TROPHIC INTERACTIONS AMONG FISHES AND ZOOPLANKTERS NEAR SHORE AT SANTA CATALINA ISLAND, CALIFORNIA[1]

EDMUND S. HOBSON AND JAMES R. CHESS[2]

ABSTRACT

Predation pressures from fishes have influenced major evolutionary trends among shallow-water zooplankters, as concluded from study at Santa Catalina Island, Calif. The predominant zooplanktivorous fishes near shore are actinopterygians, an evolutionary line that has centered around generalized visually feeding, large-mouthed predators. Historically, zooplankters threatened by these fishes have faced selective pressures favoring reduced size, transparency, and/or nocturnal planktonic habits. At present, most zooplankters in the nearshore water column by day are very small (<2 mm, approximately); included are cladocerans, copepods, and various larval forms. Their small size precludes capture by most large-mouthed fishes, thus providing protection in daylight, when the visual sense of generalized predatory fishes is most effective. Larger zooplankters in the water column by day, for example chaetognaths, tend to be transparent. The advantage of transparency to organisms threatened by visually feeding predators is obvious, and is only briefly mentioned here. Zooplankters having sizes (most >2 mm) and other features making them vulnerable to large-mouthed fishes tend to enter the water column only at night, when darkness offers some security from visually feeding predators. Included are polychaetes, mysids, cumaceans, gammaridean and caprellid amphipods, tanaids, isopods, and carideans.

Because successful defensive features of prey create pressures that modify the offensive features of predators, the tendencies toward reduced size and nocturnal habits among zooplankters have generated appropriate adaptations among planktivorous fishes. Fishes that prey as adults on zooplankters during the day (e.g., blacksmith, *Chromis punctipinnis*) have specialized features, including a small highly modified mouth, that permit even relatively large individuals to take the tiny organisms which constitute the daytime zooplankton. Some other fishes are diurnal planktivores only as small juveniles and assume different feeding habits as they grow larger (e.g., kelp perch, *Brachyistius frenatus*; señorita, *Oxyjulis californica*; smaller juvenile olive rockfish, *Sebastes serranoides*). Fishes that prey on zooplankters at night (e.g., larger juvenile olive rockfish; kelp rockfish, *Sebastes atrovirens*; queenfish, *Seriphus politus*; walleye surfperch, *Hyperprosopon argenteum*; and salema, *Xenistius californiensis*) take the larger organisms that join the zooplankton after dark. In their feeding morphologies and body form, these large-mouthed fishes have diverged less than their diurnal counterparts from the generalized predators that give rise to them all. They have, however, acquired specialized features, including large eyes, suited to detect and capture prey in the dark.

Interactions among predators and their prey are best recognized by viewing assemblages of animals that occur together in nature. Furthermore, many trophic interactions become apparent only upon considering the changes that occur from day to night, and from one season to another. These convictions shaped studies of feeding relations among tropical reef fishes undertaken between 1962 and 1970 (Hobson 1965, 1968, 1972, 1974), and similarly influenced work done in warm temperate waters from 1972 to 1975. This more recent work centered on the inshore habitats at Santa Catalina Island, Calif. (lat. 33°28'N, long.

118°29'W), where most of the attention was directed at fishes that forage on the benthos (Hobson and Chess in prep.). The present report, however, deals with that segment of the work involving certain fishes and trophically related zooplankters that interact in the water column near shore.

Only a few studies have considered feeding habits in natural assemblages of marine fishes. Limbaugh (1955) and Quast (1968) made the major contributions in southern California, but these important studies represent only a beginning.

The present study goes beyond earlier investigations by considering the organisms taken by the fishes as prey against a broader consideration of the array of similar forms present that would seem to have been equally accessible. The selection of specific prey, however, is only partially developed in discussing these data. Selectivity will

be treated in depth later (Hobson and Chess in prep.), when these data can be reconsidered along with the data on organisms simultaneously accessible on the sea floor and other substrata, as well as in the water column above habitats different from those described here.

TERMINOLOGY

In this report, the term zooplankton encompasses all the varied small organisms we collected with a plankton net during day and night, and (most important to this study) which proved to include the major foods of a well-defined assemblage of fishes. All the organisms that we consider within this definition belong to groups included in most general accounts of the zooplankton (e.g., Newell and Newell 1963; Wickstead 1965).

Nevertheless, some planktologists would exclude from zooplankton forms like large caridean shrimps that irregularly enter the water column at night. But among crustaceans such distinctions fail to establish where, along the continua of size, mobility, and time spent in the water column, forms like large carideans are apart from those minute calanoid copepods that are zooplankters by any definition. A number of terms defining certain ecological categories among zooplankton have been proposed (e.g., holoplankton, meroplankton, tychoplankton, etc.), but while such terms are useful in certain contexts, we have seen none that define categories meaningful to the concepts developed in this paper (see Discussion).

STUDY AREA

The study area is 25 to 75 m off the western shore of Big Fisherman's Cove (Figure 1). Most of the area is open water about 5 to 15 m deep over a sandy sea floor largely overgrown by the brown alga *Dictyopteris zonarioides* (most of which is anchored to tubes of the polychaete *Chaetopterus variopedatus* (Figure 2)). From the seaward edge of the study area, the bottom falls sharply to the greater depths (more than 30 m) that lie at the center of the cove. Shoreward, and at the mouth of the cove, lies a forest of giant kelp, *Macrocystis pyrifera*. This large brown alga grows to the water's surface from a rocky bottom that slopes up to the shoreline from depths of about 8 m (Figure 3). Water temperatures during the study ranged from lows around 12°C in spring, to highs around 20°C in late summer.

FISHES STUDIED

The fishes studied are those that, during either day or night, swim in the water column and feed principally on zooplankters. They are:

Family Scorpaenidae: scorpionfishes
  Olive rockfish, *Sebastes serranoides* (Eigenmann and Eigenmann)
  Kelp rockfish, *S. atrovirens* (Jordan and Gilbert)
Family Pomadasyidae: grunts
  Salema, *Xenistius californiensis* (Steindachner)
Family Sciaenidae: drums
  Queenfish, *Seriphus politus* Ayres
Family Embiotocidae: surfperches
  Walleye surfperch, *Hyperprosopon argenteum* Gibbons
  Kelp perch, *Brachyistius frenatus* Gill

FIGURE 1.—Big Fisherman's Cove, Santa Catalina Island. The study site lies near the opposite shore, between the buoy and the headland.
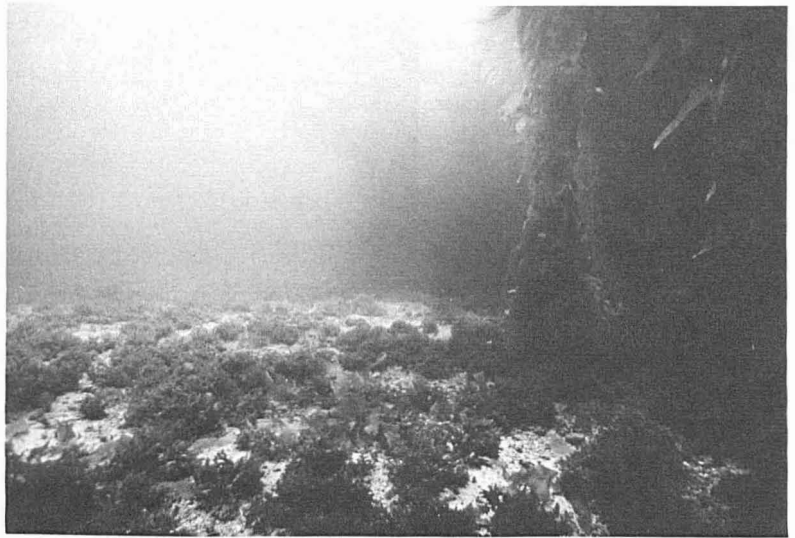
FIGURE 2.—The *Dictyopteris* field, bordered by the *Macrocystis* forest.
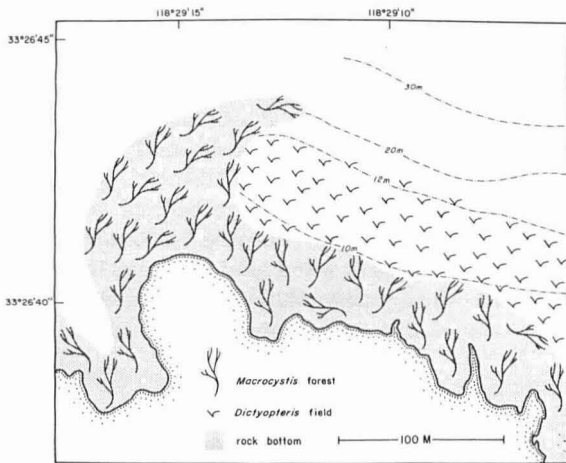

FIGURE 3.—The study area at Santa Catalina Island.

Family Labridae: wrasses
   Señorita, *Oxyjulius californica* Günther)
Family Pomacentridae: damselfishes
   Blacksmith, *Chromis punctipinnis* (Cooper)

Only two other species in the study area have similar zooplanktivorous habits: the topsmelt, *Antherinops affinis* (Ayres), and the shiner perch, *Cymatogaster aggregata* Gibbons. These two, however, are more characteristic of other habitats, where the species composition of available prey is different. Although for this reason they will be described in separate reports later, their activities are entirely consistent with what is reported and discussed below.

METHODS

Direct Observations

We used scuba and snorkeling (167 h underwater) to observe activity of the fishes and trophically related organisms during all periods of day and night. Except when collecting specimens, we tried to avoid influencing the organisms or their environment.

Collecting Zooplankters

During the same period that we collected fishes for the food-habit study, organisms in the water column that might be their prey were sampled with a 1-m plankton net (0.333-mm mesh) that we pushed through the water for 5-min periods (Figure 4). In this way, a series of paired collections sampled the waters above the *Dictyopteris* field during September 1973, February 1974, and May 1974. Of each pair, the first sampled the water column midway between the water's surface and the sea floor (in 10 to 15 m of water); and the second, which followed immediately, sampled the base of the water column to within about 10 cm above the bottom. During each sampling month, we made a set of eight collections—four at full moon, and four at new moon. Each set included a pair at night (between 2 and 4 h after last evening light), and a pair the following day (between 1200 and 1400 h). In addition, we made one set of collections in the kelp forest bordering the study

569

FIGURE 4.–Collecting plankton at middepths.

area: a pair at night, under a full moon (when there was enough light to maneuver among the kelp columns), and a pair the following midday.

Because diving lights probably influence organisms in the water column, we turned them off when collecting with the plankton net at night. At these times the moon provided ample light to navigate when it was present, but on dark nights we depended on the luminous dials of our compasses and depth gauges.

Collecting Fishes

To determine the food habits of the fishes, we speared 521 specimens of the eight species and then examined their gut contents. All specimens were taken in the study area between September 1973 and May 1974–the same period over which we sampled the zooplankton. Most of these specimens were collected either at night, within the 2 h before sunrise, or during the afternoon–times that best show differential day or night feeding. All measurements of fish size noted in this report are of standard length.

Sample Analysis

Zooplankton Samples

Generally the samples were analyzed within 2 wk after collection. Sample volumes, which ranged from 0.2 to 36.0 ml ($\bar{x} = 8.3$), were determined

after they had settled for 5 min in a graduated cylinder. The entire sample was analyzed when its volume was less than 5 ml. When the sample was larger, 5-ml aliquots were analyzed, and numbers for the entire sample then extrapolated. Whenever less than the entire sample was analyzed, the balance was searched for forms missing from the aliquot; when found–always in small numbers–these were counted and added to the list.

Fish Gut-Content Samples

The digestive tract of each fish specimen was removed immediately after collection, and preserved in a 10% Formalin[3] solution. For analysis, the contents were examined under a binocular dissecting microscope, and, when necessary, a binocular compound microscope. A note was made of the position in the digestive tract of the various items. A list was then composed of the items in the gut, with the species identified when feasible. The following data were then noted for the items in each listed category: 1) their number; 2) their size range; 3) the extent they had been digested (subjectively assessed on a scale of five, from fresh to well-digested); and 4) an estimate of their representation in the gut as percent by volume of the contents.

RESULTS

Volumes of Zooplankters, Day and Night

Our collections with the plankton net were too few, and spaced over too much time, to attach much significance to the differences in volume between various samples. Nevertheless, certain characteristics probably are meaningful.

The volumes of samples taken day and night at full moon compared with day and night at new moon are as follows: FULL MOON–daytime, middepths (n = 3): 1 to 18 ml, $\bar{x}$ = 8.3; daytime, near bottom (n = 3): 0.2 to 5 ml, $\bar{x}$ = 4; nighttime, middepths (n = 3): 2 to 13 ml, $\bar{x}$ = 4; nighttime, near bottom (n = 3): 5 to 15 ml, $\bar{x}$ = 10.3. NEW MOON–daytime, middepths (n = 3): 2 to 5 ml, $\bar{x}$ = 4; daytime near bottom (n = 3): 1.2 to 5 ml, $\bar{x}$ = 3.7; nighttime, middepths (n = 3): 3 to 13 ml, $\bar{x}$ = 8; nighttime, near bottom (n = 3): 9 to 36 ml, $\bar{x}$ = 19.6.

Thus, during the day the volumes of collections made at the middepths generally were greater than those made near the bottom, whereas the situation was reversed at night. Furthermore, volumes tended to be greater at night than during the day, with the greatest volumes of all taken near the bottom on dark nights.

Activity Patterns of the Zooplankters, Day and Night

The zooplankters are here grouped into a series of categories (Tables 1, 2),[4] most of which represent phylogenetic classes or subclasses.

Radiolarians

Based on the collections made with the plankton net (Tables 1, 2), radiolarians are consistently present in the water column during both day and night, sometimes in large numbers.

Polychaetes, Swimming

We saw polychaetes in the water column only at night. Highly motile epitokous nereids were

especially prominent when they swam at mid-depths during reproductive periods. Polychaetes are underrepresented in the plankton collections (Tables 1, 2), however, because their mobility permitted many to evade our net.

Mollusk Larvae

Based on specimens taken in the plankton net (Tables 1, 2), mollusk veligers occur in the water column in similar numbers during both day and night.

Cladocerans

Cladocerans (Figure 5C) were consistently present in the collections during both day and night (Tables 1, 2), although they were more numerous in the daytime collections.

Ostracods

We saw ostracods in the water column at night, but never during the day. Our daytime plankton collections took only a few individuals, these close to the bottom (Table 3). At night, however, several species were consistently numerous in both mid-depth and near-bottom collections (Table 3). The most numerous ostracod, *Parasterope* sp. A (Figure 5H), was numerous in the surface layers of the sand during the day (Hobson and Chess in prep.), and during the middle of the night we observed and collected it concentrated at the water's surface.

Calanoid and Cyclopoid Copepods

Calanoid and cyclopoid copepods were numerous in the water column during both day and night, based on our observations in the water as well as on our collections (Tables 1, 2). Indeed, calanoids were the most numerous of all organisms larger than about 1 mm taken in the net. Calanoids and cyclopoids were collected in greater numbers at night (Table 2), but because the plankton is generally richer after dark, they represented a smaller percentage of the sample volumes at night than during the day (Table 1).

The vast majority of calanoids and cyclopoids in the collections were subadults, and some species could be recognized only as adults. Of those identified, the major calanoids were *Acartia tonsa* (Figure 5F) and *Calanus pacificus*, with others

---

[4]The data in Tables 1 and 2 are from collections with the plankton net made above the open field of low benthic algae adjacent to the kelp forest. A set of day-night collections was also made within the forest (see Methods), where the fishes discussed below spend part (in some cases most) of their time. Because the data from these collections are essentially like those shown in the tables, they are not presented.

TABLE 1.—Organisms collected in the plankton net, day and night, showing size and mean percent of total volume represented by organisms in major taxonomic categories.

