

TROPHIC RELATIONSHIPS AMONG FISHES AND PLANKTON IN THE LAGOON AT ENEWETAK ATOLL, MARSHALL ISLANDS

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ABSTRACT

Trophic relationships among fishes and zooplankters in the nearshore lagoon at Enewetak differ sharply between day and night, and are strongly influenced by current patterns. Adults of most diurnal planktivorous fishes are numerous in certain places where tidal currents are strong, but few where such currents are consistently weak. Thus, the sea bass, *Mirolabrichthys pascualis*; the snapper *Pterocaesio tile*; and the damselfishes (*Chromis agilis*, *C. caerulea*, *C. lepidolepis*, *C. margaritifer*, and *Pomacentrus coelestus*) are numerous in strong-current areas near interisland passes, but relatively few or absent in weak-current areas close in the lee of islands or interisland reefs. The former areas are rich, the latter poor, in the major prey of these fishes—copepods, larvaceans, and fish eggs. On the other hand, the zooplankton-poor waters close in the lee of islands and interisland reefs are rich in debris from the reefs, and fishes that can subsist on these materials are abundant. *Dascyllus reticulatus* is numerous here, although less so than where currents are strong, and takes algal fragments as an important, if secondary, part of its diet; *Pomacentrus vaiuli*, equally abundant in both strong- and weak-current areas, feeds largely on algal fragments, as does *P. pavo*, which is more numerous here than where currents are strong.

In contrast, the major nocturnal planktivores are concentrated where currents are weak, but relatively sparse where these currents are strong. Included are: the soldier fishes *Myripristis pralinus* and *M. violaceus*, and the cardinalfishes *Apogon gracilis* (young also feed by day), *A. novaeguinae*, and *A. savayensis*. They are strictly carnivores that prey mostly on larger zooplankters—including large calanoids, mysids, isopods, gammarids, postlarval carideans, and brachyuran megalops—absent (except for the mysids) in the nearshore water column by day. These prey organisms generally find conditions unfavorable where strong currents flow. Most of them are sheltered on or near specific nearshore substrata during the day and enter the water column only at night; but others are in deeper water offshore by day and move inshore at night after rising toward the surface.

Limited evidence indicates that planktivorous juvenile and larval fishes, as well as the tiny plankters on which they feed, follow patterns different from those followed by larger individuals.

Many nearshore fishes find most of their food among the plankton. Clearly, the water column is a rich feeding ground. Nevertheless, fishes that would take plankters face problems perhaps not immediately apparent. Consider, for example, the feeding-related morphologies of planktivorous fishes, which obviously are products of strong selection pressures. Fishes that take plankters by day are characterized by modifications of head and jaws, including dentition, that permit even relatively large individuals to effectively consume tiny organisms in midwater, whereas fishes that take plankters at night tend to be large-mouthed species with specialized means to detect, and capture, the larger organisms that are in the nearshore water column only after dark. Awareness of

these facts evolved from studies in tropical seas (Hobson 1965, 1968, 1972, 1974; Starck and Davis 1966; Davis and Birdsong 1973) and was emphasized in more detailed study in warm temperate waters of southern California (Hobson and Chess 1976). Additional study has shown that many fishes which take plankters by day accentuate fusiform bodies and deeply incised caudal fins—features that promote rapid swimming, and which, significantly, are undeveloped among their nocturnal counterparts. Increased speed, it was suggested (Hobson 1974, 1975; Hobson and Chess 1976), has given diurnal planktivores that swim in the water column quicker access to shelter in response to severe pressures from piscivorous predators; that these speed-inducing features are comparatively undeveloped among the nocturnal species, the suggestion continued, reflects a sharply reduced threat from piscivorous predators in the water column after dark.

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The present paper considers these aspects of the interactions among the plankton and adult planktivorous fishes as expressed in the lagoon of a coral atoll. It is based on a study over 21 days at Enewetak, Marshall Islands, during April 1976.

STUDY AREA

Enewetak Atoll (lat. $11^{\circ}26'N$, long. $162^{\circ}22'E$) is a ring of shallow coral reefs and low islands encircling a lagoon about 37 km north to south and 56 km east to west. It sits amid the westward flowing North Equatorial Current and was buffeted throughout our visit (as during most of the year) by trade winds from the east. So with surface waters generally moving to the west, it was not surprising that tidal currents in passes between the open ocean and the lagoon on the windward side of the atoll were strong on the flood, but weak on the ebb. Furthermore, water over the windward interisland reefs, driven by the incessant trade winds and seas breaking over the outer reef, flowed in just one direction—into the lagoon. Presumably the situation was reversed on the leeward side of the atoll, as described for Bikini and Rongelap, two other Marshallese atolls (von Arx 1948).

From most islands, and interisland reefs, a narrow shelf of sand and isolated patch reefs extend several hundred meters into the lagoon. At the outer edge of this shelf, where the water in most places is about 20 m deep, the sea floor drops sharply to about 50 m, which is the approximate water depth over much of the lagoon. Our study centered on the lagoon's nearshore shelf along the eastern (windward) side of the atoll, where the waters are sheltered from the trade winds and prevailing seas. Initially, we made observations from Aoman Island in the north, to Enewetak Island in the south—a distance of about 32 km. Underwater visibility ranged from about 5 to over 30 m, and so at all times was suitable for observing activity. From these observations we gained a general impression of how the planktivorous fishes were distributed, as well as something of their activities.

It was soon apparent that the distribution of the planktivorous fishes was strongly influenced by nearshore current patterns. This knowledge permitted us to select fruitful locations for more intensive work, including sampling the plankton and gut contents of planktivorous fishes. Because time was short, we limited intensive study to two

sites that represented opposing extremes in prevailing current velocities, weak and strong—a variance that proved to identify certain major influences on fish-plankton interactions.

Currents were weak or nonexistent at our site in 7 m of water among coral heads on level sand about 100 m from Walt Island, close in the lee of the interisland reef (Figure 1, site A). These weak currents were most evident when water covered the reef, and always flowed from the reef. We made observations here at all hours of day and night during both spring and neap tides, and our collections sampled the full range of currents encountered, from no perceptible water movement to a velocity of 9 cm/s.

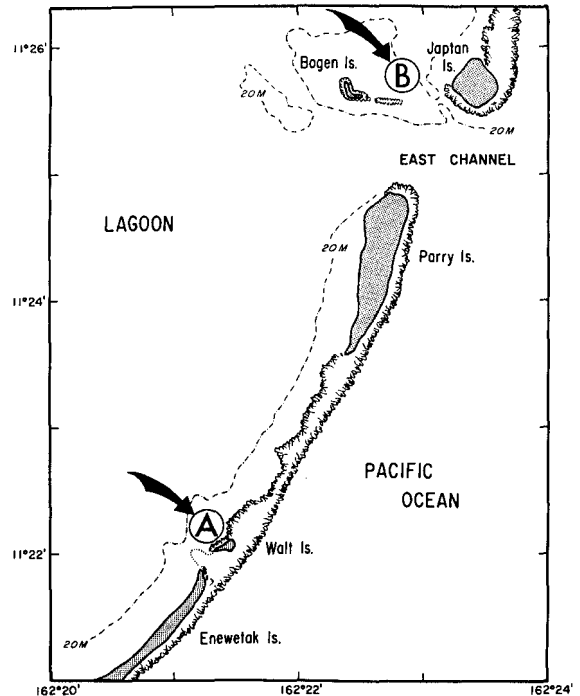


FIGURE 1.—The study area, Enewetak Atoll, Marshall Islands.

Strong tidal currents fed by water entering the lagoon through East Channel periodically swept through our site in 13 m of water among coral heads on gently sloping sand about 600 m windward of Bogen Island (Figure 1, site B). During our sampling here, currents ranged from 15 to 90, $\bar{x} = 51$, cm/s, always on flood tide. Observations (but no sampling) were also made at this station at slack water and during ebb tide when there was little perceptible current. Although there was scant evidence of an ebb current at the collection

site, a slow outflow from the lagoon was evident in East Channel itself. Even though strong currents at this site were limited essentially to flooding spring tides, their impact was clearly visible on the substrate at all times. Most notable, the sand, which swirled about in the stronger currents, was piled high in the lee of the patch reefs.

METHODS

Plankton

The methods used to collect plankton differed between the two primary sites owing to the contrast in prevailing current velocities. Nevertheless, all collections employed the same 0.333-mm mesh net and produced comparable assessments of the plankton at the two places, particularly between day and night.

Collecting Where Currents Were Weak

When sampling at the Walt Island site, we pushed the net through the water around one patch reef (Figure 2), a circuit that always took 5 min. The procedure was similar to that used at Santa Catalina Island, Calif. (Hobson and Chess 1976). When swimming with the net by day, we could watch organisms in its path, and this gave us insight into which of them might be evading the net. Mysids, for example, could do so, and often did. But these organisms reacted to us less than expected, perhaps because the meter net's opening

was large, and its approach was slow and quiet. Certainly our collections would have sampled these large mobile forms less effectively if the net had been preceded by the harness and tow line used when operating from a boat.

Three series of collections were made during midday (between 1000 and 1400 h), and three series were made at night (1 h after last evening light, at midnight, and 1 h before first morning light). We spaced the nocturnal collections over the night because earlier work had suggested that certain organisms are in the water column only briefly during specific periods of the night, a phenomenon we did not find among the diurnal plankters (Hobson and Chess 1976). Of the three collections in each series, one was made within 1 m of the bottom, one midway between bottom and surface, and one with the net breaking the surface. At night, ambient light in this clear water over white sand permitted us to collect without diving lights. Our stay at Enewetak spanned the period from full to new moon, so that we sampled both spring and neap tides, but generally there was no moonlight during the collections owing to cloud cover or time of night.

Net speed was 28 cm/s, as calculated from readings of a current meter calibrated by the speed at which the smallest fragments of algae visible to us drifted along a measured course. We decided it was necessary to determine net speed only once at this station, because all collections were made by the same two swimmers who each time exerted about the same effort, and covered the same distance.



