairs (tau = -0.32 to +0.22), as well as the single rank correla-

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TABLE 2.—Seasonal variation in relative abundance of fishes observed along a transect line. Samples are pooled over day and night transects by trimonthly intervals generally coinciding with periods of oceanographic change off Santa Barbara. Kendall's W coefficient of rank concordance among seasons = 0.77 ($P\!<\!<\!0.005$).

Species	Percent of total individuals by season			
	Dec.-Feb.	Mar.-May	June-Aug.	Sept.-Nov.
Sebastes mystinus (Juvenile)	29.5	29.4	45.3	25.2
Chromis punctipinnis	21.3	11.1	14.5	14.9
Embiotoca jacksoni	14.5	10.9	8.75	14.5
Oxylebius pictus	5.61	3.97	2.05	3.71
Embiotoca lateralis	4.97	2.34	1.49	1.86
S. carnatus	3.71	4.69	2.33	3.12
Hyperprosopon argenteum	3.29	2.71	1.40	8.27
S. mystinus (adult)	2.09	6.40	1.77	9.20
Pimelometopon pulchrum	1.95	0.36	0.84	0.42
Damalichthys vacca	1.86	3.07	2.98	2.36
Rhacochilus toxotes	1.44	1.89	0.47	1.27
Hypsypops rubicundus	1.30	1.17	1.86	1.94
Coryphopterus nicholsii	1.25	0.18	0	0.84
Paralabrax clathratus	1.21	0.36	1.30	1.86
S. chrysomelas	1.21	0.81	0.65	1.10
Medialuna californiensis	0.97	0.09	0.28	0.17
Scorpaenichthys marmoratus	0.84	0.27	0.09	0.08
Hypsurus caryi	0.56	13.6	3.17	1.86
Oxyjulis californica	0.56	2.34	1.12	2.62
Phanerodon furcatus	0.51	2.89	4.28	0.17
Ophiodon elongatus	0.46	0.18	0.09	0
Girella nigricans	0.37	0.27	2.70	3.04
Sebastes serriceps	0.19	0.36	0.37	0
S. serranoides	0.14	0.09	1.77	0.76
Cephaloscyllium ventriosum	0.19	0.09	0	0.34
S. atrovirens	0.05	0.45	0.37	0.34
Total no. of individuals	2,150	1,109	1,074	1,185
Total no. of transects	14	10	10	8

TABLE 3.—Day-night variation in abundance of fishes observed along a transect line. Samples are pooled over seasonal intervals (see Table 2). Symbols in the "Difference" column indicate for each species whether the numbers of individuals observed during the day, ordered among all transects, were significantly greater than (>), less than (<), not significantly different from (=), or too few to compare with (NC) the numbers observed at night (Wilcoxon signed-rank test for paired observations, $P\!\leq\!0.05$).

Species	No. of individuals		Percent of total individuals		Difference day vs. night
	Day	Night	Day	Night	
Sebastes mystinus (Juvenile)	1,730	8	43.80	0.51	>
Embiotoca jacksoni	492	207	12.40	13.20	>
Chromis punctipinnis	253	662	6.40	42.30	<
Oxylebius pictus	215	16	5.44	1.02	>
S. mystinus (adult)	210	34	5.31	2.17	>
Hypsurus caryi	188	31	4.75	1.98	=
Embiotoca lateralis	134	37	3.39	2.37	>
Damalichthys vacca	112	22	2.83	1.41	>
Phanerodon furcatus	91	0	2.30	0	>
Oxyjulis californica	81	0	2.05	0	>
Girella nigricans	70	6	1.77	0.38	>
Paralabrax clathratus	65	2	1.64	0.13	>
S. carnatus	56	138	1.42	8.82	<
Hypsypops rubicundus	55	29	1.39	1.85	>
Pimelometopon pulchrum	41	19	1.04	1.21	=
Coryphopterus nicholsii	38	1	0.96	0.06	>
Rhacochilus toxotes	31	41	0.78	2.62	=
S. serranoides	21	11	0.53	0.70	=
Medialuna californiensis	19	8	0.48	0.51	=
S. chrysomelas	17	38	0.43	2.43	<
Scorpaenichthys marmoratus	12	11	0.30	0.70	=
Ophiodon elongatus	10	3	0.25	0.19	=
Sebastes atrovirens	7	7	0.18	0.45	NC
S. serriceps	4	8	0.10	0.51	=
Cephaloscyllium ventriosum	2	11	0.05	0.70	NC
Hyperprosopon argenteum	0	214	0	13.70	<
Total no. of individuals	3,954	1,564	100.0	100.0	
Total no. of transects	21	21	21	21	

TABLE 4.—Vertical-zone variation in numbers of fishes observed along a transect line compared between day and night. Vertical zones are defined in Table 1; the Δh measure of a species' change in vertical position between day and night is defined in the text.

