Relationships among fishes and their prey in a nearshore sand community off southern California

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Synopsis

Trophic relationships among marine fishes in a nearshore sand environment off southern California showed that the species were distinguished by specific morphological and behavioral features adapted to capture the prey, and evade the predators, that were characteristic of that habitat. Species that foraged primarily by day included the serranid *Paralabrax clathratus*, the embiotocid *Embiotoca jacksoni*, and the labrids *Halichoeres semicinctus* and *Semicossyphus pulcher*. Primarily nocturnal foragers included the ophidiid *Chilara taylori*, the sciaenid *Umbrina roncador*, the embiotocids *Cymatogaster aggregata* and *Hyperprosopon argenteum*, and the pleuronectid *Pleuronichthys coenosus*. The bothid *Citharichthys stigmaeus* regularly fed during both day and night. The major predatory threat to these fishes came from the bothid *Paralichthys californicus*, which was primarily diurnal. In combination, these fishes possessed an array of behavioral and morphological feeding adaptations that closely matched the feeding opportunities present in that habitat. Not only did they consume, as a group, every species identified in samples of organisms from the environment (except the holoplankton, as discussed), they exploited these species over virtually the entire size ranges present. We infer from these circumstances that the species composition of fishes in this community was strongly influenced by the presence of specific feeding opportunities.

Introduction

Many distinctive features of nearshore marine fishes are adaptive because they provide means to capture prey or to thwart predators. This can be inferred from the morphology and behavior of species that interact as predator and prey, as determined by comprehensive studies of food habits (e.g. Hiatt & Strasburg 1960, Randall 1967), especially when the food habits are related to specific morphological features (e.g. Keast & Webb 1966), or to behavior (e.g. Hobson 1974). It follows, then, that interactions between predators and prey should be important forces in determining the species composition, and therefore the diversity, of marine fish communities.

There has been little attempt to study the influence of predator-prey interactions on the species composition of fishes in natural communities. It has been shown that purposeful or inadvertent introductions of exotic predators can alter the species composition in lakes, streams, or other enclosed bodies of water (e.g. Zaret & Paine 1973). And fishery managers have long recognized the potential of regulating prey populations in these habitats by manipulating predators (e.g. Swingle 1949). But these reports described relationships in closed ecosystems, where the interacting species were forced

to contend with selection pressures outside their evolutionary experience. Until now there has been virtually no consideration of how trophic interactions might influence the species composition of fishes in an open marine system, although Stephens & Zerba (1981) suggested that an 'abundant food supply' was one of several factors contributing to the diversity of fishes on a reef in southern California.

This paper shows how the species composition of fishes over a nearshore sand bottom off southern California has been influenced by the need to capture the prey, and to avoid the predators, which are characteristic of that setting. Our account describes feeding behavior, illustrates relevant behavioral and morphological features, and recounts the array of organisms in the environment that represented potential prey.

Of the many studies of trophic relations in fishes, few have attempted to assess the potential food-base, and these few have limited their coverage to just parts of trophic systems, e.g. planktivores and zooplankton (Narver 1970, Hobson & Chess 1978), and other trophic guilds (e.g. Laur & Ebeling 1983). This lack of study reflects the difficulty in coordinating observations of feeding behavior, gut-content samples, and samples of potential prey in the environment. Even when the complex timing problems in sampling have been solved, there remains the highly difficult and time-consuming task of sorting and identifying the many organisms involved. To our knowledge, the present study is the most intensive account yet made of trophic relations among the fishes and other organisms living together in a natural marine habitat.

Methods

Study site

We studied a relatively simple system in an open-sand habitat in Ripper's Cove (Fig. 1), an embayment about 400 × 150 m in area, 9 km east of the Isthmus, on the northern shore of Santa Catalina Island (lat 33° 26' N, long 118° 125' W). The cove, bordered by a sand beach, was floored largely by sand under no more than 15 m of water. At both ends of the cove a rocky substrate forested by giant kelp, *Macrocystis pyrifera*, extended 10–20 m offshore.

The sampling centered around a 50 × 4 m tract established on open sand in 10 m of water, about 100 m from shore, and 50 m from the nearest rocks or kelp. The tract was marked by a fiberglass measuring tape placed only when counts or collections were being made, but an iron rod at each end of the line remained in place during the period of study. The fishes were observed throughout the cove, but specimens collected for gut-content analysis were taken over the open sand, within 20 m of the sampling tract defined above. All fish counts and all samples of organisms that represented the potential prey in the environment were taken in, and directly above, the sampling tract.

Sampling

To effectively relate the organisms taken as prey to the samples of organisms from the environment, we had to reduce the complicating variables associated with seasonal and lunar changes. So all samples were taken at quarter moon during one month, July. And because we knew that distinctive diurnal and nocturnal modes prevail in California nearshore fishes (e.g. Ebeling & Bray 1976), the collections were timed to avoid mixing representations of the two. Thus, fishes collected for gut-content analysis were taken either late in the afternoon, or during the 2 h immediately before first morning light (one exception, noted below) – a practice that has proven effective in distinguishing diurnal and nocturnal feeding among fishes in this region (Hobson & Chess 1976). The corresponding collections of potential prey organisms in the environment were made in the middle of the day (1100–1300 h), and middle of the preceding, or following night (2300–0100 h). We assumed these times were roughly midpoints in the feeding periods of the diurnal and nocturnal fishes, respectively.

Three comparable day/night series of collections, two weeks apart, were made: one at the beginning of the month, one in the middle, and one at the end. The nocturnal collections at the begin-

Fig. 1. Ripper's Cove, Santa Catalina Island, California.

ning and end of the month occurred just before last-quarter moonrise, whereas the nocturnal collections during mid-month occurred just after first-quarter moonset. So while the moon was below the horizon when the samples from the environment were taken, the fishes collected just before dawn on these dates presumably had experienced moonlight during some portion of their feeding periods. The number of samples that could be taken was limited by two constraints: (1) the tight coordination required between the collections of fishes for gut contents, and the collections of prey samples from the environment, and (2) the risk of disturbing this relatively simple system by removing too many of its components from so small an area over such a short time.

Although the data presented in this paper represent events and circumstances during just one month, our interpretations of these data benefit from over 3 yr of intensive study of the nearshore communities of Santa Catalina Island, and over 25 yr of experience with the southern California fauna.

Fishes

Each of the three collection series included both a diurnal and a nocturnal count of post-juvenile fishes seen during one transit of the sampling tract. An underwater light was used during the nocturnal counts. Although early juveniles often were present at night, we omitted them from the counts. This is because when juveniles first appear in benthic habitats they often occur where their behavior and morphology are irrelevant to local conditions (e.g. Hobson 1984), which makes them inappropriate for this study.

The fish specimens collected for gut contents, all taken with spears, were sampled at the specified times of day and night throughout the study period. Shortly after being collected, each specimen was measured, and its digestive tract was removed and preserved in 4% formaldehyde. For analysis, the gut contents were examined under appropriate magnification. Items in the gut were identified to species when feasible, and for each taxon we recorded: number, size range, estimated stage of digestion, and estimated percent of the volume represented by that item.

Potential prey

Visual counts enumerated the few potential prey that could be readily seen. Most organisms, however, were too small, or too cryptic, to be assessed this way, and so were sampled with collecting devices. Each assessment of the benthos involved 9 circular corers, 10 cm in diameter, inserted 3 cm into the sand at roughly 5-m intervals along the 50-m tract line, alternating sides from count to count. Each assessment of organisms in the water column involved nets with 0.333-mm mesh that sampled three levels: 1–2 m above the bottom, 1–2 m below the surface, and at the surface. At each level we pushed the net for 5 min at a speed of 30 cm sec^{-1}. The net used in the near-bottom and near-surface collections had a circular opening 1 m in diameter, whereas the net used at the surface had a 20 × 50 cm rectangular opening, half of which was kept above the water while collecting. Illumination during the nocturnal plankton collections was limited to starlight because artificial light might have influenced the zooplankton.

Species of prey and potential prey selected for analysis

A calculated *level of importance* determined which of the taxa identified in samples from either the fish gut contents or the environment would be included in further analysis as prey or potential prey. Although the level-of-importance values are not presented, they are the basis of the list of *organisms present* used in Tables 2–5. This list, which is repeated for each table, includes all taxa from either the fish gut contents, or the environment, that had a level of importance exceeding the arbitrarily selected value 1.0, based on calculations as follows: For taxa in the gut contents (prey), the levels of importance are the *products of their percent frequency of occurrence, and their mean number, or mean volume* (in the case of a few exceptionally large organisms), *in the guts of any one of the fish species studied*. Similarly, for taxa in collections from the environment (potential prey), the levels of importance are the *products of their percent frequency of occurrence and the mean number pres-*

ent in any one collection, calculated for each sampled segment of the habitat, i.e. the sand, and each of the three levels of the water column. Most of the taxa listed are species, but some higher taxa were included where species could not be distinguished (e.g. natantian larvae), or where such distinction was considered unimportant to this study, and where the level of importance of the group was high (e.g. calanoid copepods). As seen below, only a few of the many organisms collected were excluded from the analysis by this procedure.

Results

During the day the study area appeared as an expanse of open sand, with relatively few visible signs of life (Fig. 2). At night, however, there was a marked increase in both visible numbers and activity among the fishes and other organisms.

Diel patterns in the fishes

Diurnal observations

Of the few species seen during the day (Table 1), some were characteristic of the open-sand habitat, while others were more characteristic of neighboring habitats of rock or algae. Those characteristic of the open sand included three flatfishes: the bothids *Citharichthys stigmaeus* and *Paralichthys californicus*, and the pleuronectid *Pleuronichthys coenosus*. Those more characteristic of rock or algae were the labrids *Halichoeres semicinctus*, and *Semicossyphus pulcher*, the embiotocid *Embiotoca jacksoni*, and the serranid *Paralabrax clathratus*.

