

Feeding Patterns among Tropical Reef Fishes

Understanding the way fishes respond to changing conditions during the day-night cycle provides insight into their feeding activities

Edmund S. Hobson

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To eat and to avoid being eaten: the impact of these concerns on activity patterns and morphologies of tropical reef fishes has been the major thrust of my research over the past fifteen years. Here I draw together major elements of these studies, which have considered the fishes in their natural habitats at widely separated locations in the Pacific Ocean, including the Gulf of California, Hawaii, and Micronesia.

Most animals in the sea ultimately are consumed by predators, even though they are armed with defenses molded through generations under predation pressures. But every successful defense evokes a modified offense, and thus a delicate balance exists today between offensive tactics of predators and defensive tactics of prey. We gain insight into this balance, and the forces that shape the feeding relationships of tropical reef fishes, by considering the situations charac-

teristic of the different segments of the diel, or day-night, cycle.

Most fishes on tropical reefs are active either by day or by night, with the diurnal species generally inactive at night and the nocturnal species remaining quiet during the day (Hobson 1965, 1968, 1972, 1974; Starck and Davis 1966; Collette and Talbot 1972; Vivien 1973). The changeover from one situation to the other is a complex process that proceeds as a well-defined sequence of events during twilight (Hobson 1972). These patterns are best illustrated by considering each segment of the diel cycle separately.

The reef in daylight

Mankind's view of the life inhabiting tropical reefs generally is what occurs during midday (Fig. 1). Fishes active on tropical reefs in daylight include the majority of highly evolved fishes in the sea, species that exhibit an especially diverse array of feeding morphologies and behaviors. Prominent forms include angelfishes (family Pomacanthidae), butterflyfishes (Chaetodontidae), damselfishes (Pomacentridae), wrasses (Labridae), parrotfishes (Scaridae), surgeonfishes (Acanthuridae), triggerfishes and filefishes (Balistidae), and puffers (Tetraodontidae). For the most part, these are colorful forms with hues arranged in distinctive, readily visible patterns. Most have highly evolved feeding mechanisms that include relatively small mouths.

Fishes that find prey on the sea floor are especially varied in their feeding morphologies and habits.



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Figure 1. The fishes that swim above this Hawaiian reef during the day illustrate the great variety of forms inhabiting shallow tropical waters. Seen here are the surgeonfishes *Zoetropterus flavescens*, *Acanthurus achilles*, *A. leucopareus*, *A. nigroris*, and *Naso lituratus*; the butterflyfishes *Chaetodon lunula* and *C. quadrimaculatus*; the sea chub *Kyphosus cinerascens*; the damselfish *Abudefduf abdominalis*; and the triggerfish *Suflamen bursa*. (All photographs are by the author.)



Many have features adapted to taking tiny cryptic crustaceans, especially amphipods, from amid benthic cover. As these prey are mostly less than a few millimeters long, feeding prerequisites seem to include a small mouth that can perform precise manipulations—and the light of day. Predators that feed this way—especially certain wrasses and butterflyfishes—usually hover within a few centimeters of the reef, inspecting its surface. When they spot prey, per-

especially among the wrasses (Fig. 3), damselfishes, and butterflyfishes. Apparently certain members of these groups assumed cleaning habits when their concept of an appropriate feeding substratum broadened to include the bodies of other animals.

Many other diurnal fishes possess specializations adapted to wrest motile nocturnal forms, especially various small crustaceans, from daytime resting places. The specialized predatory features used to exploit such prey are sometimes behavioral: for example, the triggerfish *Sufflamen verres* in the Gulf of California uncovers prey buried in the sand by lying on its side and rapidly undulating its dorsal and anal fins, thereby generating water currents that carry the sand away (Hobson 1968). Some small predators, certain wrasses in particular, characteristically hover close to the feeding jaws of large animals that disturb the sea floor, especially certain herbivores, and snap up small fishes and crustaceans as they are driven from hiding (Hobson 1968). Other predators have specialized anatomical features that provide access to prey hidden beyond the reach of more generalized forms; the Pacific butterflyfish *Forcipiger longirostris*, for example, uses its elongated snout to probe reef crevices for small shrimps that are secreted there.

Distinct from the above, the goatfishes (family Mullidae) are bottom-feeders that locate hidden prey by sensory means other than vision: they probe the sea floor with two relatively long sensory barbels carried beneath the lower jaw. One might suppose that fishes thus equipped would feed with equal effectiveness day and night, but that is untrue. Although all goatfishes are similarly equipped, and some hunt regularly during both day and night, others are primarily diurnal, and still others predominantly nocturnal (Hobson 1974). The diel activity pattern of each goatfish probably relates to the differential day-night habits of its specific prey. Some diurnal goatfishes, for example *Parupeneus multifasciatus* in Hawaii, feed heavily on nocturnal forms, especially xanthid crabs, that are concealed in daytime shelters.

