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Interactions Between Piscivorous Fishes and Their Prey

Edmund S. Hobson

Most fishes that prey on other fishes face what might seem a simple enough task: they must run down, or otherwise capture, organisms that are smaller, and weaker, than they are. Generally, their attacks are direct approaches to exposed prey that are large enough to grasp, yet small enough to manipulate. And once ingested the prey are usually swallowed whole.

These predators are well built for the job. Fish-eaters, or piscivores, generally have large, but relatively simple mouths, and short uncomplicated digestive tracts. These features have remained relatively unchanged during a long period of evolution that has seen major alterations in the feeding mechanisms of species which forage on other kinds of aquatic organisms (see Gosline 1959, Hobson 1974). Obviously, they attack with proven equipment.

Nevertheless, despite the conservative nature of their feeding apparatus, and what might seem a straightforward predatory task, other parts of their anatomies, and also their feeding related behaviors, have diversified greatly to meet severe problems that stem from capturing prey. And the finely tuned interactions between these predators and their prey are further evidence of powerful evolutionary forces. Attacks by fish-eating predators during the evolution of modern species have pressured prey to acquire effective defensive adaptations. But every successful defense has in turn evoked an appropriate offense, so that a delicate balance now exists. The opposing forces that maintain this balance, as expressed in adaptations of both predators and prey, and the patterns of predation that have resulted, are the topics of this chapter.

I have developed a synthesis based on published reports that should have widespread relevance even though most of the material draws from fishes in tropical and warm-temperate seas. These warmer marine habitats have proven most fruitful for study of the topics considered here, because feeding interactions among members of their exceptionally rich and diverse faunas exhibit especially well-defined patterns. This is largely because so many of the interacting species in these places have highly specialized feeding habits. It is one of the axioms of biology that interacting species become more specialized as their numbers increase. Nevertheless, the principles that emerge from this synthesis should apply even where species are fewer and less diverse, and where feeding patterns perhaps are less distinct.

Major Offenses of Piscivorous Fishes

Most fishes that prey on other fishes use one of four predatory strategies, each strongly reflected in the user's body features. They either (1) run down prey, (2) ambush prey, (3) habituate prey to an illusion that they are nonaggressive, or (4) stalk prey.

Predators that run down their prey are the most widespread because their major asset — speed — is particularly suited to the most widespread habitat — open water. They tend to be highly streamlined, with cylindrical, heavily muscled bodies and deeply forked tail-fins. The tunas (Scombridae) and the billfishes (Istiophoridae) are oceanic examples, whereas jacks (Carangidae) are prominent representatives in nearshore marine waters (Figure 1). The straightforward attacks that characterize these predators, however, are less effective in the confined spaces of shallow water and near the bottom, especially where prey are just a quick dart from a sheltering reef or grass bed. Such circumstances favor predators that use one of the following three ways to catch prey.

Predators that ambush prey generally rest immobile on the bottom and capture organisms that have inadvertently come within range of a short, explosive charge. The color and texture of some, for example, certain scorpionfishes (Scorpaenidae), are similar to that of the substrate on which they lie, while others, like certain flatfishes (Pleuronectiformes), may rest under a layer of sand (Figure 2).

Some ambushers capture prey without leaving their position on the bottom. When prey approach closely to the Hawaiian scorpionfishes of the genus *Scorpaenopsis* (Figure 3), for example, these big predators simply snap open their cavernous mouths and gill cavities and suck their victims in (Hobson 1974). A few species have embellished the ambushing tactic by acquiring features that actively draw prey to them; thus, certain anglerfishes (Antennariidae) have a fin spine modified as a lure that attracts potential prey (Figure 3).

Predators that habituate prey to an illusion that they are nonaggressive, including certain basses (Serranidae) and snappers (Lutjanidae), often live side by side with their ultimate victims (Figure 4). Most are sluggish, sometimes large fish, but can explode upon prey with a burst of speed over short distances. These predators often hover above the bottom in full view, which distinguishes them from the ambushers. Generally, their coloration and demeanor render them inconspicuous, so they regularly go unnoticed, if not unseen. Their success as predators depends on prey becoming accustomed to their presence, lulled by their peaceful mien and ultimately careless.

Predators that stalk prey typically include long, attenuated fishes like barracudas (Sphyraenidae), pikes (Esocidae), needlefishes (Belonidae), and cornetfishes (Fistulariidae). By drifting forward slowly, showing overt aggression only when close upon an unwary victim, they arrive within striking range of their target despite being in full view. Many stalkers have exceptional feeding structures that are in contrast to the generalized equipment of most other fish-eaters. The cornetfishes (Figure 5), for example, have an exceptionally long, tubular snout, which, when suddenly expanded, sucks in prey they have managed to approach.