The resident flatfishes were inconspicuous due to their concealing coloration and secretive behavior. The two bothids, *C. stigmaeus* and *P. californicus*, frequently went unseen because they were flush with the substrate, often buried, and rarely moved. The small size of *C. stigmaeus* (generally <100 mm SL) helped it go unnoticed (Fig. 3), but *P. californicus* was inconspicuous despite being the largest fish (often >1 m SL) routinely present, day or night (Fig. 4). *P. coenosus*, whose size was intermediate (generally 150–200 mm SL), was the most visible of the three because often its
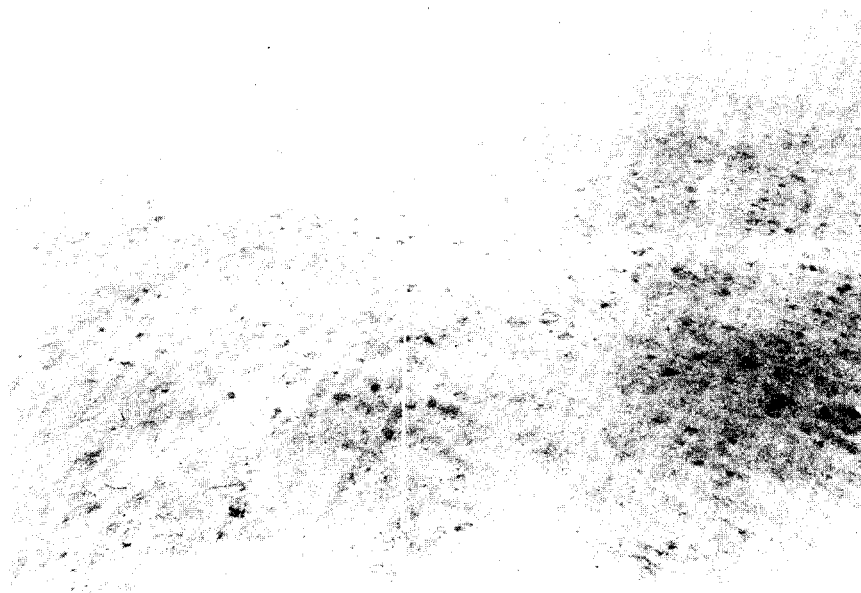
Fig. 2. The transect line in Ripper's Cove.

Table 1. Fishes counted in the sampled tract at Ripper's Cove.[1,2]

Species	Day n = 3		Night n = 3	
	% freq.	x̄ no.	% freq.	x̄ no.
1. *Heterodontus francisci*, horn shark[3]	–	–	0.33	0.3
2. *Cephaloscyllium ventriosum*, swell shark[2]	–	–	0.33	0.3
3. *Chilara taylori*, cusk-eel	–	–	0.67	2.0
4. *Scorpaena guttata*, sculpin[3]	–	–	1.00	2.0
5. *Paralabrax clathratus*, kelp bass	1.00	3.0[4]	1.00	4.3[5]
6. *Anisotremus davidsoni*, sargo[3]	–	–	0.33	1.0
7. *Umbrina roncador*, croaker	–	–	1.00	2.0
8. *Hyperprosopon argenteum*, walleye perch	–	–	0.67	1.7
9. *Cymatogaster aggregata*, shiner perch	–	–	0.67	3.7
10. *Halichoeres semicinctus*, rock wrasse	1.00	2.3	–	–
11. *Semicossyphus pulcher*, sheephead	0.67	1.0	–	–
12. *Pleuronichthys coenosus*, C-O turbot[6]	–	–	1.00	4.3
13. *Paralichthys californicus*, halibut	–	–	0.33	0.3

[1] The counts generally were consistent with what was seen in the area, but two species unrepresented in the counts frequently were present; *Embiotoca jacksoni*, the black perch, was often present during the day, and *Citharichthys stigmaeus*, the sand dab, was present day and night.

[2] Adults and subadults only. Juvenile embiotocids (surfperches) were numerous and widespread nearshore during this season and some were in the transect at night, including *Embiotoca jacksoni*, *Damalichthys vacca* and *Brachyistius frenatus*.

[3] Not considered in this paper owing to infrequent occurrence in study area.

[4] During the day all those counted in the transects, or seen in the area, were adults.

[5] At night, 77% of those counted in the transects, and about the same proportions of those seen in the area, were subadults.

[6] Frequently present in the transect during the day, although not during the counts.

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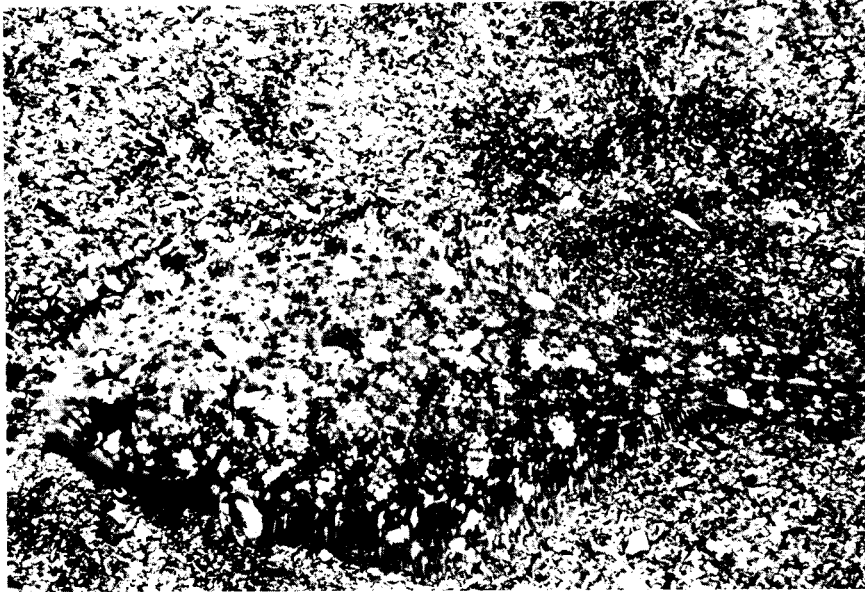
Fig. 3. The speckled sanddab, *Citharichthys stigmaeus*. A laterally compressed body, which permits lying flush on the substrate, and the ability to match its coloration to the color and texture of the surrounding sediment, enables this species to go unseen by both predators and prey. Its relatively large eyes also suit it for activity in dim light.

Fig. 4. The California halibut, *Paralichthys californicus*. Its laterally compressed body, large mouth with long canine teeth, and habit of resting motionless under a covering of sand, adapt this species to its habit of ambushing small fishes in the open-sand habitat.
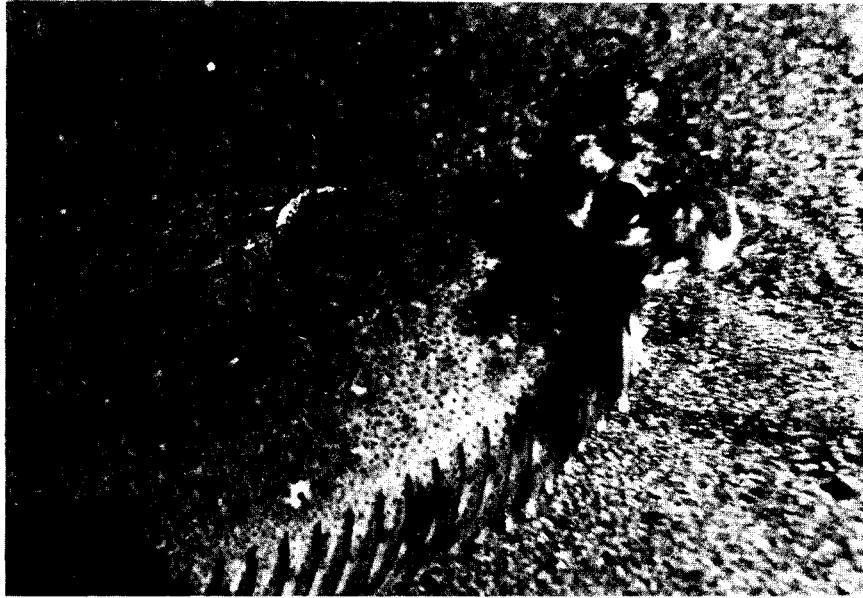
Fig. 5. The C-O sole, *Pleuronichthys coenosus*, with its forebody raised on dorsal and anal fins, and its exceptionally large, highly mobile eyes set on either side of a high, narrow ridge. This fish is suited to scan the surrounding sea floor in dim light, and its downward-projecting mouth is suited to be driven into the sediment for prey.

forebody was elevated on dorsal and anal fins, so that its head was poised above the substrate. From this position, *P. coenosus* scanned its surroundings with mobile eyes oriented vertically on either side of a high, narrow ridge, almost as if in a turret (Fig. 5). Although *P. coenosus* generally appeared inactive in daylight, occasionally an individual that had been immobile moved a meter or more across the bottom, then drove its head into the sand, apparently to feed.