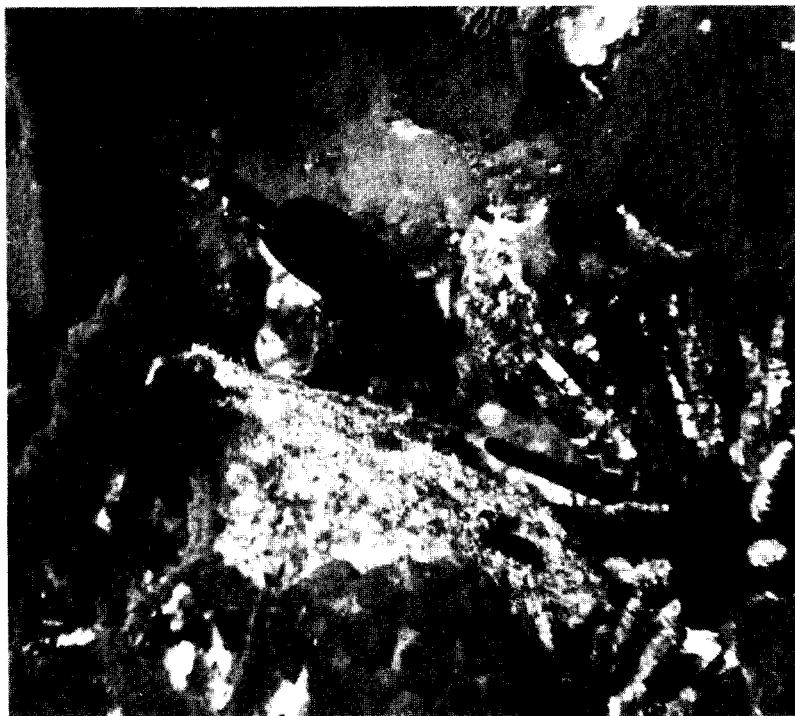


Figure 2. A damselfish, *Eupomacentrus beebei*, plucks at a tiny prey organism on a reef at the Galapagos Islands, eastern Pacific Ocean.

haps through movement or an unusual contour, they seize it in a characteristic plucking manner (Fig. 2).

The morphology and behavior suited to this habit apparently have preadapted certain fishes for cleaning other animals (Hobson 1971). Cleaning—plucking ectoparasites or other deleterious material from the bodies of other animals (see Feder 1966)—is most developed among the bottom-plucking forms,

Most predators that feed on the benthos in daylight, however, take more accessible prey, including such prominent sessile forms as sponges, coelenterates, and tunicates, as well as various slow-moving animals like echinoids and gastropods. Most of these prey organisms are fortified by such protective devices as heavy armor, nematocysts, spicules, spines, or tough fibrous tissues, and many are secreted by day deep in reef crevices or under the sand—though less consistently than the mobile secretive forms discussed above. Because of such varied defenses, the specialized feeding structures and techniques of fishes that feed on these organisms are equally varied, thus further contributing to the diversity characteristic of fishes that are active on the tropical reefs during the day.

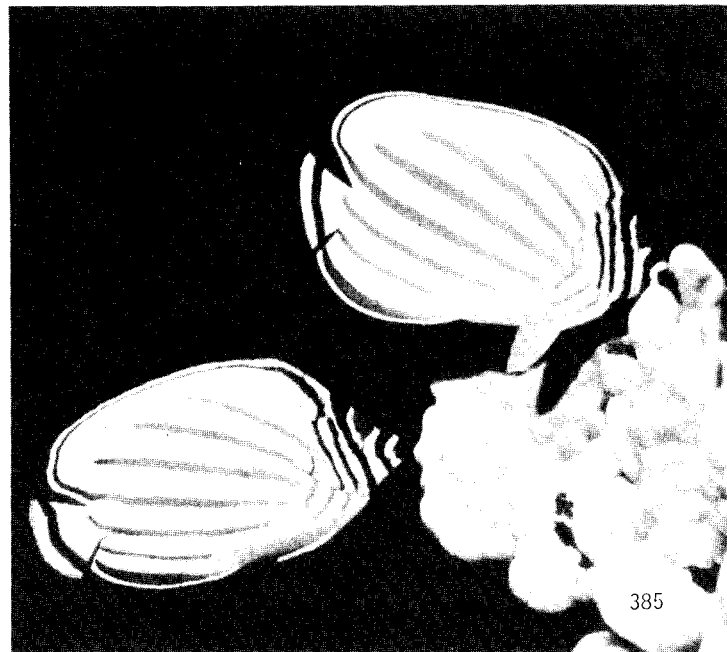
It is well known that relatively few fishes—all highly specialized—prey on coelenterates and sponges (Hiatt and Strasburg 1960; Randall and Hartman 1968). Certain fishes that feed on individual coral polyps, including such Pacific species as the butterflyfish *Chaetodon multicinctus* and the filefish *Oxymonacanthus longirostris*, tend to have protruding snouts and teeth that project from small mouths. These features permit them to snip off scleractinian coral polyps despite the surrounding calcareous armor. Another coral-feeding filefish in the Pacific, *Cantherines dumerili*, has especially powerful jaws and strong teeth, with which it bites off chunks of the skeletal rock that includes many polyps. Some species that depend on scleractinian corals for food feed not on the polyps themselves but on the mucus that the polyps have produced. Thus, the Pacific butterflyfish *Chaetodon ornatissimus*, a comparatively blunt-snouted species, scrapes away mucus that has concentrated over abrasions on the coral surface (Fig. 4).