FIGURE 2.—Collecting plankton at Walt Island, Enewetak Atoll, site of weak currents. The square frame permitted more accurate assessments at the surface and close to the sea floor.

Collecting Where Currents Were Strong

All collections at Bogen Island were made at the height of flood tide, when currents often were too strong to swim with the net, so here we worked from a boat anchored fore and aft above the study site. The net was secured to a line that passed from the boat, through a block anchored on the reef below, and returned to the boat. It was positioned at the three collecting depths—bottom, mid-depths, and surface—by pulling the line one way or the other through the block (Figure 3). The collections were extended to 15 min (compared with 5 min at the other station) to reduce error introduced by organisms taken during the few seconds it took to raise and lower the net. In presenting these data, however, we make the values equivalent to a 5-min collection. These collections depended on the current (which was measured with every collection) to carry plankton into the net, and the weakest current sampled, 15 cm/s, was judged close to the minimum necessary. Two series of collections were made during the day—at midday and in midafternoon—and two series were made at night—1 h after last evening light and at midnight.

There are problems in comparing data collected by these different methods at the two stations, but we had the advantage of sampling precisely defined positions—a critical requirement when relating the plankton to food habits of specific fishes.

The volume of water filtered by this stationary net varied with the different current velocities,

which strongly influenced the numbers of plankters taken. Nevertheless, these numbers accurately reflect the relative numbers of plankters available to fishes feeding in these currents. On the other hand, differences in volumes of water sampled must be considered when comparing estimates of the plankton in the water column from one time or place to another. Therefore, plankton volumes from the strong-current site are presented two ways: volumes actually sampled and volumes adjusted for current differences. In adjusting for current, the volumes in all collections were made equivalent to those taken in a net moving at the same relative speed that we pushed the net at the Walt Island site—28 cm/s. These adjustments also permit rough comparisons with data from California (Hobson and Chess 1976), where plankton were collected in the same way and by the same swimmers.

Fishes

A total of 154 fish specimens of 16 species were speared immediately after the plankton collections. Species names are those used by Schultz et al. (1953, 1960), except where more recent taxonomic study has indicated change.

The specimens were preserved in 10% Formalin² immediately after collection. Later, food items in the gut were identified and their positions in the gut noted. The following data were recorded for

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

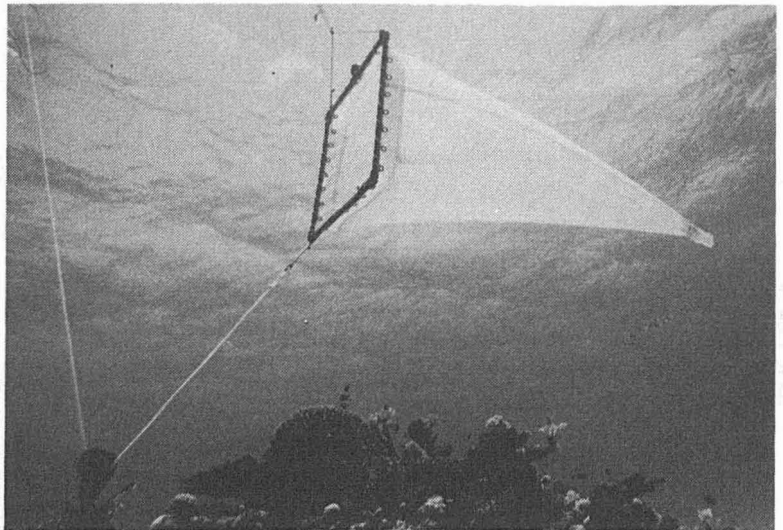


FIGURE 3.—Collecting plankton at Bogen Island, Enewetak Atoll, site of strong currents.

items of each food type: 1) number, 2) size range, 3) state of digestion (subjectively assessed on a scale of 5, from fresh to well-digested), and 4) an estimate of their representation among the gut contents as percent of the total volume.

RESULTS

Our widespread observations along the sandy shelf which rims the lagoon established that the planktivorous fishes were centered about the isolated patch reefs. At least a few planktivores foraged in the water column above virtually every reef, but more of them were above some reefs than others and there were clear patterns to their distributions. For example, during the day there tended to be more planktivores above reefs at the outer edge of the shelf than above similar reefs at comparable depths, and shallower, shoreward on the shelf. But diurnal planktivores were most numerous where strong tidal currents flowed through passes from the open sea, and least numerous where reefs or islands blocked the flow of water into the lagoon. On the other hand, the reverse was true of the nocturnal planktivores. Because the distributions and activities of these fishes proved to be closely related to current patterns, we judged that the contributing influences are best isolated by concentrating on the more extreme current situations. This was true even though in most places over the range of our observations currents were variably moderate, and prevailing conditions intermediate between the two extremes.

Where Currents Were Weak

General Observations

There is relatively little water movement near the lee shores of the islands and close behind the interisland reefs that block entry of water into the lagoon from the open sea. In some of these locations there is enough circulation to permit rich coral growth and underwater visibility that exceeds 15 m, but in other places the circulation is more limited, and living corals exist as small heads or encrustations on otherwise dead reefs, while underwater visibility often is <5 m. The lagoon floor in these regions generally is of relatively undisturbed, fine-grained sand. (A sample of sediment from the Walt Island site proved to be

75% foraminiferans, with a density of 1.32 g/ml. Grain size in over 80% of this sample was <1 mm.)

PLANKTON.—Usually we made no effort to detect the smaller plankters during our general diurnal observations, even though many of the copepods and others were visible with close inspection. Dense swarms of mysids, however, were outstanding features of the daytime scene in many places where currents were weak, especially above sand close to the patch reefs. With increasing distance from the bottom, their swarms were smaller and less numerous, though swarm-members always were closely spaced. Juveniles predominated at the lower levels, adults were more numerous above. The swarms dispersed at night, when both adults and juveniles scattered near the bottom and at middepth, but only adults were near the surface.

Although mysids were the only plankters routinely noted during the day, others were prominent after dark. Most conspicuous were large calanoid copepods—larger than any copepods present in daylight—that for a few hours after last evening light swarmed around us in dense numbers whenever we turned on our diving lights. Highly motile epitokous nereids, as well as an opheliid, *Polyopthalmus* sp., were numerous polychaetes, with other forms including hyperid and gammarid amphipods, stomatopod larvae, reptantian zoea, and brachyuran megalops. None of these forms were seen in daylight.

FISHES.—Adult diurnal planktivorous fishes were relatively few in these surroundings compared with their numbers elsewhere. Nevertheless, this seemed a favored habitat for at least one species, *Pomacentrus pavo*, which was widespread in groups of four to six individuals 2 to 5 cm above low coral-rock outcroppings in the sand, usually in the vicinity of patch reefs. *Pomacentrus vaiuli*, another abundant species, was present only as solitary individuals that rarely moved more than a few centimeters from the larger patch reefs, yet most of its food was small organisms swimming or drifting free in the water immediately adjacent to the substrate. *Dascyllus reticulatus* was numerous by day in feeding aggregations up into the midwaters, usually above large heads of branching corals, while at the same time *Amblyglyphidodon curacao*, which usually fed in groups of <10, often ranged up to the water's surface. Of the diurnal planktivores considered here that ranged into the

water column, *D. reticulatus* and *A. curacao* were the only deep-bodied forms. Other diurnal planktivores were more sparse. The more prominent of these were species of *Chromis* that usually stayed within 2 m of the reef. *Chromis caerulea*,³ mostly juveniles, generally hovered in small aggregations above heads of the coral *Pocillopora*, but *C. agilis* and *C. margaritifer* more often were solitary or in groups of just a few. At night all of these fishes were under reef shelter, and we saw no evidence of them feeding at that time.

Despite the relative paucity of adult diurnal planktivores in this habitat, planktivorous juveniles and larvae of at least several fish species frequently were numerous and fed by day. An outstanding example was the juveniles of *Apogon*

³At the distances that most of our observations were made, we were unable to consistently distinguish *Chromis caerulea* from the very similar *C. tripectoralis*, and so referred all observations to the former. Significantly, however, the behavior attributed to this species is consistent with that in all individuals observed.

gracilis, well under 50 mm long, which hovered in large, umbrella-shaped aggregations above coral heads in open sand (Figure 4). Dense schools of larval fishes, 7 to 10 mm long, (often taken on first glance as mysid swarms) were sometimes prominent, but so close to the reefs that our net sampled only an occasional outlier.

Although adult diurnal planktivores were comparatively sparse in this habitat, their nocturnal counterparts tended to be especially numerous. During daylight, dense, inactive concentrations of *Myripristis* spp. abounded at openings of reef crevices. Prominent as these concentrations were, they represented only a small part of the tremendous numbers of their species packed into the reef interstices. We became fully aware of the immensity of these populations when, about 30 min after sunset, they abruptly streamed into the open and entered the water column. Shortly after emerging, most individuals of one species, *M. murdjan*, apparently moved elsewhere, because though they were numerous initially, relatively few were seen during the night, and their numbers did not in-



FIGURE 4.—Juvenile cardinal fish, *Apogon gracilis*, approximately 25 to 30 mm long, feeding on plankton by day where currents are weak.

crease again until just before dawn. In contrast, large numbers of *M. pralinus* and *M. violaceus* remained concentrated in the waters above the nearshore patch reefs throughout the night.

Also prominent in daylight were *Apogon* spp., which concentrated close to reef cover. These included adults of *A. gracilis*, which schooled quietly at the bases of the same coral heads above which juveniles of the species (see above) actively fed; nevertheless, the true numbers of apogonids were fully appreciated only after nightfall, when many large species unseen during the day emerged from reef shelters. The most prominent of the larger apogonids entering the water column was *A. savayensis*, although some of the smaller species, notably *A. gracilis* and *A. novaeguinae*, were more numerous. Larger apogonids were solitary at night, but smaller ones often were loosely aggregated, including *A. gracilis*, of which the adults

joined the juveniles in the water column after dark.