Individuals of the four species more characteristic of neighboring habitats were relatively conspicuous when they swam into the study area. *Halichoeres semicinctus, Semicossyphus pulcher* and *Embiotoca jacksoni* continually moved about and foraged in the sand, whereas *Paralabrax clathratus* often hovered close above the sand (Fig. 6). Usually *H. semicinctus* was solitary, and much of the time made close visual inspections of the substrate (Fig. 7). Frequently it picked at the surface of the sand, apparently targeting individual prey, but also incidentally ingesting some sediment. *S. pulcher,* too, usually was solitary, but spent far less time

than *H. semicinctus* overtly inspecting the substrate and made fewer attempts to feed. It appeared to target individual prey, but often rooted in the sand (Fig. 8), and in so doing ingested much sediment, most of which it vented from its mouth and gill openings. *E. jacksoni,* which usually foraged in small groups of two or more, did not spend the time in close visual inspection so characteristic of *H. semicinctus* but spent more time ingesting food. Typically it took mouthfuls of sediment, and only then appeared to distinguish edible from inedible materials before venting clouds of debris from mouth and gill openings. Thus, it did not appear to target individual prey, as did the others and, also unlike the others, it appeared to take sediment intentionally (see Schmitt & Coyer 1982, Laur & Ebeling 1983). We only occasionally saw *P. clathratus* feed during the day; its attacks, all launched from its hovering position at prey on or close to the sand, were infrequent.
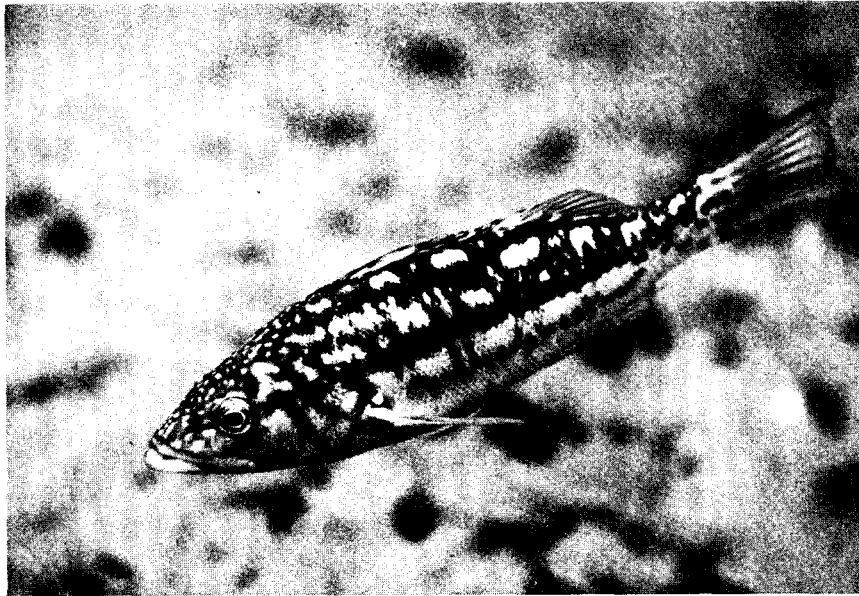
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Fig. 6. The kelp bass, *Paralabrax clathratus.* The coloration of this species is better-suited to the kelp forest which is its regular habitat. Nevertheless, its stalking mode of predation is suited to detect and capture prey that are only occasionally exposed or otherwise vulnerable – which is characteristic of many small organisms in the open-sand habitat.

Nocturnal observations

Of the increased number of fishes seen in the study area after dark (Table 1), some were in the open-sand habitat during both day and night, whereas others were there only at night. Of the species typically in the open-sand habitat during both day and night, three were described above – the flat-fishes *Citharichthys stigmaeus, Paralichthys californicus,* and *Pleuronichthys coenosus.* The fourth, the ophidiid *Chilara taylori,* was not seen in daylight because it was buried in the sand. *C. taylori* did not emerge from the sand until about 3 h after sunset, which was at least 2 h after the other nocturnal feeders had become active. When feeding, *C. taylori* swam close to the bottom, and probed in the sand with its barbel-like pelvic fins (Fig. 9). It reentered the sand about 3 h before sunrise, which was at least 2 h before the other nocturnal feeders in the study area ceased foraging. Owing to its distinctive diel activity pattern, *C. taylori* was sampled for gut contents between midnight and 0100 h.

The fishes that entered the study area only at night used the open-sand habitat as a major feeding ground. These included the embiotocids *Hyperprosopon argenteum* (Fig. 10) and *Cymatogaster aggregata* (Fig. 11), and also the sciaenid *Umbrina roncador* (Fig. 12). Foraging individuals of *H. argenteum* swam loosely spaced in groups in the water column, whereas those of *C. aggregata* hovered loosely spaced in groups, or as individuals, within a meter of the sand. Although prominent over the open sand at night, these three species spent the day in relatively inactive schools in neighboring habitats shoreward: *H. argenteum* and *C. aggregata* schooled over rocks and algae, while *U. roncador* schooled over sand near the beach. (Many *C. aggregata* also foraged by day in small groups on the sand close to rocks, and some *U. roncador* also foraged by day near their diurnal schools.)

The daytime foragers noted above as more characteristic of neighboring habitats – *Halichoeres semicinctus, Semicossyphus pulcher, Embiotoca jacksoni,* and *Paralabrax clathratus* – had returned
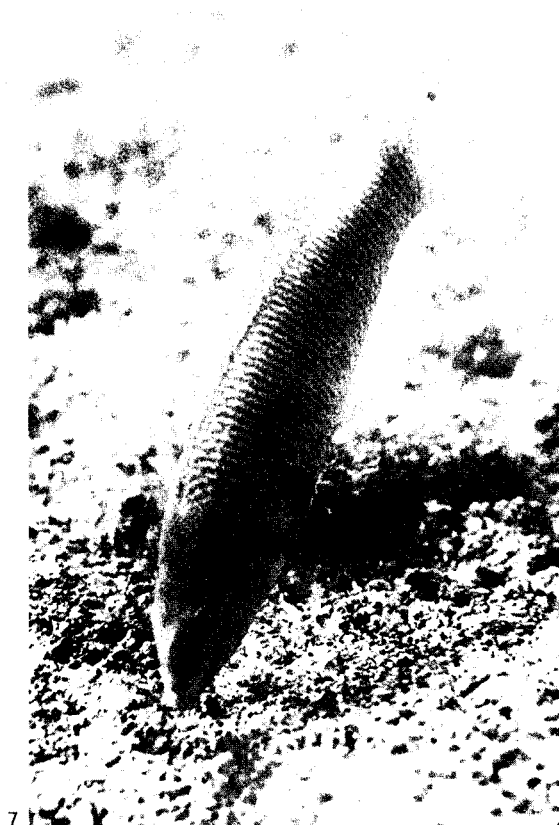
Fig. 7. The rock wrasse, *Halichoeres semicinctus*. The strictly diurnal habits and manner of intently gazing at the substrate for long periods before plucking, suggest that this species depends on acute vision to detect cryptic prey. Its pointed snout and small mouth with large canine teeth at the front of its jaws are well-adapted to pluck small organisms from the sand.

Fig. 8. The California sheephead, *Semicossyphus pulcher*. The large mouth, strong canine and pharyngeal teeth, with highly developed ability to winnow edibles from other material, permit this species to excavate, crush and ingest the heavily armored, often buried organisms, like mollusks, that are major prey. Note cloud of debris being ejected from gill openings.

to their more typical habitats by nightfall, where, like others of their kind, they sheltered amid rocks and algae (Fig. 13). The increased numbers of *P. clathratus* in the study area at night (Table 1) involved primarily subadults that were not there during the day. (Most *P. clathratus* in the study area by day were adults.) The subadult *P. clathratus* in Ripper's Cove generally were in the rock and algae habitats during daylight, but at nightfall many of them scattered over the open sand. (See Hobson et al. 1981)

Diel patterns in potential prey

Other than fishes, the only species readily observed in the study area was the holothurian *Parastichopus parvimensis*, nine of which were counted within the sampling tract during one daytime transit. With closer visual inspection of ten 0.25-m² quadrats set at 5-m intervals along the tract line, three additional species were enumerated. These were (values given are frequency of occurrence: mean number: range of numbers) the tubiculous polychaete *Spiochaetopterus costarum* (1.00:58.2:18–102), the

