CHAPTER 17

Predation as a Process Structuring Coral Reef Fish Communities

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I. INTRODUCTION

A. Background

A long-standing controversy on the major processes structuring communities of coral reef fishes has centered mainly around two alternative hypotheses. First, the **Competition Hypothesis** states that competition is the predominant interaction determining the abundance (and ultimately the distribution and local diversity) of fishes. The underlying assumption is that the population densities of adult fish are sufficiently high that resources are limiting. Consistent with this hypothesis are observations of resource partitioning among species (e.g., Smith and Tyler, 1972, 1973b, 1975; C. L. Smith, 1978; Anderson *et al.*, 1981; Gladfelter and Johnson, 1983; Ebersole, 1985; reviewed by Ross, 1986; Ebeling and Hixon, Chapter 18). Second, the **Recruitment Limitation Hypothesis,** as originally formalized by Doherty (1981), maintains that presettlement mortality of eggs (zygotes) and larvae determines adult patterns of abundance. This hypothesis asserts that mortality in the meroplankton results in such low recruitment that adult populations never reach levels at which resources become severely limiting, thus precluding significant competitive interactions (e.g., D. McB. Williams, 1980; Doherty, 1981, 1982, 1983a; Victor, 1983a, 1986b; Sale *et al.*, 1984a; Wellington and Victor, 1985; reviewed by Doherty and Williams, 1988a; Doherty, Chapter 10). (Here I equate "recruitment" with postlarval/prejuvenile settlement for fish that settle in adult habitat.)

Relatively little attention has been paid to a third alternative, the **Predation**

Hypothesis, which states that postsettlement mortality due to piscivory determines adult patterns of abundance. This hypothesis asserts that predation on new recruits, juveniles, and adults results in such low population sizes that severe resource limitation and competition are precluded. The relatively low level of interest in the predation hypothesis among reef fish ecologists is surprising (but see C. L. Smith, 1978; Doherty and Williams, 1988b; Glynn, 1988; and data papers cited below), especially considering the increasing attention given to predation in behavioral and community ecology in general (e.g., recent symposia: Feder and Lauder, 1986; Simenstad and Cailliet, 1986; Kerfoot and Sih, 1987), and in marine fisheries biology (e.g., Sissenwine, 1984; Rothschild, 1986).

The goals of this chapter are threefold: (1) to review and evaluate both direct and indirect evidence for the predation hypothesis; then (2) to show that the competition, recruitment limitation, and predation hypotheses are not so much alternatives as overlapping regions along a continuum of structuring processes; and finally (3) to suggest general means of testing the role of predation relative to other processes, adopting methods that have been used widely in other systems. I intentionally focus on evidence supporting (rather than falsifying) the predation hypothesis to provide some balance in a literature that is dominated by advocacy of other hypotheses. I personally advocate no particular hypothesis.

B. The Predation Hypothesis

Field studies have demonstrated the importance of predation in structuring various ecological systems. There is particularly strong evidence for predation effects in freshwater and rocky intertidal communities (reviewed by Connell, 1975; Clepper, 1979; Zaret, 1980; Paine, 1984; Sih *et al.,* 1985; Kerfoot and Sih, 1987). Previous studies have generated two general classes of predictions from the predation hypothesis, one evolutionary and the other ecological. First, if the predation hypothesis has operated through evolutionary time, then the morphology and behavior of prey fishes should exhibit patterns consistent with minimizing the risk of predation. Second, if predation is presently an important process in structuring reef fish communities, then the abundance (and consequently the distribution and local diversity) of prey fishes should shift in predictable ways as the density of piscivores or prey refuges changes through time or space.

From the ecological perspective of this review, the evolutionary class of predictions is relatively weak because its verification provides only circumstantial evidence that predation presently structures communities. However, documenting antipredatory patterns in the morphology and behavior of prey fishes is essential for formulating more directly ecological predictions, which

can then be evaluated by either correlative or experimental approaches. As will become obvious, circumstantial evidence that the predation hypothesis may be true for reef fish assemblages is abundant, correlative evidence is uncommon, and experimental evidence is rare.

II. Circumstantial Evidence

Indirect evidence that piscivory has exerted a strong selective force on reef fishes is plentiful, and previous reviews have compiled numerous examples (Ehrlich, 1975; Hobson, 1975, 1979; Thompson, 1976; Huntsman, 1979; Helfman, 1986a). Such circumstantial evidence indicates the widespread occurrence of both piscivorous fishes and antipredatory mechanisms among prey fishes. The evidence falls into three categories: the ubiquity of piscivores; morphological/chemical prey defenses; and behavioral prey defenses.