Family and species	Day				Night				Δh
	Mid-water	Supra-benthic	Bottom	Shelter	Mid-water	Supra-benthic	Bottom	Shelter	
Scyliorhinidae:									
Cephaloscyllium ventriosum	0	1	0	1	0	1	6	4	0.27
Serranidae:									
Paralabrax clathratus	54	11	0	0	1	0	0	1	1.33
Kyphosid-like fishes:									
Girella nigricans	65	5	0	0	0	2	4	0	1.60
Medialuna californiensis	6	13	0.	0	0	3	4	1	1.07
Embiotocidae:									
Damalichthys vacca	32	76	2	2	10	10	2	0	−0.13
Embiotoca jacksoni	101	386	4	1	66	84	51	6	0.18
E. lateralis	26	108	0	0	10	15	10	2	0.30
Hyperprosopon argenteum	0	0	0	0	213	1	0	0	—
Hypsurus caryi	97	90	1	0	7	6	16	2	0.93
Phanerodon furcatus	64	27	0	0	0	0	0	0	—
Rhacochilus toxotes	8	19	4	0	16	20	4	1	−0.12
Pomacentridae:									
Chromis punctipinnis	210	30	0	13	5	9	38	610	2.62
Hypsypops rubicundus	8	32	5	10	0	0	1	28	1.66
Labridae:									
Oxyjulis californica	73	8	0	0	0	0	0	0	[1]2.91
Pimelometopon pulchrum	29	10	0	2	0	0	0	19	2.61
Gobiidae:									
Coryphopterus nicholsii	0	0	32	6	0	0	1	0	−0.16
Scorpaenidae:									
Sebastes atrovirens	2	3	1	1	2	2	2	1	0.14
S. carnatus	3	6	32	15	0	10	84	44	0.19
S. chrysomelas	0	0	10	7	0	0	19	19	0.09
S. mystinus (adult)	178	21	10	1	4	2	8	20	2.08
S. mystinus (juvenile)	1,606	119	0	5	0	1	1	6	2.55
S. serranoides	18	3	0	0	9	0	0	2	0.40
S. serriceps	0	0	1	3	0	0	2	6	0
Hexagrammidae:									
Ophiodon elongatus	2	4	4	0	0	0	0	3	1.80
Oxylebius pictus	4	24	179	8	0	0	6	10	0.74
Cottidae:									
Scorpaenichthys marmoratus	0	1	10	1	0	0	10	1	0.09
Total no. of individuals	2,586	997	295	76	343	166	269	786	
Percent of day or night total	65.4	25.2	7.46	1.92	21.9	10.6	17.2	50.3	
Total no. of transects	21	21	21	21	21	21	21	21	

[1]Individuals are assumed to bury themselves at night.

tion for the day-night contrast with samples pooled (tau = 0.13), were nonsignificant ($P>0.05$). A Wilcoxon signed-ranks test for paired (day-night) observations indicated that numbers of eight species did not differ significantly between day and night, while numbers of four species actually increased (Table 3).

Two species commonly observed during the day were either seldom or not seen at night: *Phanerodon furcatus* and *Oxyjulis californica*. Although we often saw individuals of *P. furcatus* browsing on bryozoan-encrusted algae (mainly *Gelidium* sp.) along a crest of the reef during the day, we rarely observed them at night along the crest and never observed them during regular transects. We commonly saw small groups of *O. californica* in the mid-water zone above the transect lines during the day. At dusk, however, *Oxyjulis* individuals bury themselves in rubble and sand on the reef and

remain covered until dawn (Herald 1961; Feder et al. 1974; Bray and Ebeling 1975).

Only one species was seen at night but never during the day. *Hyperprosopon argenteum* was the second-most abundant species recorded at night, although it was never seen around the transect line during daylight hours. In over 6 yr of observations, we have seen this species in kelp beds on only a few occasions during the day. Schools of *H. argenteum* commonly occur in shallow waters along sandy beaches and shallow reefs during the day, so it appears that at least some of the larger individuals migrate offshore to kelp beds at dusk. To reach Naples Reef, fish near the surf would have to swim approximately 1.6 km offshore.

Resemblance between the day and night samples of $S = 25$ species within each of the four vertical zones was measured by coefficients of similarity or "overlap" (cf. Colwell and Futuyma

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1971). Similarity (*C*) is scaled from 0 (no resemblance at all) to 1.0:

$$C = 1.0 - \tfrac{1}{2} \sum_{i=1}^{s} \left| P_{ij} - P_{ik} \right|,$$

where P_{ij} = the proportionate abundance of species i in day sample j, and P_{ik} = that in night sample k.

Though the mid-water zone abounded with fishes during the day, it appeared sparsely populated at night (Table 4). Day-night similarity within the mid-water zone was the least ($C = 0.12$) for the four zones. Six of the 10 species recorded from the mid-water zone at night were surfperches, while three of the remaining four were rockfishes. *Hyperprosopon argenteum* accounted for 62% of the total fish recorded in this zone. *Damalichthys vacca*, along with *Sebastes serranoides* and adult *S. mystinus*, were often seen scattered in the water column at night.

Although the suprabenthic zone underwent a substantial reduction in fish abundance at night, its day-night species similarity was the highest ($C = 0.67$) for the four zones. During both day and night, the suprabenthic zone was dominated by surfperches. At night, surfperches comprised the four most abundant species, accounting for almost 80% of the total fishes observed in the suprabenthic zone (Table 4). Although Pacific electric rays (*Torpedo californica*) were never recorded over the transect lines, they were often encountered nearby, swimming slowly and hovering above the bottom (Bray, Hixon, and Ebeling unpubl. data). Swell sharks (*Cephaloscyllium ventriosum*), whose nocturnal activities were investigated by Nelson and Johnson (1970), were occasionally seen swimming just above the reef at night.

Fish observed in the bottom zone increased from 7.4% of the total individuals recorded from all zones during the day to 17.1% of the total at night (Table 4). The zone's relatively low day-night species similarity ($C = 0.28$) was due to variations in numbers of the demersal ambusher-type predators and increases in numbers of "resting" surfperches. Among the ambusher-type species, e.g., numbers of painted greenling, *Oxylebius pictus*, decreased from 179 counted during the day to only 6 at night, and numbers of two common rockfishes increased: the black-and-yellow, *S. chrysomelas*, almost doubled and the gopher, *S. carnatus*, almost tripled (Table 4).

