CHAPTER 4

Trophic Relationships of Fishes Specialized to Feed on Zooplankters above Coral Reefs

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I. INTRODUCTION

Fishes specialized to feed on zooplankters are major components of coral reef communities. They are distinctive animals, with many features that relate to their way of feeding. Although most fishes are planktivorous as larvae and early juveniles (Durbin, 1979), generally only species with appropriate adaptations remain obligate planktivores as adults (Davis and Birdsong, 1973; Hobson and Chess, 1976, 1978). This chapter examines how these species have accommodated the special needs of planktivory while retaining close ties to reef structures, generally as places to shelter when at rest or threatened.

Virtually all coral reef planktivores are among the highly diverse acanthopterygians (spiny-finned teleosts), which are the most highly evolved fishes (Gosline, 1971). Acanthopterygians dominate in coral reef communities (Smith and Tyler, 1972, Schaeffer and Rosen, 1961); for example, 98% of the species noted during a census of Hawaiian reefs are members of this group (Hobson, 1974).

Despite the great diversity of forms among coral reef acanthopterygians, however, virtually every major family includes species that are specialized as planktivores. For example, there are diurnal planktivores among the Serranidae, Chaetodontidae, Pomacentridae, and Balistidae, and there are nocturnal planktivores among the Holocentridae, Priacanthidae, and Apogonidae (Starck and Davis, 1966; Randall, 1967; Hobson, 1974). Most planktivorous acanthopterygians, including all species considered in this chapter, feed with visually oriented strikes at individual prey (Zaret, 1972; Confer and Blades, 1975; Durbin, 1979; unpublished observations). Furthermore, the major threats to planktivores feeding above coral reefs (at least during the day) come

from visually oriented attacks of large piscivorous fishes (Hobson, 1968, 1972). With vision so important, the trophic relations of coral reef planktivores—both as predators and as prey—are profoundly influenced by variations in levels of incident light (Hobson, 1972; Stevenson, 1972; Collette and Talbot, 1972). Many are adapted to specific photic conditions (Hobson, 1972; Munz and McFarland, 1973) and the vast majority feed strictly by day or by night (Hobson, 1974, 1975).

A. Need for Innovative Methods of Study

Studies of trophic dynamics among fishes and zooplankters above coral reefs have required innovative sampling procedures. The traditional methods used to sample zooplankton, for example, were developed for work in open water offshore and are ineffective in confined spaces among reefs. So studies that would sample coral reef plankton have used nets pushed by divers (Emery, 1968; Hobson and Chess, 1978) and tethered to anchors on the reef (Johannes et al., 1970; Hobson and Chess, 1978). And traps have been set on the seabed to sample the many otherwise benthic organisms that periodically join the plankton (Porter and Porter, 1977; Alldredge and King, 1977, 1980; Hobson and Chess, 1979, 1986). Similarly, assessments of trophic relations among fishes based on specimens collected from above water are limited by problems of relating gut contents to occurrences of organisms in the environment. To better define prey selection by planktivorous fishes, hand-held spears have been used to select specimens known to have been feeding at the specific time and place where the plankton was sampled (Hobson, 1968; Hobson and Chess, 1976, 1978).

Perhaps the greatest advantage these methods have over traditional shipboard operations for study of trophic interactions, however, is that they put the investigator at the site of the interactions. From there one can directly observe vital spatial and temporal relationships and behaviors that can only be inferred from above water. These methods and advantages, with emphasis on events throughout day and night, have been refined by my studies with James R. Chess of interactions among reef fishes and zooplankters at widespread locations in the Atlantic and Pacific oceans. This chapter incorporates data, observations, and impressions gained from these studies in a synthesis of present knowledge.

II. DIURNAL PLANKTIVORES

Planktivorous reef fishes that feed by day typically form aggregations in the water column (Fig. 1), and from a distance it is often difficult to distinguish one species from another. Despite differing limitations on adaptive change
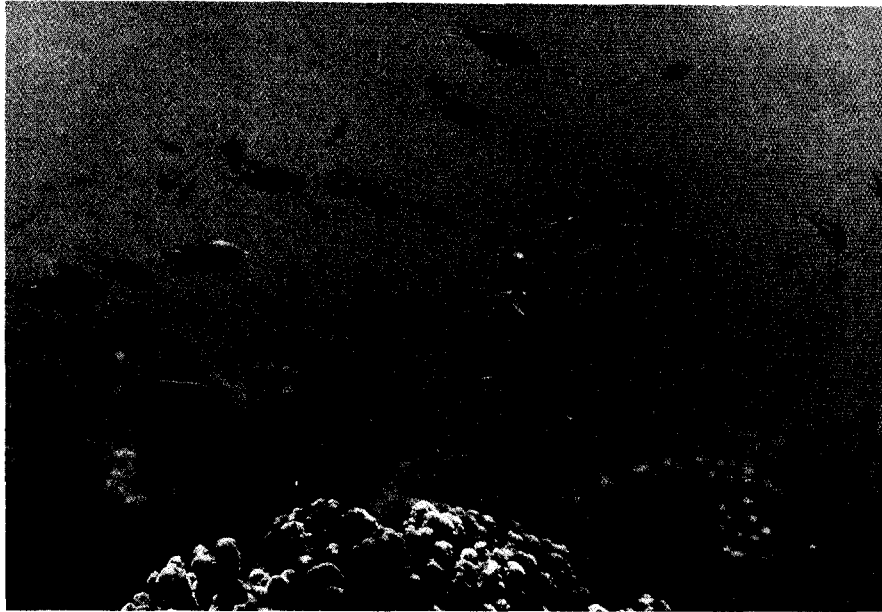
Figure 1 Feeding aggregation of *Chromis atrilobata* (Pomacentridae), a diurnal planktivore in the Gulf of California, Mexico.

related to their differing phylogenies, these fishes have acquired similar features in response to problems they have in common. This is especially evident in adaptations to the size of their prey and to feeding in exposed positions above the reefs. As a result of the remarkable degree of morphological and behavioral convergence that has developed, they tend to resemble one another more than they do other members of their own families that feed on the benthos (Davis and Birdsong, 1973).

A. Adaptations to a Diurnal Planktivorous Diet

Most diurnal reef planktivores feed primarily on swimming crustacea, particularly calanoid and cyclopoid copepods, but larvaceans or fish eggs are favored by some (Hiatt and Strasburg, 1960; Hobson and Chess, 1978; Sano *et al.*, 1984b). These prey vary in form and behavior, but those accessible during the day are largely transparent and visible mainly through their pigmented parts, such as eyes, or even gut contents (Zaret, 1980). So while planktivorous fishes generally take the larger of zooplankters available to them (Ivlev, 1961; Coates, 1980), they have been known to take the smaller of two similar forms if this one is more heavily pigmented (e.g., Zaret, 1972; Zaret and Kerfoot, 1975).

Whatever problems there may be with pigmentation, however, clearly it is an advantage to be smaller (Hobson and Chess, 1976; Obrien, 1979). And so zooplankters above coral reefs during the day tend toward not only transparency, but also reduced size. Judging from my studies with Chess, virtually all zooplankters taken by planktivorous reef fishes during the day are less than 3 mm in their greatest dimension.

Because planktivorous reef fishes have evolved from early ancestors that were adapted to feed on relatively large prey (Schaeffer and Rosen, 1961; Gosline, 1971), successful feeding depends on the performance of features modified for tasks very different from their original purpose. Particularly important have been modifications of head and jaws, including dentition, that permit even relatively large individuals to consume tiny organisms in open water. In contrast to the large, generalized mouth of the ancestral form (Gosline, 1971), most diurnal planktivores have a small mouth that in many is sharply upturned and with highly protrusible, often toothless jaws (Davis and Birdsong, 1973). Thus, whereas the primitive mouth functioned to grasp large prey, the modern planktivore mouth functions to engulf small prey.