As for sponge-feeders, the moorish idol, *Zanclus cornutus*, and the black-striped angelfish, *Holocanthus arcuatus*, are among those few specialized fishes in Hawaii that feed mainly on sponges. The moorish idol uses its long snout to reach small sponges that live within reef crevices, whereas the black-striped



Figure 3. A small yellow, black, and blue wrasse, *Labroides* sp., cleans around the eye of a large balloonfish, *Arothron* sp., at the Palau Islands, western Pacific Ocean.

Figure 4. Butterflyfish, *Chaetodon ornatissimus*, scrape tissue and mucus from coral on a Hawaiian reef.



angelfish, lacking a long snout but having more powerful jaws, takes larger sponges that encrust the more accessible rock surfaces.

Vegetation carpets many areas of most reefs and would seem ready food for fishes. The herbivorous habit, however, is an advanced trait among marine fishes (Hiatt and Strasburg 1960) and has been acquired by only a relatively few species; nevertheless, these few often predominate on tropical reefs.

The distinction between herbivorous and carnivorous groups is not sharp. The surgeonfishes, for example, include not only many predominant reef herbivores but also species that feed heavily on organic sediments and species that prey strictly on zooplankton (Jones 1968). Furthermore, there are herbivores among the butterflyfishes, damselfishes, blennies, triggerfishes, filefishes, and other families whose carnivorous representatives are discussed above. Within these groups we can see how characteristics adapted to plucking benthic invertebrates have been modified in some species for grazing on plants. It follows, then, that most herbivorous coral-reef fishes share certain characteristics with their carnivorous relatives: both groups tend to be colorful, diurnal animals with small mouths that are part of highly evolved digestive equipment.

In the waters above the reef, clusters of small fishes hover throughout the day (Fig. 5). Most of them, including many butterflyfishes and damselfishes, prey on zooplankters, especially calanoid copepods. Others, however, including certain triggerfishes, feed heavily on drifting fragments of vegetation. As do most of the varied species that take organisms from the sea floor during the day, these planktivores have relatively small mouths. But whereas the bottom-feeder's mouth usually is directed downward from its head, that of the planktivore is usually upturned. Because the upturned mouth shortens its snout, the planktivore is better able to see tiny prey in the water immediately ahead (Walter A. Starck II, cited in Rosenblatt 1967).

Diurnal planktivorous fishes have converged not only in their feeding

equipment but also toward having fusiform bodies and deeply incised (forked or lunate) caudal fins. Both of these features are also widespread among oceanic fishes like tunas and are linked to the ability to swim rapidly. Thus, one would expect diurnal planktivores that have these features to find increased speed adaptive. The advantage seems clear: small reef fishes that swim in open water, high above the sheltering reef, benefit from added speed to elude the predators that patrol these waters. Because they share these morphological tendencies, many unrelated diurnal planktivorous fishes (including certain damselfishes and seabasses) look, on casual inspection, more like one another than like members of their own families that feed on the benthos (see Davis and Birdsong 1973).

Many large, motile piscivorous fishes, including a variety of jacks (family Carangidae), patrol the waters above tropical reefs during the day. Yet despite their widespread presence and apparent readiness to feed, midday attacks are relatively infrequent—their major feeding successes come later (or earlier) in the day. These predators seem to find smaller reef fishes difficult targets during midday, even though they will attack when an opportunity arises. It is probably this threat of attack that keeps most smaller active fishes near the reef during the day. They may rise into the midwaters above the reef or swim out over the edge of adjacent open bottom, but generally they stay close enough to the reef so that shelter will be within reach if it is needed.