A. The Ubiquity of Piscivores

Piscivores are an ever-present component of all coral reef systems. At first glance, one might argue that this assertion is false for exploited systems. However, fishing disproportionally removes large piscivores, such as groupers, snappers, and jacks (Bohnsack, 1982; Munro, 1983; Koslow *et al.,* 1988; Russ and Alcala, 1989). In fact, many smaller generalized predators, which are often not the focus of fisheries, consume new recruits, juveniles, and other small fish. Table 1 summarizes major regional surveys of reef fish trophic categories and shows that 8 to 53% of the species in an area consume other fishes. This wide range of values can be partially attributed to the relative detail of the study; the higher values are from studies that included extensive analyses of gut contents (e.g., Hiatt and Strasburg, 1960; Randall, 1967; Hobson, 1974; Parrish *et al.,* 1986). Fishes from the studies in Table 1 that ate small fish at least occasionally included members of families not normally associated with piscivory, such as squirrelfishes, cardinalfishes, goatfishes, damselfishes, and wrasses.

Piscivorous reef fishes are diverse in behavior as well as taxonomy. Hobson (1975, 1979) reviewed the predatory modes of piscivores in detail and distinguished five major categories: (1) open-water species that pursue their prey, such as jacks (Potts, 1981); (2) cryptic species that ambush their prey, such as lizardfishes (Sweatman, 1984); (3) species that apparently habituate prey to an illusion that they are nonpredatory, such as groupers and snappers (Harmelin-Vivien and Bouchon, 1976); (4) species that slowly stalk their prey, such as trumpetfishes (Kaufman, 1976); and (5) species that attack prey within crevices, such as moray eels (Bardach *et al.,* 1959). Of course, a given

Table 1 Regional Surveys on the Abundance of Piscivorous versus Nonpiscivorous Coral Reef Fishes[a]

Location	Percentage piscivore abundance by			Reference
	Species number	Fish number	Fish biomass	
Caribbean Sea				
Virgin Islands	52.8	—	—	Randall (1967)
Indian Ocean				
East Africa	13.2	—	11.0	Talbot (1965)
Madagascar	13.4	2.8	—	Harmelin-Vivien (1981)
Pacific Ocean				
Great Barrier Reef	—	—	54.0	Goldman and Talbot (1976)
Great Barrier Reef	8.0	1.0	5.7	Williams and Hatcher (1983)
Hawaii (Hawaii)	28.0	—	—	Hobson (1974)
Hawaii (Oahu)	18.4	4.0	8.3	Brock *et al.* (1979)
Hawaii (NW)	41.3	6.0	19.4	Parrish *et al.* (1986)
Marshall Islands	47.6	—	—	Hiatt and Strasburg (1960)

[a] Expanded from Parrish *et al.* (1986).

piscivore may use more than one of these modes, and the final attack by all piscivores involves a rapid strike.

Some predators employ various levels of aggressive mimicry, ranging from merely hiding among nonpredatory fishes [e.g., trumpetfishes (Aronson, 1983)] to "fishing" with modified lures resembling various prey items [e.g., anglerfishes (Pietsch and Grobecker, 1987)]. In the latter case, piscivores may actually attract and consume other piscivores by utilizing fishlike lures. For example, the anterior dorsal fin of the scorpionfish *Iracundus signifer* resembles a small fish (complete with an eyespot), which undulates as if hovering (Shallenberger and Madden, 1973). Even more remarkable is the anglerfish *Antennarius maculatus*, whose lure is extremely fishlike (Pietsch and Grobecker, 1978) (Fig. 1).

The abundance as well as the diversity of piscivorous fishes is high (Table 1). At the extreme, Goldman and Talbot (1976) reported that piscivores accounted for 54% of the total fish biomass at One Tree Island on the Great Barrier Reef. Parrish *et al.* (1986) and Norris and Parrish (1988) reported over 30% piscivores by weight and over 8% by number at one of their stations in the northwestern Hawaiian Islands.

In addition to predatory fishes, a considerable host of invertebrate and tetrapod piscivores also occur on coral reefs. Invertebrate piscivores include some anemones (Gudger, 1941), cone snails (Kohn, 1956), mantis shrimps