Most of the evolution from the primitive condition, however, occurred in nonplanktivorous progenitors of modern planktivores. Protrusible jaws, for example, characterized the early acanthopterygians (Alexander, 1967; Gosline, 1971) and are now widespread among fishes (see Motta, 1984, for a review). As Gosline (1981, p. 11) stated: "The acanthopteran (acanthopterygian) system of premaxillary protrusion . . . appears to form part of the inheritance of all higher teleosts." It was to a large extent the potential of this feature that led Schaeffer and Rosen (1961, pp. 198–199) to state: "It is primarily the acanthopterygian mouth that has given rise to the enormous variety of specialized . . . feeding mechanisms for which teleosts are so well known." Among these specialized feeding mechanisms are those of diurnal planktivores, which have been refined by selection pressures specific to the planktivorous habit.

So even though some of the most protrusible jaws occur in such nonplanktivorous forms as the piscivorous *Luciocephalus pulcher* (Lauder and Liem, 1981) and the benthivorous *Gerres* spp. (Schaeffer and Rosen, 1961), the feature has nevertheless proven especially adaptive in planktivory. For example, when pomacentrids of the planktivorous genus *Chromis* are within a few centimeters of a target, their jaws shoot forward and engulf the prey (Fig. 2). According to Davis and Birdsong (1973, p. 299), jaw protrusion in planktivores "creates suction which draws prey into the cavity." This view is consistent with Lauder and Liem's (1981, p. 266) assessment that "an underlying assumption of most current research on advanced teleost feeding mechanisms is that protrusion is correlated with increased suction efficiency." But Lauder and Liem went on to show that the extremely protrusible jaws of *Luciocephalus pulcher* (among the most protrusible in teleosts) produce very little suction.
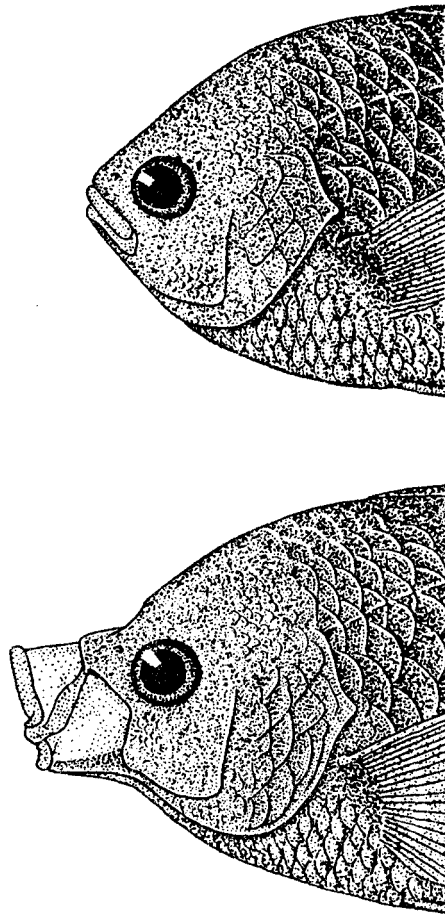
Figure 2 The protrusible upper jaw of *Chromis punctipinnis*, a typical feature of diurnal planktivores, permits projecting the mouth to engulf prey without swimming forward.

The assumption that jaw protrusion functions mainly to produce suction was earlier questioned by Nyberg's (1971) study of feeding mechanics in *Micropterus salmoides* (Centrarchidae). That species, Nyberg concluded, uses protrusion less to create suction than to bring the jaws more quickly to the prey. The advantage is greatest, he observed, in smaller bass moving slowly during the attack, and he related this to a trend in acanthopterygian evolution in which smaller, more protrusible mouths are associated with slower approaches to prey. Certainly planktivorous fishes above tropical reefs represent a culmination of this trend. *Chromis* spp., for example, generally move little, if at all, toward their prey; instead, they depend largely on their extremely

protrusible jaws to get their mouths to the target. This is the "ram-jaw" feeding mode described by Coughlin and Strickler (1990), who used high-speed cinemaphotography and video to analyze feeding by *Chromis viridis*. They concluded that this species uses "ram-jaw," low-suction feeding to capture evasive prey, but decreases jaw protrusion and increases suction when prey are less evasive.

Although the small mouth is another planktivore feature widespread among nonplanktivores, the oblique orientation of this mouth, so common among planktivores, seems to be a feature especially adaptive in fishes that would capture tiny, motile organisms in open water. Probably the advantage of this arrangement comes not from the orientation of the mouth, but rather as a consequence of the shortened snout, which places both eyes in position to train simultaneously on small targets immediately ahead (W. A. Starck, cited in Rosenblatt, 1967a).

Gill rakers, a general feature of acanthopterygians that prevents ingested prey from escaping through the gill openings, tend in planktivores to be long and especially numerous (thus closely spaced). This increases their effectiveness in fishes that would feed on small prey (Davis and Birdsong, 1973).

Despite these adaptive tendencies, however, trophic features vary among planktivores—even among close relatives. The mechanisms and structures involved in jaw protrusion, for example, vary among species of *Chromis* (Emery, 1973). So while similarities related to their common purpose unite the group, each species has been to some varying extent customized by distinctive elements of its evolutionary history.

B. Adaptations to Diurnal Threats from Predators

Interspecific convergence among diurnal planktivorous fishes in features that increase mobility are even more striking than the convergence in features that enhance feeding. Particularly evident are tendencies toward streamlined bodies and deeply forked caudal fins—features that increase swimming speeds (Norman, 1947). Significantly, these features generally are more developed in fishes that range farther from the reef (Fig. 3), which indicates an increasing need for swimming efficiency in open water. Consistent with this is a tendency to be larger, which might be expected considering the direct relation between body length and swimming speed.

Planktivores that forage farther above the reef would find that streamlining helps them maintain station in the stronger currents that flow there. They would also benefit from a speedy flight to the reef, because the survival of small fishes exposed to predators in sunlit open water often depends on how fast they get to shelter when threatened (Hartline *et al.*, 1972; Hobson and Chess, 1978).
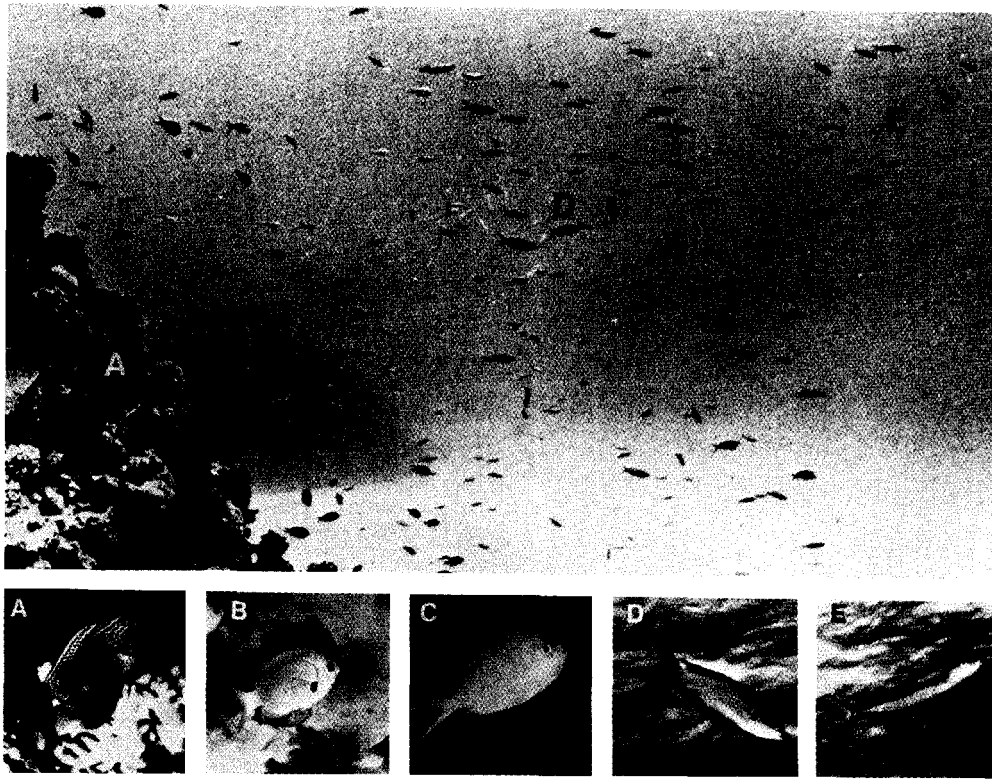
Figure 3   Planktivorous fishes foraging above a reef in the lagoon of Enewetak Atoll. Note that those farther from the reef have features that increase their swimming speed and ability to maintain station in currents. (A) *Pomacentrus vaiuli,* (B) *Chromis agilis,* (C) *Chromis viridis,* (D) *Anthias pascallus,* (E) *Pterocaesio tile.*