Fig. 9. The spotted cusk-eel, *Chilara taylori*. The eel-like body of this fish permits it to shelter in the sand by day. Although its large eyes enhance its ability to see prey and predators during its nocturnal forays, apparently at least much of its prey are detected by its modified pelvic fins, shown here probing the sand.
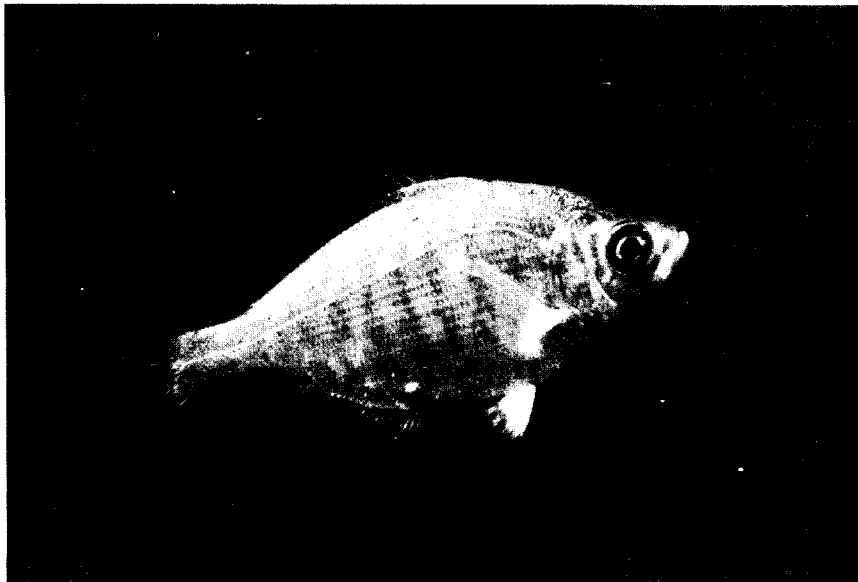
Fig. 10. The walleye surfperch, *Hyperprosopon argenteum*. Exceptionally large eyes suit this planktivore for its nocturnal hunting habits. Its upturned mouth, a characteristic of specialized planktivores, results from a shortened snout that places its eyes in position for binocular vision when targeting on small prey close ahead (W. A. Starck, cited in Rosenblatt 1967).
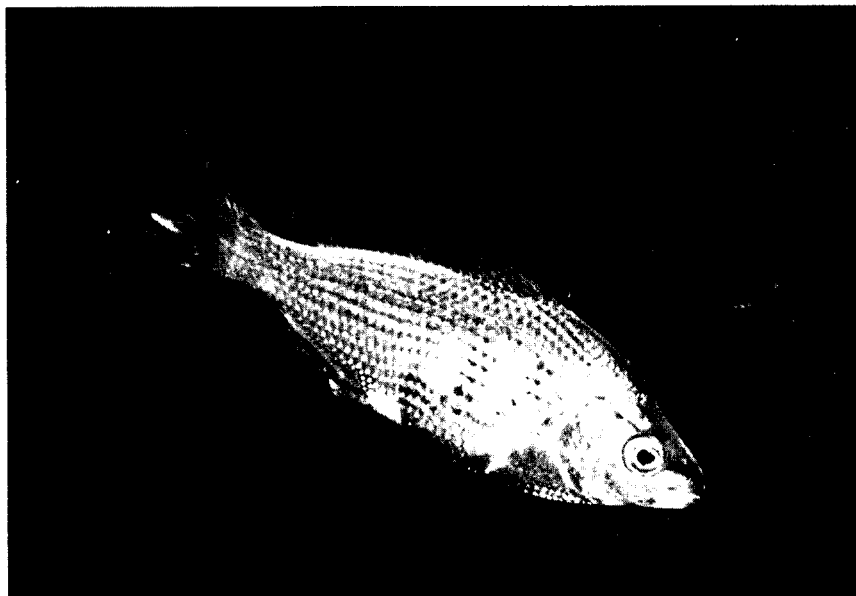
Fig. 11. The shiner perch. *Cymatogaster aggregata.* With generalized trophic features, this species is more versatile in its feeding than the others (see Hobson et al. 1981). Its slightly underslung lower jaw, however, is well-suited to its major adult feeding mode of taking prey on or close to the sand. It does this primarily at night, when reflected moonlight or starlight probably permits visual nocturnal hunting even with eyes not noticeably large.
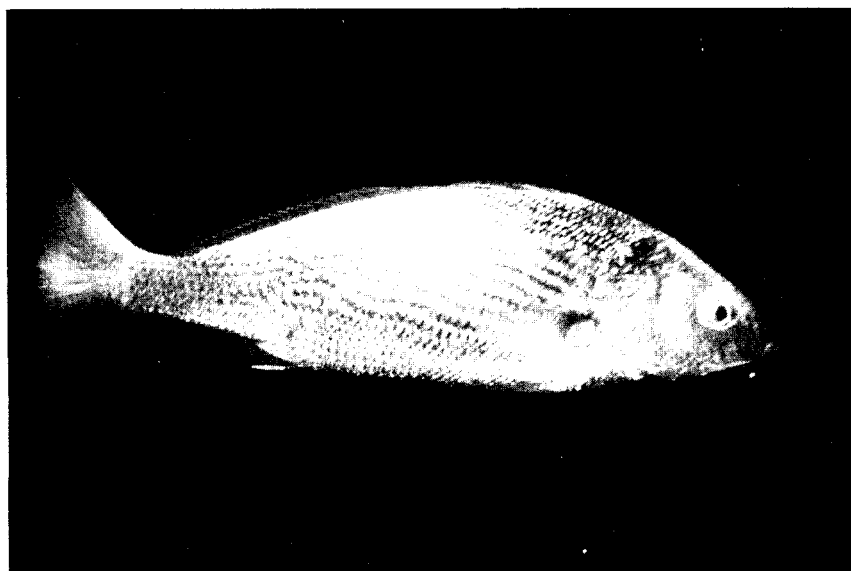
Fig. 12. The yellowfin croaker. *Umbrina roncador.* The stout conical snout projecting above the mouth, and underslung lower jaw with a single, short barbel, suit this fish for foraging in the sand.

Fig. 13. The black perch, *Embiotoca jacksoni*, a diurnal feeder, here in benthic algae at night. Although the coloration of this species is better-suited to habitats rich in vegetation, it nevertheless finds the open-sand habitat a productive foraging ground because its ability to winnow edibles from inedibles allows it to extract the many prey in heavy loads of ingested sediment.

phoronid *Phoronis vancouverensis* (0.2:0.2:0–1), and the gastropod *Olivella biplicata* (0.2:0.2:0–1). Perhaps the most visible biotic features (certainly the most visible in Fig. 1) were the sand castings produced by *P. parvimensis* (occurrence in quadrats was 0.9:1.9:0–4). These forms were counted just once, because experience elsewhere (unpublished data) had indicated that during this study their numbers would not change in ways relevant to topics considered here.

The vast majority of organisms considered as potential prey could not be assessed visually, but our collections showed that many were distributed differently between day and night (Table 2). Particularly striking, great numbers of them, mostly crustaceans, migrated upward in the water column after dark, including many that were benthonic by day. Thus, the numbers of zooplankters collected after dark in the upper level of the water column and at the surface increased almost fourfold over the numbers that were collected there during the day. Although the vertical migrations of most were limited, at least four species – the ostracods *Para-*

sterope sp. and *Rutiderma lomae* (males only), the isopod *Eurydice caudata*, and the gammaridean *Paraphoxus heterocuspidatus* – migrated from the benthos all the way through the water column to concentrate at the water's surface. Although most diel vertical migrations involved movement upward at night, limited evidence indicates the reverse in at least some fish larvae (Table 2).

Trophic relationships

Each of the fish species that foraged in Ripper's Cove took just certain of the many organisms present – some by day (Table 3), others at night (Table 4). As a group, however, they consumed virtually all sizes of every species identified in our samples of potential prey in the environment (Tables 2 and 5) – except the holoplankton, none of which were taken. With two exceptions (noted below), these fishes were benthivores, and those that foraged by day took many prey of species also taken by those that foraged at night. Of the 31 prey categories distinguished as species, 21 (67.7%) were taken

Table 2. Diel distributions of organisms in Ripper's Cove.[1]

Organisms present[2]	Day				Night			
	Bottom (3cm×1m²)	Water column (10m×1m²)			Bottom (3cm×1m²)	Water column (10m×1m²)		
	In sand n = 27	Lower 5m n = 3	Upper 5m n = 3	Surface 0.1m n = 3	In sand n = 27	Lower 5m n = 3	Upper 5m n = 3	Surface 0.1m n = 3
FORAMINIFERA								
Tretomphalus sp.	0	0.55	0	0	0	0	2.35	0.65
POLYCHAETA								
Nothria stigmatis	367.97	0	0	0	296.66	0	0	0
Owenia collaris	278.84	0	0	0	282.66	0	0	0
Spiochaetopterus costarum	38.20	0	0	0	38.20	0	0	0
Others	1,097.53	0	0	0	957.48	0	0	0
MOLLUSCA								
Veligers	0	0.40	0.05	0	0	0.40	2.10	0.69
Crenella divaricata	52.20	0	0	0	42.02	0	0	0
Parvilucina approximata	80.21	0	0	0	108.23	0	0	0
Lyonsia californica	14.01	0	0	0	24.19	0	0	0
Tellina modesta	357.78	0	0	0	376.88	0	0	0
CLADOCERA								
Evadne sp.	0	55.15	48.75	0.04	0	48.80	123.60	7.65
OSTRACODA								
Euphilomedes carcharodonta	471.10	0	0	0	631.53	0	0	0.30
Parasterope sp.	188.44	0	0	0	122.23	1.45	0.25	4.35
Rutiderma lomae	19.10	0	0	0	14.01	0	0.09	1.09
Others	127.32	0	0	0	147.70	1.05	0.20	0
COPEPODA								
Calanoids, various spp.	0	619.85	47.85	1.95	95.5	613.05	726.20	19.65
Cyclopoids, various spp.	14.01	2.15	0.60	0	0	4.00	6.60	0.80
Harpacticoids, various spp.	14.01	0.30	0	0	71.30	0	0	0.02
MYSIDACEA								
Erythropinid sp.	0	0	0	0	14.01	15.65	0.85	0
Siriella pacifica[3]	0	0	0	0	0	4.35	0.70	2.87
Others	5.09	0	0	0	5.09	0.35	0.05	0.04
CUMACEA								
Cyclaspis nubila	1,508.79	0	0	0	1,320.35	8.85	0.35	0
Others	42.02	0	0	0	61.12	0.35	0.05	0.85
TANAIDACEA								
Leptochelia dubia	292.85	0	0	0	240.64	0.10	1.00	0.05
Others	8.91	0	0	0	0	0	0	0
ISOPODA								
Eurydice caudata	5.09	0	0	0	5.09	0.25	0.15	3.01
Exosphaeroma rhomburum	47.11	0	0	0	28.01	0.05	0	0
Others	0	0	0	0	0	0	0.10	0
GAMMARIDAE								
Acuminodeutopus heteruropus	11,002.06	0	0	0	12,456.73	0	0	0
Ampelisca cristata	816.15	0	0	0	1,187.93	0.15	0	0
Amphideutopus oculatus	420.17	0	0	0	495.29	0	0	0
Batea transversa[3]	0	0	0	0	28.01	11.85	2.05	0.01
Ericthonias braziliensis	891.27	0	0	0	1,051.70	0	0	0
Metaphoxus frequens	1,381.46	0	0	0	1,838.25	0.05	0	0.01
Monoculodes hartmanae	240.64	0	0	0	263.56	2.05	0	0
Paraphoxus heterocuspidatus	2,810.04	0	0	0	2,438.25	0.05	0	0.50