The last three strategies cited are described in pure form. Although the examples given are highly distinctive, many piscivores, for example, certain sea basses, incorporate components of two, or even all three, of these strategies. Furthermore, some piscivores have adopted specialized variations of these strategies. The leather bass, *Dermatolepis dermatolepis* (Figure 6), for example, commonly gains predatory advantages by associating with both schools and individuals of other species. Sometimes the leather bass approaches prey from behind these other fishes, apparently using them as a blind to get within striking range unnoticed; other times the bass follows alongside herbivores and other grazing fishes and captures prey that are driven from cover as the grazers disturb the substrate. (Montgomery 1975).

Major Defenses of Prey

The strategies used by piscivorous predators are responses to the defenses of their prey. Major defenses include both behavioral and anatomical adaptations, and are used by most prey species in some combination. Schooling and staying within reach of shelter are important defensive behaviors, whereas spininess and body armor are important anatomical adaptations.

Virtually all small fishes school when they are away from a sheltering reef or other structure during the day, and almost invariably smaller species that spend all their time in open water school habitually. It is widely believed that fishes are protected from predators when they school, although opinions vary on how this occurs. Some suggest that when fishes school they reduce their encounters with predators (Brock and Riffenburg 1960, Olson 1964), whereas others believe that schools increase security because predators regard the group as some inedible, or threatening, object (Crawford and Powers 1953, Springer 1957).

Some note that the greater number of eyes and other sensory receptors in the group make it significantly more probable that a threatening predator will be recognized (Bowen 1931); others suggest that schools have resulted because individuals in the center are protected by those of their kind between themselves and the predators (Williams 1964, Hamilton 1971).

Any one of the above possibilities could be a factor under appropriate circumstances, but generally I favor the theory that advantage is gained through a "confusion effect" (as advocated by Allen 1920a, 1920b, Manteifel and Radakov 1961, Eibl-Eibesfeldt 1962, Hobson 1965, 1968, Starck and Davis, 1966, Neill and Cullen 1974).

The confusion effect theory contends, in essence, that predators confronted by the many targets in a school commonly fail to concentrate on an individual. Many characteristics of schools are understandable when considered as enhancing a confusion effect. Schooling fishes emphasize features that make individuals difficult to distinguish. Thus, all members of a school are about the same size and look much alike. Schooling fishes are noted for lacking external differences between the sexes. When threatened, schooling fishes typically close ranks, a maneuver that places additional individuals within the attacker's field of vision, thus further troubling those that have difficulty with multiple targets.

Schoolers under attack also swim faster and begin weaving in and out among one another, a maneuver that appears to increase the confusion effect. At this point the silvery hues that characterize so many schoolers come into play, as sunlight reflecting from their sides at rapidly changing angles would seem to present the attacker with a bewildering shower of brilliant flashes (Hobson 1968). Similarly, the bars or stripes that characterize the color patterns of many schoolers tend to blend together as a shifting maze of lines that conceal individuals (Starck 1966). And just as the protective aspect of the school requires its members to present a uniform appearance, it also requires them to present uniform behavior. Thus, it seems likely that any individual that swims abnormally, for example, because of injury, becomes a distinctive target (Hobson 1968).

Every successful defense in prey will be answered among predators by an appropriate offense. So it should be expected that some predators have solved the defensive features of schools. The sword of the swordfish (Xiphiidae) and the saw of the sawfish (Pristidae) may be effective weapons when attacking fish schools (Williams 1964), as may the long tail of the thresher shark (Alopiidae) (Nichols and Murphy 1916). But so long as the vast majority of fish-eating predators is frustrated by the defensive aspect of schools, their failures will cancel out the successes of the relatively few specialized forms that seem to have solved the problem.

The advantage of schooling as a protective device is unneeded by smaller fishes that live close to the sea floor, because these find shelter in or close to reefs and other structures. Some, like the razorfishes (Labridae, *Hemipteronotus* spp.) are specialized to dive into the sediments. Still others, like certain goatfishes (Mullidae), seem secure simply by being close to the substrate; perhaps their immediate proximity to the sea floor sufficiently inhibits the space-demanding attacks of predators that might otherwise threaten them, or perhaps they simply go unnoticed by most predators. In any event, as long as these various species are close to shelter many of them feed, and carry on other pursuits, as solitary individuals. Some of them, however, for example the damselfish *Abudefduf troschelli*, periodically swim up into midwaters, and at these times generally school with others of their kind (Hobson 1968).