Samples From Walt Island

PLANKTON.—Major materials (zooplankters, algae fragments, and crustacean molts) taken in the plankton net during day and night at the Walt Island site of weak currents are listed in Table 1. Zooplankters, grouped by major taxonomic categories and with data pooled from the three sampled depths (surface, middepth, and near bottom), are listed in Table 2. Additional data for calanoid copepods are presented in Table 3 to support certain points developed in the Discussion.

TABLE 1.—Composition of plankton at Walt Island, Enewetak Atoll, site of weak currents.

Materials	Day (n = 9)		Night (n = 9)	
	Mean vol (ml)	Mean % of total vol	Mean vol (ml)	Mean % of total vol
Zooplankters	3.4	38.3	10.7	79.0
Algae fragments	3.6	51.8	3.1	21.0
Crustacean molts	0.5	9.9	0.0	0.0
Totals	7.7	100.0	13.8	100.0

TABLE 3.—Size distribution of calanoid copepods, day and night, at Walt Island, Enewetak Atoll, site of weak currents.

Size (mm)	Midday		Night			
	(n = 9)		1 h after last light (n = 3)	Midnight and later (n = 6)		
	Percent	Mean no.	Percent	Mean no.	Percent	Mean no.
>3-5	0	0	0	0	24	¹ 138.7
>2-3	0	0	0	0	31	² 180.5
>1-2	48	³ 10.9	43	⁴ 40.1	31	⁵ 179.0
<1	52	11.8	57	53.2	14	81.3

¹Including *Euchaeta marina*, *Pleurommama xiphias*, and *Undinula vulgaris*.
²Including *Candacia* sp., *E. marina*, *Neocalanus* sp., *Pleurommama xiphias*, and *U. vulgaris*.
³Including *Acartia* sp., *Metridia* sp., *Pleurommama* sp., and *Scolothricella* sp.
⁴Including *Acartia* sp., *Candacia* sp., *E. marina*, and *U. vulgaris*.
⁵Including *Acartia* sp., *Candacia* sp., and *Euchaeta* sp.

TABLE 2.—Occurrence, number, and size of zooplankters collected day and night at Walt Island, Enewetak Atoll, site of weak currents.

Plankton categories present	Day (n = 9)			Night (n = 9)		
	Size (mm)	Percent occurrence	Mean number	Size (mm)	Percent occurrence	Mean number
Foraminiferans ¹	0.4-1.0	100	36.7	0.4-2.0	100	337.0
Siphonophores	4.0-6.0	11	0.4	4.0-8.0	38	2.6
Polychaetes	—	0	0.0	3.0-25.0	33	28.3
Mollusk larvae	0.3-1.0	78	21.0	0.5-2.0	89	55.2
Pteropods	—	0	0.0	2.0-5.0	33	2.0
Squid	—	0	0.0	3.0-12.0	22	0.3
Ostracods	0.5-1.0	67	5.4	0.6-2.0	100	26.4
Calanoid copepods	0.5-2.0	89	22.7	0.5-5.0	100	579.5
Cyclopoid copepods	0.5-1.5	56	8.0	0.5-2.0	100	39.0
Harpacticoid copepods	0.5-1.0	22	0.3	0.5-2.0	89	9.3
Stomatopod larvae	—	0	0.0	18.0-26.0	11	1.0
Mysids	2.0-8.0	89	² 1,398.7	1.0-8.0	100	³ 3,031.8
Cumaceans	—	0	0.0	1.0-1.5	56	12.4
Isopods	—	—	0.0	1.0-12.0	67	5.3
Hyperiid amphipods	0.6-2.0	33	5.0	1.0-4.0	100	17.8
Gammarid amphipods	—	0	0.0	1.0-5.0	100	23.2
Caridean larvae	2.0-3.0	89	6.0	1.0-12.0	100	504.2
Caridean adults and juveniles	—	0	0.0	4.0-15.0	100	20.0
Reptantian zoea	0.5-2.0	78	20.0	0.5-4.0	100	629.8
Brachyuran megalops	2.0-3.0	22	0.2	2.0-8.0	100	60.3
Chaetognaths	4.0-10.0	44	1.0	3.0-12.0	100	92.4
Larvaceans	—	0	0.0	2.0	11	0.4
Appendicularian larvae	2.0	11	0.1	2.0	11	0.4
Fish eggs	1.0-2.0	100	40.0	0.5-3.0	100	273.6
Fish larvae	2.0-13.0	44	11.3	2.0-25.0	⁴ 100	51.2

¹Most of them planktonic stage of *Tretomphalus*.
²All appeared to be *Mysinae* sp. Mysids constituted 52.8% of the volume of daytime collections.
³Included *Mysinae* sp. and *Siriella* sp., the latter unseen in daylight. Mysids constituted 44.8% of the volume of nighttime collections.

GUT CONTENTS OF THE PLANKTIVOROUS FISHES.—The gut contents of diurnal fishes collected at the same time, and in the same location, as the daytime plankton collections are listed in Table 4, and those from the nocturnal species, which were collected between midnight and first morning light on nights when the plankton were sampled, are listed in Table 5.

Where Currents Were Strong

General Observations

Currents were periodically strong near the passes from the open sea, and here, where patch reefs and other hard substrata typically are covered with living corals, underwater visibility consistently exceeded 20 m.⁴ The lagoon floor in

these areas generally is coarse, well-sorted sand (a sample of the sediment at the Bogen Island site proved to be about 60% fragments of calcareous algae, *Halimeda* spp., with a density of 1.25 g/ml; grain size in over 80% of this sample was greater than 1 mm).

PLANKTON.—Plankters were noted infrequently during casual diurnal observations where currents were strong. Nevertheless, the mysids so prominent where currents were weak occurred here only in small, inconspicuous swarms that concentrated close in the lee of patch reefs when currents were running. The larger zooplankters, frequently so prominent after dark in weak-current areas, were not noted here in any abundance, although nocturnal observations underwater in this habitat were limited.

FISHES.—During the day planktivorous fishes were especially numerous in these surroundings. Many diurnal species were concentrated here, the more prominent being: the serranid *Mirolabrichthys pascualis*, the lutjanid *Pterocaesio tile*, and the damselfishes *Chromis agilis*, *C. caerulea*, *C. lepidolepis*, *C. margaritifer*, *Pomacentrus coelestus*, and *Dascyllus reticulatus*. *Pomacentrus*

⁴Our concept of strong-current locations does not include those breaks in the interisland reefs where the lagoonward flow of water crossing the reef concentrated and spilled into the lagoon at sometimes exceptionally high velocities. These currents were localized and relatively shallow. Planktivorous fishes present were essentially those of nearby weak-current locations in the lee of these reefs, and although no collections were made here we would not have expected such currents to be rich in zooplankters, for reasons developed in the Discussion.

TABLE 4.—Food habits of diurnal planktivorous fishes from Walt Island, Enewetak Atoll, site of weak currents. The value outside the parentheses is the rank of the item as food of that fish species (based on incidence and volume in diet); of the two values in parentheses, the first is the percent of fish of that species containing the item, the second is the mean percent of the total diet of that fish species represented by the item.

Categories present	Mean no. ¹	1	2	3	4	5	6	7	8
Plankton:									
Foraminiferans	36.7	—	—	—	—	—	—	—	—
Siphonophores	0.4	—	—	—	—	—	—	—	—
Mollusk larvae	21.0	—	—	—	—	—	—	—	—
Ostracods	5.4	—	—	—	—	—	—	—	—
Calanoids and cyclopoids	230.7	1(100:90)	2(100:16.2)	4(17:2.5)	1(100:82.7)	2(100:23)	1(100:75)	1(100:85.8)	2(100:41.7)
Harpacticoids	0.3	4(20:0.4)	6(17:0.3)	—	—	—	—	—	—
Mysids	1,398.7	—	4(17:0.8)	—	5(33:1.0)	—	4(50:6.0)	4(20:1.4)	—
Hyperids	5.0	—	—	—	—	—	—	—	—
Caridean larvae	6.0	—	5(17:0.5)	—	4(67:2.3)	—	—	5(20:1)	—
Reptantian zoa	20.0	—	—	—	—	—	—	—	—
Brachyuran megalops	0.2	—	—	—	—	—	—	—	—
Chaetognaths	1.0	3(40:3.6)	—	—	—	—	—	—	—
Larvaceans	(³)	—	—	—	—	—	—	—	—
Apendicularian larvae	0.1	—	—	6(17:0.5)	—	—	—	2(20:8)	4(33:3.3)
Fish eggs	40.0	2(40:60)	3(67:5.0)	2(50:5.3)	3(67:7.3)	3(40:5.0)	2(100:8.5)	3(60:1.8)	3(67:8.3)
Fish larvae	11.3	—	—	—	—	—	—	—	—
Algal fragments	—	—	1(100:77.2)	1(100:85)	2(67:15)	1(100:65)	3(50:10.5)	—	1(100:46.7)
Crustacean fragments	—	—	—	—	(33:17)	—	—	—	—
Gurry	—	—	—	—	(33:10.0)	(60:7.0)	—	(20:2.0)	—
Benthic:									
Cephalaspidean mollusks	—	—	—	5(17:1.7)	—	—	—	—	—
Compound ascidians	—	—	—	3(33:5.0)	—	—	—	—	—

¹Numbers of plankters (from Table 2) provided only for rough measure of relative abundance.

²Calanoids and cyclopoids not separated in gut contents; both occurred in all fish species but calanoids predominated.

³Larvaceans not present in plankton collections but in two fish guts.

TABLE 5.—Food habits of nocturnal planktivorous fishes from Walt Island, Enewetak Atoll, site of weak currents. See Table 4 legend for explanation of listed values.