Diurnal planktivorous fishes in open water also tend to aggregate, a widely recognized defensive behavior in fishes (Eibl-Eibesfeldt, 1962; Hobson, 1968). That aggregating and a quick retreat to cover are adaptive in defense becomes evident when certain open-water predators appear, notably large *Caranx* spp. (Carangidae). In response to this threat, the planktivores assembled to feed above the reefs abruptly close ranks, and then often dive to the reef below.

Despite the convergence among so many unrelated species in features that increase swimming speed, and the obvious adaptive value of these features, certain other planktivorous fishes have accommodated the same threats by taking virtually the opposite evolutionary course. Instead of being more streamlined than their benthic relatives, species of the planktivorous pomacentrid genera *Dascyllus* and *Amblyglyphidodon* are actually deeper-bodied (and

have longer fin spines) than benthivorous pomacentrids (Hobson and Chess, 1978). These features retard rather than promote swimming speeds, so if maintaining station in currents and accelerated flight are important, how do these fishes compensate for their reduced swimming efficiency?

They can, of course, avoid strong currents simply by feeding elsewhere, but what about the problem with predators? I suggest that threats from predators are reduced by their greater body depth and spine development, because these features increase the chance of becoming lodged in the mouth or pharynx of predators that would attempt to swallow them. An effective combination of deep bodies and strong fin-spines probably protects benthivorous as well as planktivorous chaetodontids and pomacanthids (Hobson and Chave, 1972). It is significant that the planktivorous species of these two families are, as a group, indistinguishable from their benthivorous relatives on the basis of external morphologies. Many, in fact, are congeners, for example, the planktivorous and benthivorous species of *Chaetodon* (Hobson, 1974).

Clearly, the exceptionally deep bodies characteristic of these predominantly benthivorous families are suited to activities in open water, although perhaps not where strong currents flow. It would seem that while the streamlined bodies and deeply forked caudal fins of many diurnal planktivorous fishes promote eluding predators, the exceptionally deep bodies and long fin-spines of certain others tend to discourage predators. Both combinations may promote access to zooplankton in open water during the day by reducing threats from predators (Fig. 4).

Planktivorous fishes in open water above reefs become increasingly vulnerable with decreasing light, and they respond by moving closer to shelter. Thus, they forage lower in the water column when the sky is overcast than when it is clear, and they descend briefly when clouds pass in front of the sun on otherwise clear days (Hobson, 1972; Stevenson, 1972).

C. Distribution and Movement

Diurnal planktivores are most numerous along reef edges adjacent to deeper water, probably because their major prey—holoplankters from open water (Hobson and Chess, 1978, 1986)—are most accessible there. Consider, for example, their distribution (excluding juveniles) among reef habitats off the island of Hawaii, as determined by visual assessments in belt transects (Hobson, 1974). Diurnal planktivores were of 12 species and constituted 45% of the fishes counted along the drop-off into deeper water, but were only of 6 species constituting 14.6% of the fishes counted over the inner reef.

The abundance of diurnal planktivores near the reef edge comes not only from the many that reside there, but also from others that migrate each morning from nocturnal shelter sites elsewhere on the reef (Hobson, 1972,

Figure 4 The planktivorous chaetodontid *Hemitaurichthys polylepis* (left) is as deep-bodied as the benthivorous members of its family, whereas the planktivorous acanthurid *Acanthurus thompsoni* (dark fish) is far more streamlined than the benthivorous members of its family.

1973, 1974). Although reef edges tend to be irregular structures rich in shelters used by diurnal planktivores, apparently these shelters cannot accommodate all the planktivores that feed there. That the migrators are among the larger diurnal planktivores (Hobson, 1974) suggests either that there is a shortage of the more spacious shelters at the feeding site or that the smaller species lack the capacity to migrate.

Diurnal planktivores concentrate along the reef edge and feed mainly on transient zooplankters from open water, even though resident zooplankters of comparable type and size are widespread and accessible on many reefs. I refer to the resident zooplankters that occur in dense, generally monospecific swarms close to reef structures, including various copepods (e.g., *Acartia* spp. and *Oithona* spp.) as well as mysids (e.g., *Anisomysis* sp. and *Mysidium* spp.) (Emery, 1968; Hobson and Chess, 1978; Hamner and Carleton, 1979).

These diurnal swarms can be immense. For example, Hamner and Carleton (1979) described a swarm of the copepod *Oithona oculata* encircling a Palauan bay that was more than 100 m long and estimated to contain 75 million individuals. Similarly, Emery (1968) observed among reef formations in the Florida keys swarms of the copepod *Acartia spinata* that ranged in size from just a few to over 60 m^3, with densities of about 110,000 individuals per m^3.

The zooplankters in these swarms, however, seem generally unavailable to predatory fishes. Probably this is because predators confronted with multiple targets have difficulty distinguishing individuals (Welty, 1934; Eibl-Eibesfeldt, 1962; Hobson and Chess, 1978). In concluding that swarms protect their members from predators, Hamner and Carleton (1979, p. 11) noted that planktivores "swim through the swarms as if they were invisible."

Certainly there is some predation on these swarms, just as there is predation on fish schools. For example, Emery (1968) saw predators take copepods from swarms in the tropical Atlantic, and Hobson and Chess (1978) found mysids in the gut contents of diurnal planktivores taken near mysid swarms in the central Pacific. But considering how many individuals there are in these swarms, this predation is probably insignificant. Swarming, therefore, would seem to be an adaptive behavior that reduces the vulnerability of reef zooplankters to reef planktivores.

Because diurnal planktivores feed mainly on transients, they depend on water currents to supply them with food. It is well known that currents are important to feeding planktivores (Stevenson, 1972; Thresher, 1983a), and even casual observations note that there are currents where planktivores are abundant. In fact, it is because their food is transported by currents that planktivorous fishes are able to feed in the stationary aggregations so characteristic of them. As Stevenson (1972) pointed out, the aggregations dissolve when currents slacken and the planktivores are forced to swim about in search of prey. Despite their dependence on currents as transporters of food, however, planktivorous fishes find it increasingly difficult to maintain station when currents exceed optimal velocities (which vary with the species), and ultimately they are forced to shelter (Hobson and Chess, 1976, 1978).