Although small reef fishes face an intense threat from predators when they move away from shelter, some nevertheless spend their active hours in the midwaters. But even these are careful to stay within reach of shelter on the sea floor. Many such fishes, including various damselfishes (Pomacentridae, especially *Chromis* spp.) feed on zooplankton, and though they acquire a measure of security by aggregating, they nevertheless remain dependent on shelters that lie far below them. Significantly, most of these plankton-feeders, or planktivores, have acquired features that increase their swimming speed and thus hasten their descent to cover when threatened (Hobson 1974).

Compared to close relatives that spend all their time near the reef, these planktivores tend to have more cylindrical bodies and more deeply incised tailfins (Davis and Birdsong 1973) — two tendencies that increase their speed. Furthermore, these speed-inducing features are most pronounced in those species that habitually range farthest into open water (Hobson and Chess 1978). That they use this speed is demonstrated when certain predators appear — notably jacks — and the entire assemblage abruptly closes ranks and dives headlong toward the reef

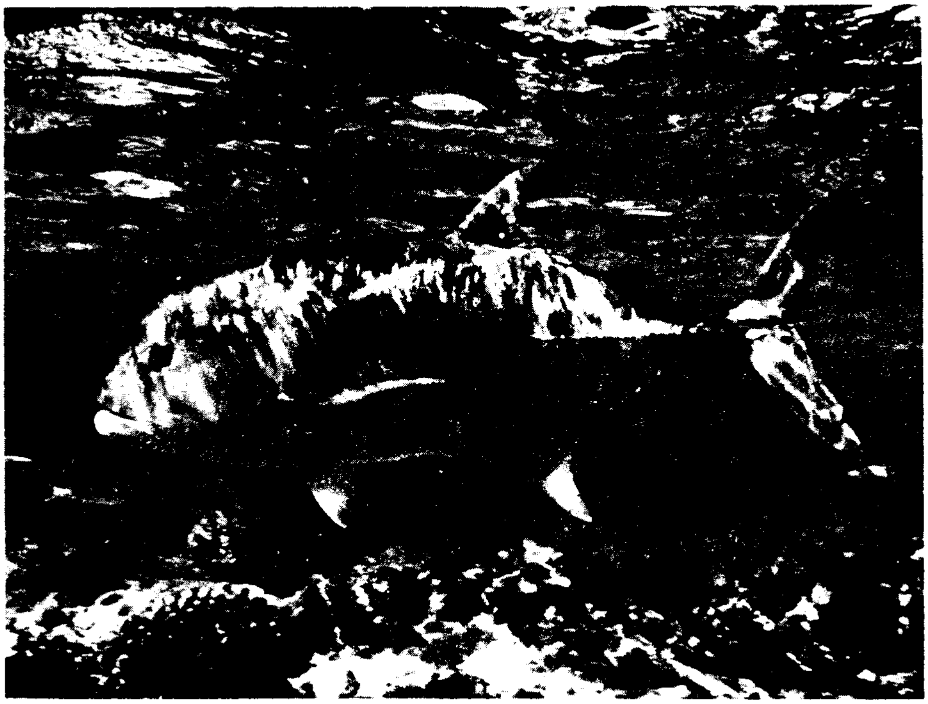

Figure 1. This large jack, *Caranx ignobilis*, here patrolling near shallow reefs at Midway Atoll, Hawaii, is built to run down prey with an aggressive, straightforward charge.