Organism category	Size (mm)	Day		Night	
		Middepth collections (n = 6)	Near-bottom collections (n = 6)	Middepth collections (n = 6)	Near-bottom collections (n = 6)
Radiolarians	0.1- 1.0	5.9	7.2	2.1	0.6
Polychaetes	1.0-55.0	0.3	0.3	0.3	2.1
Mollusk larvae	0.4- 0.8	0.2	0.2	0.2	0.1
Cladocerans	0.3- 1.0	11.2	1.0	0.9	0.5
Ostracods	0.5- 2.0	0.1	<0.1	0.8	1.9
Calanoids and cycloipods	0.6- 4.0	62.5	66.0	29.1	15.3
Harpacticoids	0.6- 1.0	0.2	1.3	0.6	0.8
Other copepods	1.0- 3.0	0.2	<0.1	0.1	0.1
Cirripedian larvae	0.6- 1.0	0.3	1.6	0.2	0.1
Nebaliaceans	3.0- 8.0	0.0	0.0	0.3	0.2
Mysids	1.0-12.0	0.0	0.7	39.1	47.3
Cumaceans	2.0- 5.0	0.0	0.0	2.0	3.7
Tanaids	1.0- 3.0	0.0	0.0	0.3	0.3
Isopods	1.0-10.0	0.0	0.3	1.7	2.4
Gammarideans	1.0- 5.0	0.1	0.2	10.0	14.2
Caprellids	3.0-18.0	0.0	0.0	0.4	0.8
Euphausid larvae	1.0- 3.0	0.6	1.0	0.5	0.3
Euphausid adults and juveniles	12.0-14.0	0.0	0.0	0.2	0.1
Caridean larvae	1.0- 5.0	2.0	2.3	4.8	3.9
Caridean adults and juveniles	4.0-10.0	0.0	0.0	1.0	0.7
Reptantian zoea	0.5- 4.0	0.4	0.6	0.9	0.7
Brachyuran megalops	2.0- 3.0	0.0	0.1	0.4	0.5
Bryozoan larvae	0.5- 1.0	0.7	0.6	0.7	0.5
Chaetognaths	4.0-10.0	1.3	3.4	0.6	0.3
Larvaceans[1]	1.0- 4.0	0.5	0.4	0.1	0.1
Fish eggs	0.6- 2.0	12.1	12.2	1.1	1.3
Fishes	3.0-11.0	1.6	1.9	1.5	1.2

[1]Underrepresented in collections, see text.

TABLE 2.—Organisms collected in the plankton net day and night, showing occurrence and mean number of individuals of organisms in major taxonomic categories.

Organism category	Day				Night			
	Middepth collections (n = 6)		Near-bottom collections (n = 6)		Middepth collections (n = 6)		Near-bottom collections (n = 6)	
	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Radiolarians	100	~500	100	~550	83	~3,500	83	~1,800
Polychaetes	0	0	0	0	33	<1	50	5
Mollusk larvae	33	3	33	2	50	3	50	4
Cladocerans	100	1,227	83	49	100	146	83	46
Ostracods	17	1	33	<1	100	20	100	73
Calanoids and cyclopoids	100	2,414	100	1,978	100	3,730	100	2,203
Harpacticoids	33	2	50	<1	83	23	100	41
Other copepods	17	1	17	1	17	1	17	1
Cirripedian larvae	50	6	50	30	50	5	17	2
Nebaliaceans	0	0	0	0	33	8	66	2
Mysids	0	0	50	1	100	1,100	100	1,721
Cumaceans	0	0	0	0	100	31	100	105
Tanaids	0	0	0	0	33	6	50	9
Isopods	0	0	33	3	100	23	100	49
Gammarideans	17	<1	17	3	100	436	100	2,121
Caprellids	0	0	0	0	50	4	50	15
Euphausid larvae	100	16	83	21	50	12	50	11
Euphausid adults and juveniles	0	0	0	0	17	<1	17	<1
Caridean larvae	83	31	67	45	100	200	100	220
Caridean adults and juveniles	0	0	0	0	50	25	83	10
Reptantian zoea	67	5	83	9	100	58	100	30
Brachyuran megalops	0		17	<1	50	2	67	4
Bryozoan larvae	83	71	83	12	100	117	67	21
Chaetognaths	100	35	83	31	83	7	33	4
Larvaceans[1]	67	7	50	7	17	2	17	2
Fish eggs	100	137	100	90	100	36	100	59
Fishes	67	19	50	5	83	33	83	19

[1]Underrepresented in collections, see text.

TABLE 3.—Ostracods collected in the water column, day and night.

| | | Day | | | | Night | | | |
| | | Middepth collections (n = 6) | | Near-bottom collections (n = 6) | | Middepth collections (n = 6) | | Near-bottom collections (n = 6) | |
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Parasterope sp. A	1-2	0	0	0	0	100	10.2	83	33.8
Cycloleberis loblancoi	1-2	0	0	0	0	67	3.5	83	18.2
Vargula americana	1-4	0	0	0	0	50	4.8	100	12.2
Philomedes sp. A	1	0	0	0	0	17	0.5	33	3.5
Unidentified species A	1	0	0	0	0	17	0.8	17	0.2
Euphilomedes carcharodonta	1-2	0	0	0	0	50	0.5	0	0
Cythereis sp.	1	0	0	17	0.2	17	0.5	0	0
Philomedes sp. B	1	0	0	0	0	17	0.5	0	0
Conchoecia sp.	1	0	0	17	0.3	0	0	0	0
Unidentified species B	2	0	0	0	0	0	0	17	0.2

present including *Candacia* spp., *Clausocalanus* sp., *Ctenocalanus* sp., *Euchaeta* sp., *Labidocera* spp., *Lucicutia* sp., *Metridia pacificus, Paracalanus* sp., and *Rhincalanus nasutus.* The major cyclopoid was *Coryceus* sp. (Figure 5E), but others, including *Oithona* sp., were present.

Harpacticoid Copepods

Our daytime collections took relatively few harpacticoids, all near the bottom. They were more numerous in the night collections, however, when they appeared in both middepth and near-bottom samples. One form predominated, a species of *Porcellidium*, probably undescribed, designated *Porcellidium* species A (Figure 5G). Our night middepth collections (n = 6) took $\bar{x}$ = 21.6 specimens of this species, whereas the near-bottom collections (n = 6) took $\bar{x}$ = 37.3. During the day *Porcellidium* species A was absent in all middepth collections (n = 6), but the near-bottom collections (n = 6) took $\bar{x}$ = 16. Only one other harpacticoid was collected in daylight, a form here designated as harpacticoid species A. Our daytime middepth collections (n = 6) took $\bar{x}$ = 1.8 specimens of this species, but it was absent in all daytime near-bottom collections, and all collections made at night. Three other forms—a second species of *Porcellidium*, and two species of *Eupelta* (all probably undescribed)—were taken only at night: a combined mean of 0.7 in the middepth collections, and a combined mean of 3.2 in near-bottom collections.

Other Copepods

No other copepods were seen in the water column, and very few were taken in the plankton net. An occasional caligoid or monstrilloid appeared in the collections, but were too few to suggest a pattern.

Cirripedian Larvae

Most of the tiny cypris larvae of the barnacles (Figure 5D) are smaller than 1 mm. Their occurrence in the collections (Tables 1, 2) was irregular, and without consistent differences between day and night, or between middepth and near-bottom samples.

Nebaliaceans

At night we occasionally observed and collected one species, probably *Nebalia pugettensis* (Figure 5J; see Smith and Carlton 1975). However, they were neither seen nor taken during the day.

Mysids

Siriella pacifica (Figure 5M) was the most widespread mysid over the study area. It remained sheltered on the sea floor and close to kelp during the day, but during late twilight moved into open water, where it spent the night (Table 4). On five evenings we noted when *S. pacifica* had first risen as much as 1 m above the bottom, and found this level attained 29 to 42 ($\bar{x}$ = 37.6) min after sunset. On six mornings, the last individual 1 m above the bottom was seen 32 to 50 ($\bar{x}$ = 38.7) min before sunrise. The stomach contents of 30 *S. pacifica* collected during day and night were examined: DAYTIME—of 10 (8.5-10.5 mm, $\bar{x}$ = 9.6) collected amid giant kelp during midafternoon (5 from the
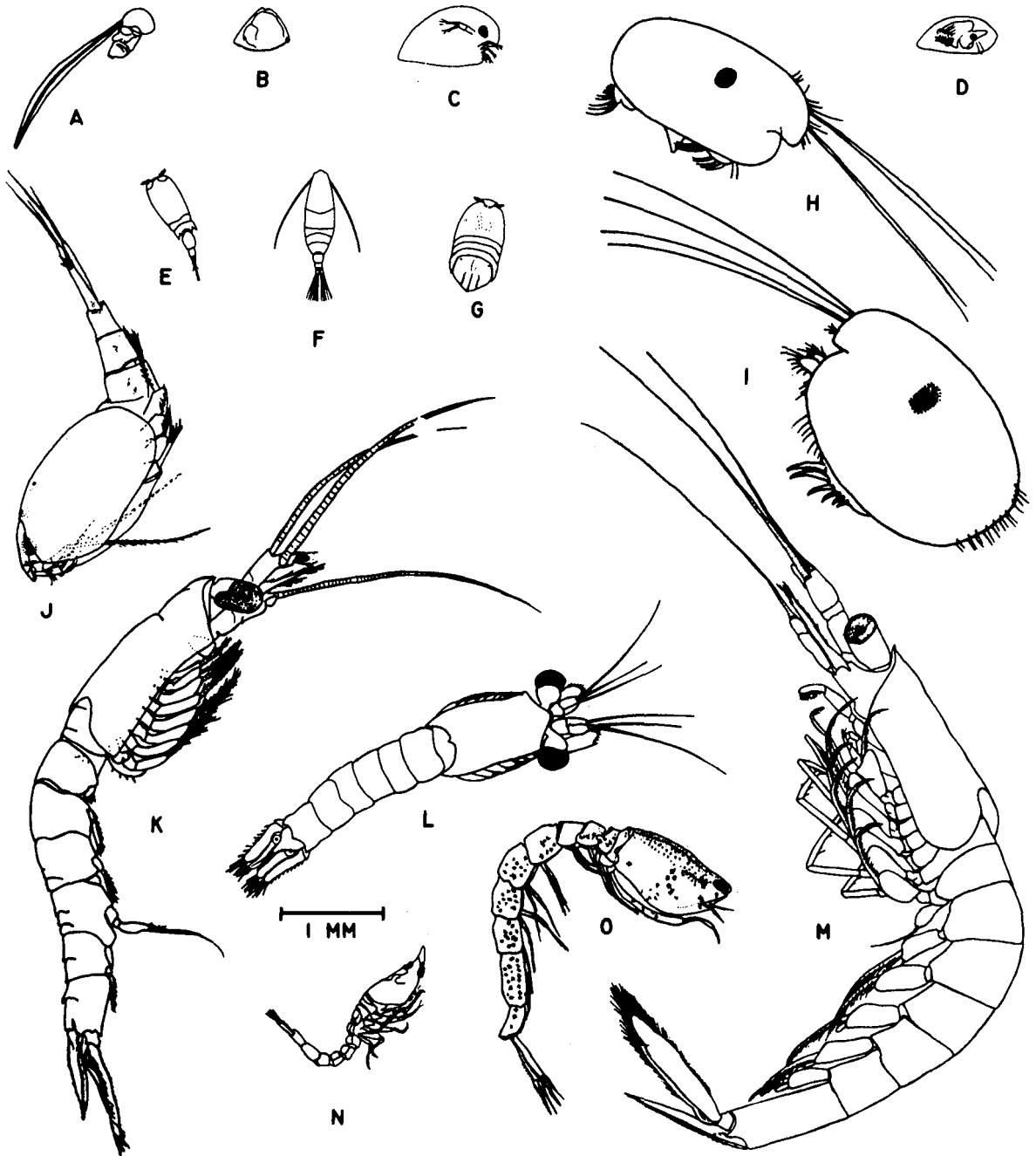
FIGURE 5.—Relative sizes of some of the zooplankters involved in this study. A to F are full-time inhabitants of the water column; G to W are species that rise into the water column after dark (R is occasionally there during daylight). A. larvacean *Oikopleura* sp.; B. bryozoan larva, cyphonautes; C. cladoceran *Evadne* sp.; D. barnacle larva, cypris; E. cyclopoid copepod *Coryceus* sp; F. calanoid copepod *Acartia tonsa*; G. harpacticoid copepod *Porcellidium* sp.; H. ostracod *Parsterope* sp. A; I. ostracod *Cycloleberis lobiancoi*; J. nebaliacean *Nebalia pugettensis*; K. mysid *Acanthomysis sculpta*; L. mysid erythropinid sp.; M. mysid *Siriella pacifica*; N. cumacean *Cumella* sp. A; O. cumacean *Cyclaspis nubila*; P. isopod *Paracercies* sp. (♀); Q. isopod *Cirolana diminuta*; R. isopod gnathiid (♀); S. gammaridean amphipod *Batea transversa*; T. gammaridean amphipod *Gitanopsis vilordes*; U. gammaridean amphipod *Ericthonias braziliensis*; V. caprellid amphipod *Caprella pilidigita*; W. caridean decapod *Hippolyte clarki*.
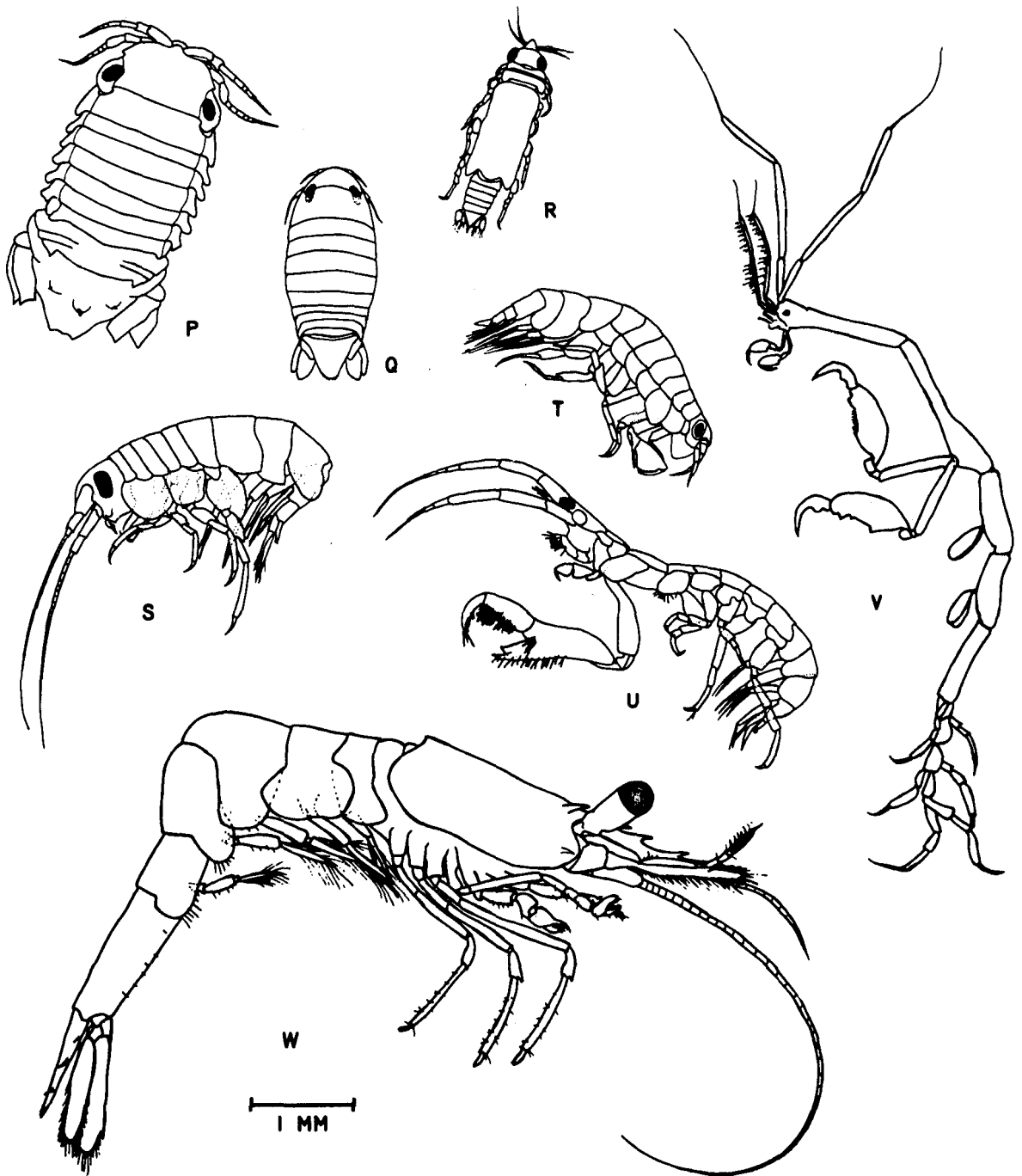
canopy, 5 from the lower portions of the plants), 7 were empty and 3, whose stomachs averaged 13% full, contained crustacean fragments (55% of total volume) and unidentified material. NIGHT-TIME—20 individuals (7-12 mm, $\bar{x}$ = 10.5) taken at middepth 2 h before first morning light had stomachs averaging 82% full, and containing crustacean fragments (100% of total volume), including copepods and cladocerans. Clearly, *S. pacifica* is a nocturnal predator.