Plankton categories present	Mean no. ¹	Fishes			
		1	2	3	4
Foraminiferans	337.0	—	—	—	—
Siphonophores	2.6	—	—	—	—
Polychaetes ²	28.3	6(20:5.3)	1(91:45.4)	5(11:5.6)	7(10:5.5)
Mollusk larvae	55.2	—	—	—	—
Pteropods	2.0	—	—	—	—
Squid	0.3	—	10(9:0.5)	—	—
Ostracods	26.4	11(10:0.2)	—	—	—
Calanoids	579.5	³ 1(100:37.0)	³ 5(36:1.4)	³ 6(11:2.2)	1(70:38.3)
Cyclopoids	39.0	—	—	—	—
Harpacticoids	9.3	—	—	—	—
Stomatopod larvae	1.0	—	4(18:4)	7(11:1.7)	—
Mysids	3,031.8	2(80:17.5)	3(56:9.7)	2(67:26.1)	5(30:4)
Cumaceans	12.4	—	—	—	—
Isopods	5.3	7(20:1.5)	—	8(11:1.1)	—
Tanaids ⁴	—	10(10:0.5)	—	—	9(10:1)
Hyperids	17.8	—	—	—	—
Gammarids	23.2	8(20:1)	11(9:0.2)	—	10(10:0.3)
Caridean larvae	504.2	—	—	9(11:0.6)	2(70:18.2)
Caridean adults and juveniles	20.0	5(50:7.0)	8(9:3.7)	4(44:7.8)	3(30:16.0)
Reptantian zoëa	629.8	—	—	—	11(10:0.2)
Brachyuran megalops	60.3	3(50:17.3)	2(82:23.1)	1(100:28.3)	6(20:3)
Chaetognaths	92.4	9(10:1)	—	—	—
Larvaceans	0.4	—	—	—	—
Apendicularian larvae	0.4	—	—	—	—
Fish eggs	273.6	—	—	—	8(10:2)
Fish larvae	51.2	4(30:8.2)	6(18:2.7)	3(56:20.6)	4(30:11.5)
Fish adults and juveniles	0.3	—	7(9:4.7)	—	—
Insects ⁴	—	—	9(27:0.9)	—	—
Algal fragments	—	—	—	—	—
Crustacean fragments	—	—	(9:2.3)	(33:6.0)	—
Unidentified fragments	—	—	(18:1.4)	—	—

¹Numbers of plankters (from Table 2) provided only for rough measure of relative abundance.

²Most polychaetes in guts of fishes were nereid epitokes.

³Predominant calanoids in the three larger fish species were *Pleurommama xiphias* and *Euchaeta marina*, which were relatively large (3 to 5 mm).

⁴Tanaids and insects were not present in plankton collections but were in several fish guts. Both are known from plankton collections elsewhere (e.g., Hobson and Chess 1973, 1976).

vaiuli was numerous, but perhaps no more so than where currents were weak (see above), and here too it confined itself to the immediate proximity of the reef.

The nature of the substrate can be important. *Chromis caerulea* and *Dascyllus reticulatus*, for example, swam in tight well-defined aggregations above specific growths of branching coral—particularly large heads of *Pocillopora* spp. (Figure 5A). *Pomacentrus coelestus* generally stationed itself low in the water column above outcroppings of coral rock and rubble, its relation to the substrate much like that of the similarly hued, but deeper-bodied, *P. pavo*. *Chromis agilis*, *C. lepidolepis*, and *C. margaritifer* generally swam in small widespread groups over patch reefs. Compared with their congener *C. caerulea*, they showed less affinity to specific substrata or locations on the reef. Thus *C. caerulea* invariably re-

sponded to a human intruder by sheltering among the branches of a large coral head directly below its feeding station (Figure 5B), whereas *C. agilis*, *C. lepidolepis*, and *C. margaritifer* frequently responded to the same stimulus by moving away, and taking shelter in a variety of places only when the stimulus was intensified.

In places where many of these diurnal planktivores were concentrated, a relation was evident between their morphologies and the distances they swam from the reef: those with feeding stations farther from the reef tended more toward cylindrical bodies and deeply incised caudal fins (Figure 6). This generalization proved valid despite exceptions among such deep-bodied forms as *Dascyllus reticulatus* (Figure 7) and *Amblyglyphidodon curacao*, in which the effect of their deeper bodies is even further enhanced by longer fin spines. Thus, for example, 7 *D. reticulatus*, 47

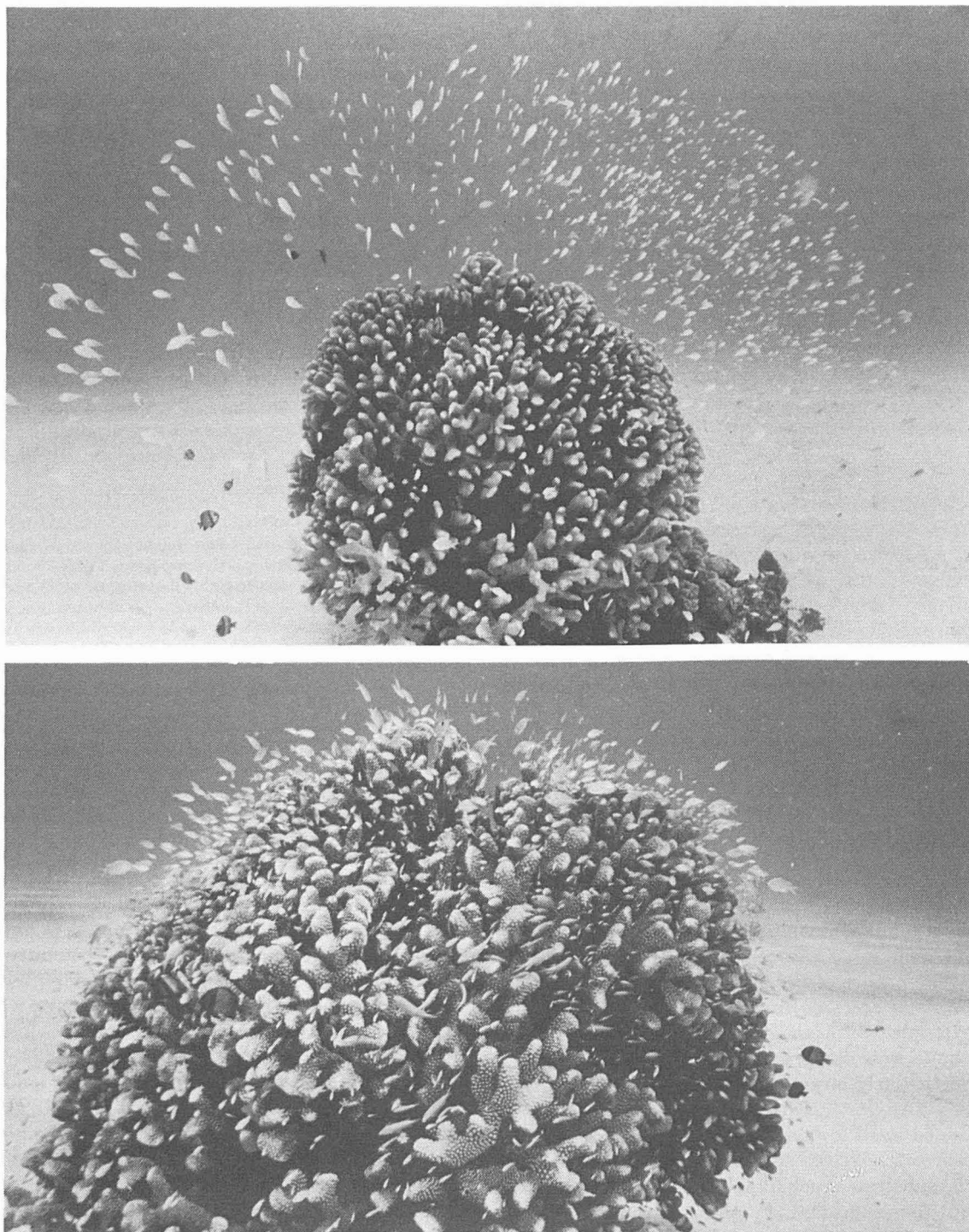


FIGURE 5.—A. *Chromis caerulea*, and a few *Dascyllus reticulatus* (lower left), feeding on plankton above a head of *Pocillopora* at the Bogen Island site. The largest fish are about 70 mm SL; the coral head is about 1.5 m in diameter. B. Upon being threatened, the fish shown in 5A dive to shelter in the interstices of the coral head.