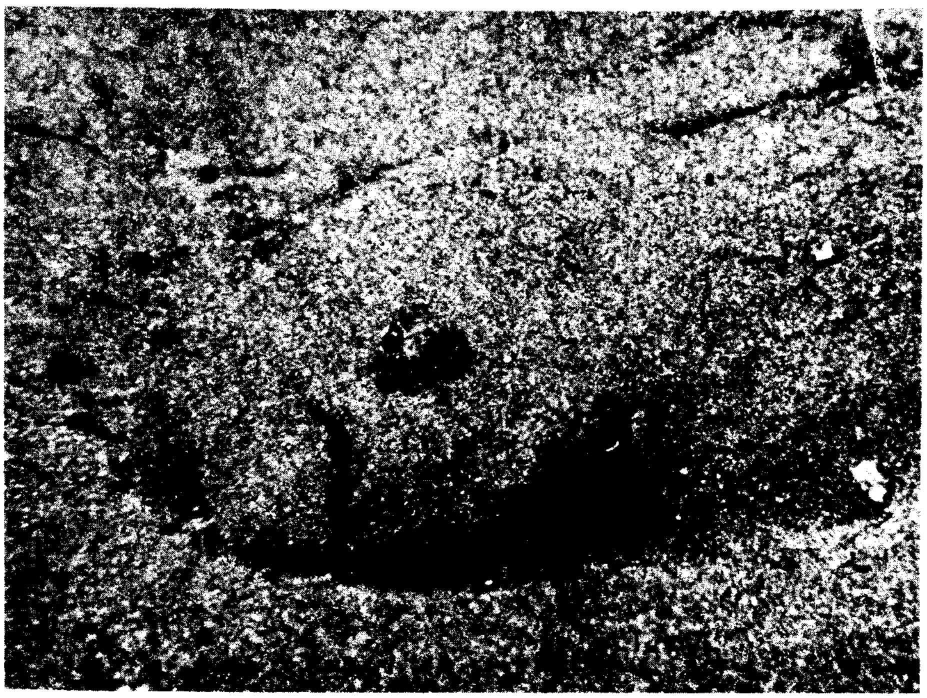

Figure 2. This California halibut, *Paralichthys californicus*, will erupt from its concealed position under the sand off the California coast to ambush small fishes that have come within range of a short, explosive charge.

Figure 3. With a sudden expansion of its cavernous mouth and gill cavities, this scorpionfish, *Scorpaenopis* sp., sucks in prey without leaving its perch on this Hawaiian reef. The small, white appendage just inside its lower lip, which often is moving and highly visible while the fish rests motionless and otherwise virtually unseen, may lure prey to within range of capture.

Figure 4. Even though these large groupers, *Mycteroperca rosacea*, hover in full view above this reef in the Gulf of California, they nevertheless feed on the small fishes about them. Perhaps their sluggish countenance habituates prey to an illusion that they are nonaggressive, and ultimately the prey become fatally careless.

Figure 5. The long, attenuated body of this cornetfish, *Fistularia commersoni*, here gliding above a reef in the Gulf of California, accentuates features that characterize stalking predators.

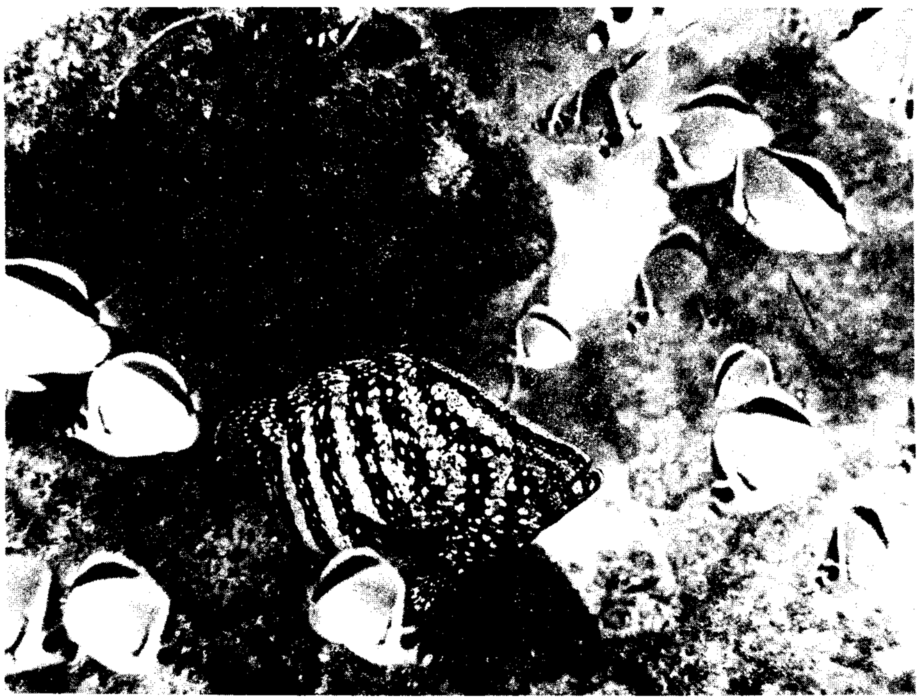

Figure 6. A leather bass, *Dermatolepis dermatolepis*, amid a school of the chaetodontid *Heniochus nigrirostris* in the Gulf of California. This chaetodontid is not prey of *D. Dermatolepis*, but apparently the serranid enhances its chances of approaching unnoticed to within striking range of prey by mingling with these and other fishes.

below. Because there is a direct relation between swimming speed and body length, it is unsurprising that within a group of closely related planktivores the smaller species remain closest to cover; thus, the smallest of the Hawaiian planktivorous damselfishes, *Chromis vanderbilti*, rarely feeds more than 0.5 m above the reefs, whereas larger relatives, like *C. ovalis*, typically feed 2 to 5 m above (Hobson 1972, 1974, Munz and McFarland 1973).