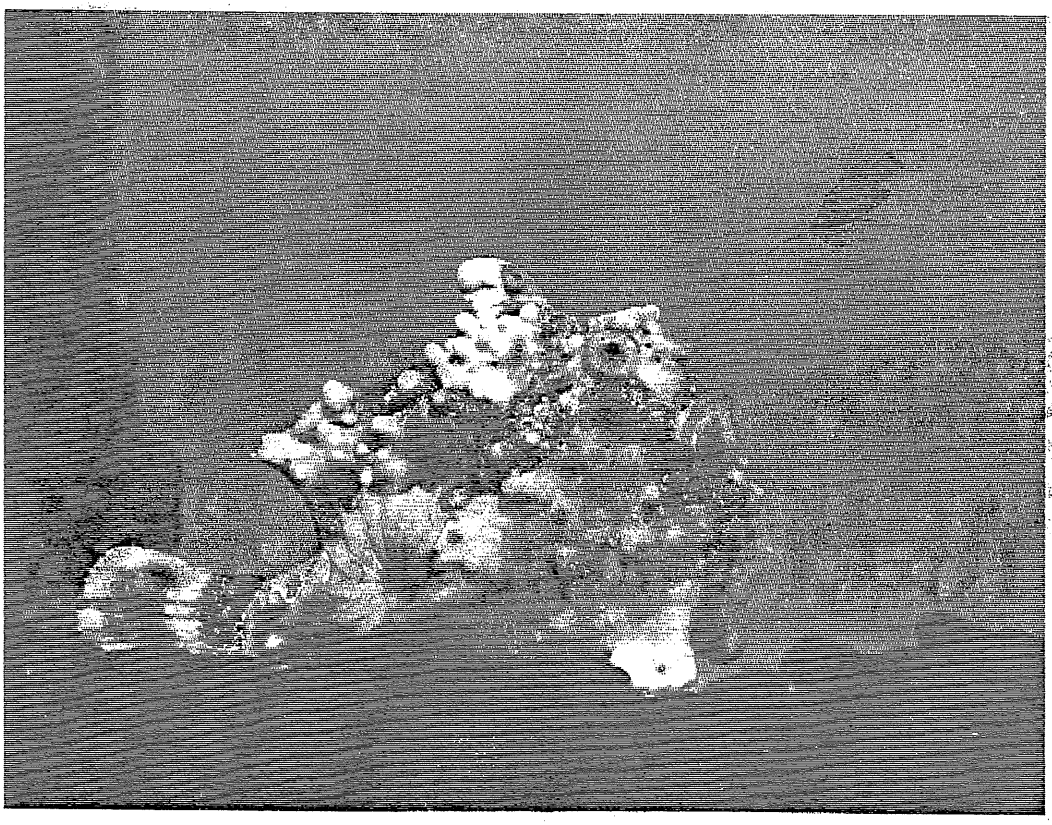


Figure 1 The anglerfish *Antennarius maculatus* (58.5 mm SL). The fishlike lure is a modified first dorsal spine, which moves in a circular pattern resembling swimming motions. The highly cryptic body provides this fish with an effective sit-and-wait ambush mode of piscivory. [From Pietsch and Grobecker (1978); copyright © 1978 by the American Association for the Advancement of Science.]

(Steger and Benis-Steger, 1988), asteroid seastars (Robilliard, 1971), and even ophiuroid brittlestars (Morin, 1988) (Fig. 2). Seasnakes (Voris and Voris, 1983) and seabirds (Hulsman, 1988) can also be major predators of reef fishes. Overall, there are probably many more piscivores on any given reef than most researchers suspect.

B. Morphological/Chemical Prey Defenses

The general mechanisms whereby prey minimize the risk of predation have been the subject of numerous books (Cott, 1940; Wickler, 1968; Edmunds, 1974; Curio, 1976) and review articles (Bertram, 1978; Harvey and Greenwood, 1978; Endler, 1986; Ydenberg and Dill, 1986). Because such mechanisms do not bear directly on the question of community structure, my goal