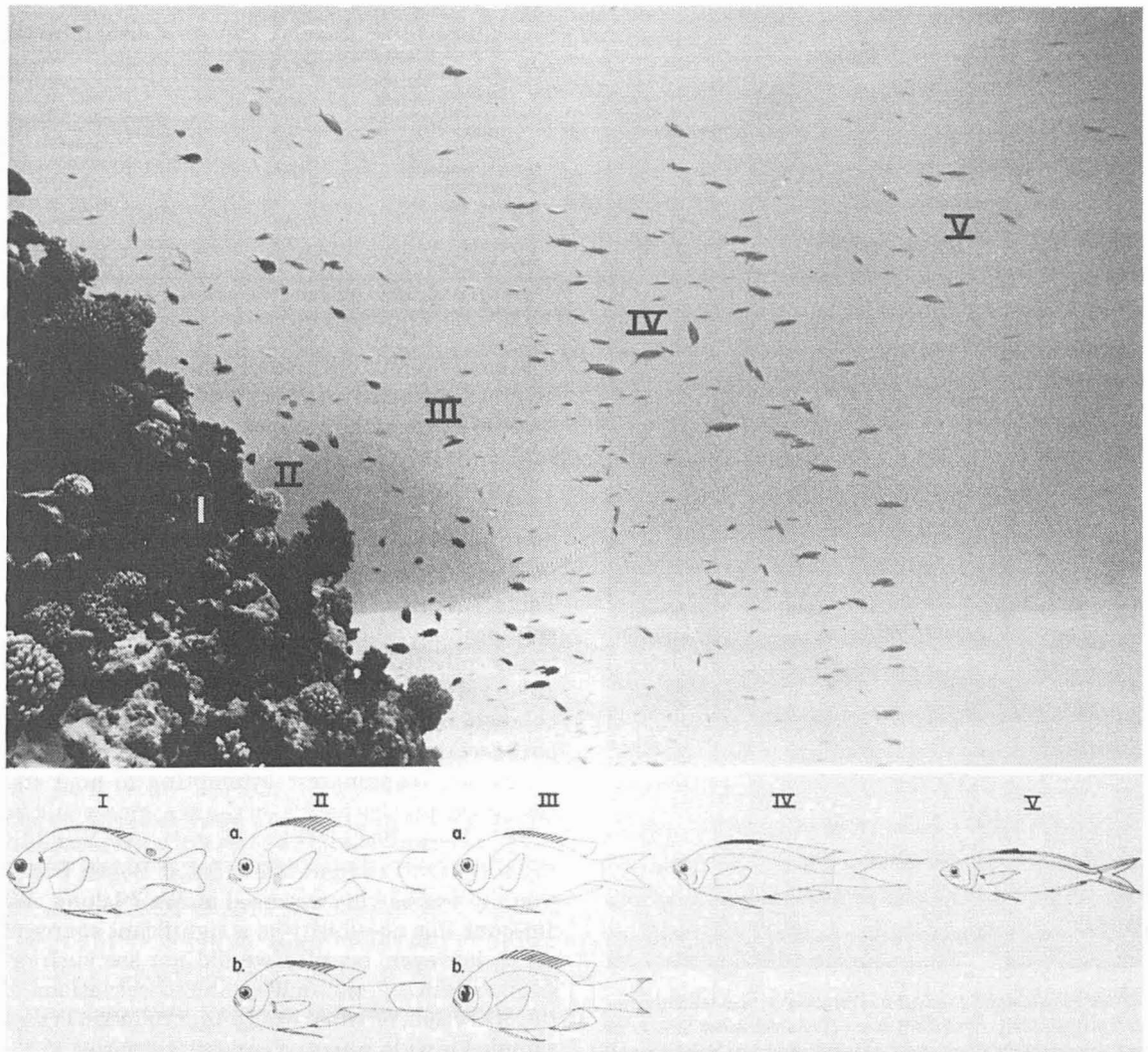


FIGURE 6.—Planktivorous fishes where currents are strong. Major species in each of the zones identified in the photo by roman numerals are illustrated in the appropriate column below the photo (placement based on observations made at the scene). I. *Pomacentrus vaiuli*; II. a, *Chromis agilis*, b, *C. margaritifer*; III. a, *C. caerulea*, b, *C. lepidolepis*; IV. *Mirolabrichthys pascualis*; V. *Pterocaesio tile*.

to 60 mm SL, $\bar{x} = 55.9$, had longest dorsal fin spines that were 20.3 to 23.4%, $\bar{x} = 21.0\%$, of their standard length, whereas these values for 13 individuals of *Chromis* spp. (4 *C. agilis*, 4 *C. caerulea*, and 5 *C. lepidolepis*), 52 to 70 mm SL, $\bar{x} = 59.4$, were 12.3 to 16.1%, $\bar{x} = 15.3\%$. The significance of these data becomes clear when possible selective values of both fusiform and deep-bodied morphologies in planktivorous fishes are treated in the Discussion.

Although most diurnal planktivorous fishes favored conditions associated with current, the

strongest currents observed at this site, approximately 1 m/s, clearly exceeded optimum velocities. When such currents flowed, most of the smaller planktivores were close to the reef, many of them concentrated in the lee, and their feeding rates had noticeably declined.

In comparison to the great numbers of adult diurnal planktivores in these surroundings, the nocturnal planktivores were sparse. Although observations underwater in this habitat at night were limited, only a relatively few individuals of

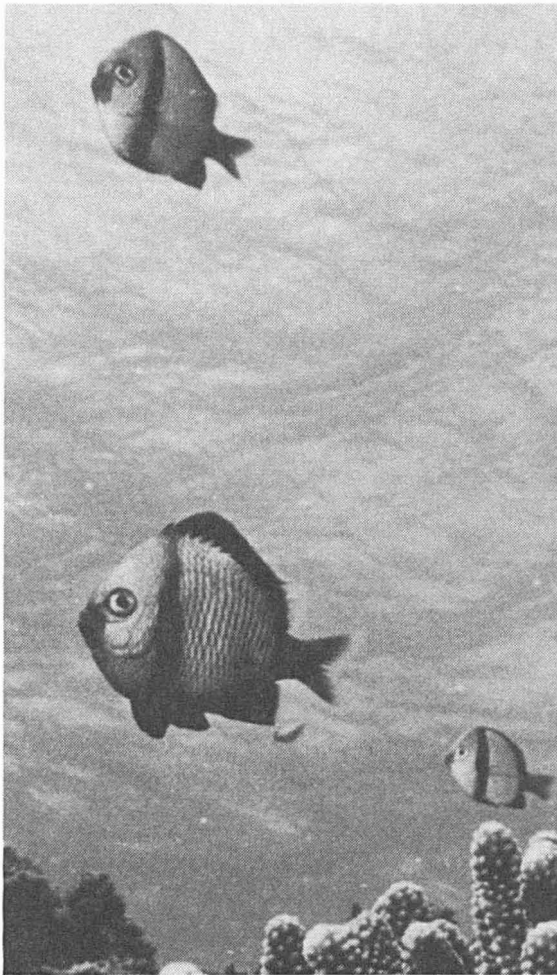


FIGURE 7.—*Dascyllus reticulatus* illustrates the tendency toward a deep body in certain diurnal planktivores that is in contrast to the tendency toward a more cylindrical body in many others.

Myripristis spp. and *Apogon* spp. were seen. Furthermore, during extensive daytime observations here we failed to note the dense concentrations of these and other nocturnal fishes in diurnal shelters that were widespread and obvious where currents were weak.

Samples From Bogen Island

PLANKTON.—The major materials taken in the net at the Bogen Island site of strong tidal currents were zooplankters and algae fragments (Table 6). To facilitate comparisons with collections from the weak-current site, all volumes are standardized to a 5-min collection. The table lists

TABLE 6.—Composition of plankton in 6 day and 6 night collections at Bogen Island, Enewetak Atoll, site of strong currents.¹

Items	Zooplankters	Algae fragments	Totals
Day collections:			
Mean vol (ml):			
Collected	2.8	5.7	8.5
Adjusted	1.2	2.7	3.9
Mean % of total vol	32.3	67.7	100.0
Night collections:			
Mean vol (ml):			
Collected	7.3	1.9	9.2
Adjusted	3.9	1.0	4.9
Mean % of total vol	78.8	21.2	100.0

¹Currents during diurnal collections: 32 to 90 cm/s, \bar{x} = 57; currents during nocturnal collections: 15 to 83 cm/s, \bar{x} = 45.

volumes of plankters actually collected, as well as volumes adjusted to the standard relative net speed of 28 cm/s (the net speed at the weak-current site).

The zooplankters collected at Bogen Island, grouped by major taxonomic categories and with data pooled from the three collection depths (surface, middepths, and near bottom), are listed in Table 7. For the reasons given above concerning volumes, the table lists numbers of plankters actually collected and numbers adjusted to the standard relative net speed. Additional data on calanoid copepods (Table 8) are presented to support certain points developed in the Discussion.

Possibly zooplankters attempting to hold station above precise points on the sea floor would be sampled less effectively by the stationary net during the slower currents sampled at Bogen Island than by the moving net used at Walt Island. We discount this possibility as a significant source of error, however, because we did not see such organisms during our underwater observations of the operation, or when examining collections that sampled a wide range of current velocities.

GUT CONTENTS OF THE DIURNAL PLANKTIVOROUS FISHES.—The gut contents of diurnal fishes collected at the same time, and in the same location, as the daytime plankton collections are listed in Table 9. Only a relatively few nocturnal planktivores (all of them *Myripristis* spp. and *Apogon* spp.) were seen during the limited observations in this habitat after dark, and none were sampled.

DISCUSSION

We were unable to intensively sample more than two stations in the limited time available to us at Enewetak. Nevertheless, data collected at these two sites under a variety of conditions,

TABLE 7.—Occurrence, number (actual and adjusted for current velocity), and size of zooplankters collected day and night at Bogen Island, Enewetak Atoll, site of strong currents.

Plankton categories present	Day (n = 6)				Night (n = 6)			
	Size (mm)	Percent occurrence	Mean no. (collected)	Mean no. (adjusted)	Size (mm)	Percent occurrence	Mean no. (collected)	Mean no. (adjusted)
Foraminiferans ¹	0.3-1.0	100	56.3	27.7	0.3-2	100	558.7	346.4
Siphonophores	4.0	17	0.6	0.3	4-8	50	5.7	3.5
Polychaetes	3.0	17	0.6	0.3	3-20	100	6.9	4.3
Mollusk larvae	0.5-2.0	100	11.1	5.4	0.5-2	100	31.1	19.3
Pteropods	0.5-6.0	100	6.3	3.1	2-12	83	33.7	20.9
Squid	—	0	0.0	0.0	3-4	50	1.8	1.1
Cladocerans	0.7-1.0	33	0.9	0.4	—	0	0	0
Ostracods	0.5-2.0	100	14.1	6.9	0.5-2	83	107.6	66.7
Calanoid copepods	0.5-4.0	100	1,726.7	846.4	0.5-5.0	100	7,751.1	4,820.1
Cyclopoid copepods	0.5-2.0	100	840.0	411.7	0.5-2.0	100	303.6	188.6
Harpacticoid copepods	0.5-2.0	100	23.0	11.3	0.8-2	67	6.2	3.8
Mysids	2.0	83	6.2	3.0	0.5-7	67	16.2	10.0
Stomatopod larvae	—	0	0	0	20-25	17	0.2	0.1
Cumaceans	—	0	0	0	2	17	0.1	<0.1
Tanaids	2.0	17	0.6	0.3	—	0	0	0
Isopods	—	0	0.0	0.0	1-3	100	57.3	35.5
Hyperid amphipods	0.4-2.0	50	32.2	15.8	0.5-6	100	76.0	47.1
Gammarid amphipods	1.0	17	0.6	0.3	3-4	100	38.4	23.8
Euphausiid larvae	0.5-7.0	50	5.0	2.5	0.8-1	33	9.1	5.6
Caridean larvae	1.0-4.0	100	81.2	39.8	1-10	100	386.1	239.4
Caridean adults and juveniles	2.0-6.0	33	2.8	1.4	5-15	83	13.1	8.1
Reptantian zoëa	0.5-2.0	100	252.8	123.9	0.5-4	100	509.7	316.0
Brachyuran megalops	1.5	17	0.6	0.3	1-6	100	115.4	71.6
Ophiroid larvae	2.0	17	0.5	0.3	—	0	0	0
Chaetognaths	2.0-15.0	100	75.3	36.9	3-55	100	440.0	272.8
Larvaceans	1.0-3.0	100	25.3	12.4	2-4	100	87.4	54.2
Salps	—	0	0	0	(?)	17	1.1	0.7
Fish eggs	0.5-2.0	100	732.2	358.8	1-2	100	3,785.6	2,347.1
Fish larvae	2.0-6.0	50	6.6	3.2	23-90	100	46.6	28.9

¹Most of them planktonic stage of *Tretomphalus*.
²A 90-mm leptocephalus larva.