TABLE 4.—Mysids collected in the water column, day and night.

		Day				Night			
		Middepth collections (n = 6)		Near-bottom collections (n = 6)		Middepth collections (n = 6)		Near-bottom collections (n = 6)	
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Siriella pacifica	2-12	0	0	0	0	100	693.0	100	1,242.2
Erythropinid sp.	1- 6	0	0	17	5.3	100	400.3	100	468.3
Acanthomysis sculpta	4- 8	0	0	0	0	33	6.2	17	2.0
Unidentified sp.	3- 8	0	0	0	0	0	0	17	1.0

An unidentified erythropinid species (Figure 5L) behaved much like *S. pacifica*, but was seen less often. Although one daytime near-bottom collection took 32 individuals (probably the net sampled a diurnal aggregation close to the sea floor), generally the species was taken in the plankton net only at night. During the day we found it numerous amid the flocculent material that often accumulates in shallow depressions on sandy bottom (Hobson and Chess in prep.).

The predominant mysid observed and collected in the canopy of the kelp forest was *Acanthomysis sculpta* (Figure 5K), which aggregated in small openings among the kelp fronds during the day. (*Siriella pacifica* also was numerous in the kelp canopy, but not the erythropinid.) At night some *A. sculpta* moved out over the adjacent open regions sampled by our net (Table 4), but most stayed close to the kelp. The stomach contents of 20 *A. sculpta* collected during day and night were examined: DAYTIME—All 10 (8.5-11 mm, $\bar{x}$ = 10.0) collected amid the canopy of giant kelp during midafternoon contained food, with their stomachs averaging 85% full. All 10 contained plant material, apparently *Macrocystis* (69% of diet volume), while 7 contained crustacean fragments, mostly copepods, (30% of diet volume). NIGHTTIME—All 10 (8-11 mm, $\bar{x}$ = 9.6) collected in the kelp canopy 30 min before first morning light contained food, with their stomachs averaging 82% full. All 10 contained plant material,

apparently *Macrocystis* (56% of diet volume), and 9 contained crustacean fragments, mostly copepods (44% of diet volume). Thus, *A. sculpta*, which does not join the other two mysid species in their mass movement into open water after dark, seems to feed on plants and animals during both day and night.

Cumaceans

Cumaceans were numerous in the water column at night, but absent there during the day. On four evenings we noted the first one to rise as much as 1 m above the bottom, and found this level attained 26 to 41 ($\bar{x}$ = 32.3) min after sunset. On four mornings we noted the last individual 1 m above the bottom, and recorded this event 37 to 50 ($\bar{x}$ = 41.3) min before sunrise. Usually we were unable to determine the species of cumaceans seen swimming in the water, but our plankton collections (Table 5) took only two species in substantial numbers: *Cumella* sp. A (Figure 5N) and *Cyclaspis nubila* (Figure 5O). Both of these species were numerous in samples of sand taken from the surface of the sea floor during the day (Hobson and Chess in prep.).

Tanaids

Tanaids were absent in the daytime collections, but one species, *Leptochelia dubia*, was collected at

TABLE 5.—Cumaceans collected in the water column, day and night.

		Day				Night			
		Middepth collections (n = 6)		Near-bottom collections (n = 6)		Middepth collections (n = 6)		Near-bottom collections (n = 6)	
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Cumella sp.A	1-2	0	0	0	0	100	11.7	100	73.5
Cyclaspis nubila	2-5	0	0	0	0	67	17.8	100	29.2
Unidentified sp.	2	0	0	0	0	50	0.7	67	1.7

night. The nighttime middepth collections ($n = 6$) took $\bar{x} = 5.8$ *L. dubia*, and the nighttime near-bottom collections ($n = 6$) took $\bar{x} = 9.5$. We found this species in tubes of cemented sand grains in daytime dredge samples from sandy bottom (Hobson and Chess in prep.).

Isopods

Isopods generally were absent from the water column during the day, although the plankton collections show that at least some juvenile and female gnathiids (Figure 5R) are present. After dark, however, a number of isopods occurred in the mid-waters (Table 6). *Paracercies* spp., in particular, were numerous. Most of the specimens of *Paracercies* were juveniles or females (Figure 5P), and their identity remains uncertain. Based on the occurrence of males, *P. cordata* is by far the most

numerous species of this genus in the study area, but at least one other is present.

Gammaridean Amphipods

Gammaridean amphipods were generally absent from the water column during the day, although *Gitanopsis vilordes*, which lived principally amid the dense surface canopy of the kelp forest bordering the study area (Hobson and Chess in prep.), was collected in small numbers (Table 7). At night, however, we saw gammarideans throughout the water column, and, with *Batea transversa* (Figure 5S) predominating, they were a major component of our catch in the nighttime collections (Table 7). *Batea transversa* was numerous during the day amid the low benthic algae that floors most of the study area (Hobson and Chess in prep.).

TABLE 6.—Isopods collected in the water column, day and night.

| | | Day | | | | Night | | | |
| | | Middepth collections ($n = 6$) | | Near-bottom collections ($n = 6$) | | Middepth collections ($n = 6$) | | Near-bottom collections ($n = 6$) | |
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Gnathiid juveniles	1-3	0	0	33	3	100	9.8	100	32.5
Paracerces sp.	1-3	0	0	0	0	50	11.3	67	11.2
Cirolana harfordi	2	0	0	0	0	33	1.5	17	2.0
Cirolana diminuta	3-5	0	0	0	0	-17	0.2	33	0.8
Eurydice caudata	2-3	0	0	0	0	0	0	33	0.8
Excorallana kathae	10	0	0	0	0	17	0.3	17	0.2
Cirolanid sp.	3	0	0	0	0	0	0	17	0.2
Exospheroma rhomburum	3	0	0	0	0	0	0	17	0.2
Limnoria sp.	3	0	0	0	0	0	0	17	0.2

TABLE 7.—Gammaridean amphipods collected in the water column, day and night.

| | | Day | | | | Night | | | |
| | | Middepth collections ($n = 6$) | | Near-bottom collections ($n = 6$) | | Middepth collections ($n = 6$) | | Near-bottom collections ($n = 6$) | |
Species	Size (mm)	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.	% freq.	Mean no. indiv.
Batea transversa	1-4	0	0	0	0	100	400.7	100	1,978.2
Gitanopsis vilordes	1-3	17	0.8	17	2.3	83	11.3	100	41.7
Ericthonias braziliensis	2-4	0	0	0	0	17	0.7	17	2.0
Synchelidium sp.	3	0	0	0	0	17	0.3	33	1.3
Orchomene sp.	2-4	0	0	0	0	17	0.2	50	1.3
Aoroides columbale	3-4	0	0	0	0	0	0	33	1.3
Pleustes platypa	2	0	0	0	0	33	0.7	0	0
Ampithoe spp.	8	0	0	0	0	17	0.2	17	0.5
Podocerus cristatus	2	0	0	0	0	0	0	33	0.3
Oedocerotid sp.	3	0	0	0	0	0	0	17	0.3
Phoxocephalid sp.	2	0	0	0	0	0	0	17	0.2
Unidentified[1]	1-4	0	0	0	0	83	79.7	100	95.5

[1]Many of the unidentified specimens are juveniles, probably at least many being of the species listed above.

On four evenings we noted the first gammaridean seen as much as 1 m above the bottom, and found this level attained 27 to 39 ($\bar{x}$ = 34) min after sunset. On each occasion, individuals had been visible close among the bottom algae for about 5 min before any of them rose to the 1-m level. The final return to the sea floor at daybreak was monitored on four mornings, when the last individual was seen 1 m above the bottom 26 to 41 ($\bar{x}$ = 35) min before sunrise. Similar to the evening situation, individuals continued to be visible close above the bottom algae for an additional 5 min, or so.

To roughly determine the proportion of gammarideans that rise from the sea floor at night, we compared the amphipods in a sample of benthic algae at night, with a similar sample taken in the same place the following day (both samples, loosely packed in a 2.3-liter plastic bag, were taken immediately after plankton collections). Both samples contained 2.5 ml of animals (including other forms besides amphipods). Nevertheless, the limited data (Table 8) indicate that the numbers of some gammarideans on the algae, notably *B. transversa*, dropped sharply after dark, those of others, including *Ericthonias braziliensis* (Figure 5U), experienced a lesser decline, and those of still others remained essentially unchanged. Data from the collections (Table 7) and direct observations indicate that there were fewer amphipods on benthic algae after dark because many have risen into the water column. But the tendency to leave the sea floor clearly varies between species and in perhaps no species is it absolute. Probably at least

TABLE 8.—Gammaridean amphipods collected in samples of benthic algae, day and night.

Species	No. of individuals	
	Day	Night
Species known from plankton collections		
Batea transversa	10	0
Ericthonias braziliensis	25	8
Ampithoe spp.	15	11
Aoroides columbiae	2	0
Pleustes platypa	2	0
Podocerus cristatus	1	0
Total	55	19
Species unknown from plankton collections		
Hyale nigra	10	9
Photis brevipes	2	0
Elasmopus antennatus	0	1
Heterophlias seclusus	1	0
Total	13	10
Unidentified forms[1]	26	22

[1]At least some of the unidenitfied forms probably are juveniles of the species listed above.

many individuals make only short excursions into the water column.

Caprellid Amphipods

We never saw caprellids above the bottom during the day, but saw them, though infrequently, in the water column at night. Consistent with these observations, caprellids were collected in the plankton net at night, but never during the day. The nighttime middepth collections (n = 6) took $\bar{x}$ = 3.2 *Caprella pilidigita* and $\bar{x}$ = 0.2 *C. californica*, whereas the near-bottom collections (n = 6) took $\bar{x}$ = 9.7 *C. pilidigita* and $\bar{x}$ = 5.2 *C. californica*. In addition, a single unidentified juvenile was taken in one nighttime middepth collection. Size ranges of specimens: *C. pilidigita* 4 to 18 mm, *C. californica* 6 to 10 mm, and the unidentified juvenile 3 mm. Both *C. californica* and *C. pilidigita* (Figure 5V) were at all times numerous amid the low benthic algae that floors most of the study area.

Euphausid Larvae

The calyptopis larvae of euphausids occurred regularly in both day and night collections.

Euphausid Adults and Juveniles

Euphasid adults and juveniles were neither seen nor collected in the water column during the day, but occasionally swarmed around our lights at night. The few individuals collected in the plankton net (Tables 1, 2) are of one species: *Thysanoessa spinifera*. The numbers collected, however, underrepresent the numbers we saw in the water (all of which appeared to be *T. spinifera*), probably because this relatively large, motile animal effectively evaded our net. Rather than rising from the sea floor at nightfall, as do so many other nocturnal components of the plankton discussed above, this euphausid seems to move in from deeper water. Unlike the other forms, euphausids were not taken in our extensive diurnal sampling of the benthos (Hobson and Chess in prep.).

Caridean Larvae

Based on the collections (Tables 1, 2), caridean larvae are numerous in the plankton during both day and night, but more so at night. Furthermore, there are more larger individuals in the water

column after dark. We made no attempt to identify our specimens to species, but probably many are larvae of the two species discussed as adults and juveniles, below.

Caridean Adults and Juveniles

Caridean adults and juveniles were observed in the water column only at night. On the one evening that the event was noted, the first individual seen rising as much as 1 m above the bottom attained this level 39 min after sunset. Adult and juvenile carideans are absent in the daytime collections, but *Hippolyte clarki* (Figure 5W), was sometimes numerous in collections made after dark. The nighttime middepth collections ($n = 6$) took $\bar{x} = 25.2$ *H. clarki*, and the near-bottom collections ($n = 6$) took $\bar{x} = 10$. Only one other adult caridean was collected, this a single *Eualus herdmani* in a nighttime near-bottom sample. The specimens of *H. clarki* were 4 to 10 mm long, the single *E. herdmani* 12 mm. *Hippolyte clarki* is numerous during the day in the kelp forest bordering the study area, where it concentrated in the dense surface canopy and upper regions of these massive plants. At the same time *E. herdmani* predominated in the lower regions of the same plants (Hobson and Chess in prep.).

The stomach contents of 20 *H. clarki* collected during day and night were examined. DAYTIME—Of 10 (8-16 mm, $\bar{x} = 10.8$) collected from giant kelp plants during midafternoon, 4 were empty, and the other 6, whose stomachs averaged 17% full, contained only extensively macerated fragments. NIGHTTIME—Of 10 (8-17 mm, $\bar{x} = 12$) collected close to giant kelp 1 h before first morning light, 1 was empty, and the other 9, whose stomachs averaged 34% full, contained a variety of prey, some of it fresh: mollusk veligers in 4 (28% of total volume); foraminiferans in 3 (9% of total volume); shrimp larvae in 1 (11% of total volume); and extensively macerated material in 7 (52% of total volume). These limited data indicate this animal is primarily a nocturnal predator, but only a relatively few seem to swim far from algal cover.

Reptantian Zoea

Based on the collections (Tables 1, 2), zoea were consistently present in moderate numbers at all levels of the water column during both day and night, but were most numerous there after dark. Usually we failed to notice zoea in the water, but one night observed them in dense swarms close to the bottom.

Brachyuran Megalops

Our plankton collections (Tables 1, 2) indicate that brachyuran megalops were frequently present, if not numerous, in the water column at night, but only infrequently present during the day.

Bryozoan Larvae

The cyphonautes larvae of bryozoans (Figure 5B) were consistently taken in substantial numbers by middepth and near-bottom collections both day and night.

Chaetognaths

Our collections regularly took chaetognaths both day and night (Tables 1, 2), but even though these animals are relatively large, we failed to see them in the water, presumably because they are largely transparent. Chaetognaths probably were more numerous in the study area than our collection data indicate, owing to a mobility that would permit many to evade our net.

Larvaceans

We collected larvaceans in our plankton net both day and night, but only in small numbers (Tables 1, 2). It became clear that these numbers far underrepresented the numbers present, however, when we examined the gut contents of the blacksmith (recounted below). Most larvaceans in the area are less than 0.5 mm in diameter, and apparently their pliable bodies readily squeeze through the 0.333-mm mesh of our net. So we made a midday tow in the study area using a 0.25-m net with a 0.253-mm mesh. Significantly, larvaceans, most being of the genus *Oikopleura* (Figure 5A), made up 20% of the sample. There was one larvacean to about every six copepods (calanoids and cyclopoids), and they ranged from 1 to 3 mm long, with a diameter of about 0.2 to 0.5 mm. Significantly, active individuals throughout much of this size range were observed passing through a piece of 0.333-mm mesh net placed among them in a petri dish. Because these animals are transparent, and so small, we failed to see them in the water.

Fish Eggs

Fish eggs were a regular component of both middepth and near-bottom plankton collections during both day and night (Tables 1, 2). Owing to their small size and transparency, however, they went unseen by us in the water.

Fish Larvae

Fish larvae were consistently seen and collected at middepths and near the bottom both day and night (Tables 1, 2).

Activity Patterns of
Planktivorous Fishes, Day and Night

Having described the zooplankters that occur in the water column during both day and night, we now consider the feeding activities of the fishes that find prey there.

Sebastes serranoides—olive rockfish

Small juveniles of this species first appeared inshore during midsummer when about 30 mm long. They remained here throughout the ensuing year, growing to about 100 to 110 mm long. Although their numbers declined sharply during the following summer, when the next crop of small juveniles arrived, many remained in the area well into a second winter, and some stayed longer. Nevertheless, few olive rockfish exceeding about 120 mm occurred in the study area. Larger individuals (to well over 200 mm) were numerous in deeper water, but were not considered in this study. Limbaugh (1955) noted: "The young appear in large schools, from May through September. The schools form behind protective reefs, in bay entrances, and in the lee of islands." Other data on this species presented by Limbaugh, and also by Quast (1968), pertain generally to individuals larger than those discussed here. The species is reported to reach 610 mm (Miller and Lea 1972).

The activity pattern of this fish changes markedly during its first year inshore. Most of the smaller juveniles are active by day and relatively inactive at night. Beginning among those about 55 mm long, however, there is a general shift toward feeding after dark. Nocturnal habits are characteristic among individuals larger than about 65 mm (to at least 120 mm—the largest considered

here). This report, therefore, recognizes three size categories, and treats each separately:

1) small juveniles, which are predominantly diurnal, are those shorter than 55 mm; 2) intermediate juveniles, which represent a transition to the nocturnal mode, are those between 55 and 64 mm; and 3) large juveniles, most of which are nocturnal, are those 65 mm and longer.

SMALL JUVENILES.—During daylight, the small juveniles generally hovered in small aggregations at middepths in less than 5 m of water. In the study area they were most numerous along the shoreward margin of the kelp forest, close to rising stands of *Macrocystis* and other large algae.