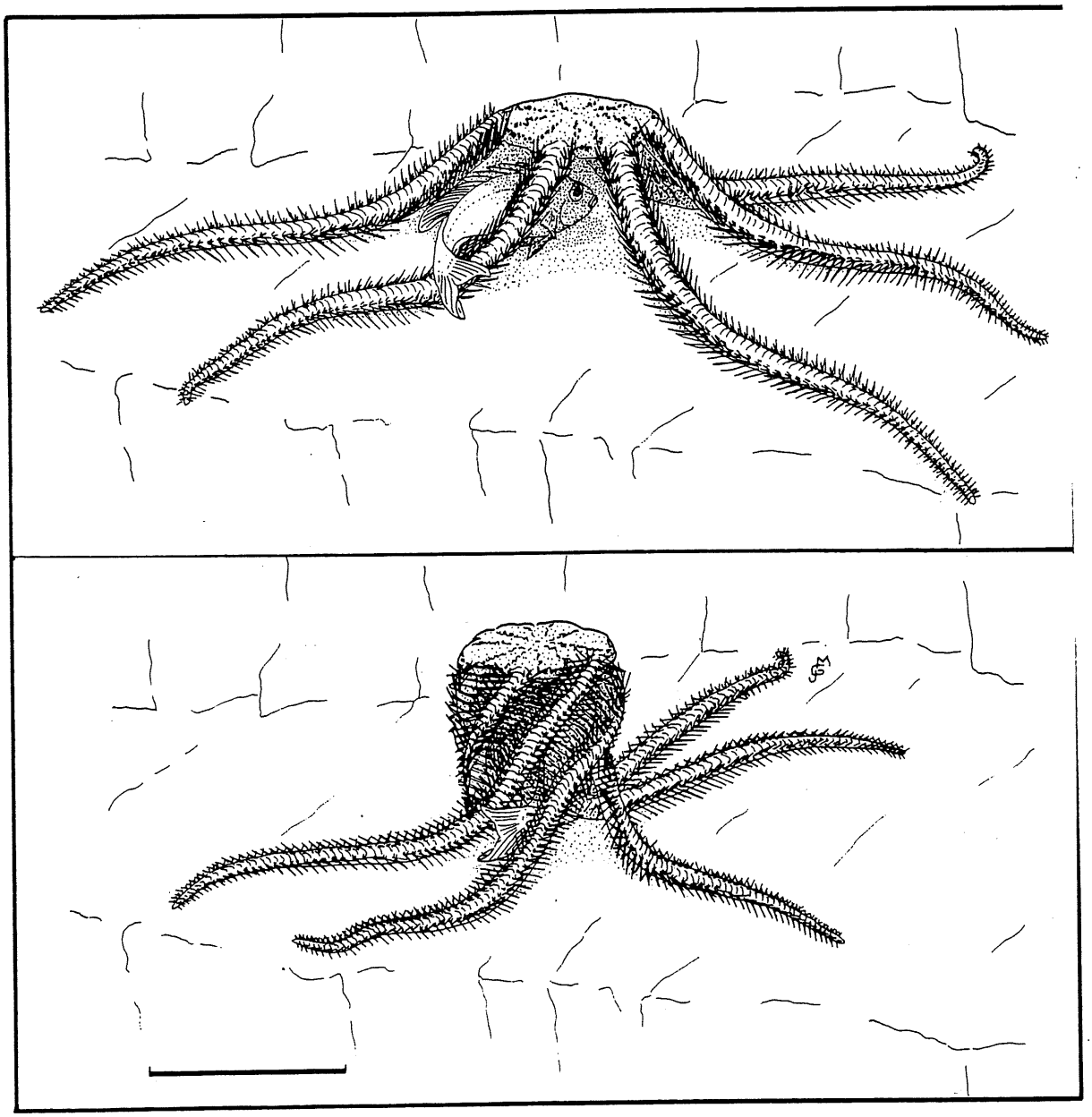


Figure 2 Piscivory by the brittlestar *Ophiarachna incrassata* (bar indicates 5 cm). *Above:* ambush posture, with a fish entering the "shelter" formed between the disc and the reef. *Below:* spiral posture, with the fish imprisoned within a helical cylinder of spines. [Reprinted from J. G. Morin (1988), in "Echinoderm Biology—Proceedings of the Sixth International Echinoderm Conference, Victoria, 23–28 August 1987" (R. D. Burke, Ph. V. Wadenor, Ph. Lambert, and R. L. Parsley, eds.), 832 pp., Hfl.155/US$80.00. A.A. Balkema, P.O. Box 1675, 3000 BR Rotterdam, Netherlands/A.A. Balkema, Old Post Road, Brookfield, Vermont 05036, U.S.A. Copyright © 1988 by A.A. Balkema Publishers.]

here is not to provide an exhaustive review, but simply to emphasize that prey defenses are both abundant and diverse among reef fishes.