Planktivorous fishes also are distributed relative to their size. Feeding at reef edges, for example, is most characteristic of larger individuals. Thus, species concentrated close to the drop-off (depth about 25 m) into deeper water off the island of Hawaii (Hobson, 1974) are, at sizes exceeding 10 cm SL, the larger of the planktivorous reef fishes there (e.g., the chaetodontids *Chaetodon miliaris* and *Hemitaurichthys polylepis*, the pomacentrid *Chromis verater*, the acanthurids *Acanthurus thompsoni* and *Naso hexacanthus*, and the balistid *Xanthichthys auromarginatus*). The smaller species are more widely distributed. Examples include the pomacentrids *Chromis agilis* and *C. hanui* (combined as *C. leucurus* in that report), which have maximum sizes of about 7 cm SL. Although these two are numerous along the drop-off, they also are abundant above the inner reef, where the larger species are comparatively scarce.

A similar difference in distribution with size exists above the shelf of sand and isolated patch reefs that rims the windward side of the lagoon at Enewetak atoll (Hobson and Chess, 1978, 1986). In that setting, zooplanktivorous fishes of all sizes abound above patch reefs along the shelf's edge (depth about

10 m), but only the smaller subadults and very small species (less than about 6 cm) are numerous above patch reefs on the inner shelf (depth < 5m). [Relatively large herbivorous planktivores are abundant above patch reefs on the inner shelf, where they feed mainly on drifting plant fragments (Hobson and Chess, 1978), but herbivorous planktivores are not considered here because many of their trophic relations are unlike those of zooplanktivorous species.]

Differences in distribution with size can be related to differences in trophic relationships. As noted earlier, the concentration of larger zooplanktivores at the shelf edge is consistent with diets dominated by transient organisms from open water (Hobson and Chess, 1978). The major planktivore above patch reefs along the shelf edge at Enewetak is the adult of *Chromis viridis*, which is larger than most other planktivores at this site even though its maximum size is only about 7 cm SL. [This species was previously known, and identified in that report, as *C. caerulea* (see Randall *et al.*, 1985a).] Tony Chess and I collected 21 of these fish (6.0–7.3, $\bar{X}$ = 6.5 cm SL) from above the patch reefs during the day, and of the 1168 zooplankters in their guts, 1047 (89.6%) were 2.5 to 3.0-mm individuals of *Undinula vulgaris*. This calanoid copepod is a major component of the plankton in the Enewetak lagoon, but during the day it is largely absent above the shelf (Gerber and Marshall, 1974; Hobson and Chess, 1986). In fact, the relatively shallow water above shelf patch reefs during daytime is virtually without zooplankters of any kind larger than 1.5 mm (Hobson and Chess, 1986), which probably is why there are so few larger zooplanktivorous fishes there in daylight.

On the other hand, the smaller zooplanktivorous fishes so abundant above patch reefs on the inner shelf at Enewetak during the day find their food readily available. Chess and I collected subadults of three species whose large plankton-feeding aggregations were prominent above the inner-shelf patch reefs: *Chromis viridis* (n = 13; 9–40, $\bar{X}$ = 25.5 mm SL), *Dascyllus aruanus* (n = 10; 16–35, $\bar{X}$ = 27.5 mm SL), and *Rhabdamia gracilis* (n = 20; 20–36, $\bar{X}$ = 30.9 mm SL). None of the varied zooplankters in their guts—mostly crustacea, but also including larvaceans and fish eggs—were larger than 1.0 mm, and plankton collections taken at the time found these smaller forms to be abundant in the water column.

That the larger planktivorous fishes feed mainly on transient zooplankters at the reef's perimeter is particularly evident above reefs swept by currents. Here these fishes concentrate above the upcurrent edge of the reef and are relatively few above the reef downcurrent. Above a southern Californian reef swept by currents that reverse with the tide, for example, Bray (1981) found that larger (>15 cm) individuals of *Chromis punctipinnis* (but not the smaller ones) concentrate to feed on cladocerans, copepods, and larvaceans at whichever end of the reef faces the current, changing ends with each reversal of current.

Furthermore, plankton samples that Bray took both upcurrent and downcurrent of the feeding *C. punctipinnis* showed that these aggregations remove from the inflowing current a significant proportion of the organisms suitable as prey.

A greater availability of suitable prey above upcurrent parts of a reef explains diel movements that I observed in the planktivorous *Clepticus parri* (Labridae) above a reef off St. Croix, U.S. Virgin Islands. From early to mid morning each day, larger individuals (>15 cm) of this species migrated toward the upcurrent end of the reef, and then from mid to late afternoon they returned downcurrent. The similarity of this pattern to the diel migrations that some Hawaiian planktivores make between inner-reef shelter sites and outer-reef feeding grounds (Hobson, 1972, 1973) suggests that the larger *C. parri* found their prey more available upcurrent.

But if prey of the larger planktivores become increasingly scarce in currents that flow over a reef, how is it that prey of the smaller planktivores apparently remain abundant? Part of the answer is that during the day the smaller zooplankters (less than about 1 mm) are vastly more numerous in currents flowing over the reefs. Perhaps a more important reason, however, is that during the day these smaller zooplankters may be relatively safe from reef predators when more than a few meters above the substrate. This is because the predators that threaten them most are themselves relatively small animals that become increasingly vulnerable with distance from shelter in daylight. Smaller planktivorous fishes that feed by day, for example, generally stay within a meter of the reef. And the various mysids and other predaceous crustacea that range into the water column to feed on still smaller zooplankters do so only at night (Hobson and Chess, 1976, 1978). Thus, during the day, smaller zooplankters may enjoy what is in essence a refuge from reef predators in all but the lower levels of currents flowing over a reef. And as the current flows along, individuals from this refuge would be there to replace those of their kind consumed at the lower levels.

D. Trophic Links with Open-Water Communities

It is widely recognized that planktivorous fishes are a major trophic link between coral reef and open-water communities (Emery, 1968; Davis and Birdsong, 1973). Food webs that have been constructed to represent coral reef trophic systems, however, assume that the primary flow of energy from planktivores to other elements of the community is through piscivorous predators (e.g., Polovina, 1984). But while undoubtedly some diurnal reef planktivores are consumed by predators (e.g., Choat, 1968; Hartline *et al.*, 1972), the numbers taken are relatively few owing to effective defenses, as described earlier.

Probably the major path of energy from diurnal reef planktivores to other components of the reef trophic system is through feces. Feeding planktivores produce prodigious amounts of feces that rain down upon the reef throughout the day, and much if not most of this material is consumed by other fishes (Robertson, 1982). Chess and I have found that when zooplankters are especially abundant in the water column, those consumed by planktivores pass through the guts so rapidly that they appear in the feces with little sign of digestion. In this situation the secondary consumers probably gain more energy from the zooplankton than do the planktivores that had consumed them first. Although planktivore feces are most readily ingested by fishes before settling on the seafloor, significant amounts are taken from the bottom by herbivores and detritivores (Robertson, 1982). Most of this coprophagy occurs below the feeding aggregations, but some material still in planktivore guts at day's end is vented at nocturnal shelter sites elsewhere on the reef, and according to Bray et al. (1981) this represents a significant importation of energy to the reef benthos.

III. CREPUSCULAR CHANGEOVER

Like virtually all members of the coral reef community, planktivorous reef fishes and their prey find twilight to be a time of transition between distinctive diurnal and nocturnal modes. The changeover process is an orderly complex of responses to specific levels of diminished daylight, with the morning and evening sequences being essentially mirror images of one another (Hobson, 1972; Collette and Talbot, 1972; Helfman, 1986b). Here I describe events during the evening changeover that involve planktivorous fishes and zooplankters.

A. Transition from Day to Night: Fishes

When the diurnal planktivores descend toward the seafloor late in the afternoon they provide the first clear indication that the reef community is shifting toward its nocturnal mode. Although the beginnings of this process cannot be distinguished from the highly variable diurnal condition described earlier by 30 min before sunset it is clear that many diurnal planktivores are descending toward shelter on the reef.