At night, most fishes were observed in the shelter zone. Although only 2% of the day total of fishes were seen in holes and crevices, 50% of the night total were observed there (Table 4). Day-night species similarity was fairly low ($C = 0.36$), largely because of the increase in numbers of individuals of *Chromis punctipinnis* observed in holes: from only 13 counted during the day to 610 counted at night (Table 4). Individuals of *Pimelometopon pulchrum* and *S. mystinus* were also commonly seen in the shelter zone at night.

These counts of fishes inhabiting holes, especially at night, may be conservative because we could not completely census the numerous deep holes and crevices along the transect line. This problem certainly influenced our counts of individuals of *O. pictus* and juvenile *S. mystinus*. Nocturnal counts of both species were much lower than those made during the day, and the individuals that were observed at night were invariably hiding deep in holes. Subsequent nighttime applications of small amounts of the anesthetic quinaldine to holes that first appeared vacant often yielded several *O. pictus* and 5 to 20 juvenile *S. mystinus*. Similar applications of this anesthetic during the daytime occasionally revealed these fishes, but in far smaller numbers.

The vertical positions of the 25 species of fishes during the day and night are summarized in Table 4. Data on some species are fragmentary because individuals of these species were rarely encountered along the transect line. However, general observations made during hundreds of hours of diving during both day and night tend to substantiate conclusions based on these data. For example, we saw but two kelp bass along the transect line at night, one in mid-water, the other on the bottom. In surrounding areas, we saw many individuals resting on the bottom, several in mid-water, but very few in holes. Eighteen of 24 species recorded during the day were most common in the suprabenthic and mid-water zones above the reef. Only the treefish, *S. serriceps*, was most common in the holes of the shelter zone. Of the 23 species recorded at night 16 were most common in contact with the reef, either in the open positions of the bottom zone or in the holes of the shelter zone. Only two species, *Hyperprosopon argenteum* and *S. serranoides*, were most common in the mid-water zone.

The day-night differences in the activities of many species involved considerable shifts among

the four zones. These shifts are measured in Table 4 by values of Δh:

$$\Delta h = \sum_{i=1}^{4} \left[(p_{i\,\text{day}})\,(i) - (p_{i\,\text{night}})\,(i) \right],$$

where $p_{i\,\text{day}}$ is the proportion of individuals of a species observed during the day in zone i ($i = 1, 2, 3,$ or 4 for the shelter through mid-water zones, respectively) and $p_{i\,\text{night}}$ is the proportion observed at night. The Δh's range from $+3.0$, when all observed individuals of a species undergo a maximum shift downward from the mid-water zone during the day to the shelter zone at night, to -3.0, when all individuals undergo the reverse maximum shift upward. A $\Delta h = 0.0$ indicates little or no shift, in that the species' proportional distribution among zones does not change from day to night.

Fish species varied considerably in the degree to which they changed zones between day and night, although the patterns of shifting upward or downward were similar within families (Table 4). Some species changed their vertical position little if at all: several species of rockfishes; the cabezon, *Scorpaenichthys marmoratus*; *Rhacochilus toxotes*; *Damalichthys vacca*; and blackeye goby, *Coryphopterus nicholsii*. Other species changed their vertical position markedly between day and night. Individuals of *Chromis punctipinnis* and *Pimelometopon pulchrum*, which had near-maximum positive values of Δh, move about in the water column during the day and shelter in holes at night. No individuals of *Oxyjulis californica* were seen at night (recall that they descend from mid-water to bury themselves in sand or gravel patches). Assuming that burying individuals are in the "shelter zone," Δh for *Oxyjulis* = 2.91. No species had a large negative value of Δh, i.e., no species mostly contained individuals that rose from the bottom to mid-water at night. Hobson and Chess (1976) noted that during the day most *Sebastes atrovirens* were "seated on rocky strata" whereas at night they "hovered in mid-water." In the present study, the Δh of *S. atrovirens* was small but positive (Table 4); however, this species was relatively rare in our transects.

Several lines of evidence indicate that many of the kelp-bed fishes observed become less active and do not regularly feed at night. The levels of activity often could be inferred from direct observations. Many species that swam about and fed on or above the reef during the day were found deep in holes and crevices at night and would flee from their shelter only when vigorously disturbed. These species included *Hypsypops rubicundus*, *C. punctipinnis*, *P. pulchrum*, and juvenile *S. mystinus*. Some individuals of *P. pulchrum* reportedly secrete a mucous envelope about themselves (Wiley 1974), and we often found this fish wedged deep in crevices in an apparent state of torpor at night. Individuals of *Girella nigricans* were also found in holes or on the bottom but were more responsive to our presence. Previous diel analyses of gut contents substantiate our present impressions that the following species are strictly daytime feeders: *H. rubicundus* (by Clarke 1970), *O. californica* (by Bray and Ebeling 1975), juvenile *S. mystinus* (by Thomas Bailey unpubl. data), and *C. punctipinnis* (by Hobson and Chess 1976; Bray unpubl. data).