Similarly, the threat of attack probably is a major reason why so many small fishes aggregate when active in exposed locations. Even fishes that are solitary when close to reef cover will join others of their kind when in open water. It may be that predators have difficulty isolating a target from among the many confronting them in a fish school (Manteifel and Radakov 1961; Eibl-Eibesfeldt 1962; Hobson 1968), and thus smaller fishes are relatively secure in these aggregations. Ordinarily, smaller fishes congregated in exposed positions draw closer to one another when

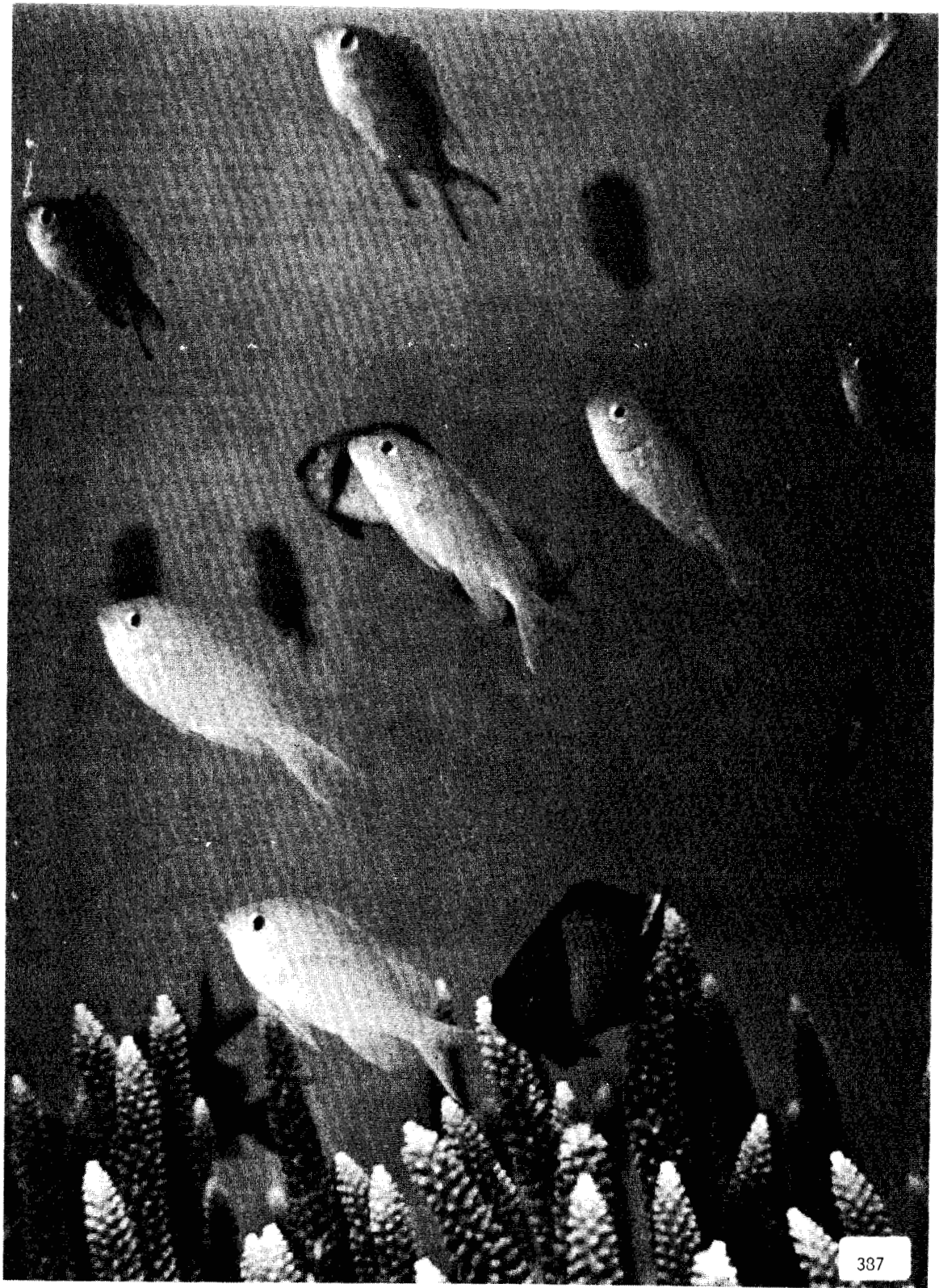
large predators approach (Hobson 1965, 1968).

Selective pressures from generations of visually orienting predators have refined defense mechanisms that protect prey species in daylight. There are, of course, occasional lapses in these defenses when the prey are briefly vulnerable. Small fishes that usually stay within retreating distance of cover sometimes stray too far into the open, and others normally secure in a school occasionally drift too far from their fellows. Often large jacks or other predators swim slowly among schooling prey for hours during the day without an aggressive move, and then suddenly attack—presumably having sensed a vulnerable target. But potential prey are sensitive to hunting predators; when one appears, they become especially alert, and thus less likely to make a defensive mistake.