The small juveniles appeared in the water column each morning, beginning about 40 min before sunrise, after a night spent sheltered under cover of algae or rocks. They occurred first as solitary individuals, but soon assembled in aggregations that were well-formed by 30 min before sunrise. Only after sunrise, however, did they feed appreciably. Then, sporadically at first, but with steadily increasing frequency, they began to snap at objects in the water indistinguishable to a human observer a few meters away.

The onset of feeding in the morning is illustrated by the decreasing incidence of empty guts in specimens collected during this period from the mid-water aggregations. Empty guts occurred in 84% of those sampled during the 40 min before sunrise (52 of 62 specimens; 42-54 mm, $\bar{x} = 49$), in 58% of those collected during the 15 min following sunrise (7 of 12 specimens; 41-53 mm, $\bar{x} = 48$), in 25% of those taken 15 to 30 min after sunrise (2 of 8 specimens; 45-53 mm, $\bar{x} = 50$), and in none of those collected 30 to 60 min after sunrise (10 specimens; 41-54 mm, $\bar{x} = 50$).

Intermittent observations throughout the day showed consistent feeding activity. The guts were full in all 11 specimens (40-51 mm, $\bar{x} = 45$) sampled from aggregations during midafternoon. Items they had taken, combined with items taken by the 31 specimens containing food that were collected during early morning (a total sample of 42 fish), document the food habits of these small juveniles.

Prey of the 44 small juveniles that had identifiable material in their guts are listed below in order of their rank as prey. (The same format is used in presenting the gut contents of the other fish species, below.) In this list, the major num-

bered categories are the same as those in which the zooplankters are organized in Tables 1 and 2 and in the text above. The few additional major categories include various nonplanktonic organisms that some of these fishes had taken in small numbers. Listed under each major category, according to rank within that category, are the species and species groups that are the actual prey of the fish. Following most entries throughout the listing are sets of three values in parentheses; these values relate certain characteristics of the entry to the food habits of the fish. (The values were derived from calculations based only on fish that contained identifiable material. Fish with empty guts or containing only unidentifiable material were not considered.) The first value in parentheses is the percent of fish that contained the item(s); the second value is the mean number of individuals of the item(s) that were taken, and the third value is the mean percent of the diet volume represented by the item(s). Rank as prey was determined by a ranking index, which is not shown, but which is the product of the first and third values in parentheses.

Following the above format, the prey organisms are:

1. CALANOID AND CYCLOPOID COPEPODS (83: 44.4: 59.5)
   calanoids, including *Acartia tonsa* and *Labidocera* sp. (81: 40.3: 54.9); cyclopoids, including *Corycaeus* sp. (38: 4.1: 4.6).
2. GAMMARIDEAN AMPHIPODS (29: 0.4: 11.4)
   Batea transversa (18: 0.3: 7.6); unidentified fragments (11: 0.1: 3.8).
3. CARIDEAN LARVAE (20: 0.4: 3.2)
   unidentified species.
4. MYSIDS (11: 0.3: 4.5)
   Acanthomysis sculpta (3: 0.1: 2.0); erythropinid sp. (3: 0.1: 0.5); unidentified fragments (7: 0.1: 2.0).
5. CLADOCERANS (20: 1.1: 2.4)
   Evadne sp.
6. OTHER COPEPODS (18: 0.3: 2.2)
   unidentified monstrilloids.
7. EUPHAUSID ADULTS AND JUVENILES (11: 0.1: 1.3)
   unidentified fragments.
8. BRACHYURAN MEGALOPS (5: 0.1: 4.8)
   unidentified.
9. HARPACTICOID COPEPODS (18: 0.4: 1.2)
   harpacticoid sp. A (7: 0.1: 0.7); *Porcellidium* sp. B (5: 0.1: 0.2); *Porcellidium* sp. A (2: 0.1: 0.1); unidentified fragments (5: 0.1: 0.2).
10. TANAIDS (10: 0.2: 2.4)
    Leptochelia dubia (7: 0.1: 1.2); unidentified fragments (3: 0.1: 1.2).
11. REPTANTIAN ZOEA (11: 0.1: 1.3)
    unidentified.
12. FISHES (5: 0.2: 2.0)
    unidentified larvae.
13. ISOPODS (2: <0.1: 1.1)
    Paracercies sp.
14. GASTROPODS (2: 0.4: 0.5)
    Tricolia sp.
15. EUPHAUSID LARVAE (2: <0.1: 0.1)
    calyptopsis.
16. CIRRIPEDIAN LARVAE (5:<0.1: <0.1)
    cypris.
17. BRYOZOAN LARVAE (2: <0.1: <0.1)
    cyphonautes.

Small juveniles took calanoid copepods as their major prey from the time they began feeding at sunrise until they ceased feeding at the end of the day. In 10 specimens collected during May and June (the only times for which calanoids in this material were identified to species), about 22% of the calanoids were *Acartia tonsa*, and although the rest remained unidentified (except for a single specimen of *Labidocera* sp.), many probably were immature individuals of this same species.

A number of the prey listed above occurred only in specimens collected during early morning. These are: the gamaridean amphipods, the tanaids, the euphausids, the lone isopod, the megalops, and all mysids except those in one individual (see below). Most of these items were extensively digested, in sharp contrast to the freshness of the calanoids and other food materials in the early-morning specimens. Clearly, they had been in the guts for some time, probably since the previous night. Nevertheless, judging from the empty guts in most individuals of this size at daybreak it would seem that nocturnal feeding is insignificant.

Only later than about 30 min after sunrise did the olive rockfish begin taking *Evadne* sp., but this cladoceran then became a consistant component of the diet for the rest of the day. *Evadne* is slightly smaller and more transparent than the other prey organisms, and to capture it the rockfish may need more light. The only mysid taken during the day was *Acanthomysis sculpta*, of which two individuals that appeared recently ingested were found in one olive rockfish during midafternoon.

INTERMEDIATE JUVENILES.—Individuals between about 55 and 65 mm long were highly inconsistent in so far as whether they fed by day or by night (many did both). The nocturnal situation among intermediate individuals is represented by 18 specimens (55-63 mm, $\bar{x} = 58$) collected before sunrise from open water during the hour before first morning light, and also from developing

aggregations of juveniles more than 30 min before sunrise. Of these, 13 (72%) were full of prey in varying stages of digestion, demonstrating nocturnal feeding, whereas 5 (28%) were empty, indicating they had been inactive that night. All the empty fish were from the developing aggregations, but many of those containing food were also taken from those aggregations. Items taken at night by the 13 intermediate juveniles containing food were as follows, with the format being that used for the small juveniles, above.

1. GAMMARIDEAN AMPHIPODS (69: 2.9: 28.5)
   including *Batea transversa* and *Ericthonias braziliensis*.
2. CUMACEANS (54: 2.7: 26.3)
   Cyclaspis nubila (46: 2.6: 26.1); *Cumella* sp. A (8: 0.1: 0.2).
3. MYSIDS (38: ?: 16.2)
   Siriella pacifica (23: 0.3: 13.1); unidentified fragments (15: ?: 3.1).
4. FISHES (15: 7.1: 5.4)
   unidentified larvae.
5. CAPRELLID AMPHIPODS (8: 0.5: 6.2)
   Caprella pilidigita.
6. POLYCHAETES, SWIMMING (8: ?: 5.0)
   unidentified fragments.
7. OSTRACODS (8: 0.1: 0.8)
   Parasterope sp. A
8. BRACHYURAN MEGALOPS (8: 0.5: 0.4)
   unidentified.

The diurnal feeding situation, as well as the changeover from day to night, is represented by 12 individuals (55-62 mm, $\bar{x}$ = 58), all with full guts, collected from among feeding aggregations of small juveniles within 1 h after sunrise. Almost all the food items in this sample were either fresh or well-digested—there was little in between. Presumably, the fresh items were those that had been taken after feeding began within the previous hour, whereas the extensively damaged items had been taken during the night before. (One would expect specimens taken as early in the morning as these to contain evidence of any nocturnal feeding they might have done, and this proved true here.) Seven of the 12 individuals sampled contained both fresh and well-digested material in large numbers, always with the fresh items forward in the gut (often in the esophagus), and the well-digested items well back in the posterior region. Clearly, these individuals had fed substantially during both day and night (a conclusion strengthened by the kinds of prey among the fresh and well-digested segments of the diet, see below). Three of the other five specimens contained only fresh items, indicating diurnal feeding exclusively, whereas two contained just well-digested ma-

terial, indicating only nocturnal feeding. Food items in this material are identified below, but with fresh items listed separately from well-digested items.

FRESH ITEMS

1. CALANOID AND CYCLOPOID COPEPODS (83: 65.9: 47.8)
   calanoids (83: 65.7: 47.5); cyclopoids (17: 0.2: 0.3).
2. CLADOCERANS (33: 0.8: 0.8)
   Evadne sp.
3. OSTRACODS (8: 0.1: 1.7)
   Cycloleberis lobiancoi.
4. OTHER COPEPODS (8: 0.1: 0.4)
   monstrilloids.
5. ISOPODS (8: 0.1: 0.4)
   gnathiid juveniles.
6. HARPACTICOID COPEPODS (8: 0.2: 0.2)
   Porcellidium sp. A.
7. CARIDEAN LARVAE (8: 0.1: 0.3)
   unidentified.

WELL-DIGESTED ITEMS

1. GAMMARIDEAN AMPHIPODS (50: 1.3: 1.1)
   including *Batea transversa*.
2. CARIDEAN LARVAE (33: 2.2: 12.9)
   unidentified.
3. EUPHAUSID ADULTS AND JUVENILES (17: 0.7: 10.7)
   unidentified fragments.
4. FISHES (17: 1.0: 9.2)
   unidentified larvae.
5. REPTANTIAN ZOEA (17: 0.3: 2.0)
   unidentified.
6. BRACHYURAN MEGALOPS (8: 0.3: 1.3)
   unidentified.
7. INSECTS (8: 0.1: 0.8)
   unidentified.
8. CAPRELLID AMPHIPODS (8: 0.1: 0.4)
   unidentified.

The fresh items apparently represent diurnal feeding, the well-digested items nocturnal feeding. Thus, among individuals within the intermediate size range there obviously are many that forage during both day and night.

LARGE JUVENILES.—During the day, olive rockfish more than about 65 mm long generally hovered in small aggregations low in the water column beneath the kelp canopy within the seaward part of the forest (Figure 6). Aggregations composed of relatively large individuals (exceeding a length of about 100 mm) sometimes hovered above others of the same size seated on the rocks below.

In contrast to the small individuals described above, large juveniles generally showed no sign of feeding during the day, an observation supported
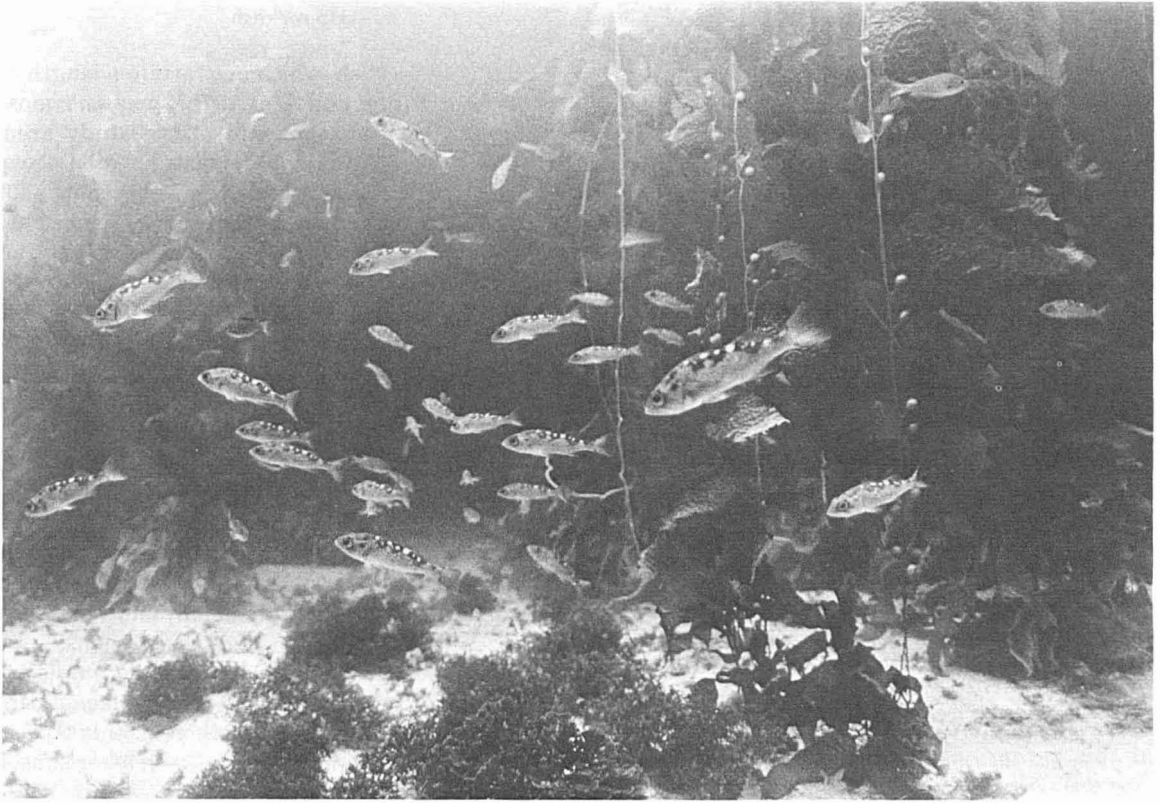
FIGURE 6.—A daytime aggregation of large juvenile olive rockfish, *Sebastes serranoides*. Many nocturnal fishes spend the day in quiet schools.

by examination of gut contents. Of 42 specimens (65-120 mm, $\bar{x} = 91$) collected from aggregations during midafternoon, 28 (67%) had empty guts, and 8 (19%) contained only well-digested fragments. Six (14%), however, contained relatively fresh prey probably captured earlier that day: the mysid *Acanthomysis sculpta* (50: 15.7: 32.5); the caridean shrimps *Hippolyte clarki* (50: 0.5: 14.2) and *Eualus herdmani* (17: 0.2: 5.2); the cladoceran *Evadne* sp. (17: 4.3: 10.0); calanoid copepods (17: 1.5: 5.2); euphausid larvae, calyptopis stage (17: 0.5: 1.6); and harpacticoid copepod *Porcellidium* sp. A (17: 0.2: 0.1). Also present were extensively digested fragments of cumaceans, tanaids, euphausids, and mysids (33: ?: 20.5) that probably had been taken the night before (a judgment influenced by knowledge of nocturnal food habits, defined below). All of the cladocerans, calanoids, and euphausid larvae among this material constituted the entire gut contents of one 82-mm individual, and the contents suggest a mode of feeding like that of the small juveniles above.

Beginning about 20 min after sunset, large juveniles began leaving the sites of their daytime aggregations. They moved away from the kelp forest, and dispersed over the adjacent field of *Dictyopteris*. Many of them rose into the upper part of the water column, but most remained within 5 m of the sea floor. They remained in these positions throughout the night, often assuming a tail-down attitude, now and then darting a few centimeters forward and snapping at objects in the dark water. The few that remained in the kelp forest usually hovered high in the water column beneath sizeable breaks in the kelp canopy. They began returning to the forest at first morning light, and by 30 min before sunrise were back in their daytime aggregations.

Clearly, olive rockfish of this size feed chiefly at night. This conclusion is supported by study of gut contents from 72 specimens (65-157 mm, $\bar{x} = 85$) collected in this area at night—later than 4 h after sunset, and before first morning light. Only two of these (less than 3%) had an empty gut, a contrast

to the high incidence of empty guts (67%) among specimens collected during the afternoon. More significant, the gut of all 70 other specimens contained many fresh items, all organisms present in the water column after dark.

Major categories of prey with included species and species groups, are listed below in order of their rank as prey.