Our analyses of fish-gut emptiness revealed that even many of the kelp-bed fishes not undergoing such obvious diel changes in vertical position may stop feeding at dusk (Figure 1, Table 5). Although all five demersal surfperches (*Embiotoca jacksoni*, *E. lateralis*, *Hypsurus caryi*, *Damalichthys vacca*, and *Rhacochilus toxotes*) generally remain in the suprabenthic and bottom zones both day and night, their diel patterns of gut emptiness indicate that all but *R. toxotes* do not feed at night. Median scores of gut fullness for *E. jacksoni* reached maximum values in the afternoon and declined after sunset; at dawn, all guts examined were empty (Figure 1a). Fully 88% of the fishes speared during daylight hours contained food in their foreguts (Table 5). Although 39% of the fishes collected at night contained food, 89% of these were collected before midnight. Thus it is likely that the food contained in the foreguts of these individuals was eaten before nightfall and had not yet passed into the second quarter of their guts. Foreguts of *E. lateralis*, *H. caryi*, and *D. vacca* show the same pattern (Figure 1b-d). In fact, all four species had significantly less food in their guts during the night than during the day (Table 5). Gnose (1968) also observed that individuals of *E. lateralis* collected from off Oregon had empty guts at dawn. Additionally, two other kelp-bed surfperches that commonly occur in mid-water, *Phanerodon furcatus* and *Brachyistius frenatus*, which is rare at Naples Reef, feed mainly during the day (Bray and Ebeling 1975; Hobson and Chess 1976).

In contrast, median scores for fullness of *R. toxotes* reached maximum values at night, and many foreguts were empty during the day (Figure
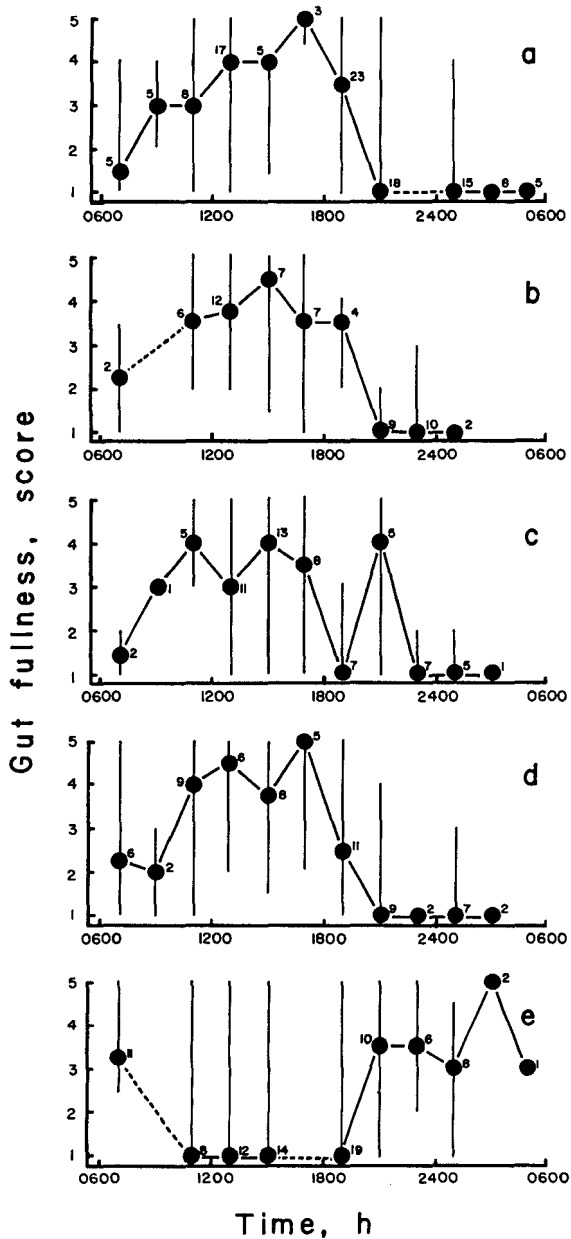
FIGURE 1.—Scored fullness (1, empty-5, full) of foreguts of five demersal surfperches: a, *Embiotoca jacksoni*; b, *E. lateralis*; c, *Hypsurus caryi*; d, *Damalichthys vacca*; and e, *Rhacochilus toxotes*. Each point represents the median score and each vertical line the range of scores for (*n*) individuals collected over a 2-h interval. Time is measured relative to sunrise (0600 h) and sunset (1800 h).

TABLE 5.—Day-night variation in "foregut" emptiness for the five species of demersal surfperches. Values of chi-square with 1 df were calculated from day-night, empty-not empty values in contingency tables for each species.

	Day		Night		Day vs. night	
Species	No. exam-ined	% empty	No. exam-ined	% empty	χ^2	P
Embiotoca jacksoni	43	12	69	61	26.4	<0.005
E. lateralis	34	5.9	25	64	23.0	<0.005
Hypsurus caryi	40	10	25	60	18.6	<0.005
Damalichthys vacca	36	8.3	31	71	27.9	<0.005
Rhacochilus toxotes	45	51	46	33	3.2	≈0.07

although this difference was not significant (Table 5).

It is likely that many of the large-mouthed demersal species feed any time that suitable prey are available. Included among these species are various rockfishes (*Sebastes carnatus*, *S. chrysomelas*, and *S. serriceps*) and *Scorpaenichthys marmoratus*, all of which are cryptically patterned and probably ambush much of their prey. Analyses of gut fullness and states of digestion relative to time of day may be of little value in determining the feeding chronology of these fishes, especially larger individuals. Kariya (1969) showed that food items may take days rather than hours to pass through the stomach of *Sebastes inermis*, a species from Japan; and Larson (pers. commun.) found that small majid crabs (10 mm carapace width) were still intact in the stomachs of adults of *S. carnatus* up to 10 h after ingestion. However, other lines of evidence indicate that they feed at night. We saw more individuals of *S. carnatus* and *S. chrysomelas* at night, probably because they were more active then, and the types of food items included in their diets suggest they feed at night as well as during the day. Their diets include medium-sized crustaceans (crabs, shrimps, etc.) and cephalopods (Quast 1968b; Larson 1972); both prey were far more active and exposed along the transect line at night. We have observed individuals of *S. carnatus* and *S. chrysomelas* at night with live, struggling crabs and octopi protruding from their mouths. Also, individuals of these species often consumed small fishes that escaped from our collecting spears during night dives. Finally, all of these fishes can be caught by hook and line at night as well as during the day (Milton Love, pers. commun.).