Ultimately, even the most elusive prey will likely find itself between the jaws of a predator. But even from this position the attacker can be deterred. The strong fin-spines that characterize many fishes certainly complicate the predator's task. A predator that has successfully taken a relatively large spiny-finned fish into its mouth now must position the prey to enter its narrow digestive tract head-first. An attempt to swallow such prey tail-first would likely result in the spines locking erect and becoming lodged in the pharynx or esophagus. I have seen many predators fatally choked this way. Also, during the split second that the predator must relax its grasp for proper positioning, I have seen predators lose the prey fish they had held firmly between their jaws.

Spininess, like most successful defenses, is developed to extremes in some species, but these extremes generally limit other abilities. Thus, certain rockfishes, *Sebastes* spp., have large bony heads that carry many fixed spines, and surely present predators with a troublesome mouthful. But the added weight of these structures ties those that bear them to a largely sedentary life on the sea floor. Significantly, more motile rockfishes, like the olive rockfish, *Sebastes serranoides*, have smaller heads with fewer and less pronounced spines.

An effective combination of strong fin spines and exceptionally deep bodies probably protects butterflyfishes (Chaetodontidae) and angelfishes (Pomacanthidae) from most of the predators that threaten their neighbors on coral reefs (Hobson and Chave 1972). Furthermore, some reef fishes that habitually swim into the exposed midwaters and feed on plankton, for example, damselfishes of the genera *Dascyllus* and *Amblyglyphidodon*, have longer fin spines and much deeper bodies than do their relatives that remain close to sheltering reefs. Thus in response to the same predatory threat that has led to more cylindrical bodies and deeply incised caudal fins in many other planktivorous damselfishes, the evolution of these species seems to have taken the opposite course. Where a cylindrical body (and deeply incised tail fin) promotes eluding predators, the deep body (with long fin spines) would seem to promote discouraging predators — two opposing routes to the same end: to reduce the threat of attack (Hobson and Chess 1978).

Patterns of Predation

Interactions between predator and prey are shaped by the way these animals perceive their surroundings. Their orienting senses, therefore, are presumably major elements in defining predation patterns. Clearly, most piscivorous fishes depend mainly on vision to capture prey. Despite notable exceptions, especially among species that frequent dark or turbid waters, the predominance of vision on a broad scale is unquestionable. Of course, the range of vision underwater is sharply limited. Light diminishes rapidly as it passes through even the clearest natural water because it is scattered by suspended particles and is absorbed by the water itself; consequently underwater objects no matter how large, are invisible beyond about 70 m (Brock and Riffenburg 1960). So predators must use some other sense to detect prey at greater distances.

Thus, certain sharks track injured or distressed fishes over long distances by orienting on odors characteristically emitted by these prey (as long as the odor trails out in a current, or behind moving prey). But even sharks drawn in by odors generally switch to visual cues when close to their target (Hobson 1963). So with visual ranges in the aquatic realm limited, the major interactions between predators and their prey are at close range — a set of circumstances that undoubtedly has contributed to most large predators being nearsighted (Walls 1942). And with visual orientation so important, feeding interactions are strongly influenced by the changes in underwater light that characterize the different times of the day-night cycle.

Because most piscivorous fishes orient visually when they feed, one might expect attacks to increase with the brightness of underwater light. By this reasoning, however, attacks should be most frequent during midday, when in fact activity among predators is at a low ebb. Probably this mild paradox reflects a long, successful evolution that has given prey defenses that effectively counter the offensive strengths of their predators. If predators can see better in bright light, so can their prey, and the lack of activity among predators during midday suggests that during this period defense has an edge over offense.

Certain prey defenses, at least, are best suited to bright light. Features of the school that would enhance a confusion effect should be most effective under bright light. These features include flashing silver sides and color patterns consisting of bars or stripes. Even the confusion effect itself, which entails presenting the attacker a complex visual image, may increase or decrease with light. Whether or not this is so, schooling fishes appear relatively safe from predators during most of the day (Hobson 1968).