Just as smaller individuals stay closer to the reef while active during the day, they also are the first to shelter in the evening. Consider, for example, the species of *Chromis* in Hawaii (Hobson, 1972): The smallest, *C. vanderbilti* (maximum size about 5 cm SL), stays within a meter or so of the reef on even the brightest days and is dispersed under cover on the reef by 15 min before

sunset. The next smallest, *C. agilis* (as *C. leucurus* in that paper; maximum size about 7 cm SL), ranges 1–2 m above the reef during the day and is under cover within a few minutes after sunset. Finally, two larger species of similar size, *C. ovalis* and *C. verater* (maximum size about 14 cm SL), range throughout the water column during the day, and the last of them take cover about 15 min after sunset. The final descent of the larger planktivores marks the beginning of the "quiet period," a 15- to 20-min interval when the waters above the reef appear relatively empty of fishes (Hobson, 1972). It is believed that reef fishes tend to avoid exposed positions at this time because of sharply increased threats from predators. Actually, as the diurnal planktivores demonstrate in descending to cover in order of increasing size, most diurnal fishes have left the water column before the quiet period begins. Apparently the smaller fishes are threatened first—the smallest well before sunset—and after that the danger continues to grow in the fading light, threatening progressively larger fishes, until by the start of the quiet period virtually all diurnal fishes that had been in the water column have been affected. Thus, the timing of the quiet period and other changeover events appears to be determined by levels of light. These events occur earlier under cloudy skies (Collette and Talbot, 1972) and are extended in the longer twilight at higher latitudes (Helfman, 1981, 1986b; Hobson, 1986).

The nocturnal planktivores enter the waters above the reef at nightfall in the same order by size that the diurnal species leave—smaller ones first. The smallest appear while some of the diurnal species still hover low in the water column, well before the quiet period has begun. The first of them are less than 3 cm in size and not readily visible (many are highly transparent). Among the first to rise above the reef are juvenile *Apogon* spp. (Apogonidae), which are prominent members of tropical reef communities worldwide. A previous discussion of the early appearance of largely transparent juvenile apogonids (Hobson *et al.*, 1981, p. 23) stated:

> This entry into exposed locations when many piscivorous predators hunt most effectively might seem in conflict with the quiet period concept. But in the dim light we are not surprised that these inconspicuous little fish seem to go unseen by the visual hunters that so seriously threaten the more visible adults. Certainly these juveniles go unseen by human eyes at this time, except under close inspection with a diving light, and so fail to detract from the aura of inactivity that characterizes the quiet period.

On many tropical reefs the quiet period comes to an abrupt end about 30 min after sunset, when hordes of *Myripristis* spp. (Holocentridae) surge into the water column from their daytime shelters in the reef (Hobson, 1972) (Fig. 5A and B). Other planktivorous fishes follow in short order, including *Priacanthus* spp. (Priacanthidae). As is the case among their diurnal counter-
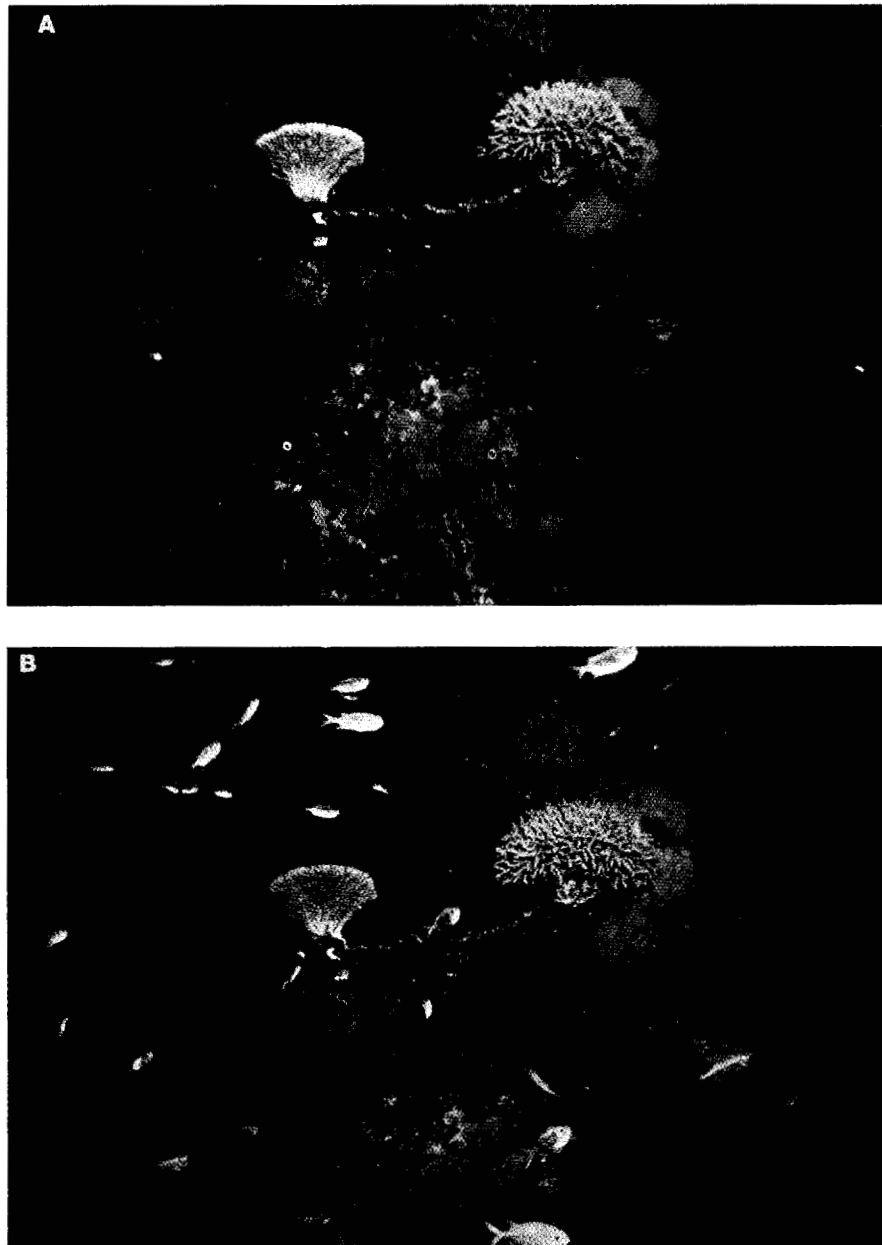
Figure 5   A reef in the lagoon at Enewetak Atoll (A) 30 min after sunset and (B) 2 min later, as numerous *Myripristis* spp. emerge from shelter.

in water that had flowed through the deeper passes from the open sea (except for individuals trapped in shallow water at sunrise, as detailed in the following). But beginning during late twilight, calanoids of this size were among the many forms that became increasingly numerous in the waters above the shelf. It was obvious that they had arrived in currents that flowed over the inter-island reefs from the open sea outside the atoll—currents that carried relatively few such forms during the day. Considering that Enewetak is in the path of the trade winds and the oceanic Equatorial Current, it seems probable that the increased numbers of zooplankters in water flowing over the interisland reef at night include organisms that shortly before had risen to the surface from ocean depths windward and upcurrent of the atoll (Hobson and Chess, 1986).

A rich assortment of reef residents join the open-water transients above reefs late during the changeover. They include the holoplankters that had been in swarms close to benthic substrata during the day, mostly copepods and mysids (Emery, 1968; Hobson and Chess, 1978; Hamner and Carleton, 1979), but that at nightfall disperse throughout the water column. Even more prominent, however, are a variety of semipelagic organisms that enter the water column during the night from positions in or on the seafloor. Many of these are primarily benthic organisms that spend only a relatively short period of time in the water column. They include various polychaetes, ostracods, copepods, mysids, isopods, amphipods, and crustacean larvae (Alldredge and King, 1977, 1980; Robichaux *et al.*, 1981; McWilliam *et al.*, 1981). The residents vary widely in size, from well under 1 mm to more than 10 mm, and generally include the largest of the zooplankters above reefs at night (Hobson and Chess, 1978, 1986).