Along the transect line during the day, fishes congregate in mid-water to pick plankton and browse on kelp surfaces. At night, on the other hand, almost all of the foraging by fishes occurs on

1e). Some 67% of the fish collected at night contained food in their foreguts, and 49% of those collected during the day also contained food,

or near the bottom. *Hyperprosopon argenteum* was an exception in that individuals of this species occurred alone or in small, loose groups in mid-water at night. Hobson and Chess (1976) and Bray (unpubl. data) found that guts of specimens speared at night were full of recently ingested prey, whereas almost all guts from individuals speared during the day were empty. However, the fact that this fish constitutes a large portion of the catch made by shore fishermen (Frey 1971) indicates that at least some individuals feed during the day.

We know little about the feeding periods of the remaining six species seen along the transect line. The halfmoon, *Medialuna californiensis*, often appeared to be more sensitive to our presence than were individuals of other species near the bottom, and we cannot deny the possibility that *Medialuna* feeds at night. It reportedly eats mainly algae supporting a variety of attached epiphytic animals and much smaller quantities of free animals (Quast 1968b; Follett et al. 1960). The fact that two small demersal species, *Coryphopterus nicholsii* and *Oxylebius pictus*, were seen much less often at night suggests that they retreat deep into holes and crevices then. Larger individuals of lingcod, *Ophiodon elongatus*; *Paralabrax clathratus*; and *S. mystinus* eat cephalopods as well as fishes and other prey (Love 1974; Miller and Geibel 1973; Quast 1968c), so it is reasonable to suspect that they too feed, at least occasionally, at night.

DISCUSSION

During the day, large numbers of fishes pervade the study area of reef and kelp off Santa Barbara. Most fishes inhabit the mid-water zone well off the bottom, while smaller numbers of ambusher-type predators remain in contact with the reef bottom. In contrast, the same kelp forest appears almost abandoned at night. Most notably, large numbers of fishes disappear from mid-water, while the numbers of fishes increase markedly in the shelter zone of holes and crevices.

Although day-night changes in fish abundance may be partly attributable to sampling error caused by our use of lights at night, etc., these changes most certainly reflect differences in the fishes' requirements and distributional patterns between their periods of activity and inactivity. During the day, the area in the vicinity of our transect line seems to constitute a focal point of

fish activity. Daytime fish diversity and abundance appeared to be greater along the transect line than in adjacent areas, 5 to 10 m away. Loose aggregations of juvenile *S. mystinus* and, less frequently, *Chromis punctipinnis*, *P. clathratus*, and *Girella nigricans*, formed in the water column above the transect line. Likewise, other fishes gathered closer to the bottom. Perhaps this local richness relates to the position of the transect about the reef crest. The transect line was attached to one of the highest rocky prominences on the reef, and it ran along the inner margin of a dense stand of giant kelp. Quast (1968a) noted that the combination of high-relief rocks and kelp augments the surface area available for invertebrates, the principal food of the fishes, and serve as orientation points for fishes throughout the water column. Also, inshore and offshore margins of kelp beds often demonstrate the "edge-effect," in that the fauna is richer there than in areas on either side (Feder et al. 1974). At Naples Reef, surfperches, especially individuals of *Embiotoca lateralis* and *Phanerodon furcatus*, tend to congregate about the reef crest and the south dropoff 20 m away where thick stands of *Gelidium* and other red algae flourish. Individuals of *E. lateralis* gorge themselves on the caprellid amphipods that occur in great numbers amongst the algae (Robert Cowen and David Laur, pers. commun.). Also we noticed that fishes tend to aggregate in sunlit areas like the reef crest and avoid the shaded areas on either side. In tropical reefs, diurnally schooling fishes that migrate to adjacent sand flats at night return in daylight to the same prominent topographic features on the reef (Hobson 1973). Other factors that influence local fish abundance and diversity are: availability of food (e.g., Hobson 1968, 1972, 1974), proximity to shelter (e.g., Low 1971; Sale 1972), and the presence of "cleaner" fish that rid larger fish of their ectoparasites (Slobodkin and Fishelson 1974). At least some of these factors may also have contributed to the high numbers of fish along our transect line.

After dark, fishes that seek shelter and/or become inactive are no longer attracted by richer feeding grounds and orientation points characteristic of the reef crest. As darkness falls, midwater aggregations of *C. punctipinnis*, *Paralabrax clathratus*, *Girella nigricans*, and young *S. mystinus* dissolve as the fish disperse singly or in small groups over the bottom to shelter in the many holes and crevices in surrounding areas. During the day, for example, individuals of *C.*

punctipinnis occur patchily in small mid-water aggregations over the transect line and in much larger aggregations along the outer margins of the kelp bed. At night, however, they shelter in holes throughout the entire study area. In freshwater lakes of Ontario at night, day-active fishes move into shallow water where there is sufficient cover for sheltering (Emery 1973), but in the tropics, most day-active reef fishes shelter in holes deep in the coral and so their exposed numbers decrease at night (see Hobson 1974).