1. GAMMARIDEAN AMPHIPODS (90: 16.9: 43.9)
    Batea transversa 76: 8.5: 21.9); *Ericthonias braziliensis* (19: 1.1: 2.6); *Ampithoe* spp. (20: 1.3: 2.4); *Photis brevipes* (14: 1.2: 0.8); *Ampelisca* sp. (3:<0.1: 1.6); *Synchelidium* sp. (9: 0.1: 0.6); *Aoroides columbiae* (9: 0.1: 0.4); *Hyale nigra* (3: 0.1: 0.3); *Monoculoides* sp. (3: 0.3: 0.2); *Podocerus cristatus* (4: <0.1: 0.1); phoxocephalid sp. (3: <0.1: 0.1); lysianassid spp. (1: <0.1: 0.1); *Paraphoxus* sp. (1:<0.1: 0.1); *Pleustes platypa* (1: <0.1: 0.1); unidentified gammarideans, including unknown forms and those unrecognized due to damage (73: 3.9: 12.6).
2. MYSIDS (69: 2.7: 12.5)
    Siriella pacifica (47: 1.7: 9.2); erythropinid sp. (40: 0.9: 3.1); *Acanthomysis sculpta* (3: <0.1: 0.2).
3. CUMACEANS (57: 4.9: 8.4)
    Cyclaspis nubila (37: 4.1: 7.2); *Cumella* sp. (40: 0.8: 1.1); unidentified (3: <0.1: 0.1).
4. POLYCHAETES, SWIMMING (36: 0.5: 8.6)
    at least most of them nereids.
5. CAPRELLID AMPHIPODS (36: 1.4: 7.0)
    Caprella pilidigita (24: 0.8: 4.2); *C. californica* (19: 0.5: 2.6); *C. brevirostis* (1: <0.1: 0.1); unidentified species (1: 0.1: 0.1).
6. OSTRACODS (43: 1.6: 3.8)
    Parasterope sp. A (37: 1.0: 2.9); *Vargula americana* (9: 0.3: 0.5); *Philomedes* sp. (4: 0.1: 0.2); *Cycloleberis lobiancoi* (3: <0.1: 0.1); unidentified (1: <0.1: 0.1).
7. ISOPODS (39: 1.7: 3.3)
    Paracercies sp. (27: 0.8: 2.1); gnathiid juveniles and females (21: 0.8: 0.8); *Idotea* spp. (4: 0.1: 0.1); *Cirolana diminuta* (3: <0.1: <0.1); *Limnoria lignorum* (1: <0.1: 0.1); *Excorallana kathae* (1: <0.1: <0.1).
8. CARIDEAN ADULTS AND JUVENILES (24: 0.4: 4.1)
    Hippolyte clarki (20: 0.2: 2.2); *Eualus herdmani* (6: 0.2: 1.9).
9. TANAIDS (26: 0.5: 1.2)
    Leptochelia dubia (25: 0.4: 1.0); unidentified (4: 0.1: 0.2).
10. EUPHAUSID ADULTS AND JUVENILES (7: 0.1: 2.0)
    Thysanoessa sp. (1: <0.1: 0.7); unidentified (6: 0.1: 1.3).
11. FISHES (9: <0.1: 1.6)
    unidentified larvae.
12. BRACHYURAN MEGALOPS (10: 0.2: 0.7)
    unidentified.
13. CARIDEAN LARVAE (9: 4.0: 0.6)
    unidentified.
14. HARPACTICOID COPEPODS (13: 0.2: 0.2)
    Porcellidium sp. A.
15. REPTANTIAN ZOEA (6: 0.6: 0.4)
    unidentified.
16. CALANOID AND CYCLOPOID COPEPODS (4: <0.1: 0.2)
    unidentified cyclopoids.
17. OTHER COPEPODS (1: <0.1: 0.1)
    unidentified caligoids.
18. NEBALIACEANS (1: <0.1: <0.1)
    Nebalia pugettensis.

Sebastes atrovirens—kelp rockfish

The kelp rockfish, which may attain a length of 425 mm (Miller and Lea 1972), was the most numerous adult scorpaenid in the study area. During the day, a few individuals hovered above the sea floor in shadow under the kelp canopy, but most spent the daytime seated on rocky substrata within the forest—quiet but alert. At night this fish generally hovered in mid-water close to the rising kelp stipes (Figure 7), and often amid the kelp canopy, near the water's surface. Occasionally at night it hovered in open water close along the seaward margin of the forest. Differences in activities between day and night have gone unnoted in previous reports of this species. Limbaugh (1955) reported that it lives in the lower levels of the kelp and among the rocks, and feeds on "crustaceans and small fish." Quast (1968), on the other hand, reported that it ranges all the way from the bottom to the kelp canopy and apparently utilizes "all available foods in these regions."

Of 29 specimens (89-240 mm, $\bar{x}$ = 175) collected for study of food habits, all 6 (100%) taken during midafternoon were empty, whereas only 3 of 23 (13%) taken at night (more than 4 h after sunset) were empty. Clearly, this fish is predominantly a nocturnal feeder. Quast (1968) noted that many of the kelp rockfish he examined had an empty stomach but did not suggest nocturnal feeding. He noted that his specimens "appeared quite thin," and though recognizing this may be a natural condition, thought perhaps "the high frequencies of empty stomachs and the broad variety of food items found may indicate malnutrition." The kelp rockfish of our study area, we have noted, often have deeply concaved bellies during the day, which we assume is due to the emptiness of their guts at this time.

Almost all food materials taken by this fish were from the water column. The major food categories, which included species and species groups, are listed below in order of their rank as prey.

1. MYSIDS (90: 22.3: 39.5)
    Acanthomysis sculpta (60: 18.3: 30.1); *Siriella pacifica* (65: 3.6: 9.2); erythropinid sp. (15: 0.4: 0.2).
2. CARIDEAN ADULTS AND JUVENILES (85: 7.0: 16.2)
    Hippolyte clarki (65: 4.4: 10.0); *Eualus herdmani* (40: 2.6: 6.2).
3. GAMMARIDEAN AMPHIPODS (95: 13.8: 13.7)
    Batea transversa (95: 9.3: 9.5); lysianassid spp. (50: 1.2: 1.1); *Ampelisca* sp. (10: 1.4: 1.3); *Pleustes platypa* (25: 0.3: 0.3); *Podocerus cristatus* (5: 0.1: 0.2); *Ampithoe tea* (5: 0.1: 0.2);
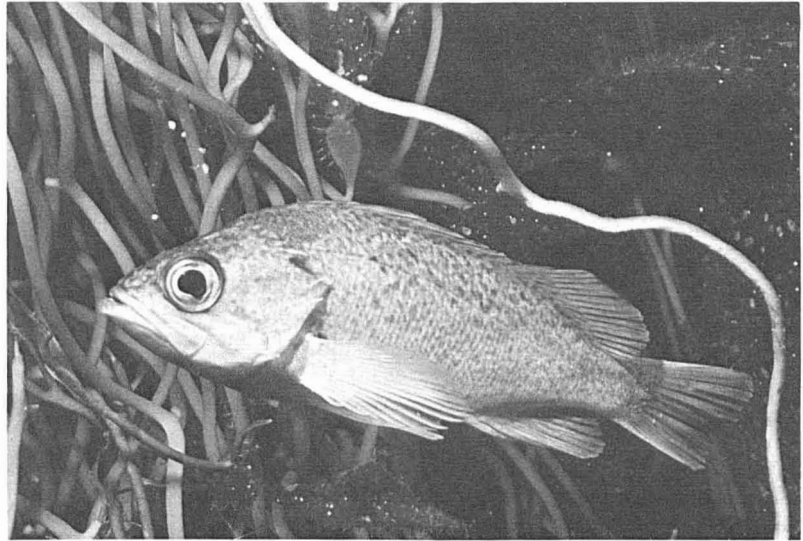
FIGURE 7.—A solitary kelp rockfish, *Sebastes atrovirens*, close to rising stipes of a giant kelp plant at night.

Aoroides columbiae (15: 0.2: 0.1); *Hyale nigra* (5: 0.1: 0.1); *Ericthonias braziliensis* (5: 0.2: 0.1); unidentified (40: 0.9: 0.8).

4. ISOPODS (75: 3.7: 14.3)
    Paracercies sp. (75: 3.3: 11.8); *Pentidotea resecata* (5: 0.1: 1.8); gnathiid juveniles (10: 0.1: 0.3); *Cirolana harfordi* (10: <0.1: 0.2); *Idotea rectolineata* (5: <0.1: 0.2).
5. POLYCHAETES, SWIMMING (20: 0.3: 7.1)
    unidentified, but only certain epitokous nereids were significant, these being prominent in the guts on nights when they swam in mid-water.
6. BRACHYURAN ADULTS (10: 0.1: 4.2)
    all *Pugettia producta*.
7. OSTRACODS (30: 0.5: 0.9)
    Cycloleberis lobiancoi (20: 0.2: 0.5); *Vargula americana* (10: 0.2: 0.3); *Parasterope* sp. A (5: 0.1: 0.1).
8. FISHES (15: 0.1: 1.2)
    larvae (10: 0.1: 0.8); scales (5: ?: 0.4).
9. NEBALIACEANS (5: 0.1: 1.1)
    Nebalia pugettensis.
10. CUMACEANS (5: 0.3: 0.7)
    all *Cyclaspis nubila*.
11. GASTROPODS (5: 0.1: 0.1)
    Lacuna unifasciata.
12. EUPHAUSID ADULTS AND JUVENILES (5: 0.1: 0.1)
    unidentified.

Xenistius californiensis—salema

We never saw salema in the study area during the day, but at night frequently encountered solitary individuals (Figure 8), or loosely spaced groups of four to six. Usually they swam high in the mid-waters above the open fields of *Dictyopteris* within 10 m of the forest. Their first appearance in the evening consistently occurred about 40 min after sunset, apparently after they had come from some distance away. The relatively few times we saw this species in daylight (always more than 400 m from the study area), it swam in schools of more than 50 individuals, closely spaced and seemingly inactive, at middepths within the forest. Reportedly this fish reaches 255 mm (Miller and Lea 1972).

Fresh material filled the stomachs of all five specimens (163-180 mm, $\bar{x}$ = 170) collected for study of food habits. They were taken at night, more than 3 h after sunset, and before daybreak, and so nocturnal feeding is apparent. All three
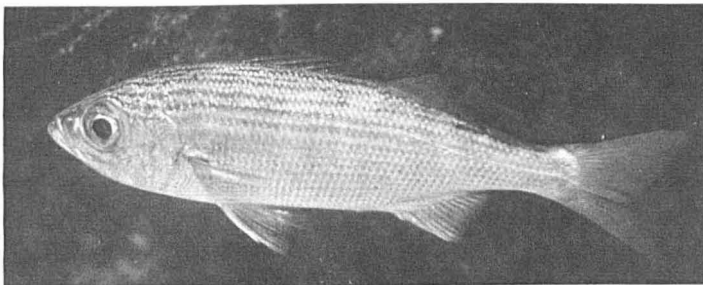

FIGURE 8.—A solitary salema, *Xenistius californiensis*, swims above the sea floor at night.

585

taken before midnight had their intestines empty; this, considering also the inactive appearance of those in diurnal schools, suggests lack of daytime feeding. Quast (1968) reported a high incidence of empty stomachs in specimens that he collected during the day, but did not relate this to nocturnal feeding.

All food material in the guts of specimens collected during this study are organisms that occured in the water column. Major categories of prey, which included species and species groups, are listed below in order of their rank as prey.

1. GAMMARIDEAN AMPHIPODS (100: 44.8: 38.2)
   Batea transversa (100: 26.0: 30.0); *Ampithoe plumulosa* (20: 5.2: 3.0); *Ericthonias braziliensis* (20: 2.0: 1.0); lysianassid spp. (20: 0.2: 0.4); *Gitanopsis vilordes* (20: 0.2: 0.2); *Ampithoe* spp. (20: 4.0: 1.0); unidentified species (60: 7.2: 2.6).
2. MYSIDS (100: 22.0: 28.0)
   Siriella pacifiica (100: 20.2: 26.8); erythropinid sp. (60: 1.8: 1.2).
3. POLYCHAETES, SWIMMING (40: ?: 20.0)
   unidentified species, mostly epitokus nereids.
4. CUMACEANS (60: 2.0: 2.6)
   Cyclaspis nubila (60: 1.6: 2.2); unidentified juveniles (20: 0.4: 0.4).
5. CAPRELLID AMPHIPODS (40: 5.6: 3.0)
   Caprella pilidigita (40: 4.4: 1.8); *C. californica* (40: 1.2: 1.2).
6. OSTRACODS (80: 2.2: 1.0)
   Parasterope sp. A (60: 1.2: 0.6); *Cycloleberis lobiancoi* (20: 0.6: 0.2); *Vargula americana* (20: 0.4: 0.2).
7. NEBALIACEANS (20: 1.0: 3.0)
   Nebalia pugettensis.
8. ISOPODS (40: 2.4: 1.2)
   Cirolana harfordi (20: 0.8: 0.4); *Paracercies* sp. (20: 1.0: 0.2); *Excorallana kathae* (20: 0.4: 0.2); gnathiid juveniles (20: 0.2: 0.4).

9. FISHES (20: ?: 1.8)
   scales.
10. CARIDEAN LARVAE (20: 1.2: 0.6)
    unidentified.
11. CARIDEAN ADULTS AND JUVENILES (20: 1.2: 0.6)
    unidentified.
12. REPTANTIAN ZOEA (20: 3.6: 0.4)
    unidentified.
13. CALANOID AND CYCLOPOID COPEPODS (20: 0.2: 0.2)
    calanoid, *Labidocera* sp.

This list indicates a diet much like that of salema collected from a kelp bed near La Jolla by Quast (1968), although Quast questioned the validity of his data because of the collecting methods used.

*Seriphus politus—*queenfish

The queenfish, which can grow to 304 mm (Miller and Lea 1972), consistently appeared in the study area about 40 min after sunset and remained active there throughout the night. Generally, solitary individuals, or loosely spaced groups of two to six swam several meters above the sea floor, usually close to the seaward edge of the kelp forest, but frequently above the open fields of *Dictyopteris*. Then, shortly after first morning light, 40 to 50 min before sunrise, they abruptly left the area.

During the day queenfish hover in dense, relatively inactive schools close to shore (Figure 9), but we have not seen them within 1.5 km of the study site in daylight. Limbaugh (1955), presumably assessing the daytime situation, stated:

FIGURE 9.—A daytime aggregation of queenfish, *Seriphus politus.*

"Queenfish school in tightly packed aggregations over sandy bottom."

Four of five individuals (124-171 mm, $\bar{x}$ = 148) collected shortly after they had arrived in the study area at nightfall had an empty gut, and the fifth contained just a single freshly ingested shrimp (unidentified). We conclude that these individuals had passed the previous day without feeding. The evidence further suggests they do not feed while en route from daytime schooling sites to their feeding ground in the study area.

All 31 specimens (114-193 mm, $\bar{x}$ = 151) sampled in the study area at night, later than 3 h after sunset and before first morning light, had material in their guts—much of it fresh. All prey belonged to groups known to occur in the water column. Limbaugh (1955) reported that this species feeds on "small free-swimming crustaceans and fish." Below are ranked the species and species groups taken as prey by this fish.

1. MYSIDS (84: 22.5: 44.7)
   Siriella pacifica (84: 21.0: 39.6); *Acanthomysis sculpta* (52: 1.4: 5.0); erythropinid sp. (6: 0.1:<0.1).
2. GAMMARIDEAN AMPHIPODS (89: 16.0: 21.6)
   Batea transversa (84: 15.6: 20.2); *Ampelisca* sp. (9: 0.2: 0.3); lynsianassid spp. (6: 0.1: 0.2); *Ampithoe* sp. (3: 0.1: 0.1); unidentified (3: <0.1: 0.8).
3. POLYCHAETES, SWIMMING (31: 0.8: 21.8)
   Epitokous nereids (22: 0.7: 18.4); unidentified (9: <0.1: 3.4).
4. CARIDEAN ADULTS AND JUVENILES (44: 0.7: 5.9)
   Eualus herdmani (28: 0.4: 2.0); *Hippolyte clarki* (19: 0.3: 2.0); unidentified (3: <0.1: 1.9).
5. ISOPODS (34: 0.7: 3.6)
   Paracercies sp. (22: 0.5: 1.7); gnathiid juveniles (13: 0.1: 0.2); *Limnoria* sp. (3: 0.1: 1.1); *Excorallana kathae* (3: <0.1: 0.5); *Cirolana harfordi* (3: <0.1: 0.1).
6. FISHES (6: 0.6: 1.4)
   scales.
7. NEBALIACEANS (6: 0.1: 0.2)
   Nebalia pugettensis.
8. OSTRACODS (13: 0.3: 0.2)
   Vargula americana (6: 0.1: <0.1); *Cycloeberis lobiancoi* (3: 0.1: <0.1); *Parasterope* sp. A (3: 0.1: <0.1).
9. CARIDEAN LARVAE (3: <0.1: 0.3)
   unidentified.
10. BRACHYURAN MEGALOPS (3: <0.1: 0.2)
    unidentified.
11. EUPHAUSID ADULTS AND JUVENILES (3: <0.1: <0.1)
    unidentified.
12. CUMACEANS (3: <0.1: <0.1)
    Cyclaspis nubila.