IV. NOCTURNAL PLANKTIVORES

The fishes that forage on zooplankters above tropical reefs at night have been strongly influenced by the difficulty of visually locating prey in dim light, as evidenced by the exceptionally large eyes of *Myripristis* spp. (Fig. 7). The differences in morphology and behavior between nocturnal planktivores and their diurnal counterparts shows that selection pressures affecting planktivore form and function differ greatly between day and night.

A. Adaptations to a Nocturnal Planktivorous Diet

The major prey of most nocturnal reef planktivores are among the relatively large (>2 mm), semipelagic residents of the local habitat that rise into the water column at some time during the night (Hobson, 1974; Hobson and Chess, 1978; Gladfelter, 1979). Other important prey are larger holoplankto-
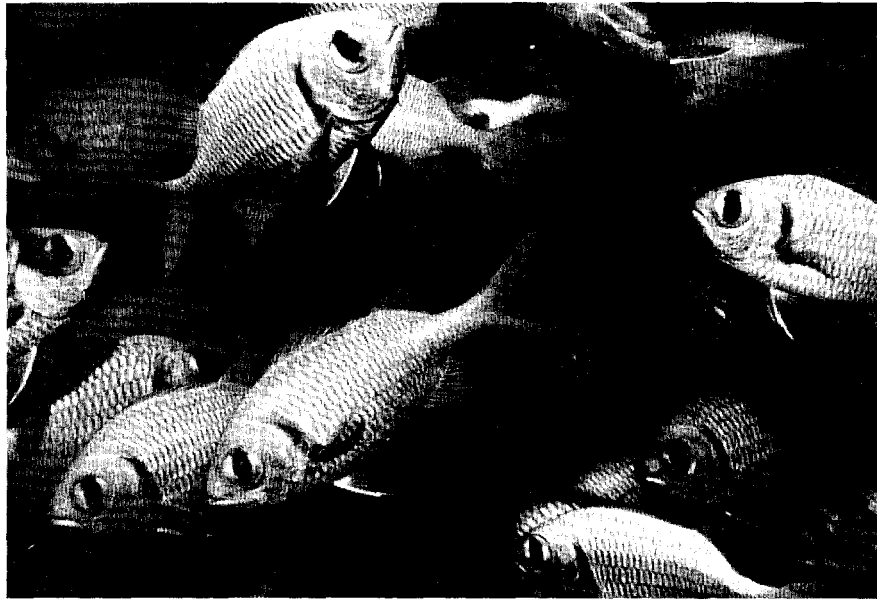
Figure 7   An aggregation of the nocturnal planktivore *Myripristis amaenus* (Holocentridae) in a Hawaiian reef cave during the day.

nic residents, such as mysids, and still others are larger transients from open water, like euphausids (Hobson and Chess, 1978). Conspicuously absent from this diet, however, are the relatively small transient holoplankters that are major prey of the diurnal planktivores, even though these organisms are more abundant at night than during the day (Hobson and Chess, 1978, 1986).

One might take these findings as evidence that nocturnal planktivores make a choice based on preference for larger prey, citing the widespread belief that planktivorous fishes choose the largest organisms available to them (Zaret, 1980). A corollary to this belief is that incentive to take the smaller zooplankters is lost in the presence of larger alternatives, which is consistent with the observation that natural selection for abilities to consume smaller prey is much reduced at night. (Consider, for example, that nocturnal planktivores generally lack the highly evolved modifications of head and jaws that enable even the larger diurnal planktivores to consume tiny prey in open water.) But despite compelling arguments that support this reasoning, I believe larger zooplankters are taken at night, not because they are preferred or that it is more efficient to do so, but rather because they simply are more vulnerable.

That nocturnal planktivores feed mainly on the larger components of the plankton may have less to do with preference for larger prey than with inability to see the smaller ones. Studies that have shown preference for larger prey have been done in daylight (e.g., Brooks and Dotson, 1965; Coates, 1980) and so

fail to consider how lack of light would influence what is available to plankti-
vorous fishes at night. Most nearshore fishes that use vision to feed at night
have sacrificed visual acuity for visual sensitivity, which limits their ability to
see smaller objects (Walls, 1967; Munz and McFarland, 1973). The greatly
enlarged eyes of *Myripristis* spp. and *Priacanthus* spp., for example, permit
these fishes to sense visual cues in the nocturnal water column, but apparently
these cues do not include the smaller zooplankters. This limitation readily
accounts for the observed lack of selection for features that permit a diet of
smaller prey, noted earlier, because obviously predators that feed by sight
would have little use for trophic mechanisms that accommodate prey too small
for them to see.

An inability to see the smaller zooplankters would also explain why my
studies with Chess have found that generally even the smallest nocturnal reef
planktivores are limited to zooplankters larger than about 1 mm, even where
comparably sized diurnal planktivores feed primarily on organisms smaller
than this. One might attribute this to the smaller mouths generally found in
"comparably sized diurnal planktivores," but our studies have shown that
nocturnal planktivores feed on larger prey even when they have feeding
structures similar to those of their diurnal counterparts.

Consider, for example, the juveniles of two closely related apogonid species,
Apogon cyanosoma and *Rhabdamia gracilis* [considered congeners by Lachner
(1953), with *A. cyanosoma* as *A. novae-guineae*]. Despite similar feeding mech-
anisms (both have the generalized trophic features of basal percoids), the
juveniles of *A. cyanosoma* feed at night and consistently take larger zooplank-
ters, whereas the juveniles of *R. gracilis* feed by day and consistently take
smaller zooplankters. This finding is based on data from specimens that Chess
and I collected above a patch reef on the lagoon shelf at Enewetak during one
night and the following day. Here, the 45 calanoid copepods in the guts of five
nocturnal *A. cyanosoma* (20–27, $\overline{X}$ = 23.6, mm SL) were 2 to 3 mm in size,
whereas the 70 calanoids in the guts of five diurnal *R. gracilis* (17–37, $\overline{X}$ = 27,
mm SL) were 0.3 to 2 mm. Clearly this difference in size of prey, day
compared to night, was determined by something other than size of mouth in
these morphologically similar predators.

The absence of larger copepods in the diet of the diurnal *R. gracilis* is readily
explained by the scarcity of these prey in the daytime water column above the
shelf, as noted earlier. But similar reasoning cannot account for the absence of
smaller copepods in the diet of the nocturnal *A. cyanosoma* because these are so
abundant at night—far more numerous than the larger ones, in fact. Although
it is possible that the smaller zooplankters were simply ignored when the
larger ones became available at night, I would expect the juvenile *A. cyanosoma*
to have taken at least some of them if they could, and the fact that they did not
seems best explained by visual limitations.

I know of one nocturnal planktivore that feeds regularly on zooplankters

smaller than 1 mm, but this exception to the generalization can be explained. *Praneseus pinguis* (Atherinidae), which is peripherally associated with reefs in the lagoons of western Pacific atolls, feeds heavily on organisms as small as 0.2 mm during nighttime excursions from nearshore schooling sites to off-shore feeding grounds. But this fish feeds right at the water's surface, where submarine starlight and moonlight are strongest (Hobson and Chess, 1973), so its visual capabilities likely differ from those of species adapted to dimmer light at greater depths.