The decrease in nocturnal abundance of fishes in the transect area might have been caused by their migrations to nearby areas of sand. Over coral reefs, many of the more prominent fishes seen in large stationary schools during the day are actually nocturnal species that leave the reef at dusk (Hobson 1968). Among these are croakers (Sciaenidae), snappers (Lutjanidae), and grunts (Pomadasyidae), which move to surrounding sand flats to feed on their invertebrate prey during the night (see papers by Hobson). However, we found no evidence of a pronounced nocturnal migration of fishes from reef and kelp to the surrounding sand. Essentially all of the fishes observed during the day were accounted for at one part or another of the reef at night. On several occasions at night, while swimming considerable distances over the surrounding sand flats, we saw only species that occur commonly at kelp-bed margins and do not actively forage at night (e.g., *Phanerodon furcatus* and *Damalichthys vacca*), or that typically inhabit sandy bottoms (e.g., the spotted cusk-eel *Chilara taylori*, and various skates and rays). We have occasionally seen relatively inactive schools of black croaker, *Cheilotrema saturnum*, on the reef during the day, and although we have not seen the fish at night, it is possible that they migrate to adjacent sandy areas to feed. Limbaugh (1961) reported that they are most active at night.

In a study of the night habits of coral reef fishes, Starck and Davis (1966) noted that the feeding times of reef fishes are closely related to the type and activities of their prey. Microcarnivorous and omnivorous fishes that browse and pick at sessile organisms are generally active only during the day. Mesocarnivorous fishes (i.e., those that feed on larger motile invertebrate prey) are largely nocturnal, because their prey (e.g., crustaceans) are active and exposed at night. Planktivorous fishes feed during both day and night, the nocturnal species having larger eyes than their diurnal counterparts. Piscivorous fishes feed opportunis-

tically during the day and night, but are most active at dawn and dusk when their prey fish are exposed while moving to and from foraging and sheltering areas. This feeding pattern has also been observed in other tropical areas (Hiatt and Strasburg 1960; Collette and Talbot 1972; Hobson 1974) and in freshwater lakes (Emery 1973).

Kelp-bed fishes also tend to show this general feeding pattern, though perhaps not so distinctly. Small-mouthed microcarnivores that pick or graze sessile invertebrates and hidden prey from off the bottom and other substrates are generally active only during daylight hours. Such foragers, including most of the surfperches, as well as *Oxyjulis californica*, *Pimelometopon pulchrum*, and *Hypsypops rubicundus*, readily converge on urchins broken open during the day, but completely ignore such chum at night.

Also as in the tropics, though less extensively so, different planktivores feed in the mid-water zone of kelp beds during the day and night. The most visible daytime planktivores, *Chromis punctipinnis* and juvenile *S. mystinus*, often form mixed aggregations of individuals that pick small zooplankton from the incoming currents. At night, neither was seen exposed outside its shelter, and individuals collected by spear and later examined had empty stomachs. Instead, the mid-water zone is dominated at night by the large-eyed species, *Hyperprosopon argenteum*, which darts about, actively feeding throughout the water column. Though we have little data on kelp-bed mesocarnivores, some, such as various rockfishes, *Scorpaenichthys marmoratus*, and *Ophiodon elongatus*, may feed at night.

We emphasize the fact that many kelp-bed fishes show considerable intraspecific variability in vertical distribution and feeding activity. Although a large majority of the population of *C. punctipinnis* usually feeds in mid-water during the day, e.g., a few individuals can usually be found in holes. Likewise, a small proportion of the day-sampled individuals of *Embiotoca jacksoni* had empty foreguts even though the species is strictly a diurnal forager. Even more variable is the feeding schedule of *Rhacochilus toxotes*. Most individuals probably have empty guts at any daylight hour, although others are satiated. We have observed that at any given time during the day, most of these surfperch assemble as schools of varying sizes just above the bottom or even in mid-water (see also Alevizon 1975). However, a lone individual may suddenly leave the school to

feed rapidly over the bottom for several minutes before rejoining the same or another school of lazily swimming, nonfeeding fish. But we do not know yet if any particular individuals tend to feed in this sporadic manner during the day to a greater extent than do most others which may feed more consistently during the night. Hobson (1971, 1976) stressed the probably widespread occurrence of individual variation in the tendency of fishes to "clean" ectoparasites from larger host species. Specifically, Hobson (1976) observed that even though cleaning is not considered to be characteristic of the rock wrasse, *Halichoeres semicinctus*, this feeding mode was repeatedly a major activity in what was probably the same individual. Thus, as far as fish activities are concerned, the behavior of an individual is not always predictable from the general characteristics of its species.

Temperate-Tropical Differences

Some phenomena that characterize the day-night change in activities of fishes inhabiting tropical coral reefs appear less well developed or absent in the activity cycles of the Santa Barbara kelp-bed fishes. For one thing, no kelp-bed species that we observed forms inactive schools over the reef during the day and disperses elsewhere to feed at night, as do snappers and grunts in tropical systems. Another noticeable lack in the kelp forests is the widespread replacement of daytime mid-water planktivores by nighttime counterparts. In tropical areas, this replacement involves more species and, to some extent, occurs vertically: at night, the diurnal planktivores (a few pomacentrids, the unusual labrid *Clepticus*, etc.) take refuge in reefs that had provided shelter for the nocturnal planktivores (some holocentrids, apogonids, priacanthids, etc.) during the day (Hobson 1968, 1972; Collette and Talbot 1972). In our kelp-bed system at Naples Reef, however, the only noticeable replacement of the abundant daytime mid-water planktivores is *Hyperprosopon argenteum*, which, moreover, is probably a "horizontal replacement" from inshore areas. In this system, the only common fish that shelters during the day and may emerge at night is *Cephaloscyllium ventriosum*, a rather slow-moving piscivore that probably eats sheltering or inactive prey (Nelson and Johnson 1970). The cryptic demersal mesocarnivores (i.e., carnivores that feed on medium-sized prey, e.g., rockfishes, *Scorpaen-*

ichthys marmoratus, etc.) may shelter either day or night between feeding bouts.