1. Structures

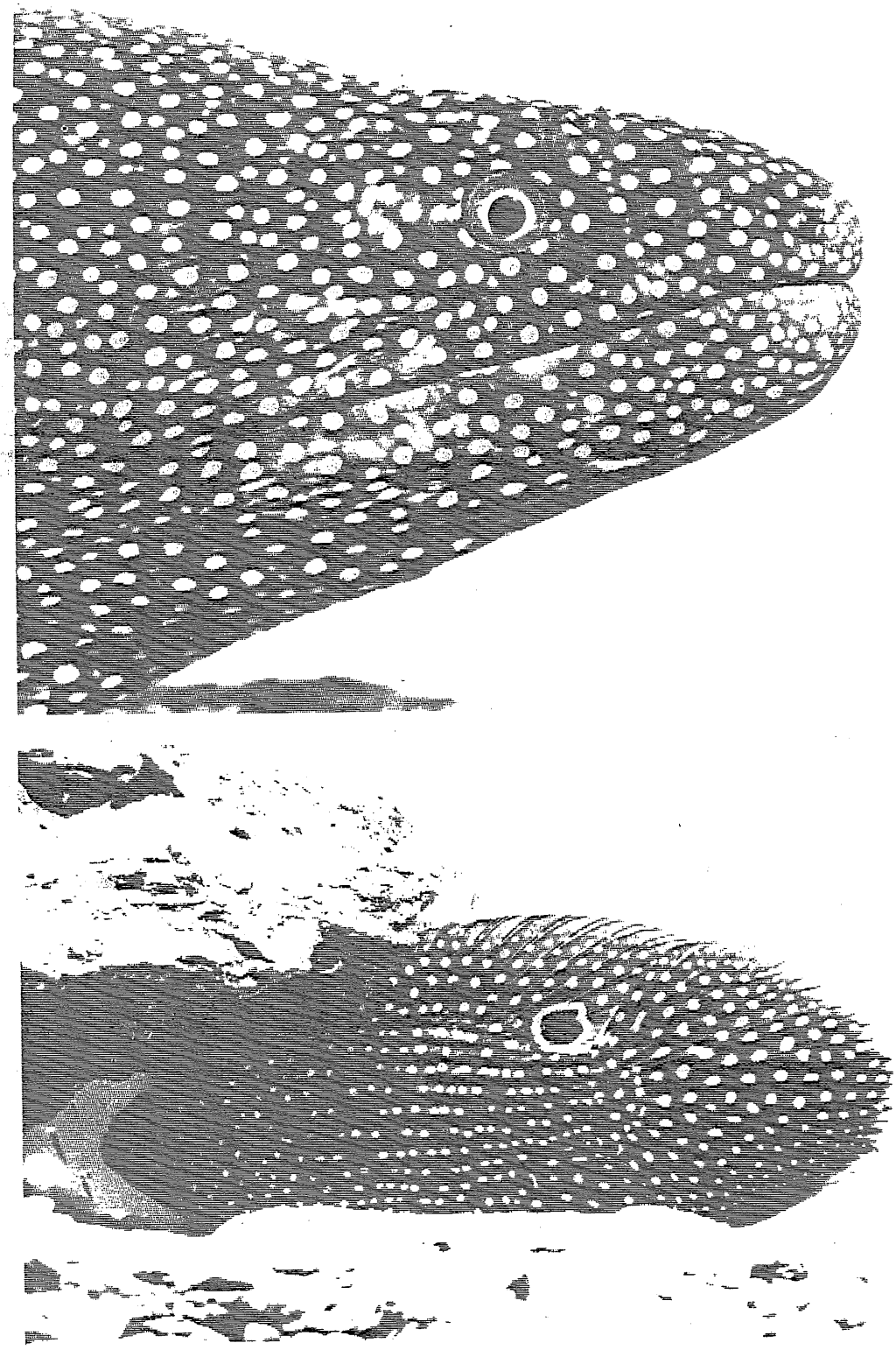
Reef fishes exhibit a wide variety of body shapes and structures that are clearly useful in discouraging attack. Tough skin (e.g., boxfishes), fin spines (e.g., scorpionfishes), exceptionally deep bodies (e.g., angelfishes) that can be expanded in some cases (e.g., triggerfishes), and the ability to inflate (e.g., puffers) interfere with a piscivore's ability to grasp and consume its prey. The mucous envelope produced by some parrotfishes during nocturnal inactivity may inhibit olfactory detection by moray eels (Winn and Bardach, 1959). Beyond obvious structures, the threat of predation has also undoubtedly selected for the swimming morphology of prey fishes that allows for rapid escape responses (Hobson and Chess, 1978).

2. Colors

Cryptic coloration, often associated with cirri and other structural modifications, is widespread among benthic reef fishes (e.g., clinid blennies). Crypsis may involve masquerade mimicry of inedible objects (Randall and Randall, 1960), often associated with special behaviors (e.g., pipefishes resembling seagrass). Prey fish may even resemble piscivores [Batesian mimicry (reviewed by Russell *et al.*, 1976)]. For example, a harmless cardinalfish of the genus *Fowleria* strongly resembles the venomous and piscivorous scorpionfish *Scorpaenodes guamensis* (Seigel and Adamson, 1983). The plesiopid *Calloplesiops altivelis* dives into a hole when frightened, but leaves its tail exposed. The tail strongly resembles the head of the moray eel *Gymnothorax meleagris*, complete with an appropriately placed eyespot (McCosker, 1977) (Fig. 3). An eyespot on the tail, especially when combined with obliterative coloration around the eye (e.g., some butterflyfishes), may also cause piscivores to misdirect their attacks (Neudecker, 1989). Finally, conspicuous "warning" (aposematic) coloration may advertise fish that are toxic (e.g., some puffers) or otherwise unpalatable (e.g., some butterflyfishes) (Neudecker, 1989).

3. Toxins

The slowest swimming and presumably most vulnerable reef fishes, the Tetraodontiformes, include many toxic species (Halstead, 1978). Puffers contain tetrodotoxin, among the most potent of neurotoxins, and the demersal eggs and larvae of some species are unpalatable to predators (Gladstone, 1987). Trunkfishes excrete ostracitoxin, which can kill other fish in confined areas. Skin toxins (crinotoxins) have also been identified in the moray eels *Gymnothorax nudivomer* and *Muraena helena*, soapfishes, some gobies, and soles of the



genus *Pardachirus* (Halstead, 1978; Randall *et al.*, 1981; Tachibana *et al.*, 1984). The blenniid *Meiacanthus atrodorsalis* not only has toxic buccal glands providing a defensive venomous bite, but also two nonvenomous mimics (the blenniids *Ecsenius bicolor* and *Runula laudanus*) that are apparent examples of Batesian mimicry (Losey, 1972b).

C. Behavioral Prey Defenses

The most obvious ways that reef fishes avoid predation are, first, by remaining close to shelter [including urchins and anemones (reviewed by Ehrlich, 1975)] and, second, by dodging a piscivore's final attack. Helfman (1986a, 1989) reviewed the behavioral interactions between prey fish and approaching piscivores. Three more subtle, but clearly important means of avoiding predation involve schooling behavior, spawning patterns, and daily activity patterns. The ubiquity of these behaviors bolsters the conclusion that the risk of predation is severe and widespread on coral reefs.