TABLE 8.—Size distribution of calanoid copepods, day and night, at Bogen Island, Enewetak Atoll, site of strong currents.

Size (mm)	Midday (n = 6)		Night (n = 6)	
	Percent	Mean no. ¹	Percent	Mean no. ¹
>3-4	0	0	5	² 246.7
>2-3	3	³ 26.2	25	⁴ 1,203.6
>1-2	54	⁵ 453.7	60	⁶ 2,888.6
<1	43	366.5	10	481.4

¹Numbers from collections in varying currents adjusted for equivalence to collections from the Wait Island site.
²Including *Euchaeta marina*.
³Including *Candacia* sp. and *E. marina*.
⁴Including *Candacia* sp., *E. marina*, *Neocalanus* sp., and *Undinula vulgaris*.
⁵Including *Acartia* sp. and *Euchaeta* sp.
⁶Including *Acartia* sp., *E. marina*, and *Metridia* sp.

supplemented by widespread observations elsewhere, permit a synthesis that we hope stimulates needed additional study. The following discussion pertains to adults of the planktivorous fishes and to plankters collected by our 0.333-mm mesh meter net. All food items found in the fish guts occurred in these plankton collections, so the combined assemblage can be considered a trophic unit. The situation described from these data, however, may not apply to smaller individuals. Limited data, including that from *Apogon gracilis*, the only planktivore studied as an early juvenile, suggest that the smaller plankters which passed through our net, and their predators among

juvenile and larval fishes, may follow significantly different patterns (see Miscellaneous Considerations below).

Diurnal Relationships

Probably diurnal planktivores concentrated where strong tidal currents flowed into the lagoon through the passes because these waters were rich in zooplankters, particularly calanoid copepods (Table 7). We presume that at least many of these were oceanic zooplankters carried to within reach of inflowing tidal currents on the eastern side of the atoll by the westward flowing North Equatorial Current—a phenomenon amplified by the trade winds. In addition, some of the materials carried from the lagoon on the preceding ebb tide probably return. Although this outflow is minimal on the windward side of the atoll, at least during the trade-wind season (see von Arx 1948), it probably contains significant amounts of certain kinds of organisms. Gerber and Marshall (1974) noted that the waters of the Enewetak lagoon are much richer in zooplankton than the surrounding ocean. Describing the same condition at Bikini, Johnson (1949) stated: "Much of the oceanic plankton

TABLE 9.—Food habits of diurnal planktivorous fishes from Bogen Island, Enewetak Atoll, site of strong currents. See Table 4 legend for explanation of listed values.

Plankton categories present	Mean no. (from Table 2) ¹	Fishes								
		1	2	3	4	5	6	7	8	9
Foraminiferans	27.7	—	—	9(10:0.1)	—	—	—	—	—	—
Siphonophores	0.3	—	—	—	—	—	—	—	—	—
Polychaetes	0.3	—	—	—	—	—	—	—	5(25:1.1)	—
Mollusk larvae	5.4	—	—	—	—	—	—	—	—	—
Pteropods	3.1	—	—	—	—	—	—	—	—	—
Cladocerans	0.4	—	—	10(10:0.1)	—	—	—	—	—	—
Ostracods	6.9	—	—	—	—	—	—	—	—	—
Calanoids and cyclopoids ²	419.5	1(100:70.4)	1(100:80.7)	3(100:18.9)	2(100:33.6)	1(100:61.1)	1(100:43)	3(100:11.8)	1(88:33.5)	2(80:6.2)
Harpacticoids	11.3	8(10:0.8)	—	8(20:0.6)	5(20:0.2)	5(11:0.6)	5(11:0.6)	—	7(13:0.3)	—
Mysids	3.0	—	—	—	—	—	—	—	—	—
Tanaids	0.3	—	—	—	—	—	—	—	—	—
Hyperids	15.8	9(10:0.2)	—	—	—	—	—	—	—	—
Gammarids	0.3	—	—	—	—	—	—	—	—	—
Euphausiid larvae	2.5	—	—	—	—	—	—	—	—	—
Caridean larvae	39.8	2(50:20.4)	2(80:6.0)	5(20:1.3)	4(30:0.7)	5(11:1.1)	4(22:2.6)	4(40:1.2)	4(50:4.3)	—
Caridean adults and juveniles	1.4	—	—	—	—	—	—	—	—	—
Reptantian zoea	123.9	3(50:2)	3(20:0.8)	7(20:0.7)	—	4(11:1.3)	—	—	—	—
Brachyuran megalops	0.3	—	—	—	—	—	—	—	—	—
Ophiuroid larvae	0.3	—	—	—	—	—	—	—	—	—
Chaetognaths	36.9	7(20:0.7)	4(20:0.4)	—	—	—	—	—	—	—
Larvaceans	12.4	6(20:1.2)	—	1(100:40.9)	1(100:49.6)	2(67:17.8)	3(67:20.4)	1(100:61.2)	—	—
Apendicularian larvae ³	0.0	—	—	6(10:2)	—	—	—	5(10:0.5)	—	—
Fish eggs	732.2	4(30:2.5)	5(20:0.2)	4(90:7.7)	3(100:8)	3(78:12.6)	2(89:20)	2(100:24.1)	2(100:26.3)	3(80:5)
Fish larvae	6.6	5(20:1.5)	—	—	—	—	6(11:0.6)	—	6(13:0.4)	—
Fecal pellets	—	—	—	—	7(10:0.3)	—	—	—	—	—
Algal fragments	—	—	—	2(90:21.2)	6(20:0.2)	—	—	6(10:0.2)	3(75:23.9)	1(100:84.8)
Crustacean fragments	—	—	—	3(30:0.8)	—	—	—	—	13(3:0.6)	—
Unidentified fragments	—	—	4(40:5.0)	2(20:5.7)	—	—	—	—	33(8:3)	—
Gurry	—	—	—	—	5(50:7.4)	3(33:5.5)	4(44:12.8)	2(20:1.0)	13(13:1.3)	2(20:4.0)

¹Numbers of plankters (adjusted values from Table 7) provided only for rough measure of relative abundance.²Calanoids and cyclopoids not separated in gut contents; both occurred in all fish species, but calanoids predominated.³Apendicularian larvae not present in plankton collection, but in two fish guts.

swept into the lagoon thrives there and becomes concentrated so that the average concentration per cubic meter of the eleven most common animal groups is about four times higher than outside." In addition, by the time the incoming current passed our Bogen Island station it presumably had picked up lagoon materials upstream, so its contents probably were of diverse origin.

Of course, currents in themselves enhance the planktivorous habit because planktivores holding station above a reef receive more plankters in currents than in equally rich waters without currents. Most of these fishes, however, take shelter by the time a current reaches 1 m/s, so that optimal velocities are somewhat below this. As the current increases, the advantage of receiving more plankters is progressively outweighed by the difficulty of holding station (as was pointed out for *Chromis punctipinnis* in California by Hobson and Chess 1976).

The relatively few adult diurnal planktivores that foraged where currents were weak probably owed their low numbers to the lack there during the day of calanoids and other zooplankters suitable as prey (Table 2). The many zooplankters that tidal currents carried to planktivores elsewhere were unavailable to fishes here, and those taken as prey or otherwise lost were not quickly replaced. Although the volume of zooplankters collected at the weak-current site by day (Table 1) actually exceeded the volume at the strong-current site (Table 6), it consisted largely of swarming mysids (Table 2) which are local residents seemingly unavailable as prey to diurnal planktivores (possibly for reasons discussed below under Miscellaneous Considerations). The strong-current site was in fact much richer in copepods, caridean larvae, larvaceans, and fish eggs—the major prey of the diurnal planktivores (compare Tables 2 and 7).

Locations in the lee of reefs, however, can be rich in drifting debris from these reefs (Gerber and Marshall 1974). This situation existed at the Walt Island site, where *Pomacentrus pavo* and *P. vaiuli*, the most numerous diurnal planktivores there, subsisted largely on algal fragments. Furthermore, the only other diurnal planktivores numerous in weak-current areas, *Amblyglyphidodon curacao* and *Dascyllus reticulatus*, demonstrated a capacity to utilize algae even though both species are largely carnivorous. Gerber and Marshall (1974), too, found that *D. reticulatus* fed on algal fragments when zooplankters were sparse. Obviously, the capacity to utilize algae as food is highly

adaptive for planktivorous fishes that would live where drift from a reef is rich in algal fragments, though relatively poor in zooplankters (Table 1).