However, feeding on plankton at night may be more widespread in areas farther south. Hobson and Chess (1976) concluded that several species eat plankton at night off Santa Catalina Island. Though they are relatively rare at Naples Reef, for example, individuals of *Sebastes atrovirens* and larger juveniles of *S. serranoides* are important mid-water planktivores at night in kelp beds off Santa Catalina. Also, *Xenistius californiensis* picks plankton in the relatively clear waters around this island, but this species does not commonly occur as far north as Santa Barbara. Naples Reef is located just south of a faunal boundary at Point Conception (cf. Hubbs 1960; Quast 1968; Briggs 1974). Also, our mainland assemblage differs noticeably from nearby insular communities (Ebeling et al. unpubl. data). Nonetheless, it is reassuring to find that many of our results parallel those of Hobson and Chess.

Figure 2 summarizes the day-night distributions of kelp-bed fishes from an evolutionary point of view. Fish are depicted as being distributed vertically, based on their proportionate abundances in each of the four zones, from the mid-water zone to the shelter zone, and as comprising four ecological groups, based on their habits and phylogenetic origins. Belonging to taxa with temperate origins, all species in group A are demersal species of the bottom-habitat group, which generally move but little from their perches on the bottom during the day or night (see Table 4, $\Delta h = 0.42$). Groups B, C, and D are composed of more active species that commonly occur in the suprabenthic zone and in mid-water during the day, but there the similarity ends. Also with temperate origins, species in group B are large-mouthed generalized predators, which can switch from plankton to larger prey including small fishes as the occasion arises (Love 1974), and simply descend to rest on the bottom at night ($\Delta h = 1.92$). Group C and D species are small-mouthed microcarnivores of mixed origins, which either forage over the substrate or pick plankton from mid-water. Group C fishes are all surfperches with a common temperate origin, whose day-night change in vertical position is relatively slight ($\Delta h = 0.22$), and whose nocturnal behavior is relatively unspecialized, in that the fish simply slow down over the bottom and do not generally seek shelter in holes and crevices. But in contrast with all the others, group D fishes appear to be rela-
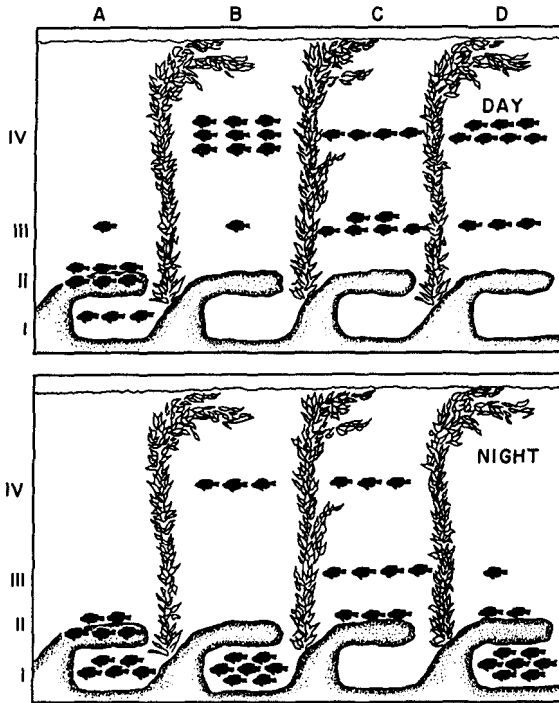
FIGURE 2.—Day and night positions of four ecological groups of fishes inhabiting Santa Barbara kelp beds: A) demersal species (*Coryphopterus nicholsii, Ophiodon elongatus, Oxylebius pictus, Sebastes carnatus, S. chrysomelas, S. serriceps,* and *Scorpaenichthys marmoratus*); B) large-mouthed generalized predators (*Paralabrax clathratus, Sebastes serranoides,* and adult *S. mystinus*); C) surfperches (*Embiotoca jacksoni, E. lateralis, Hypsurus caryi, Phanerodon furcatus, Rhacochilus toxotes,* and *Damalichthys vacca*); D) small-mouthed grazing and picking tropical derivatives (*Chromis punctipinnis, Hypsypops rubicundus, Medialuna californiensis, Oxyjulis californica,* and *Pimelometopon pulchrum*). Vertical zones (I-IV) are defined in Table 1. Each fish symbol represents 10% of the total individuals in the group expressed proportionally to the relative abundances of the different species in the group.

the pictures of renewed (albeit lessened) activity painted of the community of coral reef and outlying sand-flat fishes at night (Starck and Davis 1966; Collette and Talbot 1972; etc.). Perhaps the relatively clear and well-lighted tropical waters are more conducive to nocturnal activity for the many visually oriented fish. Denied much of the moonlight by the dense kelp canopy and frequent low clouds, the relatively turbid, temperate waters are often a dark and gloomy place at night. In fact, even during the day when the water is particularly turbid, the usually active planktivores, grazers, and browsers tend to stop foraging and often seek shelter, as do their tropical counterparts under similar conditions (Collette and Talbot 1972).