1. Schooling

That prey derive antipredatory benefits from living in groups is well documented among animals in general (reviewed by Bertram, 1978; Harvey and Greenwood, 1978), as well as fishes in particular (reviewed by Radakov, 1973; Hobson, 1978; Shaw, 1978; Partridge, 1982; Pitcher, 1986). Various mechanisms have been proposed to explain how schooling (polarized or nonpolarized) lowers the risk of predation. Besides social and foraging advantages, there is general agreement that avoiding predation is a major reason why so many reef fishes school or otherwise occur in groups. Heterospecific schools are common, although the foraging advantages of such groups are difficult to separate from the safety advantages (e.g., Ehrlich and Ehrlich, 1973; Ormond, 1980; Wolf, 1987). In an unusual case, postlarval haemulid grunts school on reefs with similarly sized mysid "shrimp," which they apparently use as a source of both safety and food (McFarland and Kotchian, 1982).

There is considerable evidence that groups of reef fishes may actually mob and otherwise harass piscivores (Johannes, 1981; Dubin, 1982; Motta, 1983; Donaldson, 1984; Sweatman, 1984; Ishihara, 1987). Reciprocally, by attacking in groups, some piscivores effectively isolate individual prey from schools (Major, 1978; Schmitt and Strand, 1982). In any case, large spawning

Figure 3 Batesian mimicry by the plesiopid *Calloplesiops altivelis*. *Above:* the model moray eel *Gymnothorax meleagris*, in typical posture with its head exposed from a reef crevice (ca. 15 cm head length). *Below:* intimidation posture by the mimic, which enters crevices when frightened but leaves its tail exposed (ca. 15 cm TL). (Photos courtesy of Tom McHugh, Steinhart Aquarium.)

aggregations of reef fishes appear to suffer little predation, although their eggs are often not so lucky (Colin, 1976, 1978, 1982, 1989; Colin and Clavijo, 1978, 1988; Bell and Colin, 1986).

2. *Spawning Patterns*

Johannes (1978a, 1981) compiled a large body of evidence suggesting that the timing, location, and behavior of spawning in reef fishes are strongly affected by the risk of predation on adults and their eggs (see also Thresher, 1984). Table 2 summarizes Johannes' interpretation of various patterns. Overall, reef fishes appear to spawn when and where both the risk of predation on adults is minimized and the probability of eggs and larvae drifting safely away from the reef is maximized. Johannes (1978a, 1981) argued convincingly that the planktonic dispersal of reef fish larvae evolved primarily as a refuge from the severe risk of predation by planktivores on reefs (documented by Hobson and Chess, 1978; Leis, 1981; Hamner *et al.*, 1988). Corroborating these ideas, Gladstone and Westoby (1988) showed that relatively invulnerable toxic reef fishes do not display the patterns listed in Table 2. Instead, toxic fishes unhurriedly court and spawn throughout the day, do not defend their toxic demersal eggs, and spawning and hatching are unrelated to tidal cycles. Note, however, that one can provide adaptive explanations for virtually any observed behavior. Johannes' (1978a) hypotheses remain largely untested (Shapiro *et al.*, 1988), and other hypotheses for larval dispersal have been proposed (Barlow, 1981; Doherty *et al.*, 1985).

3. *Daily Activity Patterns*

Reef fishes worldwide exhibit pronounced behavioral shifts associated with daily cycles of sunlight. Detailed studies of this phenomenon have been made

Table 2 Hypothesized Ways That Spawning Coral Reef Fishes Minimize the Risk of Predation from Reef-Based Piscivores and Planktivores[a]

Reproductive behavior	Hypothesized advantage
Broadcast Spawners (most species)	
Offshore spawning migration	Reduces predation on eggs and larvae
Spawning near shelter	Reduces predation on spawners
Vertical spawning rush	a. Reduces time spawners are exposed b. Reduces predation on eggs (off bottom)
Spawning during ebbing spring tides	Reduces predation on eggs (offshore)
Spawning at night	Reduces predation on spawners and eggs
Demersal Spawners	
Brood defense	Reduces predation on eggs
Live-bearers	Eliminates predation on eggs and larvae

[a] Extracted from Johannes (1978a).

in the Gulf of California (Hobson, 1965, 1968), Hawaii (Hobson, 1972), the Caribbean (Collette and Talbot, 1972), and the Great Barrier Reef (Domm and Domm, 1973). Hobson (1975, 1979) and Helfman (1978, 1986b) provide general reviews of these patterns. Crepuscular periods (dawn and dusk) are times when the specialized visual systems of both diurnal and nocturnal prey fishes, suited for detecting their own small prey, are ineffective for detecting piscivores (Munz and McFarland, 1973; McFarland and Munz, 1975c; McFarland, Chapter 2). Piscivores, on the other hand, have visual systems with maximum sensitivity in twilight, presumably because they do not require the specialized vision needed by strictly diurnal or nocturnal species. These relative constraints leave prey fishes particularly vulnerable to predation at twilight, a period when virtually all such species seek shelter. This behavior results in a brief "quiet period" when neither diurnal nor nocturnal species occupy the water column. Consistent with the risk of predation causing these patterns, smaller and more vulnerable fish seek shelter earlier and emerge later than larger individuals.