A single small juvenile queenfish, 38 mm long, was collected on 2 November shortly before first morning light as it swam alone close over the sand. Its full gut contained mysid *Siriella pacifica*, gammaridean amphipod *Batea transversa*, and isopod *Limnoria* sp. All of these forms are also

prey of larger queenfish, but those taken by this small individual were less than half the size of prey routinely taken by the larger fish.

Material that we collected at La Jolla in 1971 included some information on smaller juveniles. Ten individuals (10-27 mm, $\bar{x}$ = 19) were collected on the same day during the hour before first morning light—all from the stomachs of larger individuals of their own species. Of these, only the two largest, 23 and 27 mm, contained prey of the types taken by larger conspecifics: mysids and gammaridean amphipods constituted 99% of the diet of these two, with calanoid copepods representing the remainder. In contrast, calanoid copepods were the major prey of the seven smaller individuals (in six, 80% of the total diet). Fish larvae (in one, 11% of the total diet), and cladocerans (in one, 9% of the total diet), constituted the rest. These limited data indicate that the queenfish, like the olive rockfish above, changes as it grows from a diet of copepods to one of mysids and other plankters that appear after dark. The queenfish, however, seems to make the change at a smaller size, perhaps because it has a larger mouth. Moreover, the data fail to show that the queenfish, like the olive rockfish, feeds by day when subsisting on copepods.

Hyperprosopon argenteum— walleye surfperch

The walleye surfperch, which can grow to 304 mm (Miller and Lea 1972), consistently schooled during the day in about 2 to 5 m of water over sand at the edge of the forest at the head of Fishermen's Cove. Usually these schools included 20 to more than 100 closely spaced individuals. Members of these schools appeared inactive, an impression supported by the eight empty guts found in nine individuals (115-173 mm, $\bar{x}$ = 140) taken during midafternoon (and the ninth contained only well-digested fragments). Presumably describing the daytime situation throughout southern California, Limbaugh (1955) stated: "They school in an aggregate cloud ... over sand patches among rocks."

The schools dispersed at nightfall, and many individuals spread along the seaward edge of the forest at the perimeters of the cove. They swam individually (Figure 10) or in small groups 1 to 3 m above the bottom, usually over sand within a few meters of, but sometimes within, the forest. Of the 35 (60-151 mm, $\bar{x}$ = 111) collected in the study area between 4 h after sunset and daybreak, only one
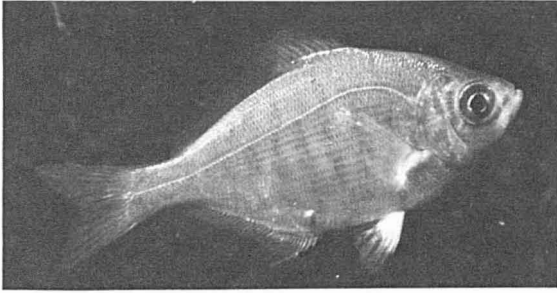
FIGURE 10.—A solitary walleye surfperch, *Hyperprosopon argenteum*, swims in the water column at night.

was empty; the rest were full of prey, much of it fresh.

Clearly, this is a nocturnal fish. Those seen in the study area at night, however, tended to be smaller on the average than those seen in the diurnal schools, suggesting that the larger fish might range farther away. All prey in the 34 individuals containing identifiable material were organisms that occur in the water column, as listed below.

1. GAMMARIDEAN AMPHIPODS (100: 63.6: 47.0)
   Batea transversa (85: 39.8: 24.2); *Ampithoe* spp. (41: 3.3: 3.8); *Hyale nigra* (9: 2.8: 2.9); *Ericthonias braziliensis* (15: 0.5: 1.1); *Ampelisca* sp. (15: 0.6: 1.0); *Synchelidium* sp. (24: 0.4: 0.3); lysianassid spp. (15: 0.6: 0.2); *Heterophilias seclusus* (6: 0.1: 0.1); *Photis* sp. (3: <0.1: 0.1); *Paraphoxus* sp. (3: <0.1: <0.1); *Aoroides columbiae* (3: <0.1: 0.1); unidentified (91: 15.4: 13.2).
2. CUMACEANS (85: 52.9: 25.2)
   Cyclaspis nubila (76: 51.2: 24.8); *Cumella* sp. A (18: 1.7: 0.4).
3. ISOPODS (72: 21.1: 10.2)
   Paracercies sp. (65: 19.5: 7.6); gnathiid juveniles (21: 1.0: 0.6); *Pentidotea resecata* (15: 0.2: 0.6); *Excorallana kathae* (3: 0.1: 1.0); *Cirolana diminuta* (15: 0.2: 0.2); *Rocinella belliceps* (6: <0.1: 0.2); *Exospheroma* sp. (6: <0.1: <0.1); idoteid sp. (3: <0.1: 0.1).
4. CAPRELLID AMPHIPODS (41: 2.1: 6.0)
   Caprella pilidigita (24: 1.4: 4.7); *C. californica* (21: 0.7: 1.2); *C. penantis* (3: <0.1: <0.1); *Tritella laevis* (3: <0.1: <0.1).
5. POLYCHAETES, SWIMMING (35: <0.7: 6.4)
   epitokous nereids (9: 0.7: 5.5); unidentified fragments (26: ?: 0.9).
6. OSTRACODS (62: 1.7: 1.6)
   Parasterope sp. A (38: 0.7: 0.6); *Cycloleberis lobiancoi* (23: 0.5: 0.4); *Philomedes* sp. (9: 0.4: 0.4); species O (3: <0.1: <0.1); species N (3: <0.1: <0.1).
7. MYSIDS (21: 0.6: 1.3)
   Siriella pacifica (15: 0.5: 1.2); *Acanthomysis sculpta* (3: <0.1: <0.1); unidentified fragments (3: 0.1: <0.1).
8. CARIDEAN ADULTS AND JUVENILES (21: 0.9: 0.9)
   Hippolyte clarki (3: 0.2: 0.1); unidentified (24: 0.7: 0.8).
9. BRACHYURAN MEGALOPS (26: 0.7: 0.5)
   unidentified.
10. TANAIDS (15: 0.5: 0.5)
   Leptochelia dubia (6: 0.2: 0.3); unidentified (9: 0.3: 0.2).
11. NEBALIACEANS (6: <0.1: <0.1)
   Nebalia pugettensis.
12. CARIDEAN LARVAE (3: <0.1: <0.1)
   unidentified.

Brachyistius frenatus—kelp perch

The kelp perch, which Miller and Lea (1972) claimed can attain a length of 214 mm, was numerous close among the rising stands of giant kelp. It often aggregated immediately under the canopy (Figure 11), but occurred along the entire length of the plants from water's surface to the

FIGURE 11.—Kelp perch, *Brachyistius frenatus*, aggregated close to kelp, pluck zooplankters from the water column during the day.

sea floor, with larger individuals mostly in the lower regions. Far fewer numbers also occurred close above low fields of benthic algae some distance from the kelp forest. It assumed similar attitudes in the same places during both day and night, but after dark there seemed to be more of them in the mid-waters along the outer edge of the kelp.

Most kelp perch feed by plucking material from the surface of algae, but plankton-feeding is widespread, especially among those aggregated in the mid-waters at the edges of the forests. Limbaugh (1955) reported that the kelp perch feeds on small crustaceans, particularly those that occur on giant kelp. Quast (1968) also reported a predominantly crustacean diet, with a preponderance of amphipods, but also including mollusks and bryozoans.

Preliminary assessment of our food-habit data, along with direct observations, showed that in this species it is primarily the smaller individuals that feed on plankton. Consequently, we consider for this paper only those less than 100 mm long, leaving the larger individuals for a later paper. This point is drawn somewhat arbitrarily, although plankters generally become noticeably less prevalent in the diet at about this size. With kelp perch more so than with the other species treated in this paper, however, many of the individuals considered had mixed a diet of plankters with organisms plucked from a substrate. Bray and Ebeling (1975) reported that kelp perch feed mainly on tiny plankters, mostly copepods, based on a sample of predominantly small individuals (43–142 mm, $\bar{x} = 103$).

All 35 specimens (40–99 mm $\bar{x} = 81$) collected during the afternoon as they swam over various locations in the study area, usually close to kelp, contained food, much of it fresh. On the other hand, of 34 specimens (38–99 mm, $\bar{x} = 76$) collected during the 2 h of night before first morning light 25 (74%) were empty. The other nine, however, contained food, including relatively fresh items. Thus, although the kelp perch within this size range clearly fed mostly by day, some apparently fed at night. Individuals evidencing nocturnal feeding ranged from 81 to 99 ($\bar{x} = 95$) mm long, and so were among the larger ones in the sample.

Recognizing that the contrasting conditions between day and night undoubtedly influenced the composition of the diet, food data from individuals collected during the afternoon (when presumably most fresh items in the gut had been taken by day) were considered separately from food data from individuals collected during the last hours of the night (when presumably most fresh items in the gut had been taken after dark).

In addition to the high incidence of empty guts in kelp perch collected at night, the guts of those that had taken prey after dark averaged 50% full, compared with an average of 72% full for the day feeders. Furthermore, the night feeders contained an average of 38 prey items, compared with an average of 252 for the day feeders (at least in part, however, this difference reflects the larger size of nocturnal prey). These data strengthen our conclusion that over the size range studied, nocturnal feeding is relatively unimportant to this species. Bray and Ebeling (1975) also noted that kelp perch feed mainly by day.

Foods taken by individuals that had been feeding during the day are ranked below:

1. CALANOID AND CYCLOPOID COPEPODS (94: 157.7: 49.1)
   calanoids, including *Calanus pacificas*, and *Rhincalanus nasutus* (71: 137.2: 44.2); cyclopoids, including *Corycaeus* sp. and *Oncea* sp. (74: 20.5: 4.9).
2. GAMMARIDEAN AMPHIPODS (63: 57.9: 37.0)
   Microjassa litodes (46: 23.1: 15.1); *Ericthonias braziliensis* (14: 3.9: 2.6); *Gitanopsis vilordes* (11: 3.0: 0.1); *Ampithoe* spp. (3: 0.1: 0.2); *Hyale nigra* (3: 0.3: 0.2); *Batea transversa* (3: 0.1: 0.1); unidentified (63: 27.4: 18.7).
3. CLADOCERANS (37: 26.1: 6.9)
   Evadne sp.
4. CIRRIPEDIAN LARVAE (31: 1.8: 0.9)
   cypris stage.
5. POLYCHAETES, NONSWIMMING (11: 0.4: 1.9)
   Spirorbis sp. (9: 0.4: 1.8); unidentified (3: 0.1: 0.1).
6. HARPACTICOID COPEPODS (14: 1.6: 0.7)
   Porcellidium sp. A (11: 1.5: 0.6); *Porcellidium* sp. B (3: 0.1: 0.1).
7. OSTRACODS (26: 0.6: 0.6)
   Cythereis sp. (17: 0.3: 0.2); *Philomedes* sp. B (11: 0.2: 0.1); unidentified sp. C (3: 0.1: 0.3).
8. CAPRELLID AMPHIPODS (9: 0.3: 0.7)
   Caprella pilidigita (6: 0.2: 0.4); *C. californica* (3: <0.1: 0.3).
9. FISH EGGS (14: 0.4: 0.3)
   unidentified.
10. PELECYPODS (11: 0.4: 0.3)
    Hiatella arctica (9: 0.3: 0.3); *Halodakra brunnea* (3: <0.1: <0.1).
11. ISOPODS (14: 0.7: 0.2)
    Paracercies sp. (6: 0.5: 0.1); gnathiid juveniles (6: 0.1: <0.1); unidentified fragments (3: 0.1: 0.1).
12. BRYOZOAN LARVAE (9: 0.1: 0.2)
    cyphonautes.
13. CARIDEAN LARVAE (9: 0.2: <0.1)
    unidentified.
14. FISHES (6: 0.2: <0.1)
    unidentified larvae.

15. MYSIDS (3: <0.1: <0.1)
    Siriella pacifica.
16. CUMACEANS (3: <0.1: <0.1)
    Cyclaspis nubila.
17. CARIDEAN ADULTS AND JUVENILES (3: <0.1: <0.1)
    Hippolyte clarki.

Although these fish preyed heavily on zooplankters, clearly many of the organisms in the above list were plucked from a substrate. The major gammaridean, *Microjassa litodes*, was never seen or taken by us in the water column, but was a predominent form on the surface of giant kelp (Hobson and Chess in prep.) Similarly, the many forms known to occur in the water column only at night, e.g., *Siriella pacifica, Cyclaspis nubila, Paracercies* sp., *Batea transversa,* and *Hippolyte clarki* were probably plucked by these day feeders from the algae or sand where they occur in the daytime.

Foods taken by individuals that had been feeding at night are ranked below.

1. GAMMARIDEAN AMPHIPODS (100: 33.8: 71.1)
    Batea transversa (66: 8.1: 22.1); *Ericthonias braziliensis* (44: 0.9: 2.6); *Microjassa litodes* (22: 1.6: 1.7); *Ampithoe* spp. (22: 0.3: 0.9); *Hyale nigra* (11: 0.4: 0.9); *Aoroides columbiae* (11: 0.1: 0.3); unidentified, at least some probably juveniles of the above (100: 22.4: 42.6).
2. CAPRELLID AMPHIPODS (66: 4.4: 15.0)
    Caprella californica (55: 2.0: 9.5); *C. pilidigita* (11: 2.0: 4.1); unidentified (22: 0.4: 1.4).
3. ISOPODS (44: 0.5: 6.6)
    Paracercies sp.
4. CARIDEAN ADULTS AND JUVENILES (55: 0.7: 5.1)
    unidentified.
5. MYSIDS (22: 0.2: 1.1)
    Siriella pacifica (12: 0.1: 1.0); erythropinid sp. (11: 0.1: 0.1).
6. POLYCHAETES, NONSWIMMING (22: 0.2: 0.3)
    Spirorbis sp.
7. OSTRACODS (22: 0.2: 0.2)
    Parasterope sp. A (12: 0.1: 0.1); *Cytheresis* sp. (11: 0.1: 0.1).
8. FORAMINIFERANS (11: 0.1: 0.2)
    unidentified.
9. HARPACTICOID COPEPODS (11: 1.0: 0.1)
    Porcellidium sp. A.

Two specimens also contained fragments of algae (*Macrocystis* in one, *Sargassum* in the other) that probably had been taken incidentally along with prey. Clearly this fish took at least some of its nocturnal prey from a substrate—*Spirorbis* sp., for example. Nevertheless, because the diet is comprised mostly of organisms that swim in the water column at night, we believe this was probably where most of them were taken. Most of these prey organisms also occurred on rocks and algae after dark, but if substrate-feeding had predominated, we would have expected a greater proportion of strictly substrate-dwelling forms.

Oxyjulis californica—señorita

The señorita, which can attain a length of 250 mm (Miller and Lea 1972), is perhaps the most widespread fish in nearshore habitats at Santa Catalina Island. It is strictly a diurnal species that, like other labrids, rests under cover on the sea floor at night (Hobson 1971). Often during the day it swims in large assemblages 1 to 2 m above the sea floor (Figure 12).

Most señoritas feed by plucking material from the surface of algae—often from algae drifting as fragments in the mid-waters—but plankton-feeding is widespread, and predominates in smaller juveniles. Limbaugh (1955) concluded that the señorita is an omnivorous carnivore that feeds "on almost any animal protein." Hobson (1971) found that specimens between 110 and 195 mm long had fed primarily on bryozoans that encrust algae, and on caprellid amphipods. Quast (1968) reported the principal foods to be small gastropods and crustaceans commonly associated with algae, but noted that specimens 50 to 60 mm long had fed heavily on copepods, ostracods, and bryozoan larvae.