The problem of being within striking range when small fishes become momentarily vulnerable during the day because of a defensive lapse has been solved by predators that lie in wait under cover or camouflaged—the ambushers—or by those that stalk. These tactics are used by some highly specialized forms. Typically, the ambushers are cryptically hued forms that remain unseen as they rest immobile on the sea floor. From here they attack unwary prey that stray within reach of a sudden explosive charge. Ambushers include lizardfishes, scorpionfishes (Fig. 6), and flatfishes. The stalkers, on the other hand, must arrive within striking distance of vulnerable prey while they themselves are in full view. They do this by drifting slowly toward smaller fishes, showing overt aggression only when close to an unwary victim. The stalkers—typically long, attenuated fishes—include barracuda (family Sphyraenidae), needlefishes (Belonidae), trumpetfishes (Aulostomidae), and cornetfishes (Fistulariidae).

Many fishes are adapted for life in the caves and crevices that honeycomb tropical reefs. Prominent

Figure 5. Damselfishes rise into the waters above a reef at the Palau Islands, where they will feed on zooplankters.



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among them are the moray eels, which remain largely unseen on the reef top even though they are among the predominant fishes in the area. Although generally described as nocturnal, many morays are in fact most active during the day (Hobson 1968, 1974; Chave and Randall 1971). Some of them forage in exposed locations, but most confine their activities to reef crevices. Many specialized features, including an extremely solid skull and an

quickly to stimuli emanating from fishes in distress. Thus, although many organisms find reef crevices a haven from predators that hunt on the surface of the reef, they become vulnerable in those shelters to other predators, including moray eels, that have developed adaptive means to exploit this situation.

Some of the more prominent fishes on the reef during the day are in fact nocturnal forms that assemble here in large, stationary schools while inactive. Included are many of the herrings (family Clupeidae), silversides (Atherinidae), grunts (Pomadasyidae), snappers (Lutjanidae), and croakers (Sciaenidae). Although fish in these schools are a major component of the daytime scene on many tropical reefs, most leave the reef at nightfall and forage elsewhere.

Other nocturnal fishes make themselves less conspicuous during the day by assembling in reef crevices and caves. Included in this category are many of the squirrelfishes and soldierfishes (family Holocentridae), cardinalfishes (Apogonidae), bigeyes (Priacanthidae), and sweepers (Pempheridae). Although most are out of sight during daylight, some frequently are visible around the bases of coral heads or at the openings to caves (see cover).

The reef during twilight

A human observer has difficulty recognizing when the daytime situation first begins moving toward the nocturnal mode. The early transition is indistinguishable from variations in activity during midday when light levels fluctuate with changing cloud cover and water transparencies. Within the hour before sunset, however, the transition events are unmistakable.

Probably the first obvious sign of changeover occurs among the planktivorous fishes. After having been aggregated in the midwaters above the reef throughout the day, these fishes descend progressively closer to the reef as light diminishes (Hobson 1972; Collette and Talbot 1972). By the time they are in the lower regions of the water column, it is clear that many other diurnal fishes are similarly moving closer to cover. The sequence in which they

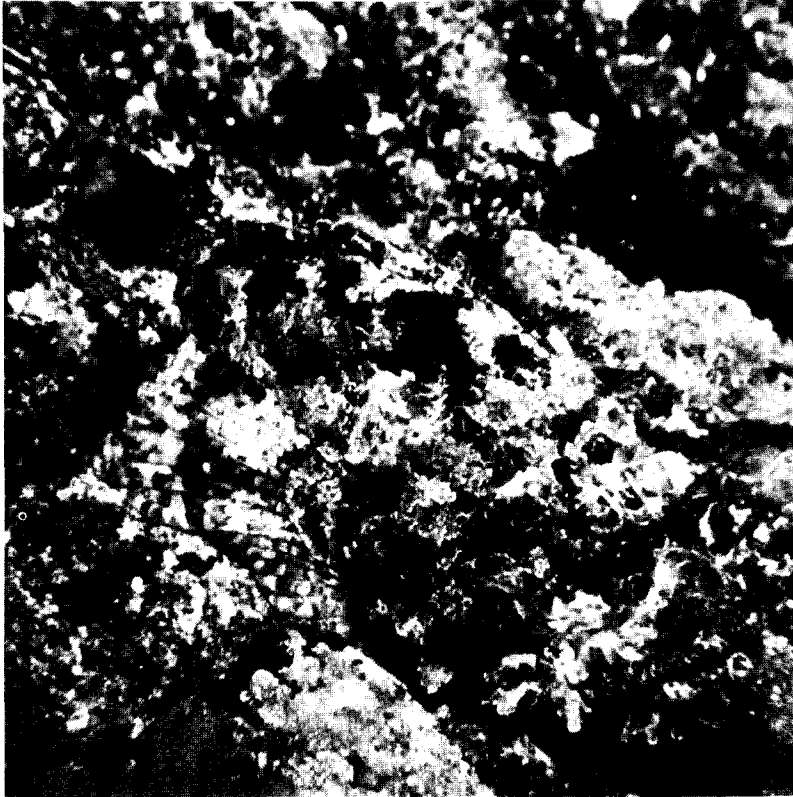


Figure 6. A scorpionfish, *Scorpaena* sp., lies virtually unseen on a reef at the Galapagos Islands, where it will attack small fishes and crustaceans that venture near.

elongated body, enable moray eels to wedge through narrow spaces within the reef (Gosline 1971).