Associated with day–night shifts in activity are daily migrations between safe resting areas and relatively exposed feeding areas. Grunts spend the day schooling inactively on reefs, and after dusk migrate to nearby seagrass beds and feed (Ogden and Ehrlich, 1977). The fish migrate along predictable routes, where they are frequently intercepted by waiting lizardfish (McFarland *et al.*, 1979; Helfman *et al.*, 1982). Helfman's (1986a) manipulations of lizardfish models suggested that the timing of migration is influenced by the activity of these piscivores.

III. Correlative Evidence

The evidence reviewed in the previous section suggests that the risk of predation on coral reefs is great and that reef fishes have evolved a variety of mechanisms that minimize this risk. Such evidence is consistent with but not sufficient for demonstrating the importance of predation in structuring reef fish communities. Predation structures a prey assemblage by altering the absolute and relative abundances of species, thus affecting the distributions and perhaps the local diversity of the prey. There are both indirect and direct sources of evidence for such population- and community-level effects. In this section, I first review relevant predictions generated by the predation hypothesis, then evaluate the correlative evidence for each.

A. Predictions from Theory

Although a wide variety of specific predictions can be generated from the predation hypothesis, only a handful can presently be evaluated by data on reef

fishes. Two indirect predictions can be derived from general concepts, one concerning patterns of survivorship of prey cohorts and the other concerning prey refuge space. Two more direct predictions involve relationships between the abundance of predators and prey, and between predator abundance and local prey diversity.

1. Prey Survivorship

A general pattern from the literature is that small, young, or otherwise naive animals are more susceptible to predation than larger, older, experienced adults (Murdoch and Oaten, 1975; Taylor, 1984; Werner and Gilliam, 1984). Therefore, if predation affects prey abundance, then mortality is likely to be more severe for early-aged individuals than for adults, as has been argued for reef fish eggs, larvae, and juveniles (Johannes, 1978a). The resulting prediction is that cohorts of reef fishes under intense predation should suffer disproportionally high mortality early in life. Such a pattern is called "type III" survivorship (Pearl and Miner, 1935; Deevey, 1947) (Fig. 4A).

The inferential power of this prediction is weakened (but not destroyed) by two facts. First, mortality is not necessarily equivalent to death by predation, and acts of predation among reef fishes are notoriously difficult to observe. However, other sources of mortality (physical disturbances and pathogens) can be detected by careful monitoring. In the case of physical disturbances, storms may (Lassig, 1983) or may not (Walsh, 1983) be a source of mortality for reef fishes, while hypothermal events can be locally catastrophic (Bohnsack, 1983a). Considering pathogens, I know of no evidence of fatal epidemics among reef fishes, except perhaps the occasional mass mortalities of fantail filefish (*Pervagor spilosoma*) in Hawaii (unpublished observations), the causes of which have not been determined.

Second, as discussed in detail in Section V,B,6, type III survivorship provides evidence for the predation hypothesis only if initial population densities exceed levels at which resources become limiting. However, of the three types of survivorship curves depicted in Fig. 4A, type III is the pattern that would most quickly lower population size below some competitive threshold, and is the pattern most consistent with population size being limited by predation (Deevey, 1947).

2. Prey Refuge Availability

If the predation hypothesis is true, then the possibility exists that predators cause prey to compete for refuge space (Holt, 1984, 1987; Jeffries and Lawton, 1984). In this scenario, the competition and predation hypotheses intersect. Predation limits prey population sizes, with refuge availability setting the extent of this limit, as mediated by competition for refuges. Applied to reef fishes, such predation-induced competition has been advocated as the