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Organisms present[2]	Day Bottom (3 cm × 1 m²) In sand n = 27	Day Water column (10 m × 1 m²) Lower 5 m n = 3	Day Upper 5 m n = 3	Day Surface 0.1 m n = 3	Night Bottom (3 cm × 1 m²) In sand n = 27	Night Water column (10 m × 1 m²) Lower 5 m n = 3	Night Upper 5 m n = 3	Night Surface 0.1 m n = 3
Photis brevipes	85.31	0	0	0	113.32	0	0	0
Rudilemboides stenopropodus	406.16	0	0	0	296.66	0	0	0
Synchelidium rectipalmum	240.64	0	0	0	226.64	0.65	0	0
Others	654.45	0	0	0	1,137.00	0.75	0.90	0
CAPRELLIDAE								
Caprella pilidigita	5.09	0	0	0	14.01	0	0	0
Mayerella banksia	296.66	0	0	0	179.53	0	0	0
Others	85.31	0	0	0	28.01	0.40	0	0.01
NATANTIA								
Larvae and juveniles	0	0	0.05	0.02	10.19	63.95	91.20	0.08
Crangon holmsi	5.09	0	0	0	8.91	0	0	0
Others	0	0	0	0	0	0	0	0
REPTANTIA								
Zoeae	0	0	0	0	5.09	11.10	27.60	0.50
Others	0	0	0	0	0	0	0.10	0
ECHINODERMATA								
Dendraster excentricus	56.02	0	0	0	61.12	0	0	0
Others	28.01	0	0	0	43.29	0	0	0
CHAETOGNATHA								
Various spp.	0	2.85	4.15	0.05	0	2.25	14.55	0.16
LARVACEA								
Various spp.	0	2.70	0	0	0	1.15	9.15	0.90
FISHES								
Eggs (planktonic)	0	42.15	184.65	2.27	0	20.50	37.45	4.33
Larvae	0	0.25	0.10	0.01	0	1.10	0.25	0
Others	0	0	0	0	8.91	0	0	0.01
MISCELLANEOUS[4]	117.14	2.50	4.50	0.06	81.49	0.01	0.13	0.09

[1] Tabulated values are estimated mean numbers present within the designated segments of a hypothetical 1-m² × 10-m high column that extends from the sand to the water's surface. The values were derived as follows: (1) *Bottom, in sand.* – The estimated mean numbers of organisms in the sand (to a depth of 3 cm) at the base of the column were extrapolated from the mean numbers collected in the circular cores (r = 0.05 m) by multiplying by 127.324 (based on the relationships of A = πr^2). (2) *Water column, lower.* – The estimated mean numbers in the lower 5 m of the water column were extrapolated from the mean number collected in the circular plankton net (r = 0.5 m) 2–3 m above the sand by multiplying by 0.0787 (based on the volume of water filtered during each collection, 70.868 m³, as calculated from collection time and net speed: see Methods). (3) *Water column, upper.* – The estimated numbers in the upper 5 m of the water column were extrapolated as for the lower water column, but from the collections within 2–3 m of the water's surface. (4) *Water column, surface.* – The estimated mean numbers in the column within 0.1 m of the surface were extrapolated from mean numbers collected in the modified plankton net (0.5 m × 0.2 m rectangular opening, half-submerged: see Methods) by multiplying by 0.0222 (based on the water filtered, 4.5 m³, as calculated from collection time and net speed).

[2] The list includes all taxa designated as important, either in the habitat or in the gut contents, by the procedures described in Methods. The category 'others' in the list includes the species whose calculated level of importance was below the designated level, and also a variety of individuals that could not be identified to species (presumably many of these were young stages of species distinguishable only as adults and these are included among the unidentified taxa of that group).

[3] *Siriella pacifica* and *Batea transversa* inhabit algae during the day (Hobson & Chess 1976). Their absence in our daytime collections suggests that those we collected at night came from daytime shelter in neighboring habitats.

[4] Includes those collected in small numbers that are not referable to one of the other categories. Figures for diurnal water column inflated by large numbers of bryozoan and cirripedian larvae that were present one day.

Table 3. Mean numbers of prey taken by the major fish species during the day from among the organisms present in Ripper's Cove.

Organisms present[2]	Fish species[1] 1. *Paralabrax clathratus* n = 4 (1 empty) 115.9 (89–140) mm SL 2. *Embiotoca jacksoni* n = 4 (0 empty) 137.8 (113–165) mm SL 3. *Halichoeres semicinctus* n = 10 (0 empty) 171.1 (106–218) mm SL 4. *Semicossyphus pulcher* n = 6 (0 empty) 221.7 (206–265) mm SL 5. *Citharichthys stigmaeus* n = 4 (0 empty) 81.3 (63–94) mm SL 6. *Pleuronichthys coenosus* n = 4 (2 empty) 180 (170–190) mm SL					
	1	2	3	4	5	6
FORAMINIFERA						
Tretomphalus sp.	0	0	0	0	0	0
POLYCHAETA						
Nothria stigmatis	0	0	0	0	0	0.5
Owenia collaris	0	0	1.0	0.3	0	0
Spiochaetopterus costarum	0	3.8[3]	7.7	0.3	1.0	0
Others	0	0	4.1	4.0	1.0	1.0
MOLLUSCA						
Veligers	0	0	0	0	0	0
Crenella divaricata	0	3.8	0.3	3.3	0	0
Parvilucina approximata	0	0	0.1	3.2	0	0
Lyonsia californica	0	0.3	0.3	1.8	0	0
Tellina modesta	0	0	0.4	9.7	0	0.5
Others	0	0.3	1.4	8.6[4]	0	0
CLADOCERA						
Evadne sp.	0	0	0	0	0	0
OSTRACODA						
Euphilomedes carcharodonta	0.3	2.3	0.8	1.2	0	0
Parasterope sp.	0	7.0	0.8	0.3	0	0
Rutiderma lomae	0	0	0	0	0	0
Others	0.3	1.5	0.3	0	0	0
COPEPODA						
Calanoids, various spp.	0	0	0	0	0	0
Cyclopoids, various spp.	0	0	0	0	0	0
Harpacticoids, various spp.	0	0	0	0	0	0
MYSIDACEA						
Erythropinid sp.	0	0	0	0	0	0
Siriella pacifica	0	0	0	0	0	0
Others	0	0	0	0	0	0
CUMACEA						
Cyclaspis nubila	0.3	13.8	3.5	0	0.3	0
Others	0	0.5	0	0	1.0	0
TANAIDACEA						
Leptochelia dubia	0.3	6.5	3.6	0	0	0
Others	0	0	0	0	0	0
ISOPODA						
Eurydice caudata	0	0	0	0	0	0
Exosphaeroma rhomburum	0	0	0	0	0	0
Others	0	4.3	0	0	0.8	0
GAMMARIDEA						
Acuminodeutopus heteruropus	10.7	126.3	22.9	0.3	4.3	0
Ampelisca cristata	0.7	3.3	0.7	11.2	1.5	24.5
Amphideutopus oculatus	0	2.1	0.1	0	0	0
Batea transversa	0	0	0	0	0	0
Ericthonias braziliensis	1.0	16.3	1.5	0	0.5	0
Metaphoxus frequens	0.7	5.5	1.6	0	0	0.5
Monoculodes hartmanae	0	1.5	0.8	0.3	1.0	0

Table 3. (Continued).

Organisms present[2]	Fish species					
	1	2	3	4	5	6
Paraphoxus heterocuspidatus	0	0.8	0.6	1.5	0	0
Photis brevipes	0	13.8	45.2	0.5	0	0
Rudilemboides stenopropodus	0.7	3.3	0.9	1.0	0	0
Synchelidium rectipalmum	0	0.8	0.1	0	0	0
Others	5.0	87.7	28.3	15.2	0.8	0
CAPRELLIDAE						
Caprella pilidigita	0.3	0	4.0	0	0	0
Mayerella banksia	1.0	1.0	3.8	0	0.3	0
Others	4.3	2.0	0	0	0	0
NATANTIA						
Larvae and juveniles	0	0	0	0	0	0
Crangon holmsi	0	0	0	0	0	0
Others	0	0	0.1	0.5	0	0
REPTANTIA						
Zoeae	0	0	0	0	0	0
Others	0	0	0	0.5	0	0
ECHINODERMATA						
Dendraster excentricus	0	0	0.3	9.3	0	0
Others	0	0		0.3	0	0
CHAETOGNATHA						
Various spp.	0	0	0	0	0	0
LARVACEA						
Various spp.	0	0	0	0	0	0
FISHES						
Eggs (pelagic)	0	0	0	0	0	0
Larvae	0	0	0	0	0	0
Others	1.3	0	0	0	0	0
MISCELLANEOUS	0	0	1.3	4.0	0	0
SAND ($\bar{x}$ % of diet volume)	6.3	17.3	10.6	8.5	0	7.5

[1] For all species, size range of specimens approximated size range of individuals present.

[2] See Footnote 1, Table 2.

[3] Tube fragments only.

[4] Fragments of relatively large, heavily-shelled bivalves (including *Americardium biangulata*) and gastropods (*Lirularia* sp. and *Olivella baetica*). Most larger items in the gut contents of *S. pulcher* even when fresh, were crushed. Often this made identification difficult, and measurements only estimates.

during both day and night, whereas only 4 (12.9%) were taken strictly by day, and 6 (19.4%) were taken just at night. Species not taken in similar numbers during both day and night included the more sedentary, heavily armored forms like mollusks and echinoids, which were prey primarily of the diurnal feeders, and the polychaetes, which were prey primarily of the nocturnal feeders. The two fish species that did not forage on the benthos were *Paralichthys californicus* and *Hyperprosopon argenteum*. We did not examine gut contents of *P.*

californicus from Ripper's Cove, but reportedly the species feeds primarily by day (Haaker 1975) on smaller fishes of the types considered here as predators (Limbaugh 1955, Quast 1968). *H. argenteum*, a nocturnal planktivore, did not prey on holoplankters (most <2 mm; Table 5), even though holoplankters constituted the majority of nighttime zooplankton; rather, it preyed entirely on certain forms (most >2 mm; Table 5) that were among the zooplankton only after dark (Table 2).