Besides being home for organisms that remain secreted at all hours, the caves and crevices are daytime havens for many other forms seeking shelter when injured or distressed. It is not surprising, therefore, that many morays and other predators in these places respond

shelter themselves varies with species and size. For example, the wrasses are among the first to settle down, and among all species that shelter at nightfall the smaller individuals are first to move from view. By sunset many diurnal fishes are no longer visible, and the numbers of others in the water column rapidly diminish.

At the same time that many diurnal fishes are leaving the water column, others, including certain parrotfishes, surgeonfishes, and damselfishes, move in long drawn-out processions from one part of the reef to another. Clearly, many reef species redistribute themselves at this time, in essence moving between feeding grounds and resting places that sometimes are widely separated. Certain species follow the same routes at the same time, relative to sunset, day after day. The patterns remain poorly defined, however, because instead of joining the movements, many individuals of these same species find cover where they have been active throughout the day (Hobson 1972).

More and more diurnal fishes take cover as twilight progresses, but a substantial number still occupy the lower regions of the water column 10 to 15 minutes after sunset. Then, abruptly, the vast majority drop to the reef below, leaving the water column essentially deserted.

Now there ensues on most reefs a span of about 20 minutes that can aptly be called the quiet period. At the outset, many diurnal species still mill about close among the coral, but their activity steadily diminishes. Prominent among them are certain surgeonfishes, damselfishes (Fig. 7), and butterflyfishes, some already showing colorations different from those of daylight. Amid these increasingly inactive diurnal fishes some nocturnal forms begin to circulate, having emerged from the reef crevices that harbored them in daylight. Usually these include some of the larger cardinalfishes and squirrelfishes, which remain close to the reef. Despite this activity, however, the reef overall appears still.

About 30 minutes after sunset, hordes of soldierfishes and other nocturnal species come boiling out

of their caves. These are fishes that will forage up in the midwaters during the night, and their sudden appearance abruptly ends the quiet period. It is now almost dark, and a human observer can just dimly distinguish in the last vestige of rapidly fading daylight the major features of the reef around him.

One might wonder why these crepuscular events follow a well-defined sequence, and why, during



Figure 7. At day's end, damselfish, *Chromis lepidolepis*, shelter among soft corals at the Palau Islands.

that quiet segment of twilight, both diurnal and nocturnal reef fishes are largely absent from the midwaters. Answers to these questions, I believe, become evident if one observes places where large fish-eating predators find their prey concentrated and accessible, as for example in large schools. Many predators apparently find dusk's half-light to their advantage, and under appropriate circumstances certain



Figure 8. A moray eel, *Gymnothorax petelli*, hunts for prey on a Hawaiian reef at night.

Figure 9. Two parrotfishes, *Scarus sordidus* (on the left) and *S. dubius*, are protected from predators by a mucus covering as they rest under a coral ledge in Hawaii at night.

large piscivores whip the sea into a froth of predatory activity during that same period of twilight that is quiet on so many other reefs.

These crepuscular attacks can be seen in certain parts of the Gulf of California, where massive schools of herrings, grunts, and other species concentrate near shore. Although members of these schools are relatively safe from predators during most of the day, the mechanism providing this protection seems increasingly ineffective during twilight (Hobson 1965, 1968). In their attacks, jacks and other large predators need room to maneuver, and, as we have seen, most small reef fishes, by moving close to the reef, shelter themselves from such attacks during this vulnerable period. But havens amid reef structures cannot be used by most schooling fishes, which must face predators in relatively open water.

Although the large piscivores seem

to attack most effectively in the reduced light of dusk, their attacks abruptly diminish about 30 minutes after sunset, suggesting that they become ineffective when light falls below a certain level. Not surprisingly, schooling fishes that endure these crepuscular attacks generally remain close together until their attackers have withdrawn (Hobson 1968). And, significantly, at about the same time that the schooling fishes disperse over their nocturnal feeding grounds, nocturnal soldierfishes are streaming out of their reef caves to end the quiet period (Hobson 1972).