It is paradoxical that the "tropical derivatives" (Figure 2D) persist in their complex nocturnal shelter-seeking while many primarily temperate fishes remain exposed. One explanation assumes that selection pressures brought about by nocturnal (or crepuscular) predation are either different or more relaxed in our temperate system of kelp forest and reef than in the tropical reef system. Observing a similar set of circumstances, Hobson (1972) noted that Hawaiian reef fishes, which enjoy a relative dearth of crepuscular predators, show the same specialized sheltering behavior during twilight as do their close relatives in the Gulf of California, which have many such predators. He suggested that these complex behavior patterns may evidence historic selection pressures from predators. These patterns may persist on Hawaiian reefs today even though they are currently perhaps less critical to the survival of the refuge-seeking species than in reef systems elsewhere. An alternative explanation holds that crepuscular and nocturnal predation by, e.g., the Pacific electric ray, is important in kelp beds, but that the tropical derivatives compete more successfully against the primarily temperate species for shelter.

CONCLUSIONS

As indicated by paired day-night observations along a transect line, kelp-bed fishes occur in about the same relative abundances throughout the year in an area of reef and kelp along the mainland side of the Santa Barbara Channel. During the day, most fishes occupy the "mid-water zone" higher than 1 m off the bottom. Far fewer are "exposed on the bottom" or in the "shelter zone" of holes and crevices in the reef itself. During the night, when

tively recent derivatives of primarily tropical families (Pomacentridae, Labridae, etc.), and essentially all show extreme changes in their vertical distribution ($\Delta h = 2.07$) as they actively seek the shelter zone refuge. Some at least, like *Chromis punctipinnis*, are specialized to the extent that they tend to "home" to the same hole on successive nights (Bray unpubl. data).

Thus, in the kelp beds, there is no broad replacement for the "day shift" of fishes at night, even though the fishes' invertebrate prey appear to be more active and exposed then. And, in general, after the dusk period of intensified activity, the notably lackluster night life gives the kelp forest an aura of desolation, as compared with

the number of individuals appears reduced by more than half, most fishes occupy the bottom and shelter zones.

Thus, like that of tropical reefs, the vertical distribution of fishes changes markedly between day and night. Planktivores that pack the mid-water zone during the day virtually abandon the area at night to rest on the bottom or seek shelter in reef holes. The vacated mid-water space is only partly reoccupied by a relatively sparse population of nocturnal planktivores and a few remaining generalized carnivores. The largest relative increase of individuals occurs in the shelter zone, where superabundant daytime planktivores, such as the blacksmith, hide at night. With so many fishes commuting extensively between the mid-water and shelter zones, it is understandable that the intervening suprabenthic zone shows the greatest species similarity between day and night. Many ambusher-type foragers are always oriented to the bottom and change their positions relatively little for the night shift.

It seems likely, therefore, that at night feeding on plankton decreases and most of the foraging by fishes takes place over the bottom. The large-mouthed demersal ambushers—various rockfishes, the cabezon, and others—probably feed almost any time that suitable prey are available. The rubber-lip seaperch may actually feed more actively at night. Nonetheless, many of the fishes that wander over the bottom at night may stop feeding at dusk. Most demersal surfperches remain exposed at night, although their foreguts soon empty, and the fish appear more lethargic than they do during the day when they are actively foraging.

Focal points of daytime fish activity, such as the productive crest of the reef and other prominent landmarks, appear to lose their attractiveness at night. Most aggregations disappear at dusk as fishes generally disperse out over the reef bottom. But unlike many tropical-reef fishes, kelp-bed species do not normally move off the reef to forage over the adjacent sand flats.

Kelp-bed fishes often show considerable intraspecific variation in vertical distribution and feeding activity. During the day, e.g., noticeable numbers of typically mid-water species invariably seek shelter, while at night some individuals remain in the water column. And fishes differ in the intensity at which they feed during any given period during the day. All this suggests that certain individuals may assume and even maintain distinctive habits that differ from the species "norm," i.e., the behavior of a particular fish is not always predictable from the general characteristics of its species.

Thus, in comparing the diel behavior of kelp-bed fishes as a group with that of their tropical counterparts, it becomes apparent that even though both groups follow the same basic patterns, the kelp-bed community is the more loosely "programmed." In the kelp-bed system, for example, there is less large-scale replacement of fishes between discrete areas or vertical zones at dusk. Here, the night shift offers no real substitute for the dense aggregations of daytime planktivores or demersal microcarnivores, even though these fishes' invertebrate prey are active and exposed at night. Perhaps the better lighted tropical waters allow more specialized activities because here the visually oriented fishes can better see what they are doing, even by moonlight. In the kelp forest, the level of fish activity decreases even during the day when the water becomes very turbid, as often happens with the onset of dense blooms of phytoplankton during the spring and summer.

The kelp-bed species that belong primarily to tropical families tend to show the same specialized pattern of nocturnal shelter seeking as do their close tropical relatives, even though the general program of diel activity in the kelp forest appears to be comparatively unstructured. Perhaps the specialized refuge-seeking procedures of kelp-bed pomacentrids and labrids are simply "evolutionary holdovers" that contribute relatively little to the present fitness of these fishes. But alternatively, the "tropical derivatives" may actually compete more successfully against primarily temperate species such as surfperches for shelter on the reef. Even though the intensity of predation at twilight and perhaps at dark may be somewhat less in our temperate system than in the tropics, a few ingenious and effective predators, such as the Pacific electric ray, patrol the Santa Barbara kelp forests throughout the night.

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