No matter how effective the daytime, or diurnal, defenses may be, however, there are bound to be lapses during which the prey are briefly vulnerable. For example, small fishes that ordinarily stay within reach of shelter will sometimes stray too far into the open, and others normally secure in schools will briefly separate from their group. Still others, usually alert to developing dangers, will be momentarily distracted. The most successful diurnal piscivores are those best able to exploit such defensive mistakes.

But prey are unlikely to make errors of this sort in the presence of jacks and other aggressive free-swimming predators. Prey recognize signs that mark hunting predators, and take appropriate action when aware that one is about. Those that find safety in the reef move toward these shelters, and those that are secure in schools tighten their ranks. Above all, the prey are alerted, so that few suitable targets are available to those predators that characteristically run down their prey with a highly overt, straightforward charge.

Of course, such predators enjoy occasional midday successes. Sometimes groups of jacks charge into schools of small fish, seemingly in a coordinated effort to scatter the school and thus isolate individuals (Eibl-Eibesfeldt 1962, Starck and Davis 1966). Using a different tactic, jacks and skipjacks (Scombridae) may accompany schooling prey for hours without making an aggressive move, then suddenly attack (Hiatt and Brock 1948, Hobson 1968), presumably having sensed a vulnerable individual. But these are relatively infrequent successes; predators of this type remain better suited to hunt under other conditions.

Adaptations that place predators within striking range when smaller fishes become momentarily vulnerable during the day characterize the ambushers, those that habituate prey to their apparent nonaggressiveness, and the stalkers. Included here are most of the species that capture smaller fishes through the day on tropical marine reefs (Hobson 1974, 1975). Their closely related feeding strategies express a common goal: to catch prey unaware in a vulnerable position. That their most distinctive features seem designed to exploit relatively infrequent lapses in the defenses of their prey testifies strongly for the considerable strengths of these defenses.

If the major defenses of smaller fishes are most effective in daylight, what becomes of these fishes at night? It appears that after dark they are comparatively free of the intense threats from predators that so strongly influence their every move during the day. Predators that threaten smaller fishes on tropical marine reefs by day are largely inactive, or shift to some other prey, at night (Hobson 1968, 1973, 1974). This observation is true despite some fish-eaters that are specially equipped to capture their prey at night. One such predator is the big-eye jack, *Caranx marginatus*, a large fish whose name describes the distinctive feature that permits it to see better in the dark; it hunts smaller fishes at night in the eastern Pacific Ocean (Hobson 1968). But compared to the number of piscivores abroad in daylight, few are active at night.

Some of the smaller night-active, or nocturnal, predators that feed chiefly on crustaceans and other free-swimming invertebrates — including soldierfishes (*Myripristis* spp.), glasseyes (*Priacanthus* spp.) and cardinalfishes (*Apogon* spp.) — take small fishes, especially larval forms, but only as a relatively minor part of their diets (Hiatt and Strasburg 1960, Randall 1967, Vivien 1973, Hobson 1974). Perhaps smaller fishes fail to generate the stimuli that orient nocturnal predators, or perhaps they simply are too elusive to be caught consistently by most predators that feed in the dark.

The smaller fishes themselves offer evidence that at night they enjoy a sharply diminished threat from predators. The two major defensive behaviors that protect them by day — schooling and staying close to shelter — are greatly relaxed at night. Breder (1959) stated, "The dispersion of schools in darkness has been so often reported that it is to be expected unless otherwise shown." Although some fishes maintain their schools during the night, especially certain open-water species, generally the assemblages are much looser, and individuals are much farther apart.

Proximate shelter certainly becomes less critical at nightfall, as many species that stay close to reefs in daylight range into open regions after dark. Thus, the open sandy expanses adjacent to reefs in the Gulf of California are largely without visible signs of life during the day, but are transformed into centers of nocturnal activity as fishes flood from the reefs into these expanses at nightfall (Hobson 1965, 1968). Evidence of a diminished threat at night also exists among the body features of the smaller fishes. For example, the widespread tendencies among planktivorous reef fishes toward more cylindrical bodies and deeply incised tails — features that permit a speedier retreat to cover when threatened — occur only in species that feed in the midwaters by day. Features of this sort are lacking among nocturnal counterparts, including certain soldierfishes, and cardinalfishes (Hobson 1974, 1975).

So far I have described a system that would seem to favor the prey; they are well protected by effective defenses during most of the day and face only a relatively minor threat from predators at night. But conditions change drastically during the morning and evening transitions between day and night. Defenses effective in bright daylight falter as light diminishes, so that the transition periods, though relatively brief, provide many piscivorous fishes their major feeding successes.