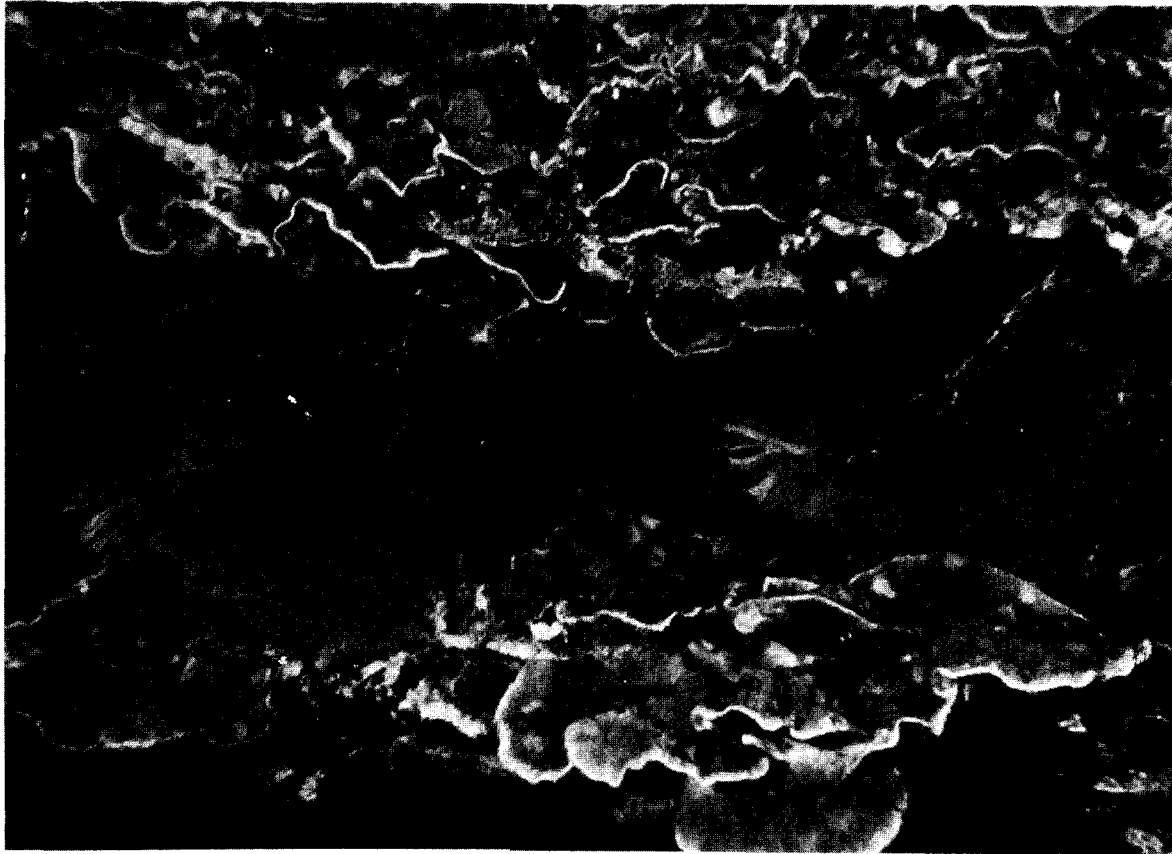
The threat from crepuscular predators, I believe, has shaped the twilight activities of tropical reef fishes into an established, well-defined sequence of events. The reef undergoes a quiet period when large piscivores are relatively few or dispersed and when schooling fishes are insignificant. But even when overt attacks are infrequent, the

advantage of proximate cover during this period is probably strong. Significantly, the sequence of events characterizing activities of reef fishes during evening twilight is essentially reversed during the corresponding period of morning twilight (Hobson 1972).

The reef after dark

Having reoccupied the midwaters above the reef at nightfall, some of the soldierfishes forage there on zooplankters until daybreak, but many others mass together and swim offshore to feed. Bigeyes are among the species that behave similarly (Gosline 1965; Hobson 1972). The soldierfishes and others that migrate to off-reef feeding grounds behave much like the many schooling fishes that perform similar migrations at nightfall.

On the reef below, meanwhile, many other nocturnal fishes, including squirrelfishes (genera *Adio-*



ryx, *Flammeo*, *Holocentrus*, and *Holotrachys*) and scorpionfishes (*Dendrochirus*, *Pterois*, and *Scorpaena*), have emerged from the caves that harbored them in daylight and will hunt close among the coral throughout the night. Many moray eels, too, as well as conger eels (family Congridae) swim on the darkened reef-top, most of them in transit from one crevice to another (Fig. 8).

Despite the nocturnal hunters, however, a casual observer sees relatively little activity on the reef at night. Compared to the many fishes one sees there in daylight, few are visible after dark. Even discounting all those fishes that leave the reef at nightfall to forage elsewhere, there seems a dearth of active fishes among the darkened corals. Nocturnal fishes tend to be inconspicuous, most being rather small (less than 30 cm long) and only intermittently exposed close to shelter on the reef-top. Moreover, in com-

parison to the many diurnal fishes that display bright hues in bold patterns, most nocturnal fishes are drab.