Direct observations, complemented by our food habit data (see below), agree that smaller individuals mostly pluck their prey from the water column, whereas larger individuals mostly pluck their prey from some substrate. In this respect, then, the señorita is similar to the kelp perch, described above. So, as with the kelp perch, this paper considers only those individuals less than 100 mm long, leaving the larger individuals for a later paper. We have better reason for drawing the dichotomy at this point with the señorita than with the kelp perch: the smallest señorita we found containing prey obviously plucked from a substrate was 101 mm long, and although planktivorous habits predominated in certain individuals up to 175 mm (which were among the largest taken), most over 100 mm seemed to feed primarily on a substrate. So unlike the diverse feeding habits of smaller kelp perch, the smaller señoritas seemed strictly planktivorous. Bray and Ebeling (1975) stated: "Unlike kelp perch, señoritas did not exploit the plankton as a major source of food." Although this view would seem to disagree with our findings, their samples of the two species were not comparable on this point. Most of their kelp
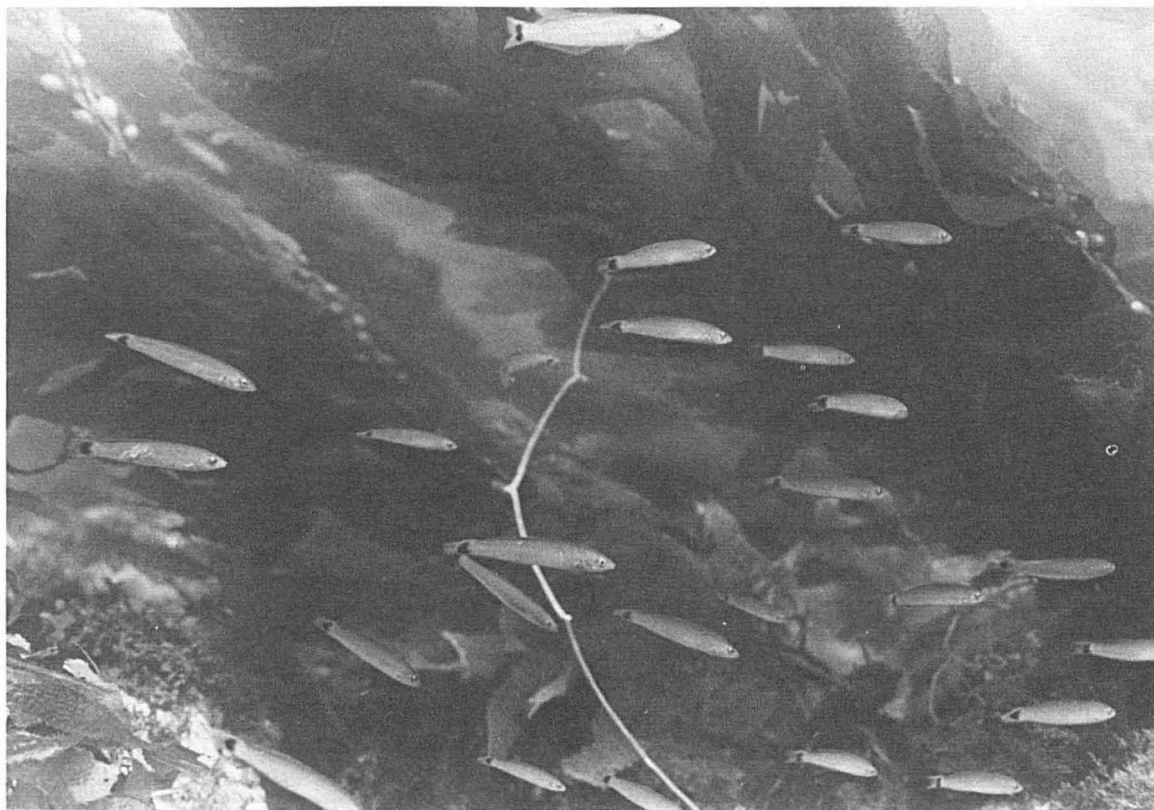
FIGURE 12.—An aggregation of señoritas, *Oxyjulis californica*, passes along the edge of a kelp forest during the day.

perch were small, as noted above, whereas their señoritas were relatively large (110-223 mm, $\bar{x}$ = 169).

All 24 specimens (19-99 mm, $\bar{x}$ = 51) collected during the afternoon as they swam in groups above the sea floor were full of relatively fresh prey, as ranked below:

1. CALANOID AND CYCLOPOID COPEPODS (100: 68.7: 74.1)
   calanoids (75: 44.3: 43.8); cyclopoids, including *Corycaeus* sp. and *Oncaea* sp. (67: 24.4: 30.3).
2. BRYOZOAN LARVAE (58: 7.3: 4.3)
   cyphonautes.
3. HARPACTICOID COPEPODS (42: 7.1: 4.8)
   Microsetella sp. (25: 3.1: 2.1); *Porcellidium* sp. A (8: 0.1: 0.2); unidentified spp. (21: 3.9: 2.5).
4. CIRRIPEDIAN LARVAE (46: 2.8: 2.8)
   cypris stage.
5. GAMMARIDEAN AMPHIPODS (25: 1.8: 4.7)
   unidentified fragments.
6. CLADOCERANS (21: 4.8: 5.4)
   Evadne sp.
7. MOLLUSK LARVAE (46: 1.1: 1.0)
   veligers.
8. FISH EGGS (4: 0.1: 0.3)
   unidentified.

9. RADIOLARIANS (4: 0.1: <0.1)
   unidentified.

With the likely exception of the gammarideans, which were unidentifiable, all of the items in the above list are organisms present in the water column at the time these fish were feeding.

Chromis punctipinnis—blacksmith

The blacksmith, which can attain a length of 300 mm (Miller and Lea 1972), is probably the most numerous fish in the nearshore waters at Santa Catalina Island. During the day it concentrated along the seaward edge of the kelp forests, but occurred in varying numbers in most nearshore habitats, usually aggregated in the mid-waters (Figure 13). At nightfall it sheltered among the rocks, often considerable distances inshore from where it spent the day.

Other species of the genus *Chromis* are widespread in tropical seas, where they are known to be planktivores, e.g.: West Indies (Randall 1967); Gulf
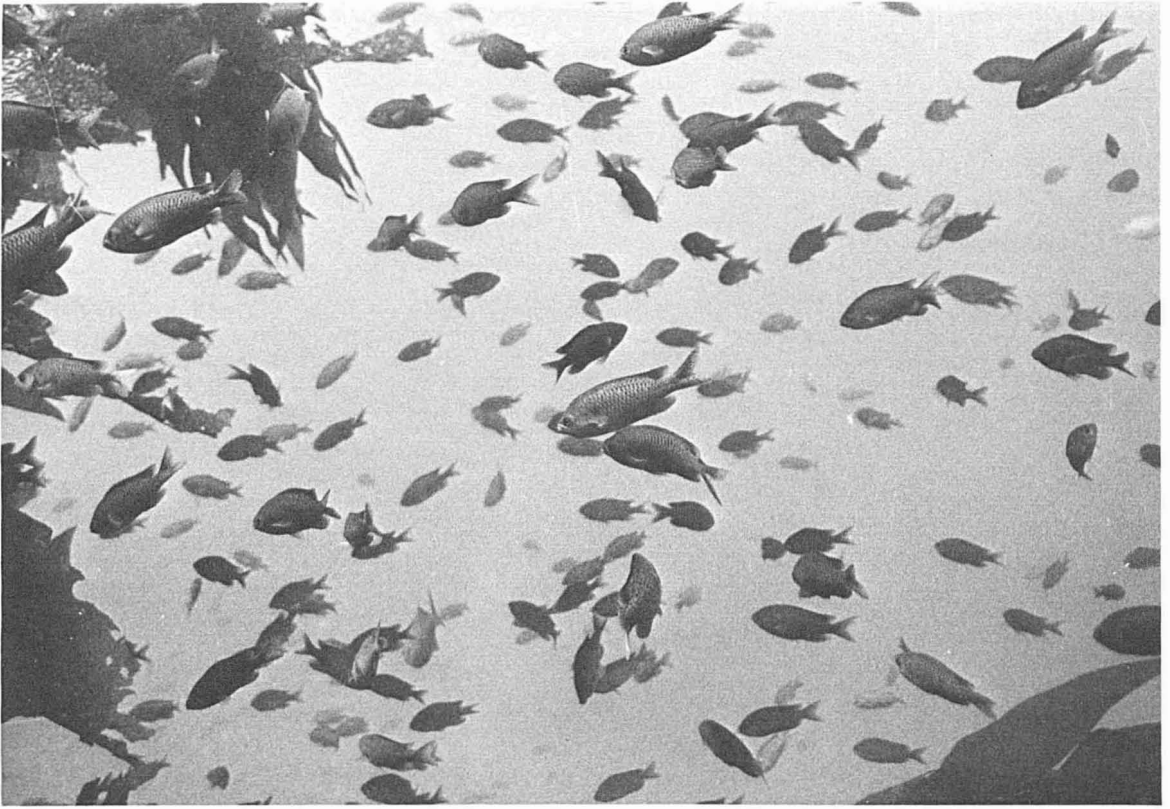
591

FIGURE 13.—Blacksmiths, *Chromis punctipinnis*, aggregated at the edge of a kelp forest, pluck zooplankters from the water column during the day.

of California (Hobson 1968); Hawaii (Swerdloff 1970; Hobson 1974). It is also well-known that *C. punctipinnis* is a planktivore. Limbaugh (1955) noted that it feeds on "particulate plankton such as small fish, squid, and crustaceans," and "may materially affect the amount of plankton entering kelp beds because they eat it as it enters." Quast (1968) listed the principal food of the blacksmith as "minute swimming crustacea and crustacean eggs and larvae gleaned from open water species of kelp beds and over rocky areas." In taking its tiny prey from the water column in what seems a visually directed action, the blacksmith suddenly thrusts both of its highly protrusible jaws forward, then immediately retracts them, presumably sucking plankters into its rapidly expanding oral cavity. This way of feeding has also been noted among its tropical congeners (Swerdloff 1970; Hobson 1974).

Aggregations of blacksmiths feeding on plankton occurred throughout the water column, with each member of an aggregation acting indepen-

dently. They aggregated according to size: the discrete aggregations of small juveniles (which first appeared inshore during late summer, when about 15 to 25 mm long) generally were closer to the sea floor than were aggregations of the adults.

Blacksmiths fed throughout the day, but the rate at which they ingested prey varied. In the tropical Atlantic, *Eupomacentrus partitus*, another planktivorous pomacentrid, feeds more rapidly with increased light and with increased current (Stevenson 1972). Blacksmiths, too, feed more rapidly in a current than at slack water, presumably (as Stevenson suggested of *E. partitus*) because they receive more plankters. To measure this effect, we counted the characteristic mouth movements of feeding adult blacksmiths, first in a moderate current, and then at slack water. The observations were made during midafternoon under a clear sky at a depth of 5 m in 10 m of water. The fish were part of an aggregation with members ranging from about 109 to 130 mm long (these being the sizes of the two in-

dividuals collected later judged to be the largest and smallest in the group). In the moderate current, with the giant kelp lying over at about 25° (attempts to measure the current in this habitat proved unsatisfactory owing to complex eddy systems), 10 individuals (selected haphazardly) plucked at plankters 50 to 73 ($\bar{x} = 58$) times during 1-min periods. One hour later, when there was no discernible current, 10 individuals in a similar, if not the same aggregation, each plucked at plankters 30 to 51 ($\bar{x} = 39$) times during 1-min periods. Probably there is an optimum current speed beyond which the fish find the increasing difficulty of maintaining station outweighs the advantage of added food. We lack data on feeding rates, but have noted that in strong currents blacksmiths abandon the open places within the forest, where they had been dispersed and feeding, and concentrate in dense numbers close in the lee of individual kelp columns.

Of 41 adults (92-145 mm, $\bar{x} = 118$) collected from aggregations in the water column throughout the study area during the afternoons, 36 were full of food, much of it fresh. The other 5, all collected during midafternoon along the margin of the forest bordering the inshore edge of the *Dictyopteris* field, were empty. All prey taken by these blacksmiths, ranked below, are forms we have collected in the water column during the day.

1. LARVACEANS (100: 448.1: 57.5)
    most of them *Oikopleura* spp.
2. CALANOID AND CYCLOPOID COPEPODS (100: 256.3: 33.7)
    calanoids, including *Calanus pacificus*, *Acartia tonsa*, *Labidocera* sp., and *Rhincalanus nasutus* (100: 253.6: 32.4); cyclopoids, including *Corycaeus* sp., *Oncaea* sp., and *Oithona* sp. (72: 2.7: 1.3).
3. FISH EGGS (69: 17.9: 4.1)
    unidentified.
4. CLADOCERANS (75: 24.6: 2.5)
    Evadne spp.
5. CARIDEAN LARVAE (33: 1.4: 0.9)
    unidentified.
6. EUPHAUSID LARVAE (33: 5.1: 0.6)
    calyptopis stage.
7. CIRRIPEDIAN LARVAE (33: 3.5: 0.6)
    cypris stage.
8. BRYOZOAN LARVAE (17: 1.2: 0.2)
    cyphonautes.
9. CHAETOGNATHS (3: 0.1: 0.5)
    unidentified.
10. REPTANTIAN ZOEA (3: 0.4: 0.1)
    unidentified.
11. HARPACTICOID COPEPODS (3: <0.1: <0.1)
    Microsetella sp. A.
12. FISHES (3: <0.1: <0.1)
    unidentified larvae.
13. ISOPODS (3: <0.1: <0.1)
    gnathiid juvenile.

In feeding so heavily on larvaceans, their major prey, these adult blacksmiths differ from other species treated in this report. Significantly, however, larvaceans are also major prey of other species of *Chromis* elsewhere, e.g., in Hawaii (Hobson 1974) and in the West Indies (Randall 1967). Probably larvaceans are important food of the blacksmith throughout its range, even though they have gone unreported in previous food-habit studies of this species. Larvaceans are difficult to recognize, especially if digestion is advanced or preservation faulty, and this may account for them going unreported.

Because juvenile blacksmiths were in feeding aggregations distinct from those of the adults, we analyzed their gut contents separately. Of 14 juveniles (16-47 mm, $\bar{x} = 34$) collected from aggregations during the afternoon, all were full of food, much of it fresh. All prey, ranked below, are forms that we have collected from the water column during the day.

1. CALANOID AND CYCLOPOID COPEPODS (100: 394.4: 54.1)
    calanoids, including *Acartia tonsa* (100: 366.2: 50.5); cyclopoids, including *Corycaeus* sp. and *Oncaea* sp. (93: 28.2: 3.6).
2. LARVACEANS (93: 48.9: 26.4)
    most of them *Oikopleura* spp.
3. CLADOCERANS (100: 108.8: 12.5)
    Evadne spp.
4. CIRRIPEDIAN LARVAE (79: 63.6: 4.6)
    cypris stage.
5. BRYOZOAN LARVAE (79: 63.6: 4.6)
    cyphonautes.
6. HARPACTICOID COPEPODS (57: 6.4: 0.8)
    Microsetella sp. A.
7. FISH EGGS (43: 2.1: 0.7)
    unidentified.

Differences in the diet between juvenile and adult blacksmiths can be related to the sizes of the various organisms in the water column. Most prey of the juveniles were less than 0.5 mm long. Compared to the prey of adults these included more cladocerans, copepods, and larvae of barnacles and bryozoans, but fewer larvaceans and fish eggs (there were no larvaceans in the smallest blacksmith, 16 mm long, and no fish eggs in all six <34 mm).

During the day, the heaviest concentrations of adult blacksmiths in the vicinity of the study area were at the mouth of the cove seaward of the kelp

forest. The sea floor in this region is sand, and lies under more than 30 m of water. Because blacksmiths habitually settled among rocks at night, the offshore feeders migrated to resting areas inshore at day's end. At the migration's peak, groups of 100 or more blacksmiths spaced perhaps 50 m apart streamed along established routes.

As the migrators swam between feeding grounds and shelter areas, they passed among many other blacksmiths, most of which were actively feeding and which gave the migrators no overt notice. Most of the blacksmiths in the vicinity of the study area were nonmigrators that found nocturnal shelter among rocks lying below their mid-water feeding grounds.

Most of the blacksmiths within the forest bordering the study area began descending toward the sea floor by sunset, and by 35 min after sunset the vast majority had taken shelter among the rocks. They rested here throughout the night, and their lack of feeding during this period is indicated by the empty guts we found in all 11 individuals (111-143 mm, $\bar{x}$ = 122) collected among rocks during the 2 h immediately before first morning light.

In the morning, blacksmiths among the rocks became noticeably active about 40 min before sunrise. They began to rise among the kelp columns about 25 to 30 min before sunrise, and to feed about 5 to 10 min later. At about the same time that blacksmiths within the forest were rising into the water column, the migrating individuals streamed along their courses to the offshore feeding grounds, reversing the courses they had followed inshore the night before.

DISCUSSION

Trophic relationships among the fishes and zooplankters near shore at Santa Catalina Island differ strikingly between day and night (Table 9), broadly paralleling the situation described earlier in the water column above tropical reefs (Hobson 1965, 1968, 1972, 1973, 1974). This section discusses these differences and their evolutionary implications.

The Mid-Waters in Daylight

Zooplankters populating the nearshore water column at Santa Catalina during the day—including radiolarians, cladocerans, copepods, and

TABLE 9.—Percent of each fish species that took prey in each major food category.