Table 4. Mean numbers of prey taken by the major fish species at night from among the organisms present in Ripper's Cove.

Fish species[1]
1. *Chilara taylori* n = 11 (1 empty) 129.9 (109–152) mm SL
2. *Paralabrax clathratus* n = 11 (5 empty) 100.1 (72–148) mm SL
3. *Umbrina roncador* n = 8 (0 empty) 201 (191–228) mm SL
4. *Cymatogaster aggregata* n = 15 (1 empty) 98.6 (70–109) mm SL
5. *Hyperprosopon argenteum* n = 10 (0 empty) 110.5 (110–148) mm SL
6. *Citharichthys stigmaeus* n = 8 (2 empty) 56 (42–65) mm SL
7. *Pleuronichthys coenusus* (sm) n = 5 (0 empty) 86 (60–115) mm SL
8. *Pleuronichthys coenosus* (lg) n = 5 (1 empty) 153.3 (140–167) mm SL

Organisms present[2]	1	2	3	4	5	6	7	8
FORAMINIFERA								
Tretomphalus sp.	0	0	0	0	0	0	0	0
POLYCHAETA								
Nothria stigmatis	0	0	24.9	0	0	0.2	0.6	2.3
Owenia collaris	0	0	0	0	0	0	0	0
Spiochaetopterus costarum	0	0	0	2.1	0	6.0	0	76.5
Others	0	0	2.3	0	0.3	0	0.2	2.3
MOLLUSCA								
Veligers	0	0	0	0	0	0	0	0
Crenella divaricata	0	0	0	0.1	0	0	0	0
Parvilucina approximata	0	0	0	0	0	0	0	0
Lyonsia californica	0	0	0.1	0.1	0	0	0	0
Tellina modesta	0	0	0	0	0	0	0	0
Others	0	0	0.1	0	0	0	0	0.3
CLADOCERA								
Evadne sp.	0	0	0	0	0	0	0	0
OSTRACODA								
Euphilomedes carcharodonta	0	0	0	1.8	0.2	0	0	0
Parasterope sp.	0	0	0.3	0.1	2.3	0	0	0
Rutiderma lomae	0	0	0	0	0.3	0	0	0
Others	0	0	0	0.4	0.1	0	0	0
COPEPODA								
Calanoids, various spp.	0	0	0	0	0	0	0	0
Cyclopoids, various spp.	0	0	0	0	0	0	0	0
Harpacticoids, various spp.	0	0	0	0	0	0	0	0
Others	0	0.2	0	0	0	0	0	0
MYSIDACEA								
Erythropinid sp.	0	0.2	0	0	0	0	0	0
Siriella pacifica	0	0	0	0	1.6	0	0	0
Others	0	0.7	0	0	0.2	0	0	0
CUMACEA								
Cyclaspis nubila	0.2	0.2	0.4	9.3	10.9	0.3	0.4	0
Others	0	0	0.3	0.1	2.6	0	0	0
TANAIDACEA								
Leptochelia dubia	0	0	0.3	5.1	3.0	0	0	0
Others	0	0	0	0	0.4	0	0	0
ISOPODA								
Eurydice caudata	0	0	0	0	0.2	0	0	0
Exosphaeroma rhomburum	0	0.2	0	0.4	0.1	0	0	0
Others	0	0.2	0	0.1	1.0	0	0	0
GAMMARIDEA								
Acuminodeutopus heteruropus	1.5	0.2	1.5	66.9	0	1.5	2.2	0

Table 4. (Continued).

Organisms present[2]	Fish species							
	1	2	3	4	5	6	7	8
Ampelisca cristata	7.2	0.5	35.3	3.8	4.4	2.0	8.4	4.8
Amphideutopus oculatus	0.6	0.3	1.5	1.0	0	0	0.4	0
Batea transversa	0	0.3	0	0.1	85.3	0	0	0
Ericthonias braziliensis	0.2	0	0	3.5	0	0	0	0
Metaphoxus frequens	0	0	0.4	1.1	1.0	0	0	0.3
Monoculodes hartmanae	0.4	0	0.6	1.7	1.3	0.2	0	0.3
Paraphoxus heterocuspidatus	0.1	0	3.4	0.1	2.4	0.2	0	0
Photis brevipes	1.9	0	2.3	4.1	0	2.4	2.4	4.0
Rudilemboides stenopropodus	0	0.2	0.5	4.6	0	0.2	1.2	0
Synchelidium rectipalmum	0	0	0.3	0.4	0.1	0	0	0
Others	0.8	0.3	1.4	25.6	37.3	0.5	0.4	1.5
CAPRELLIDAE								
Caprella pilidigita	0	0.3	0	0.9	9.7	0	0	0.3
Mayerella banksia	0	0	0	0.2	0	0	0	0.8
Others	0	1.6	0.3	0.4	0	0	0	0
NATANTIA								
Larvae and juveniles	0	0	0	0	0	0	0	0
Crangon holmsi	0.8	0	0.4	0	0	0	0	0
Others	0	0.2	0.1	0	0.1	0.2	0.2	0
REPTANTIA								
Zoeae	0	0	0	0	0	0	0	0
Others	0	0	0	0	0	0	0	0
ECHINODERMATA								
Dendraster excentricus	0	0	0	0	0	0	0	0
Others	0	0	0	0	0	0	0	0
CHAETOGNATHA								
Various spp.	0	0	0	0	0	0	0	0
LARVACEA								
Various spp.	0	0	0	0	0	0	0	0
FISHES								
Eggs (pelagic)	0	0	0	0	0	0	0	0
Larvae	0	0	0	0	0	0	0	0
Others	0.1	0.3	0	0	0	0	0	0
MISCELLANEOUS	0	0	0.4	0	0.9	0	0.4	0
SAND ($\bar{x}$ % of diet volume)	0	0	5.5	14.9	0	0	0	0

[1] See Footnote 1, Table 3.
[2] See Footnote 1, Table 2.

Discussion

Structurally and behaviorally, the fishes that frequented the open-sand habitat in Ripper's Cove were a diverse group, and much of their diversity related to the ways they extracted food from the environment. Their thoroughness in exploiting the prey resources of this habitat resulted from having an array of feeding adaptations that closely matched the array of feeding opportunities present. Based on these facts, and considering diurnal and nocturnal conditions separately, we first discuss how characteristic trophic features in these species meet requirements of foraging in the open-sand habitat. We then generalize from these findings to consider predator-prey relations as primary

Table 5. Sizes of organisms in collections from the habitat and in gut contents of the fishes.

Organisms present[1]	Size ranges (mm)					
	Day			Night		
	Sand	Plankton	Prey	Sand	Plankton	Prey
FORAMINIFERA						
Tretomphalus sp.	–	0.3–0.5	–	–	0.3–0.7	–
POLYCHAETA						
Nothria stigmatis	5.0–20.0	–	10.0	4.0–30.0	–	8.0–28.0
Owenia collaris	10.0–26.0	–	N.R.[2]	12.0–35.0	–	N.R.
Spiochaetopterus costarum	12.0	–	10.0–15.0	10.0–20.0	–	2.0–15.0
Others	2.0–30.0	–	8.0–12.0	1.0–55.0	3.0–18.0	8.0–15.0
MOLLUSCA						
Veligers	–	0.5	–	–	0.5–1.0	–
Crenella divaricata	2.0–3.0	–	1.0–4.0	1.0–3.0	–	2.0–4.0
Parvilucina approximata	2.0–5.0	–	3.0–5.0	2.0–5.0	–	–
Lyonsia californica	2.0–15.0	–	4.0–16.0	4.0–10.0	–	4.0
Tellina modesta	1.0–10.0	–	3.0–7.0	1.0–7.0	–	–
Others	1.0–22.0	–	3.0–10.0	1.0–20.0	–	3.0
CLADOCERA						
Evadne sp.	–	0.5–2.0	–	–	0.5–1.0	–
OSTRACODA						
Euphilomedes carcharodonta	0.5–2.5	–	1.0–2.0	1.0–3.0	2.0–3.0	1.0–2.0
Parasterope sp.	1.0–2.0	1.0	1.0–2.0	1.0–2.0	1.0–2.5	1.0–2.0
Rutiderma lomae	1.5–2.0	–	–	1.0–2.0	1.5	2.0
Others	0.4–3.0	–	1.0–2.0	0.8–2.0	1.0–2.0	2.0
COPEPODA						
Calanoids, various spp.	–	1.0–2.0	–	–	1.0–2.0	–
Cyclopoids, various spp.	–	1.0	–	–	1.0	–
Harpacticoids, various spp.	0.8–1.0	0.5–1.0	–	0.5–0.8	0.8–1.0	–
Others	0.4	–	–	–	–	2.0
MYSIDACEA						
Erythropinid sp.	–	–	–	4.0	2.0–5.0	3.0
Siriella pacifica	–	–	–	–	3.0–12.0	5.0–8.0
Others	4.0	–	–	4.0	3.0–8.0	5.0–10.0
CUMACEA						
Cyclaspis nubila	2.0–6.0	–	2.0–5.0	2.0–6.0	2.0–5.0	3.0–4.0
Others	1.0–3.0	0.5	2.0	2.0–4.0	1.0–2.0	2.0–5.0
TANAIDACEA						
Leptochelia dubia	1.0–5.0	–	2.0–5.0	1.0–5.0	1.0–3.0	2.0–4.0
Others	3.0	–	–	–	–	–
ISOPODA						
Eurydice caudata	2.0	–	–	2.0	2.0–5.0	2.0–6.0
Exosphaeroma rhomburum	1.0–3.0	–	–	2.0–3.0	2.0–4.0	2.0–3.0
Others	–	–	–	–	1.0–2.0	2.0
GAMMARIDEA						
Acuminodeutopus heteruropus	1.0–4.0	–	1.0–3.0	1.0–3.0	–	1.0–2.0
Ampelisca cristata	2.0–11.0	–	3.0–11.0	2.0–13.0	4.0–6.0	3.0–9.0
Amphideutopus oculatus	2.0–7.0	–	4.0	2.0–7.0	–	3.0–6.0
Batea transversa	–	–	–	3.0–4.0	1.0–5.0	2.0–4.0
Ericthonias braziliensis	1.0–6.0	–	2.0–4.0	2.0–5.0	–	2.0–4.0
Metaphoxus frequens	1.0–5.0	–	2.0–5.0	1.0–5.0	3.0	1.0–4.0

Table 5. (Continued).