Presumably factors other than size contribute to the relative vulnerability of various zooplankters at night. Many of the semipelagic residents, in particular, are more opaque than the more numerous holoplankters among which they occur after dark, and these are appropriate targets in dim light. Others are awkward swimmers, for example, caprellid amphipods, and therefore are less elusive and also more likely to create the turbulence and resulting bioluminescence thought to direct many nocturnal attacks (Hobson *et al.*, 1981).

That nocturnal planktivores have generalized feeding mechanisms does not mean they lack specialized trophic features. The mouths of some resemble the mouths of diurnal planktivores in being sharply upturned (Fig. 7), so obviously the advantage of this arrangement, noted earlier for diurnal species, has adaptive value among nocturnal planktivores as well. I have mentioned the exceptionally large eyes of many, which certainly are highly specialized means to orient visually in dim light and presumably to locate prey. Significantly, eyes of species active at middle depths tend to be larger than eyes of species active at the base of the water column, probably because the light available close to the seafloor is increased by reflected moonlight and starlight (Hobson *et al.*, 1981).

B. Adaptations to Nocturnal Threats from Predators

There is morphological and behavioral evidence that threats from predators are significantly reduced at night. For example, the streamlined bodies and deeply forked caudal fins so widespread among diurnal planktivores are much less developed among their nocturnal counterparts. So if these features are adaptive in providing the speed needed to evade attacks, as suggested earlier, their general absence among the nocturnal species could mean there is less threat of attack after dark (Hobson, 1973, 1979).

Similarly, the tendency to aggregate while feeding in the water column, which is thought to be a defense against predators (Eibl-Eibesfeldt, 1962) and is so strong by day, is much weaker at night. Some, including various *Myripristis* spp., are active in loose aggregations, especially in moonlight, but many others, including various *Apogon* spp., are solitary (Hobson, 1968, 1974). Some individuals of *Priacanthus cruentatus* school high in the water column as

they migrate seaward shortly after nightfall, but other individuals of this species are solitary as they remain above the reef during the night (Hobson, 1974).

Even those nocturnal planktivores commonly described as "schooling fishes" based on their daytime assemblages, for example, various clupeids and atherinids (Randall, 1967), generally disperse at night in favor of independent activity and small, loosely associated feeding groups (Starck and Davis, 1966; Hobson, 1968). So if aggregations are adaptive by reducing the threat of attack, the nocturnal condition would indicate relative freedom from such threats.

Certainly the visually directed attacks that threaten smaller fishes during the day would be limited by the sharp decrease in ambient light at night. Nevertheless, it would seem that at least some of the reduced nocturnal threat comes from conventional attackers. Examples include *Caranx marginatus* and *Selar crumenophthalmus* (Carangidae), which hunt smaller fishes at night in the Gulf of California (Hobson, 1968). These two species have morphologies typical of aggressive, open-water predators, but with large eyes that may allow them to attack in the ordinary way using the much lower levels of ambient light produced by moon and stars. Support for this possibility comes not only from the tendency of nocturnal planktivores like *Myripristis* spp. to aggregate under moonlight, but also from the countershaded nocturnal coloration of *Myripristis* spp., that is, dark above and light below (Hobson, 1968). If Longley (1917) and others are correct that such countershading effectively conceals midwater fishes from predators, this feature in nocturnal planktivores would suggest that they are threatened by predators that use light from above—presumably moonlight or starlight—to direct their nocturnal attacks.

The major visual cues above coral reefs on darker nights or in deeper water, however, probably are the emissions of luminescent organisms, which must have profound effects on nocturnal interactions between predators and prey (Hobson, 1966; Hobson *et al.*, 1981). Certainly the straightforward charge typical of predators that threaten diurnal planktivores would be less effective amid luminescent organisms on dark nights. Because luminescence among the plankton is greatly increased around moving objects, an aggressive charge by a large predator would be advertised as soon as launched, giving prey time for evasive maneuvers. Furthermore, while a charging predator could target on luminescence around its prey, I question whether this tactic would be successful if the attack is launched from some distance away. This is because the luminescent organisms that elicited the attack would be left behind as the fish darts away, thus leading the attacker to the wake of the fleeing fish (Hobson *et al.*, 1981). On the other hand, nocturnal piscivores may attack the leading edge of the luminescent trail.

But even if nocturnal planktivores are relatively free of attacks like those that

threaten diurnal species, they may be threatened by some other type of predator in situations where defenses effective in daylight are irrelevant (Hobson, 1973). A predator that is effective amid luminescent organisms at night might be one that hovers motionless, waiting for prey to betray themselves by movement that produces turbulence and resulting luminescence. This tactic would be in essence an ambush, and effective only at short range. Although the predator could be led by luminescence to prey some distance away, probably its approach must involve great stealth to avoid turbulence and resulting bioluminescence (Hobson et al., 1981). In this regard, one might consider the carangid *Selene brevoorti*, a predator that feeds on smaller fishes at night in the Gulf of California (Hobson, 1968). The extraordinary morphology of this species suggests unusual feeding behavior; in fact, its deep body, laterally compressed to an extreme, might well prove adaptive in maneuvering with minimum turbulence to approach unseen close to prey in the dark.

C. Distribution and Movement

Nocturnal planktivores generally are more widespread throughout the reef area than are their diurnal counterparts. Presumably this distinction has developed because the nocturnal species feed mainly on reef residents that are themselves widespread over the reef, whereas the diurnal species take mainly open-water transients that are most available at reef edges. In addition, a decreased threat of predation at night is evident in the tendency of the nocturnal species to disperse, at least during moonless nights, while the diurnal species tend to cluster.

Although most nocturnal planktivores feed near their shelter sites, many migrate to feeding grounds elsewhere—much as do certain diurnal planktivores. Some of the migrators go to other parts of their home reef, where they nevertheless continue to feed mainly on semipelagic reef residents, apparently they find them more abundant in these other places. An example is *Pempheris schomburgki*, which migrates during twilight from shelters along the inside of a Virgin Island reef to feeding grounds along the outside (Gladfelter, 1979). Other migrators that apparently go to the edge of the reef or beyond and feed on open-water transients. For example, while some individuals of *Priacanthus cruentatus* remain to feed in the local area after emerging from Hawaiian reefs, many others migrate seaward; and when they return, about 40 min before sunrise, their stomachs are full of pelagic organisms, including cephalopods and crab megalopae (Gosline, 1965; Hobson, 1972, 1974).

Nocturnal and diurnal planktivores tend to differ in their distributions relative to the effects of water currents on availabilities of their major prey—resident and transient zooplankters, respectively. The nocturnal planktivores are less numerous in stronger currents, perhaps because their resident prey

tend to avoid currents that would carry them from their home grounds. The diurnal planktivores, on the other hand, concentrate in currents that carry their transient prey from deeper water (Hobson and Chess, 1978, 1986). This is not to say that nocturnal planktivores always avoid currents, or that diurnal planktivores always are attracted to currents. To the contrary, nocturnal planktivores often feed to advantage in currents that can be tolerated by their resident prey (Thresher, 1983a), and diurnal planktivores avoid currents that exceed velocities in which they themselves can maintain station (Hobson and Chess, 1978).

Furthermore, stronger currents from deeper water should benefit nocturnal planktivores that prey heavily on larger transient zooplankters that appear above reefs after dark, as does *Myripristis pralina* at Enewetak (Hobson and Chess, 1978). Similarly, if the seaward twilight migrations of *Myripristis murdjan, M. amaenus,* and *P. cruentatus* in Hawaii are headed for feeding grounds above the outer drop-off, as surmised (Hobson, 1972, 1974), then they too would benefit from currents strong enough to supply them with zooplankters from the open sea.