Actually the balance begins to shift from prey to predator long before twilight. Even during midday, in fact, small fishes that are feeding on plankton in the midwaters descend closer to sheltering reefs whenever visibility is reduced. This descent occurs either with a drop in light, as when clouds pass before the sun, or through a drop in water transparency, as when turbid water inundates an area (Hobson 1972, Stevenson 1972). Presumably this descent by the planktivores is in response to a measurably greater threat from predators that accompanies even slightly decreased visibility. As light continues to fade with the advancing afternoon, the planktivores descend progressively closer to the bottom — a descent that probably provides a rough index of increasing danger.

As day's end approaches, the fishes that had been active above many tropical reefs show a clear relation between their size and the time they go under cover. The smaller individuals, which are most vulnerable to predators, seek shelter first, and by sunset many of them already are out of sight (Hobson 1972). Many of the larger diurnal fishes, however, remain above the bottom for some time into twilight. Then, about 15 minutes after sunset, these too move from exposed positions, and the reef experiences what has become known as the "quiet period" (Hobson 1972, Munz and McFarland 1973, Major 1977).

It is during this "quiet period," a short span of about 20 minutes during both morning and evening twilight, that smaller fishes appear to be most vulnerable. The evening quiet period on tropical reefs is that time shortly after sunset when the day-active fishes have retired to shelter, but the night-active fishes have not yet emerged, and the morning quiet period is the comparable time shortly before sunrise when the sequence is reversed. The term quiet period, then, describes a general absence of fishes in exposed — and therefore vulnerable — locations. Although descriptive of most tropical reefs, the term clearly is a misnomer in reference to others. Where schooling fishes abound, this often is a time when large predators attack most intensely. The major attackers under these conditions are those aggressive piscivores like jacks whose feeding seems most inhibited during midday. Unlike so many other smaller fishes, the schoolers generally are unsuited to shelter in the reefs and so remain exposed to what obviously are precarious circumstances. Thus, the waters around herring (*Harengula*) schools in the Gulf of California (Hobson 1965, 1968), and silverside (*Pranesus*) schools in Hawaii (Major 1977), often are whipped into a frenzy of predatory activity at a time when conditions appear tranquil elsewhere.

The end of the quiet period, about 35 minutes after sunset, is marked by a surge of nocturnal fishes, notably soldierfishes, that abruptly emerge from their daytime shelters, and swim straight away into the midwaters. The intense predation on schooling fishes has subsided, and the schools are dispersing, or migrating to night-time feeding grounds. It is almost dark — only a trace of fading sunlight remains on the water's surface overhead. The large piscivores have withdrawn, and apparently the severe danger that prevailed moments earlier has passed (Hobson 1968, 1972).

Clearly twilight is a critical period for many fishes. It is so critical, in fact, that certain visual features of many species seem specially designed for better vision during this brief period even though it is only a small segment of the 24-hour day. Important studies by Munz and McFarland (1973) have shown that twilight is slightly bluer than the light of day or night. Significantly, they have also shown that some of the light-receiving elements in the eyes of many coral-reef fishes appear more sensitive to this unique quality of twilight (which is apart from the light's brightness) than to the quality of light at other times. This is a striking find, because the study included both diurnal and nocturnal fishes. Munz and McFarland hypothesized that this added sensitivity to the quality of twilight, which presumably lets them see slightly better at this time than they could otherwise, is an adaptation to the severe evolutionary pressures that have long been exerted on predator-prey interactions during this critical period. But sensitivity to twilight blue is a feature of predators as well as prey. We still must ask why predators become relatively more effective during twilight.

The visual equipment of piscivorous fishes may be better suited after all to the half-light of dusk than is the visual equipment of their prey. Fishes on tropical reefs, including prey of the piscivores, tend to be most active either by day, or by night (Hobson 1965, 1968, 1972, 1974, Starck and Davis 1966, Vivien 1973), and adaptations to these activities quite likely limit their abilities during the transition periods. The typical diurnal fishes, including various wrasses, butterflyfishes, and damselfishes, feed on small organisms, a task requiring exceptionally sharp vision. On the other hand, most of the nocturnal fishes, including cardinalfishes, squirrelfishes, and soldierfishes, feed on comparatively large prey, but in relative darkness, a task requiring sensitivity to dim light (Hobson 1974). The two groups, then, have different visual needs; in fact, they accentuate aspects of vision that tend to be mutually exclusive; visual structures that stress perception of detail are poorly suited to dim light, whereas visual structures that stress sensitivity to dim light are poorly suited to perceiving detail (Walls 1942).