Major food category	Day feeders 1. olive rockfish <55 mm, n = 42 2. kelp perch <100 mm, n = 35 3. señorita <100 mm, n = 24 4. blacksmith >90 mm, n = 36 5. blacksmith <50 mm, n = 14					Night feeders 1. olive rockfish >65 mm, n = 70 2. kelp rockfish, n = 20 3. salema, n = 5 4. queenfish, n = 32 5. walleye surfperch, n = 34 6. kelp perch <100 mm, n = 9					
	1	2	3	4	5	1	2	3	4	5	6
Radiolarians	0	0	4	0	0	0	0	0	0	0	0
Polychaetes, swimming	0	0	0	0	0	36	20	40	31	35	0
Mollusk larvae	0	0	46	0	0	0	0	0	0	0	0
Cladocerans	20	37	21	75	100	0	0	0	0	0	0
Ostracods	0	26	0	0	0	43	30	80	13	62	22
Calanoid and cyclopoid copepods	83	94	100	100	100	4	0	20	0	0	0
Harpacticoid copepods	18	14	42	3	57	13	0	0	0	0	11
Other copepods	18	0	0	0	0	1	0	0	0	0	0
Cirripedian larvae	5	31	46	33	79	0	0	0	0	0	0
Nebeliaceans	0	0	0	0	0	1	5	20	6	6	0
Mysids	11	3	0	0	0	69	90	100	84	21	22
Cumaceans	0	3	0	0	0	57	5	60	3	85	0
Tanaids	10	0	0	0	0	26	0	0	0	15	0
Isopods	2	14	0	3	0	39	75	40	34	72	44
Gammaridean amphipods	29	63	25	0	0	90	95	100	89	100	100
Caprellid amphipods	0	9	0	0	0	36	0	40	0	41	66
Euphausid larvae	2	0	0	33	0	0	0	0	0	0	0
Euphausid adults and juveniles	11	0	0	0	0	7	5	0	3	0	0
Caridean larvae	20	9	0	33	0	9	0	20	3	3	0
Caridean adults and juveniles	0	3	0	0	0	24	85	20	44	21	55
Reptantian zoea	11	0	0	3	0	6	0	20	0	0	0
Brachyuran megalops	5	0	0	0	0	10	0	0	3	26	0
Bryozoan larvae	2	9	58	17	79	0	0	0	0	0	0
Chaetognaths	0	0	0	3	0	0	0	0	0	0	0
Larvaceans	0	0	0	100	93	0	0	0	0	0	0
Fish eggs	0	14	4	69	43	0	0	0	0	0	0
Fishes	5	6	0	3	0	9	15	20	6	0	0
Other	2	22	0	0	0	0	15	0	0	0	33

various larval forms (see Tables 1, 2)—tend to be less than 2 mm in their greatest dimension. Forms appreciably larger than this—including chaetognaths and some larvaceans—tend to be transparent. These organisms are equally numerous in the water column at night, and none are residents of the study area. The species are widespread in the water columns of the various inshore habitats, and also offshore.

This assemblage resists a common label. Most of the species have been considered holoplankton (planktonic throughout the whole of their life histories: Newell and Newell 1963), but this term excludes the larval forms so prominent here. The larval forms generally are considered meroplankton (planktonic during some stage in their life histories, but benthonic during some other: Newell and Newell 1963), but this term has been used in general reference to organisms that are planktonic at night, but benthonic by day (e.g., Williams and Bynum 1972). As noted above, we do not use these terms because they fail to define categories meaningful to the concepts developed in this paper.

Fishes that forage in the water column by day have certain characteristics relating to the problems they face as diurnal planktivores. Significantly, of the four diurnal planktivores studied at Santa Catalina, three—the señorita, the kelp perch, and the small juvenile olive rockfish—outgrow this habit. Apparently as they grow larger they find the tiny organisms in the mid-waters increasingly inappropriate as prey. We believe that each is limited in taking very small prey by the size and structure of its mouth, a problem solved by changing either feeding place, or feeding time. Thus, the señorita and kelp perch (noted by Hubbs and Hubbs 1954, to have similar dentition and feeding habits) increasingly abandon the water column as a hunting ground as they grow and shift to prey on organisms that live on algae. The small juvenile olive rockfish, on the other hand, continues to feed in the water column, but assumes nocturnal habits that bring it into contact with the larger organisms that rise above the sea floor at night (see below). The señorita and kelp perch, both relatively small-mouthed species, generally shift their food habits when about 100 mm long; the olive rockfish, with a much larger mouth (compare Figures 6, 11, 12), generally shifts when under 65 mm long.

The fourth diurnal planktivore studied at Santa Catalina, the blacksmith, retains its planktivorous diet through adulthood. It does so despite growing to a relatively large size because it has, among other adaptive features, a small mouth specialized for this habit. Judging from its numbers, the blacksmith is highly successful in the warm temperate waters of southern California. But it does not range far into the colder waters northward, and all its many congeners live in the tropics. The blacksmith embodies morphological features uncharacteristic of temperate-zone fishes, but which are widespread among tropical species. In writing of reef fishes in the tropical Atlantic Ocean, Davis and Birdsong (1973) described morphological specializations adaptive for foraging on small organisms in the mid-waters, and although they do not make the point, all their examples are species that feed by day. Especially striking are the modifications of head and jaws, including dentition, that permit even relatively large individuals to effectively capture tiny prey in open water.

The Mid-Waters at Night

The nocturnal zooplankton include, in addition to the organisms also present during the day, a large array of forms that rise at the onset of darkness from daytime shelters on, in, or close to the sea floor or other cover. These nocturnal additions to the zooplankton include various polychaetes, mysids, cumaceans, gammaridean and caprellid amphipods, isopods, tanaids, carideans, and others (see Tables 1, 2). Most exceed 2 mm in their greatest dimension, and many are 7 to 10 mm, and longer. Unlike the full-time zooplankters, which have no particular relation to the study area, these part-time zooplankters are local residents that rise at night from substrata they are closely associated with during the day.

The nocturnal components of the zooplankton seem to have reasons for rising into the water column at night that are as diverse as their morphologies. Because they have diverse habits that are little known, we feel that terms defining ecological categories among them are premature. Bousfield (1973), and others, have referred to many such forms as tychoplankton, but this term implies that presence in the water column is by chance, or accident—a description that fits very few, if any, of the forms considered here. Many are nocturnal feeders; e.g., when the mysid *Siriella pacifica* moves into the mid-waters after dark, it feeds on copepods and other smaller zooplankters. Similar-

ly, nocturnal foraging may be the rule among species like the ostracod *Perasterope* sp. A, the cumacean *Cumella* sp. A, and the amphipod *Batea transversa*, where it seems the majority spend most of the night in the water column. Working in the tropical Atlantic Ocean, Emery (1968) noted that polychaetes, cumaceans, and zoea rise into the water column at night after spending the day under reef shelter and speculated that they make this ascent to forage. But most of the polychaetes entering the water column after dark at Santa Catalina are epitokus nereids, whose mid-water activities probably relate to reproduction.

Williams and Bynum (1972) doubted the nightly ascents of amphipods in North Carolina estuaries relate to feeding because they subsist on detritus. But detritus can be available to zooplankters in the water column, as reported by Gerber and Marshall (1974) from a coral atoll in the central Pacific. Significantly, however, many of the amphipods that enter the mid-waters at night appear morphologically maladapted for swimming. The oedicerotids (including *Monoculodes* and *Synchelidium*), for example, are modified for burrowing in unstable sand (Bousfield 1973), and the caprellids (Figure 5V) seem especially unsuited for existence in mid-water. It is unlikely that such forms are in the water column to feed, especially as relatively small proportions of their populations are up there. Probably these and similar forms make only brief, or infrequent excursions into the water column for reasons yet undetermined. Williams and Bynum (1972) suggested that relative numbers of caprellids entering the water column may correlate with seasonal deterioration of their benthic habitats. They also felt that among gammaridean amphipods the tubicolous forms (e.g., *Ampelisca* and *Ericthonias*) may facilitate reproduction by entering the water column, where mating pairs would have free access to each other.

We reject Williams and Bynum's additional suggestion that the nightly ascent may be an attempt to escape from predatory bottom-feeding fishes. Most bottom-feeding fishes that prey heavily on amphipods (and other similar organisms) are diurnal. (Some of the relatively few fishes that prey on amphipods at night, and the circumstances surrounding this predation, will be discussed later; Hobson and Chess in prep.) Most predaceous fishes feed visually, and tiny, cryptically hued forms on dark substrata seem to go unseen in the low levels of illumination that prevail at night (Hobson and Chess in prep.; see also Hobson 1968, 1974, for accounts of the same situation on tropical reefs). For whatever the reason, most amphipods that fall prey to predatory fishes after dark are species that rise into the water column.

Compared to their diurnal counterparts, the nocturnal planktivorous fishes are of relatively large sizes and have large mouths—both characteristics reflecting the relatively large size and accessibility of organisms in the mid-waters after dark.

Evolutionary Implications

Since early in the Mesozoic period, the evolution of actinopterigian fishes has centered on a mainstream of generalized predators (Schaeffer and Rosen 1961). Because such predators are adapted for straightforward attacks at prey in exposed positions, the water column, with its absence of cover, has been a risky place for smaller organisms throughout the evolution of modern nearshore marine communities. In discussing the earliest actinopterigian fishes, Schaeffer and Rosen stated that food was probably first obtained by biting and was swallowed whole. Although advances in mouth structure have refined their means of seizing food (Schaeffer and Rosen 1961; Gosline 1971), generalized teleosts have continued to take their prey intact. Consequently, these fishes have found appropriate prey to be organisms large enough for them to entrap in their relatively large mouths, yet small enough for them to swallow whole. As demonstrated at Santa Catalina, prey of appropriate size include animals that rise into the nearshore water column after dark—mysids, amphipods, isopods, and others.

The present situation at Santa Catalina Island suggests that since early times predation pressures from large-mouthed, generalized predators have influenced major evolutionary trends among shallow-water zooplankters. Most apparent are trends toward nocturnal planktonic activity in those zooplankters that would spend only part of their time in the water column, and toward reduced size among those zooplankters that would spend all of their time in the water column. At the same time it would appear that each of these trends has elicited an evolutionary response among planktivorous fishes, as discussed below. We do not suggested that pressures exerted in predator-prey interactions have been the only force shaping these trends, but we believe their

impact has been significant. (A trend toward transparency, most developed in the larger zooplankters present in the water column during the day, is obviously adaptive for organisms threatened by visually feeding predators. Although this trend is only briefly mentioned here, its importance in defense against predators is emphasized by Hamner et al. 1975.)

Because most generalized predaceous fishes probably have been visual feeders since early times, their prey would have long since found water-column activities most safely performed under cover of darkness. Not surprisingly, the zooplankters that are vulnerable to large-mouthed fishes are mostly nocturnal forms that spend the daytime amid benthic cover. But only organisms that have the capacity to leave the water column can enjoy the advantage of cover during vulnerable periods.

The organisms that spend all their time in the water column have had to adapt to being fully exposed during daylight, when the visual sense of their predators is most effective. Under this circumstance one would expect long-established selective pressures favoring sizes smaller than those that can be entrapped by the relatively large mouths of generalized predators. That such selective pressures operate today among zooplankters in daylight is well documented. Brooks and Dotson (1965), for example, described the larger zooplankters in a lake being eliminated by the planktivorous clupeoid fish *Alosa pseudoharengus*, reported by Emery (1973) to feed by day.

Because successful defenses in prey create pressures that modify the offenses of predators, early tendencies in prey toward nocturnal habits or reduced size would have generated appropriate evolutionary responses among predators. Certainly a long-standing selection for nocturnal capabilities is evidenced by the many large-mouthed predaceous fishes that forage in the mid-waters at Santa Catalina after dark, including the walleye, the salema, and the queenfish. Large eyes, an obvious advantage in predators that hunt at night, have been widely acquired by these fishes (see Figures 6-10). Similarly, the small mouth and other specialized features of diurnal planktivorous fishes, like the blacksmith, clearly are adaptive for feeding on the very small organisms that constitute the diurnal zooplankton (see Figures 11-13). In their feeding morphologies and body forms, the nocturnal planktivores have diverged less than have their diurnal counterparts

from the generalized predators that gave rise to them all. This does not necessarily mean that the diurnal planktivores are more recently evolved. Each is the product of an equally long evolution, and while the diurnal planktivores have been molded by selective pressures favoring the capacity to take tiny organisms, the nocturnal species have been influenced during the same period by selective pressures favoring the capacity to detect and capture prey in the dark.

LITERATURE CITED

BOUSFIELD, E. L.
   1973. Shallow-water gammaridean Amphipoda of New England. Cornell Univ. Press, Ithaca, 312 p.
BRAY, R. N., AND A. W. EBELING.
   1975. Food, activity, and habitat of three "picker-type" micro-carnivorous fishes in the kelp forests off Santa Barbara, California. Fish. Bull., U.S. 73:815-829.
BROOKS, J. L., AND S. I. DODSON.
   1965. Predation, body size, and composition of plankton. Science (Wash., D.C.) 150:28-35.
DAVIS, W. P., AND R. S. BIRDSONG.
   1973. Coral reef fishes which forage in the water column. Helgoländer wiss. Meeresunters. 24:292-306.

EMERY, A. R.
  1968. Preliminary observations on coral reef plankton. Limnol. Oceanogr. 13:293-303.
  1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. J. Fish. Res. Board Can. 30:761-774.
GERBER, R. P., AND N. MARSHALL.
  1974. Ingestion of detritus by the lagoon pelagic community at Eniwetok Atoll. Limnol. Oceanogr. 19:815-824.
GOSLINE, W. A.
  1971. Functional morphology and classification of teleostean fishes. Univ. Press Hawaii, Honolulu, 208 p.
HAMNER, W. M., L. P., MADIN, A. L. ALLDREDGE, R. W. GILMER, AND P. P. HAMNER.
  1975. Underwater observations of gelatinous zooplankton: Sampling problems, feeding biology, and behavior. Limnol. Oceanogr. 20:907-917.
HOBSON, E. S.
  1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia 1965:291-302.
  1968. Predatory behavior of some shore fishes in the Gulf of California. U.S. Fish Wildl. Serv., Res. Rep.73, 92 p.
  1971. Cleaning symbiosis among California inshore fishes. Fish. Bull., U.S. 69:491-523.
  1972. Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fish. Bull., U.S. 70:715-740.
  1973. Diel feeding migrations in tropical reef fishes. Helgoländer wiss. Meeresunters. 24:361-370.
  1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fish. Bull., U.S. 72:915-1031.
HUBBS, C. L., AND L. C. HUBBS.
  1954. Data on the life history, variation, ecology, and relationships of the kelp perch, Brachyistius frenatus, an embiotocid fish of the Californias. Calif. Fish Game 40:183-198.
LIMBAUGH, C.
  1955. Fish life in the kelp beds and the effects of kelp harvesting. Univ. Calif. Inst. Mar. Resour., IMR Ref. 55-9, 158 p.
MILLER, D. J., AND R. N. LEA.
  1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.
NEWELL, G. E., AND R. C. NEWELL.
  1963. Marine plankton. Hutchinson, Lond., 221 p.
QUAST, J. C.
  1968. Observations on the food of the kelp-bed fishes. In W. J. North and C. L. Hubbs (editors), Utilization of kelp-bed resources in southern California, p. 109-142. Calif. Dep. Fish Game, Fish Bull. 139.
RANDALL, J. E.
  1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. (Miami) 5:665-847.
SCHAEFFER, B., AND D. E. ROSEN.
  1961. Major adaptive levels in the evolution of the actinopterygian feeding mechanism. Am. Zool. 1:187-204.
SMITH, R. I., AND J. T. CARLTON (editors).
  1975. Light's manual: Intertidal invertebrates of the central California coast. 3rd ed. Univ. Calif. Press, Berkeley, 716 p.
STEVENSON, R. A., JR.
  1972. Regulation of feeding behavior of the bicolor damselfish (Eupomacentrus partitus Poey) by environmental factors. In H. E. Winn and B. L. Olla (editors), Behavior of marine animals. Vol. 2: Vertebrates, p. 278-302. Plenum Press, N.Y.
SWERDLOFF, S. N.
  1970. The comparative biology of two Hawaiian species of the damselfish genus Chromis (Pomacentridae). Ph.D. Thesis, Univ. Hawaii, 202 p.
WICKSTEAD, J. H.
  1965. An introduction to the study of tropical plankton. Hutchinson and Co., Lond., 160 p.
WILLIAMS, A. B., AND K. H. BYNUM.
  1972. A ten-year study of meroplankton in North Carolina estuaries: Amphipods. Chesapeake Sci. 13:175-192.