Many nocturnal planktivores have distinctive defensive needs that affect their distributions during diurnal periods of rest. Unlike the diurnal planktivores, which generally are solitary while at rest during the night, many nocturnal planktivores are highly gregarious in their daytime resting mode. This is particularly evident in the clupeids, engraulids, and atherinids that shelter in dense, inactive schools close to reefs during the day. Examples from the tropical Atlantic include *Jenkinsia lamprotaenia* (Clupeidae) and *Allanetta harringtonensis* (Atherinidae), which school among reef structures by day and disperse to feed above the reef at night (Starck and Davis, 1966). Other nocturnal planktivores, more secretive than the schoolers, aggregate by day deep in the shadows of reef caves and crevices. These include *Myripristis* spp. in Hawaii (Hobson, 1972, 1974) and *Pempheris schomburgki* in the Virgin Islands (Gladfelter, 1979).

D. Trophic Links with Open-Water Communities

Nocturnal planktivores that feed mainly on resident zooplankters do not represent direct trophic connections with open-water communities, as do most diurnal planktivores. They are, of course, intermediate links in the transfer of energy between the two realms because so many of their resident prey consume oceanic materials. Their importance in this role, however, is diluted by the many other predators that consume these same prey close to the reef. On the other hand, those nocturnal planktivores that feed on transient zooplankters from the open sea do represent direct trophic connections with the oceanic realm.

The subsequent flow of energy from nocturnal planktivores to other elements of coral reef communities goes primarily through piscivorous predators, which, as noted earlier, probably is not true of diurnal planktivores. In contrast to the diurnal species, which seem relatively secure from predators, many of the nocturnal planktivores are primary prey—particularly the schooling clupeids and atherinids (Randall, 1967; Hobson, 1968). These fishes are most vulnerable to predators not while active in the water column at night, or even while at rest in schools during the day, but rather during the crepuscular transition between these conditions (Hobson, 1968).

It seems unlikely that feces of nocturnal planktivores can compare with feces of diurnal planktivores as transporters of energy to other elements of the community. Two problems limit the effectiveness of nocturnal coprophagy among fishes: first, the feces are more difficult to see in the dim light of night and, second, the more dispersed nocturnal planktivores do not offer the focal points of activity that greatly facilitate coprophagy by day. Furthermore, because the nocturnal planktivores take larger and fewer prey, digestion is slower and evacuation less frequent.

Thus, the continuous rain of feces beneath aggregations of diurnal planktivores that makes coprophagy such a viable feeding mode during the day is unlikely to be duplicated at night. Still, feces that settle on the reef beneath nocturnal planktivores, at either feeding sites or resting places, are likely to enter the coral reef food chain through vertebrate or invertebrate detritivores. One study found exceptional growth among corals at the daytime resting places of juvenile grunts (Haemulidae), which are nocturnal planktivores, and attributed this to nourishment from the excretory and fecal products of these fishes (Meyer et al., 1983).

V. VULNERABILITY OF ZOOPLANKTERS ABOVE REEFS

It is clear that zooplankters of more than about 1 mm in size are highly vulnerable to planktivorous fishes when in the water column above coral reefs during the day. Most that experience this vulnerability are of open-water species and have encountered the reef habitat by chance. There are few reef residents among them because most of these shelter by day in swarms or under benthic cover. That this sheltering behavior is adaptive as a defense is evident in the intensity of predation suffered by transients that come within reach of reef planktivores.

Zooplankters are less vulnerable above coral reefs at night, as evidenced by the great numbers of them there during that period. The nocturnal increase involves reef residents that had abandoned their daytime shelters and also open-water transients that had arrived in the reeftop flow after upcurrent populations made their nightly ascent into the surface waters. Those taken by

nocturnal planktivores tend to be relatively large, opaque forms that are unavailable by day; the far more abundant smaller forms so heavily exploited by diurnal planktivores are relatively unimportant as prey of nocturnal planktivores despite their greatly increased numbers above the reef after dark. It would appear that vulnerability to nocturnal planktivorous fishes involves features visible in dim light.

That zooplankters above reefs are more generally vulnerable in daylight is reaffirmed at dawn. At this time, reef residents that had been dispersed in the water column during the night rejoin swarms or return to benthic shelter, while open-water transients are left exposed to the developing threat from diurnal planktivores. Although the number of transients arriving in the reef-top flow had dropped sharply after upcurrent populations made their regular predawn descent into the depths, many that had been carried above the reef during the night are still there at daybreak and these become vulnerable to diurnal planktivores (Hobson and Chess, 1986). The problem of transients from the open sea trapped in relatively shallow water at daybreak is one widely experienced by zooplankters that make diel vertical migrations in deep water close to reefs, shelves or banks. Reports have cited occurrences above continental shelves (e.g., Issacs and Schwartzlose, 1965; Pereyra *et al.*, 1969) and at the edge of submarine canyons (Chess *et al.*, 1988).

The vulnerability of open-water zooplankters trapped by a relatively shallow sea bed at daybreak exaggerates the more widespread vulnerability of transients that experience incidental contact with reef habitats during the day. These are problems of organisms lacking an effective defense in situations outside their evolutionary experience. Clearly they are a rich and vulnerable source of food for reef fishes, as demonstrated by the range of specialized features these fishes have acquired to exploit them.

I suggest, therefore, that it is the vulnerability of organisms in unfamiliar surroundings that accounts for most planktivory among fishes above coral reefs, at least during the day. It should be expected that zooplankters adapted to the pelagic environment would be vulnerable to predators in reef habitats because they are unlikely to have defenses specific to that setting. Their encounters with reefs must be exceptional events and features that would adapt them for this experience are likely to be maladaptive in their normal open-water habitat.

VI. TOPICS FOR FURTHER STUDY

Certain key features of topics considered in this chapter call for further study, for example:

1. We need more data on the distribution of planktivorous fishes and zooplankters relative to size. I have described the larger planktivorous

fishes concentrated at reef edges, with smaller species and subadults more widely distributed over inner reefs, and attributed this to the pattern of availability of zooplankters of different sizes. This assessment is based on widespread observations, sampling, and impressions, but more data are needed. Confirmation calls for extensive censusing of the planktivorous fishes with concurrent sampling of the plankton, both with emphasis on distribution by size.

2. It is clear that currents are important in the trophic dynamics between fishes and zooplankters, but we need to refine our knowledge of the relationships involved. I have noted that diurnal planktivores tend to concentrate in currents because these carry their transient prey, whereas nocturnal planktivores tend to concentrate away from stronger currents because these are avoided by their resident prey. But there are many exceptions to these generalizations that should be thoroughly analyzed because they provide insight into the relationships involved. For example, one might consider circumstances where nocturnal planktivores feed on transient zooplankters in currents, or on resident zooplankters in relatively weak or intermittent currents.

3. Judgments on adaptive significance generally are based heavily on inference, and they call for further study. For example, I have suggested that streamlining is adaptive both in accelerating flight to shelter and in maintaining station in current. With one complementing the other, the two could be an exceptionally powerful evolutionary force. Whether either or both are active in a specific instance may be evident in the extent of streamlining in planktivores exposed to the prevailing current, especially if there is a concurrent measure of relative danger from predators. The same analysis would provide some basis for accepting or rejecting my suggestion that an exceptionally deep body and strong fin spines allow some fishes to feed in the water column with an acceptable degree of safety. These species would not of course be expected where there is need to maintain station in a strong current.

4. The role of trophic interactions among reef fishes and zooplankters in transferring energy from open water to the reef community is a rich area for study. This chapter identifies major routes involving predation and coprophagy, but the energetics at each link remain to be quantified.

5. What is the nature of nocturnal threats to planktivorous fishes? Nocturnal planktivores lack certain morphological and behavioral features thought to protect their diurnal counterparts from predators, and I have noted this as evidence that threats from predators are reduced at night. It is possible, however, that nocturnal planktivores simply have no use for these defenses because they face different kinds of threats.

ACKNOWLEDGMENTS