Recognizing these relationships, Munz and McFarland (1973) examined the eyes from a limited number of coral reef fishes and found that visual structures in the diurnal species differed from those in the nocturnal species precisely as might have been predicted based on their contrasting feeding circumstances. There were only two piscivores in their sample — the jack, *Carangoides ajax*, and the grouper, *Epinephelus merra* — but significantly these constituted a third group which have eyes with visual structures intermediate between those in the diurnal and nocturnal groups, and which Munz and McFarland assumed to be twilight feeders. Perhaps this development should have been expected. These piscivores take relatively large prey, so are free of the need to perceive great detail; and they do not feed at night, so they are free of the need for extreme visual sensitivity. Consequently, during the transitions between day and night these predators should have a marked visual edge over at least many of their prey. They can see well enough in light that is too dim for those diurnal prey that have sacrificed visual sensitivity for visual acuity, and they have better attention to detail than is possible for those nocturnal prey that have sacrificed visual acuity for visual sensitivity.

Apart from any sensory advantage that piscivores may have during twilight, however, they unquestionably gain an edge by choosing the time and place of the attack. The prey can only respond. During most of twilight the sky is light, but little of the light penetrates the water. As a result, predators positioned near the bottom find prey in the water above them readily visible against a light background, but prey in the midwaters find predators below them hidden in the gloom (Hobson 1966, 1968, Munz and McFarland 1973). Obviously, under these circumstances small fishes find life in the midwaters especially risky, and their reason for vacating this region is obvious. Schools, however, must remain in this highly vulnerable position through twilight even though many of the features that protect them in bright light have lost effectiveness. The colorations of their members, for example, are no longer helpful in masking individuals. Predatory fishes typically attack from below at this time, and each schooler is silhouetted against the bright surface — a distinct target (Hobson 1966).

Summary

Most fishes that prey on other fishes use one of four predatory tactics each of which is strongly reflected in its body features. They either (1) run down their prey with an overpowering charge (examples: jacks and billfishes), (2) ambush their prey (examples: scorpionfishes and flatfishes), (3) habituate prey to their apparent nonaggressiveness (examples: basses, snappers), or (4) stalk their prey (examples: barracudas and pikes).

These tactics relate closely to the defenses of their prey. Some prey defenses are behavioral, such as schooling and staying within reach of shelter, whereas others involve some adaptive body feature; for example, the development of spines, or concealing colorations. Generally, these defenses are used in combination. Schooling fishes, for instance, often have color patterns and other body features that make individuals in the assemblage less conspicuous and therefore poorer targets for predators. And small reef fishes that characteristically swim a distance from shelter often have body features that permit them to swim faster and so speed their retreat to cover when threatened.

Predator-prey interactions are strongly influenced by the varying characteristics of underwater light at different times of the day-night cycle because most of the fishes involved orient mainly by vision. Prey defenses are most effective during midday, and the smaller fishes are relatively secure then. The most successful predators at this time are those at the scene when prey fishes make momentary errors. Those best able to succeed are among the ambushers, stalkers, and those that have habituated prey to their apparent nonaggressiveness.

Predators that characteristically run down their prey with a highly overt, straightforward charge find suitable targets rare during midday because prey are unlikely to make a defensive error in their obvious presence. Most large piscivores find light at night insufficient for hunting, thus greatly reducing their threat to small fishes then. Many prey defenses, including schooling and remaining within reach of shelter, are greatly relaxed at this time.

Piscivores are most active during the transition between day and night, with their attacks peaking during twilight. Their major prey are primarily diurnal or nocturnal species ill-equipped for the rapidly changing conditions that prevail during the transition periods. At these vulnerable times most of the smaller reef fishes abandon the exposed midwaters, but schooling species, which are unsuited to shelter in the reefs, cannot do so, and are attacked severely. The major twilight attackers are those large, aggressive predators that are most inhibited in their feeding during midday.

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Edmund S. Hobson is a fisheries research biologist with the Southwest Fisheries Center, Tiburon Laboratory, National Marine Fisheries Service, Tiburon, California, and a research associate with the Scripps Institution of Oceanography. He holds a doctorate from the University of California, Los Angeles. His research during the past twenty years has centered on predator-prey relationships among fishes. He is the author of over thirty-five scientific and popular articles, most of them on predation in fishes.