Organisms present[1]	Size ranges (mm)					
	Day			Night		
	Sand	Plankton	Prey	Sand	Plankton	Prey
Monoculodes hartmanae	2.0–7.0	–	2.0–5.0	2.0–5.0	2.0–6.0	2.0–3.0
Paraphoxus heterocuspidatus	1.0–3.0	–	2.0–3.0	1.0–4.0	2.0–3.0	2.0–4.0
Photis brevipes	2.0–5.0	–	1.0–3.0	1.0–6.0	2.0–3.0	1.0–4.0
Rudilemboides						
stenopropodus	2.0–5.0	–	2.0–4.0	2.0–5.0	–	2.0–5.0
Synchelidium rectipalmum	1.0–7.0	–	2.0–4.0	1.0–6.0	2.0–4.0	2.0–3.0
Others	1.0–10.0	–	1.0–4.0	1.0–7.0	2.0–4.0	1.0–10.0
CAPRELLIDAE						
Caprella pilidigita	9.0	–	–	5.0–7.0	–	4.0–10.0
Mayerella banksia	3.0–5.0	–	–	2.0–5.0	–	4.0–5.0
Others	2.0–5.0	–	2.0–4.0	2.0–4.0	4.0	2.0–8.0
NATANTIA						
Larvae and juveniles	–	2.0	–	3.0–4.0	1.0–7.0	–
Crangon holmsi	7.0	–	–	7.0–11.0	5.0	5.0–12.0
Others	–	–	–	–	–	4.0–10.0
REPTANTIA						
Zoeae	–	–	–	1.0	1.0–2.0	–
Others	–	–	–	–	2.0–4.0	–
ECHINODERMATA						
Dendraster excentricus	5.0–14.0	–	–	1.0–9.0	–	–
Others	0.6–1.0	–	–	1.0–2.0	–	–
CHAETOGNATHA						
Various spp.	–	4.0–10.0	–	–	2.0–10.0	–
LARVACEA						
Various spp.	–	2.0–4.0	–	–	1.0–4.0	–
FISHES						
Eggs (pelagic)	–	1.0–2.0	–	–	1.0–2.0	–
Larvae	–	3.0–7.0	–	–	2.0–12.0	–
Others	–	–	–	–	–	–
MISCELLANEOUS	0.3–50.0	0.6	–	3.0–26.0	1.0–4.0	–

[1] See Footnote 1, Table 1.
[2] Not recorded.

forces in shaping trophic characteristics and species composition of fishes in natural communities.

Diurnal trophic interactions

Of the many fishes of varied species with access to the open sand in Ripper's Cove, only a relatively few with certain offensive and defensive abilities foraged there during the day. They included transients as well as residents. Here we consider the trophic adaptations that permitted diurnal exploitation of the prey in this habitat.

Cryptic features were adaptive for daytime activities over the open sand. This was demonstrated by the resident bothids, *Citharichthys stigmaeus* and *Paralichthys californicus*, which often compensated for the lack of environmental cover by matching their colorations to that of the substrate (Fig. 3), or by resting under a covering of sand (Fig. 4). Both species seemed to use their capacity for camouflage to ambush prey, and probably *C. stigmaeus*, the smallest species regularly observed in the study area, also used it to escape detection by

predators. *P. californicus* would have had less need for protection from predators as an adult, when it is relatively large, but probably found such protection important as a juvenile.

Although cryptic features were far less evident among those fishes that moved from neighboring habitats to forage over the open sand during the day, these species had other characteristics that equipped them to seek prey there. One was the ability to detect, and capture, organisms that were highly cryptic. The way *Halichoeres semicinctus* intently inspected the substrate (Fig. 7) as it roamed about the area suggested reliance on acute vision to detect well-concealed prey. And its small mouth, with anterior canines, was suited to pluck tiny organisms from the sand. Clearly these features were adapted to exploit many of the species that we took in our samples from the environment (Tables 2 and 5). Presumably the exposed targets of *H. semicinctus* were motionless, because the organisms on which it preyed (Table 3) would be likely to avoid moving in the presence of an active predator. *H. semicinctus* apparently captured at least one major prey, the gammaridean *Photis brevipes*, by snipping off exposed tips of the tubes of the polychaete, *Spiochaetopterus costarum*, in which this amphipod lives (Table 3, footnotes 3 and 4). *Paralabrax clathratus*, on the other hand, appeared to be an opportunist that hovered, or rested, in place until nearby prey were momentarily detectable, or otherwise vulnerable. Often, it appeared that predators using this tactic depended on going unnoticed to strike at nearby organisms that drew attention to themselves by moving. *Embiotoca jacksoni* avoided the problem of detecting cryptic prey through its ability to winnow organisms from ingested sediments – a successful feeding mode in Ripper's Cove because there were so many organisms in the sand (Table 2).

When *Semicossyphus pulcher* entered the open-sand habitat from adjacent areas during the day, it foraged on some of the few potential prey that were readily visible. Despite their visibility, these prey had defenses that protected them from most fishes, if not from *S. pulcher*. Many were encased in heavy armor (e.g. the mollusk *Olivella biplicata*), but *S. pulcher* crushed them with its strong jaw teeth and

pharyngeal plates. And most bivalved mollusks were buried in the sand (even though their siphons were readily visible at the surface, e.g. *Americardia biangulata*), but *S. pulcher* rooted them out with its well-developed ability to excavate. On the other hand, the many small organisms in the gut contents of even the larger *S. pulcher*, e.g. the gammarid *Ampelisca cristata* (Table 3), indicate that, like *E. jacksoni*, above, they winnowed prey from the sand and debris vented from gill and mouth openings immediately after ingestion. It is unlikely that adult *S. pulcher* could selectively ingest such tiny prey with its large mouth and heavy jaw teeth.

The four species that entered the open-sand habitat from neighboring rocks and algae probably represent a distinctive and widespread trophic category. Three of these – *P. clathratus*, *S. pulcher*, and *E. jacksoni* – (along with *Oxyjulis californica*, a labrid similar to *H. semicinctus*) have been reported to regularly leave kelp forests to forage in adjacent open sand at Santa Cruz Island, 100 km NW of Santa Catalina (Ebeling et al. 1980). Because they lacked the capacity for concealment so well developed in the residents, the fishes that ranged over the open sand from neighboring habitats during the day would seem vulnerable to such predators as *Paralichthys californicus*, which ambushes smaller fishes from concealed positions in the sand (Fig. 4) (Haaker 1975). But at least many of the transients, e.g. *Halichoeres semicinctus*, directed their attention at the sea floor as they foraged, and their highly developed abilities to detect cryptic organisms in the sand should also have helped them to detect, and thus evade, cryptic predators. Of those species that did not demonstrate particular abilities to detect cryptic organisms (although they may well have had such abilities), *Semicossyphus pulcher* gained some level of protection from its relatively large size, and *Embiotoca jacksoni* from its relatively deep body – both features that have been reported to reduce threats from predators (Hobson 1979).

The absence of planktivorous fishes in the water column of the study site during the day probably can be attributed to threats from predators. Although such prominent diurnal planktivores as *Chromis punctipinnis* and *Atherinops affinis* were

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numerous above the neighboring rocks and algae at this time (Quast 1968, Bray 1980), they did not venture above the exposed study site even though zooplankton were abundant there (Table 2). This is consistent with earlier assertions (Hobson 1968, 1979) that unacceptable risks of predation keep smaller fishes out of the more exposed regions of the water column during the day. With their attentions directed at the water column, planktivorous fishes would be especially vulnerable to predators that attack from concealed positions in the sand.

We suggest, therefore, that the relatively few fishes which foraged over the open sand of Ripper's Cove during the day were benthic feeders able to cope with the predatory threats characteristic of that habitat, and which also had either: (1) a well-developed ability to detect, and capture, species that were difficult to see, and perhaps at least partly buried, or (2) the specialized capacity to take forms that, while more visible and exposed, were heavily armored.

Nocturnal trophic interactions

The sharp increase in numbers of fishes that foraged in the open-sand habitat at night – most of them after migrating from daytime shelters elsewhere – indicated nocturnal relaxation of the constraints that limited fishes' access to that habitat during the day. Diel migrations between diurnal shelter sites and exposed nocturnal feeding grounds are widespread among nearshore fishes (Hobson 1968, 1973, McFarland et al. 1979), and appear based on two developments on the exposed feeding grounds at night: prey become more accessible, and predators become less threatening.

Much of the difference in trophic relations from day to night can be attributed to diel differences in visual capabilities. In bright light the visual systems of most nearshore fishes stress visual acuity, but in dim light visual acuity is sacrificed for visual sensitivity (Walls 1942, Munz & McFarland 1973). So at night the fishes lose much of their ability to target smaller organisms, and probably at least many sense only those prey that move. Certainly at night there is less need among both predators and prey for the cryptic features that are so adaptive by day.