Despite the adaptiveness of herbivory to planktivores under these circumstances, most of the fishes studied by us were strictly, or predominantly, carnivores. Drifting algal fragments were plentiful in nearly all nearshore habitats, but where zooplankters were also numerous the algae were insignificant in the diets of most planktivores. To be sure, certain species capitalized on drifting algae even where zooplankters were numerous. For example, *P. vaiuli*, which we frequently observed plucking items from the water column, was herbivorous and numerous at the zooplankton-rich Bogen Island site, just as it was at the zooplankton-poor Walt Island site. And *P. coelestus*, which may have replaced *P. pavo* where currents were strong, fed heavily on algal fragments where zooplankters were readily accessible. Yet the pattern is clear—zooplankters were favored by most. Generally *Chromis* spp. have been reported as strictly carnivores even where other planktivorous pomacentrids fed substantially on drifting algae (e.g., in the Marshall Islands by Hiatt and Strasburg 1960; in the West Indies by Randall 1967; and in Hawaii by Hobson 1974). Nevertheless, species of *Chromis* display some capacity to accept algal fragments, as we found in *C. margaritifer* and Gerber and Marshall (1974) found in *C. caerulea*. Thus, where waters are rich in reef debris but poor in zooplankters, we should expect to find *Chromis* spp. in relatively low numbers, just as we did at Walt Island. On the other hand, *Mirolabrichthys pascalus* (a serranid) and *Pterocaesio tile* (a lutjanid) are members of strictly carnivorous families, a fact that probably limits them to places adequately supplied with zooplankters. This view finds support from Gerber and Marshall (1974), who reported that *M. pascuales* (as *M. tuka*) and *P. tile* fed entirely on zooplankters. They noted the same for *A. curacao*, *C. agilis*, and *C. lepidolepis* but did not indicate where any of these fishes had been collected, nor whether anything but zooplankters had been available to them. This may be important because one of their major stations was in East Channel, where their plankton collections were without algae, and though they found *A. curacao* strictly carnivorous, we found that it fed heavily on algal fragments where zooplankters were in short supply (Table 4). Gerber and Marshall also noted that *P. vaiuli* fed mainly on algal fragments while

cooccurring pomacentrids concentrated on zooplankters, but concluded from this that the species is a benthic grazer.

Nocturnal Relationships

Nocturnal planktivores probably concentrated where currents were weak because their prey—including polychaetes, large calanoids, mysids, isopods, gammarids, postlarval carideans, and brachyuran megalops—were most numerous there (Table 2). With the probable exception of at least most of the calanoids (see below), most of these zooplankters were local residents that rose into the water column at night after spending the daytime sheltered on or near the sea floor. This pattern has been adequately documented among these groups of organisms from both Atlantic and Pacific Oceans (Emery 1968; Williams and Bynum 1972; Alldredge and King 1977), and its importance in shaping the activities of nocturnal planktivorous fishes has been stressed (Hobson 1968, 1972, 1974; Hobson and Chess 1976). Food-habit studies have shown that these groups include the major prey of apogonids, holocentrids, and other tropical nocturnal planktivores (Atlantic Ocean: Randall 1967; Indian Ocean: Vivien 1973, 1975; and Pacific Ocean: Hobson 1974).

Only a relatively few nocturnal planktivorous fishes occurred where currents were strong, probably because prey suitable to them were relatively scarce there (Table 7). Many of the organisms on which these fishes feed most likely find conditions in places with strong currents adverse. For example, those nocturnal zooplankters that return each morning to shelter in specific habitats would likely be transported to foreign surroundings should they encounter strong currents while in the water column. The mysids, which include some of the strongest swimmers, probably cannot hold station in currents much over 15 cm/s (based on the maximum swimming speeds of several species: Steven 1961; Clutter 1969) and currents at the Bogen Island station regularly exceeded this six-fold. Organisms that need to spend only a few hours in the water column each night might time their emergence to avoid currents, as pointed out by Alldredge and King (1977), but probably even these would find it advantageous to live without this complex timing problem. Furthermore, many of these nocturnal forms rest in sediments by day (Hobson and Chess 1976; Alldredge and King 1977) and might find the coarse, unstable sand

characteristic of strong-current areas unfavorable.

Only part of the increased numbers of zooplankters at night were suitable prey of the nocturnal planktivores. These were individuals more than about 2 mm long, which predominated among the nocturnal visitors at the weak-current site but which were a much smaller segment of the zooplankters that appeared after dark at the strong-current site. Among calanoids, for example, only individuals longer than 2 mm (mostly *Euchaeta marina*, *Pleurommama xiphias*, and *Undinula vulgaris*) were important prey of such larger nocturnal planktivores as *Myripristis* spp., and while these larger calanoids were never seen or collected by us at the weak-current site during the day, they were more numerous than the smaller ones at that station after dark (Table 3). On the other hand, most of the dramatic increase in calanoids at the strong-current site involved only slightly larger individuals of essentially the same species that were there by day, including *Acartia* sp., *Candacia* sp., and *E. marina* (Table 8), and these were largely unexploited by nocturnal planktivores. At 3 mm or less, the majority may be too small to be taken by the relatively large mouths of most of the nocturnal fishes considered here (see Hobson and Chess 1976), although they were important prey of some of the smaller species, such as *Apogon novaeaguinae*.

The daytime location of the many calanoids which appear above the reefs at night remains in question. Our nearshore plankton collections in southern California (Hobson and Chess 1976) showed far less increase in calanoids after dark, and we concluded they were in the nearshore water column day and night. But the dramatic increase in calanoids nearshore after dark at Enewetak suggests a different situation. We recognize one or a combination of two possibilities: 1) that some calanoids reside under shelter on the sea floor by day, and join the plankton at night, or 2) that some calanoids reside elsewhere by day, and migrate, or are transported, to the nearshore waters only after dark. There is evidence for both possibilities. The large calanoids that swarmed around our lights shortly after last evening light (but not taken in our collections) could not have traveled far. Alldredge and King (1977) reported calanoids emerging at night from nearshore benthic substrata on the Great Barrier Reef in numbers that could readily account for the increase in calanoids we observed after dark at

Enewetak; but there may be a problem with Alldredge and King's sampling technique. Their samples were taken with Plexiglas traps that rested on the bottom and collected zooplankters that rose into the water column at night; however, there were gaps between the rigid lower edges of these traps and irregularities on the sea floor. Conceivably, as Alldredge and King themselves recognized, the samples could have included swimming organisms from the base of the surrounding water column that entered the traps through these gaps. These collections need to be repeated with this possibility for error eliminated. While it would be surprising if the numbers of calanoids they collected had actually entered the traps through these gaps, we are concerned that the only calanoid identified in their samples, *Acartia* spp. (listed as cyclopoids), are of a genus known to include species that are exceedingly numerous in the water column during both day and night (e.g., Emery 1968; Hobson and Chess 1976). We would expect organisms that live in the substrate by day to have morphological features reflecting this habit that distinguish them from holoplanktonic relatives at the generic level or higher. So although there may have been nearshore residents among the calanoids whose numbers sharply increased after dark at Enewetak, we believe that at least most of them, especially the larger ones, appeared following regular movements from deeper water.

The calanoids that visited the nearshore waters after dark seemed to be part of a nocturnal move shoreward made by many zooplankters, including chaetognaths and larval fishes. Because each of our primary collecting sites probably received nocturnal visitors from different sources, the two are discussed separately.

Walt Island

Perhaps some of the nocturnal plankters that visited the weak-current site were carried from the open sea by the turbulent flow of water that crossed the interisland reef at higher tides, but this would have been a hazardous transit for most zooplankters, and we doubt that significant numbers came this way. If many had come by this incidental route, at least some would still have been there at daybreak—probably somewhat disoriented in these foreign surroundings. But they were always gone by early morning twilight, suggesting they followed a well-established pat-

tern with consistent and predictable arrivals and departures.

Probably most of the nocturnal plankters that visited Walt Island came from the deeper waters of the lagoon, moving over the lagoon's shallow periphery as part of a regular nocturnal rise into the surface waters. The general rise of zooplankters at night in lagoons of the Marshall Islands has been documented (at Bikini by Johnson 1949; and at Majuro by Hobson and Chess 1973). It has also been noted that by day the mid-lagoon is much richer in zooplankters than is the shallow periphery (Gerber and Marshall 1974), but a shoreward movement among zooplankters at night would reduce this difference between the two regions. Probably it is widespread that zooplankters rising from the depths at night spread out over shallow water near shore. At Kona, Hawaii, where great depths lie adjacent to a coastal shelf (see Hobson 1974), one of us (E. Hobson) often observed myctophids (lanternfishes), and other deep-water forms, in <5 m of water close to shore after dark (unpubl. obs.).

Swimming to the Walt Island site from the deeper water of the lagoon would usually entail moving against the drift from the reef. Although comparatively weak, this current would nevertheless obstruct small or weak-swimming forms. The nocturnal shoreward movement of zooplankters at this location, then, would favor the larger, stronger swimming components of the plankton—forms like chaetognaths, larval fishes, and the larger calanoids. Likely for this reason most of the calanoids among the increased numbers of zooplankters at Walt Island were >2 mm (Table 3), whereas at Bogen Island, where zooplankters were carried by currents, most of a much greater number were 1 to 2 mm long (Table 8). Distinction between the two locations is important because it is the larger zooplankters that were important prey of the nocturnal planktivores. Of course, the upcurrent swim from deeper water would take even the most mobile zooplankters some time. Thus, it is significant that larger calanoids were absent in the plankton collections made at Walt Island 1 h after last evening light, but were numerous in the collections made here at midnight and later (Table 3).

Bogen Island

We presume that most of the zooplankton collected in the flooding tidal currents at Bogen Is-

land had been carried in through East Channel from outside the lagoon—just as during the day. The greatly increased numbers at night probably followed a general rise of zooplankton toward the surface waters in the open sea. Some of these zooplankters were larger than any that were present by day, but such forms represented a lesser proportion of the nocturnal plankton here than they did at the weak-current site. Presumably the collections also included lagoon organisms from upstream, but we would expect these to be relatively few because the entrance to East Channel is only about 1.2 km away (Figure 1). Although the incoming tidal currents probably carried materials that had been transported from the lagoon on earlier ebb tides, we would not expect many of the larger mobile organisms to be among them. Most large mobile forms, it would seem, could avoid being transported from the lagoon by the comparatively weak outgoing currents. But certainly the incoming tide could be returning substantial numbers of passive drifters, like fish eggs and algal fragments, in addition to forms like the smaller calanoids. In any event, we can understand the relative scarcity in the flooding tidal currents of the relatively large nearshore residents (e.g., polychaetes, mysids, and postlarval carideans) that are so important in the diets of nocturnal planktivores.