The nocturnal fishes are predators, most with large but relatively simple mouths. The diverse array of specialized feeding structures and behaviors found among diurnal reef fishes are largely missing among fishes active at night. Most of these features are adaptations for coping with the formidable defensive structures that protect such highly varied sessile organisms as sponges, corals, and tunicates, and fishes that forage at night prey insignificantly on these forms, perhaps because in the dark they cannot detect prey that do not move (Hobson 1968, 1974).

The major prey of nocturnal fishes are motile crustaceans, most about 2 to 10 mm in their greatest dimension. They are small enough for a fish under 30 cm to swallow whole,

which is the way most of them feed, yet large enough for a fish this size to entrap in its relatively large mouth. The majority are nocturnal creatures that rest under cover during the day, secure from all but diurnal predators specialized to seek them out. Upon moving into the open at night, they become exposed to direct attacks of generalized predators that can operate in the dark.

Of course, there are nocturnal fishes that take prey from other than exposed locations. Examples include the nocturnal goatfishes, which use their sensory chin barbels just as their diurnal relatives do—to probe the sea floor for hidden prey. At least one, the Hawaiian *Parupeneus bifasciatus* (which feeds regularly during both day and night), preys after dark on such diurnal fishes as blennies and damselfishes, probably taking them from where they shelter themselves at night (Hobson 1974). Other ex-

amples include eels, both morays and congers, that actively hunt prey among reef crevices after dark.

Although most nocturnal fishes have relatively simple feeding equipment, they tend to have large eyes, and several prominent species are highly specialized. For example, the spiny puffers (family Diodontidae) have powerful beaklike jaws, with which they ingest large, heavily armored prey like gastropods and echinoids that move slowly on the reef after dark.

The soldierfishes, and others that predominate in the midwaters above the reef at night, take zooplankters unlike those taken by fishes that forage in these same places during the day. The diurnal planktivores take primarily small, full-time residents of the water column, like calanoid copepods, cladocerans, and larvaceans. Although these zooplankters are equally numerous in the water column after dark, when calanoids, at least, are important prey of certain smaller nocturnal planktivores, including many herrings, silversides, and juveniles of other species, the soldierfishes and other larger nocturnal planktivores direct their attacks instead at forms like mysids, crab megalops, and nereid polychaetes. (I use a broad, perhaps loose, concept of the term *zooplankton* here). These prey tend to be larger than zooplankters taken by diurnal fishes, and, like many of their nocturnal predators, most rise into the midwaters at nightfall from daytime positions on, in, or close to the sea floor.

Nocturnal planktivores, like their diurnal counterparts, tend to have sharply upturned mouths (presumably related to taking small prey from open water), but their mouths generally are larger than those of the diurnal species, which is consistent with the larger size of their prey. Some major characteristics common among diurnal planktivores, however—especially their increased tendencies toward fusiform bodies and deeply incised caudal fins—are less evident among planktivores in the midwaters at night. Soldierfishes, for example, are actually deeper-bodied than most of the bottom-feeding members of

their family. If these features are adaptive because they provide added speed to elude predators in open water, then the general absence of such features among small free-swimming species that rise into the midwaters at night suggests that there is a diminished threat from piscivorous predators in the water column after dark (Hobson 1973, 1974). One arrives at this same conclusion when considering the many other fishes that spend the day close to shelter on the reef—in schools or congregated in crevices—but that range out into exposed locations at night.

Further evidence bearing on the relative threat of large piscivorous predators to reef fishes at night is found among the many diurnal species that rest on the bottom after dark. The smaller individuals (less than about 15 cm) move out of sight into crevices at nightfall, indicating that they would be vulnerable in the open. But some moderately sized (over about 18 cm) butterflyfishes, surgeonfishes, and others rest in exposed or semiexposed positions, seemingly unthreatened. On the other hand, the mottled coloring that some diurnal fishes assume when they rest on the sea floor at night would seem to have selective advantage in making them less visible to nocturnal predators (Schroeder and Starck 1964). Furthermore, the mucous sheaths that some smaller parrotfishes and wrasses secrete around themselves at night (Fig. 9) are probably adaptive because they protect these fishes from predators, especially those moray eels that detect prey by direct contact with sensory receptors on their snouts (Bardach, Winn, and Menzel 1959).

Adaptions related to feeding—either to improve the fish's ability to obtain food or to elude predators—account for most of the great diversity of form among tropical reef fishes. Clearly, the evolution of these adaptations has been influenced from the beginning by factors associated with the different segments of the diel cycle.

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