With the nocturnal loss of visual acuity in fishes removing many of the threats that kept smaller organisms hidden in the sand during the day, many potential prey (e.g. various mysids, tanaids, isopods, and amphipods) became active in exposed locations, including the water column. For every organism of a predominantly benthic species that entered the nocturnal water column, however, many more of the same species remained in the sand (Table 2). So the numbers that came under threat from nocturnal planktivores were relatively few compared to the numbers of conspecifics still on the bottom that remained threatened by nocturnal benthivores. For example, while the tubiculous amphipod *Ampelisca cristata* recurred in the diet of the strictly planktivorous and nocturnal *Hyperprosopon argenteum*, it was far more numerous in the diet of the strictly benthivorous, and nocturnal, *Umbrina roncador*.

Most of the fishes that foraged in the open-sand habitat at night captured their prey in, on, or close to the sand, and they showed their suitability for this task by capturing representatives of virtually every species present – except the sedentary, armored mollusks and echinoids. The absence of sedentary forms from their diet is consistent with earlier assertions that prey must move to be effective targets for at least most nocturnal predators (e.g. Hobson 1979).

At night the fishes seemed to hunt more effectively on the open sand than among the neighboring rocks and algae. Probably prey not only were more accessible in the exposed habitat, but also more visible due to moonlight and starlight reflected from this light substrate (Hobson et al. 1981). Thus, elevated light levels over sand at night may account for the presence and predatory success there of the predominantly diurnal, subadult *Paralabrax clathratus*. Some of the nocturnal fishes in this habitat, however, may not have depended on vision to capture prey. For example, *Chilara taylori* apparently detected prey with its barbel-like pelvic fins (Fig. 9), just as the closely related *Otophidium scrippsi* has been reported to do (Greenfield 1969). Probably *Umbrina roncador* used the single short barbel at the tip of its lower jaw (Fig. 12) in a similar way.

The only fish species that regularly foraged more than 2 m above the sand in the study area at night was *Hyperprosopon argenteum*. This species fed almost entirely on the primarily benthic crustaceans that entered the water column after dark, even though these were only a small minority of the nocturnal plankton (Table 2). Certainly these prey made better nocturnal targets than did the far more abundant holoplankters, which probably were too small or transparent to be effectively seen in dim light. Not only were the crustaceans that entered the water column at night generally much larger and more opaque than the holoplankters, many were awkward swimmers (e.g. caprellids), and therefore less elusive, and also more likely to create the turbulence and resulting bioluminescence that is thought to direct many nocturnal attacks (Hobson et al. 1981). Significantly, *H. argenteum* as small as 44 mm SL (unpublished data collected elsewhere) similarly fed on these same crustaceans, especially gammarids and caprellids, rather than on the more numerous, but smaller and less visible holoplankters.

We make two inferences from the exceptionally large eyes of *H. argenteum* (Fig. 10): first, that it hunted visually, and second, that there was less light in the mid regions of the water column, where it foraged, than in the lower regions of the water column, close to the sand, where related fishes with smaller eyes, e.g. *Cymatogaster aggregata*, captured similar prey (Table 4, Fig. 11).

Nocturnal planktivores may find foraging less productive above the open sand than above neighboring rocks and algae, which reverses the situation involving benthivores, described above. While benthivores seemed to find the open-sand habitat more favorable because of higher light levels, and more accessible prey, the planktivores would have found prey more diverse and abundant above rocks and algae. Apparently the number and diversity of benthic organisms that entered the water column at night reflected the relative complexity of their benthic habitats. Thus, at night zooplankters were fewer in kind and number above the sand in Ripper's Cove than above more complex fields of benthic algae in Fishermen's Cove, 9 km away (Hobson & Chess 1976). And this difference in the numbers and diversity of nocturnal zooplankters may have influenced the numbers and diversity of planktivorous fishes, because while just *H. argenteum* foraged regularly above the open sand in Ripper's Cove at night, five planktivorous species foraged regularly above the fields of benthic algae in Fishermen's Cove after dark (Hobson & Chess 1976).

The visual limitations of nocturnal predators that reduced threats to smaller benthic invertebrates at night should also have reduced nocturnal threats to smaller fishes. But as with benthic invertebrates, the safety would have been only relative. At least one piscivorous ambusher that frequents the open-sand environment at Santa Catalina Island – the angel shark, *Squatina californica* – is most active at night (Standora & Nelson 1977). *S. californica* feeds primarily on active fishes (Limbaugh 1955), which it attacks by lashing upward from a position at rest on the sand (Pleshner 1983). At least many of its nocturnal strikes may be directed by a bio-electric sense – a capability widely developed among elasmobranchs (Kalmijn 1971). *S. californica* prefers depths of about 20 m (Limbaugh 1955), but occurs shoreward to the water's edge (Pleshner 1983). So while we did not see this shark in Ripper's Cove, it co-occurs with the fish species considered here over much of their ranges (Miller & Lea 1972), and so is likely to have influenced the evolution of their defenses. Furthermore, although the piscivorous *Paralichthys californicus* has been reported to feed mainly by day (Haaker 1975), we would expect its ambushing tactics to be successful under at least some nocturnal circumstances. There may be enough light from moon or stars to direct some attacks, and on even the darkest nights certain targets may be suitably marked by bioluminescence (Hobson et al. 1981).

The impact of predator-prey interactions on trophic features and community structure

Clearly, the variety of form and habit in fishes that foraged over the open sand of Ripper's Cove was closely related to the variety of form and habit in their prey. But many fishes with access to that habitat, and capable of exploiting its inhabitants,

e.g. the diurnal planktivores, did not do so, probably because they lacked means to evade the predators there. Thus, the fish species present in the open-sand habitat were characterized by a combination of morphological and behavioral characteristics which enabled them to both capture prey and evade predators under the circumstances that prevailed in that setting.

A species can be defined by a combination of morphological and behavioral features adapted to its specific mode of life, and certainly among the more prominent of these features are the means to capture prey, or to thwart predators. These relationships are evident in even the most casual appraisal of trophic characteristics and of course is the distribution of morphological and behavioral types among individuals that live together is the basis of their community structure. But while it is recognized that trophic relationships are important forces in structuring animal communities, a prevailing view identifies the primary mechanism as competition between predators for prey (e.g. MacArthur 1972, Moermond 1979, Hixon 1980, Larson 1980). Generally this view recognizes predation as important, but usually in the sense that it modifies patterns of competition (for space, as well as food: Paine 1966, Pianka 1974, Connell 1975, Roughgarden & Feldman 1975). In fact, until recent criticism (e.g. Lewin 1983), the concept of competition as the major force determining the structure of animal communities had become so firmly entrenched in ecological thought as to approach dogma (Wiens 1977).

The impact of interspecific competition for food on trophic features of fishes, and on the species composition of fish communities, would seem to have been greatly overstated. This is true even where forceful competition for food is on occasion likely, as where the interacting elements are locked together in lakes, streams or other closed ecosystems. (The strongest evidence of competitive trophic interactions affecting ecological relationships comes from closed systems, e.g. Johannes & Larkin 1961). Often in such situations it has been asserted as simple statement of fact that interspecific differences in trophic characteristics reduce competition, and generally there are in-

ferences that the advantage of reduced competition for food has been the major selective advantage of these characteristics. In their classic study of fishes, for example, Keast & Webb (1968, p. 1845) stated, without benefit of supporting evidence, that '... mouth and body structures combined with food specializations ... to greatly reduce interspecific competition'. And, in reference to birds, Cody (1974, p. 87) stated '... the variety of feeding methods is necessary to allow coexistence' (by reducing competition). Although distinctive trophic features reduce the chance of interspecific competition, we suggest that in most cases this reduced competition is simply an incidental result of evolutionary processes driven primarily by interactions between predators and prey. This view agrees with Connell (1980), who, in questioning the importance of competition in community structure, was of the opinion that species divergence leading to niche separation is more likely to result from interactions (coevolution) between two species on different trophic levels than between two species competing on the same trophic level.

Certainly there can be little doubt that trophic characteristics in fishes are largely products of interactions between predators and prey. Furthermore, the evolution of feeding adaptations in predators is inseparable from the evolution of defensive adaptations in prey. As stated earlier (Hobson 1979, p. 231): 'Attacks by ... predators during the evolution of modern species have pressured prey to acquire effective defensive adaptations. But every successful defense has evoked an appropriate offense, so that a delicate balance now exists.' This balance between predator and prey, based on a system of coevolved offenses and defenses, should be a stabilizing influence on community structure. But while the usual condition of balanced predator-prey relationships should establish relative stability, it nevertheless involves intense conflicts between predator and prey which continue to refine the distinctive trophic features that distinguish the species.

Thus, the fishes of Ripper's Cove were distinguished by morphologies and behaviors that would seem adaptive responses to the defensive structures or tactics of their prey. *Semicossyphus*

pulcher, for example, was characterized by being strongly diurnal, by having heavy pharyngeal teeth, and by a highly refined ability to excavate organisms from the sediments. These features provided visual conditions and capabilities suited to detect, capture, and digest its major prey – armored organisms that were motionless and at least partially buried in the sand. Similarly, *Hyperprosopon argenteum* was characterized by exceptionally large eyes and nocturnal habits, which were adaptive in feeding on organisms that entered the water column only under cover of darkness. Obviously these distinctive characteristics are products of evolutionary processes that greatly transcend interspecific encounters in any single environment. The specialized dentition of *Semicossyphus pulcher,* for example, adapted this species over its geographic range to crush a greater variety of armored prey than occurred in the limited setting of our study area. So the combination of fishes that occurred in Ripper's Cove during the present study was, in effect, a mix of species with access to that habitat that were able to exploit the prey, and to tolerate the predators, that existed there at that time.

Acknowledgements

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