Probably at least some zooplankters from the deeper waters of the lagoon visited the Bogen Island site at night during periods between flooding tides, but we made no collections at these times. Nevertheless, it would seem that the impact of such forms on the area would be limited, considering how long it takes them to travel without benefit of transport by current, and the fact that a flooding tide sweeps through here during much of most nights.

Miscellaneous Topics

The Nocturnal Increase in Fish Eggs

Planktonic fish eggs represent a special case. Unlike most other zooplankters, which are mobile forms that strongly influence their own distributions, fish eggs are passive drifters that are quickly carried from where they are released if there is any current. Presumably their relative numbers in the water column closely follow the incidence of their release by fishes on the reefs below, and certainly the circumstances of this re-

lease have been strongly influenced by the threat from predators that abound over the nearshore reefs. Planktonic fish eggs were a major food of diurnal planktivores (Tables 4, 9) but, despite an almost sevenfold increase in numbers at night (Tables 2, 7), they were insignificant in the diets of nocturnal planktivores (Table 5). Clearly these large transparent eggs are relatively safe from predatory fishes after dark, probably because they are then invisible. Thus, it would be highly adaptive for reef fishes to release planktonic eggs late in the day, or early in the night, when the eggs have maximum time for dispersing in the dark, relatively free of threat from planktivorous reef fishes.

Possible Influences of Water Depth and Size

Among the promising topics we lacked time to pursue during our short stay at Enewetak were ways that water depths, and the sizes of interacting fishes and zooplankters, may influence trophic relationships.

We believe that the difference in water depth between our primary collecting sites (7 vs. 13 m) did not significantly influence our findings, especially as the deeper station was well away from the deep part of the lagoon (Figure 1)—farther, in fact, than the shallower station. It was apparent to us, nevertheless, that water depth in the lagoon can, directly or indirectly, influence fish-zooplankton interactions. Obviously both fishes and zooplankters are physically limited in extreme shallows, especially in turbulent waters above shallow reefs. But probably the major depth-related influence stems from the general tendency of lagoon zooplankters to seek deeper water during the day (e.g., Johnson 1949; Hobson and Chess 1973)—a tendency that apparently increases with size. We suggest above that many of the larger zooplankters active above the nearshore shelf at night were in the deeper lagoon waters by day, when the water column of the nearshore shelf was largely without such forms. Perhaps the concentrations of planktivores along the outer edge of the nearshore shelf during the day were in contact with the fringe of these deep zooplankton populations.

This leads to a possible influence related to size. Very small zooplankters (those passing through the mesh of our net, and so unrepresented in the collections), and their predators among juvenile and larval fishes, may follow patterns sig-

nificantly different from patterns followed by the larger forms studied here. The zooplankters descending into the depths by day tend to be the larger individuals, so we wonder where the very small ones are located. In sharp contrast to the relatively few adult planktivores active in weak-current areas of the nearshore shelf by day, large numbers of juvenile and larval fishes (Figure 4) clearly found planktonic food abundant. It may be that very small zooplankters, unsampled by our net and too small to be taken by most adult planktivores, remain numerous in shallow weak-current areas during the day.

Mysids as Prey During the Day

It is striking that when mysids swarm in dense numbers near many reefs during the day they are relatively unimportant as prey of the major planktivorous fishes. They seem to escape the interest not only of diurnal planktivores, but also of the many nocturnal planktivores (e.g., *Myripristis* spp.) that hover within easy reach close among the coral.

To be sure, a number of the fishes we studied took some of these mysids by day. *Chromis caerulea*, *C. agilis*, *Dascyllus reticulatus*, and *Pomacentrus pavo* included mysids as minor components of their diet at the weak-current site. Furthermore, Hiatt and Strasburg (1960) reported that *C. atripectoralis* preyed significantly on mysids. But considering the preponderance of mysids in the water column at so many places during the day, these fishes took only token numbers.

Probably the relatively large size of the mysids is important in this context. The evolution of feeding morphologies in diurnal planktivores appears to have been determined by strong selective pressures to take tiny prey (Davis and Birdsong 1973; Hobson and Chess 1976). Significantly, most of the zooplankters taken by these fishes (e.g., copepods, larvaceans, and fish eggs) were <2 mm long, and the size range of mysids that swarmed around these reefs in daylight was 2 to 8 mm (Tables 2, 7). In reporting a similar situation in the tropical Atlantic Ocean, Emery (1968) speculated that planktivorous pomacentrids fail to prey on swarming mysids because normally these fishes feed on smaller prey.

The failure of *Myripristis* spp. and other large-mouthed nocturnal planktivores to exploit this diurnal resource cannot be attributed to the size of

the mysids, however, because these fishes find the same mysids major prey at night. Apparently the nocturnal fishes simply do not react to these readily accessible mysids as prey during daylight. In warm-temperature waters of southern California the large juvenile olive rockfish, *Sebastes serranoides*, feeds primarily on zooplankters after dark, but during the day sometimes preys on mysids that are within reach of the rockfish where it hovers in relatively inactive diurnal schools (Hobson and Chess 1976). However, predominantly nocturnal habits seem to be characteristic of the olive rockfish only during its large juvenile stage—both before and after this stage it feeds mainly by day (Hobson and Chess 1976). Therefore, even at that time of its life when the olive rockfish feeds primarily at night, we should not expect it to be as strongly nocturnal as *Myripristis* spp. and the other more specialized nocturnal forms that ignore mysids by day at Enewetak.

Possibly swarming mysids are protected from predators by the nature of their aggregations. Emery (1968) noted that mysid swarms respond to predators just as fish schools do. The analogy can be expanded. Like these nocturnal mysids, many nocturnal fishes congregate in dense numbers above the reef during the day, and at this time they too are relatively undisturbed by the many predators at large in the same area (Hobson 1965, 1968). It is widely believed that fishes are less vulnerable to predators when they aggregate (e.g., Bowen 1931; Springer 1957; Brock and Riffenburgh 1960; Manteifel and Radakov 1961; Williams 1964). Of the many theories that would explain this circumstance, we favor the existence of a confusion effect, as advocated by Allen (1920) and others. This theory suggests that visually orienting predators which select individual prey have trouble singling out a target among the many alternatives they confront in an aggregation. That mysids achieve some safety from predators by aggregating is further supported by the experiments of Welty (1934), who found that goldfish, *Carassius auratus*, consumed fewer daphnia when these prey were concentrated. (These comments apply as well to the relative lack of diurnal predation on larval fishes, which, in their dense schools close to the reef, resembled swarming mysids.)

Planktivore Morphology and Their Distance From the Reef

It was suggested earlier (Hobson 1974) that in

their tendencies toward more fusiform bodies and deeply incised caudal fins, diurnal planktivores have acquired added speed that is adaptive in quickening their return to reef shelter when threatened. Expanding this suggestion, these features are more developed in planktivores that swim farther from the reef because threats from predators probably increase in more exposed locations. Although morphology that permits faster swimming would also enhance holding station in a current, we believe the major selection pressures shaping these features in planktivores have come from predators.

Despite the obvious adaptiveness of fusiform bodies and of deeply incised caudal fins in many planktivores, the morphologies of certain other highly successful diurnal planktivores have taken the opposite course. For example, among the fishes we studied, *Dascyllus reticulatus* (Figure 7) and *Amblyglyphidodon curacao* are among the deepest bodied of pomacentrids, and yet they range farther into the water column than the species of *Chromis* or *Pomacentrus*. Similarly, the many planktivorous chaetodontids in Hawaii (e.g., species of *Chaetodon* and *Hemitaurichthys*), all deep-bodied forms with truncate caudal fins, are highly successful planktivores that range widely in the water column (Hobson 1974).

We suggest that whereas fusiform bodies increase the chance of eluding predators, deep bodies increase the chance of discouraging predators. The basis of this second suggestion is the fact that piscivores live with the danger of choking on spiny-rayed prey lodged in their pharynx or esophagus. Over the years we have seen many predators in this predicament—often fatally. Piscivores generally swallow their prey head-first, frequently after manipulation to ensure proper orientation. Reasons for not swallowing a spiny-rayed fish tail-first are obvious. Assuming, then, that a prey fish is swallowed head-first, the danger of it becoming lodged in the pharynx or esophagus increases with its depth or width. Thus, predators equipped to take prey from among the variety of planktivores in the water column (where those at a given level tend to be about the same length) would find greater risk ingesting deeper bodied forms, especially those with prominent fin spines. Of course, this advantage of a deep body and prominent spines in thwarting predators extends beyond planktivores; the entire family Chaetodontidae, for example, would benefit (Hobson and Chave 1972).

ACKNOWLEDGMENTS

We thank Stephen V. Smith, Director, and Laboratory Managers Philip and Janet Lamberson, of the Mid Pacific Marine Laboratory at Enewetak Atoll, for making facilities available to us. The laboratory is supported by the Division of Biomedical and Environmental Research of the U.S. Energy Research and Development Administration and is operated as an extension of the Hawaii Institute of Marine Biology, University of Hawaii. For constructive criticism of the manuscript we thank Carl L. Hubbs and Richard H. Rosenblatt, Scripps Institution of Oceanography; William M. Hamner, Australian Institute of Marine Science; Robert E. Johannes, Hawaii Institute of Marine Biology; and William Lenarz, Tiburon Laboratory. John E. Randall, Bernice P. Bishop Museum, Honolulu, identified *Mirolabrichthys pascalus*; Kenneth Raymond, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, drew Figure 1 and the fishes in Figure 6; and Alice Jellett, Tiburon Laboratory, typed the manuscript.

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