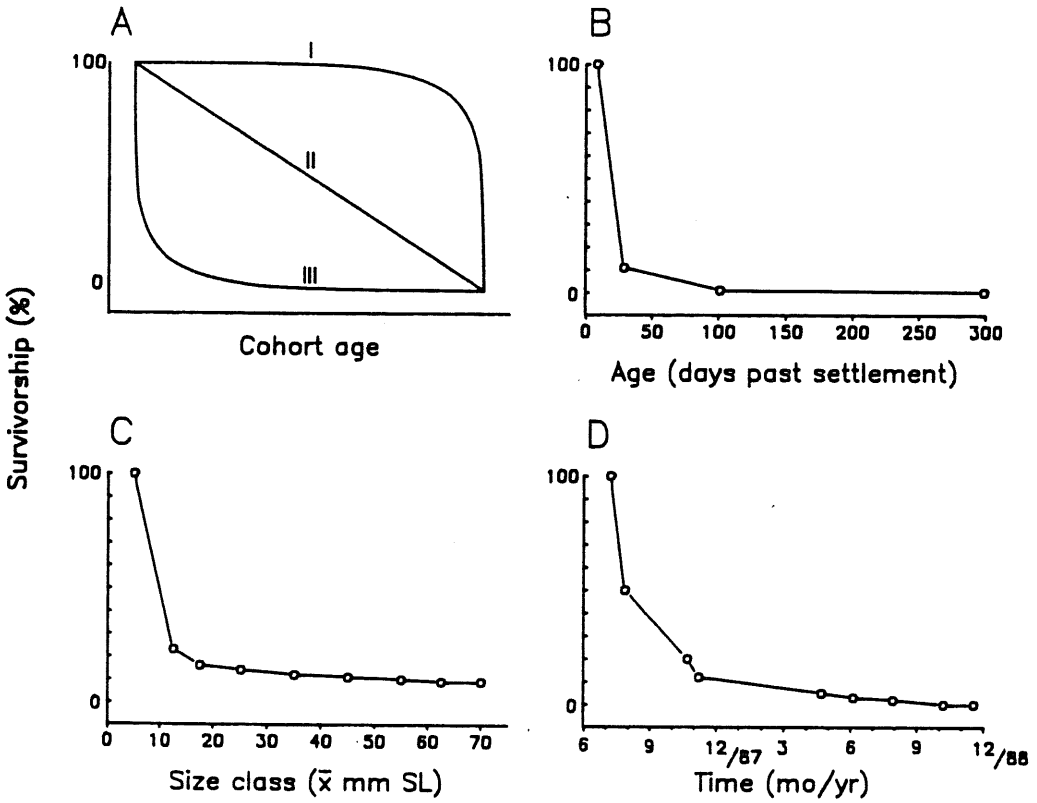


Figure 4 (*A*) The three basic types of survivorship curves, type III being most consistent with the predation hypothesis. Actual survivorship curves for: (*B*) French grunt (*Haemulon flavolineatum*) at St. Croix, U.S. Virgin Islands (extracted from Shulman and Ogden, 1987); (*C*) bluehead wrasse (*Thalassoma bifasciatum*) at the San Blas Islands, Panama (extracted from Warner and Hughes, 1988); and (*D*) blackbar soldierfish (*Myripristis jacobus*) at St. Thomas, U.S. Virgin Islands (M. A. Hixon and J. P. Beets, previously unpublished information).

hypothesis that structural shelters (holes) of the appropriate size are a primary limiting resource for reef fishes (e.g., Randall, 1963; Smith and Tyler, 1972, 1973b, 1975; Luckhurst and Luckhurst, 1978b; C. L. Smith, 1978). The correlative prediction is that comparing different reef systems should result in a positive relationship between refuge availability and prey fish densities.

Two problems in testing this prediction are, first, the potential difficulty of accurately characterizing and measuring refuge availability and, second, the fact that refuge availability may be correlated with other factors affecting fish densities independent of piscivory. In any case, the relationship between refuge availability and prey-fish densities is likely to change through time as the prey grow. In particular, prey fish may outgrow juvenile refuges and/or face different suites of predators, resulting in "ontogenetic niche shifts" between different subhabitats (reviewed by Werner and Gilliam, 1984).

3. Predation Effects on Prey Density

A more forthright means of detecting predation effects on community structure involves predictions concerning the relative abundances of piscivores and their prey. Applying predictions from general models of predator–prey population dynamics (reviewed by Taylor, 1984) is not directly possible because such models assume closed populations, where predator and prey birth and death rates are interactively linked. Local reef fish populations are generally open systems, where adult reproductive output is probably not linked to subsequent larval recruitment at the same site.

Nonetheless, the most basic prediction from the predation hypothesis is easy to derive without mathematics (see Warner and Hughes, 1988, for a more formal approach). First, in the absence of piscivores, the density of prey fish occupying a particular reef would reach a limit imposed by other processes, such as recruitment limitation or competition. Second, if the density of piscivores increased to a level at which they reduced the density of prey, then predation would become the predominant process limiting prey-fish abundance. The resulting correlative prediction is that, if the predation hypothesis is true, then a comparison of otherwise similar reef systems with broadly different piscivore densities should result in a negative relationship between piscivore and prey-fish densities.

4. Predation Effects on Prey Diversity

If the predation hypothesis is true, then local prey species richness and/or evenness should shift in predictable ways as predation intensity increases over a broad range. The two major patterns observed in other systems and predicted by various models are that prey diversity should either decline monotonically or initially increase then subsequently decrease as predation intensity increases from zero to high levels (reviewed by Hixon, 1986; Ebeling and Hixon, Chapter 18).

B. Patterns of Prey-Fish Survivorship

Having derived specific correlative predictions from the predation hypothesis, what is the evidence? As explained in Section III,A,1, cohorts of reef fishes regulated by predation are likely to exhibit type III survivorship curves (Fig. 4A). Unfortunately, field survivorship data for reef fishes have been virtually nonexistent until recently. Most studies have investigated survival only during the first few weeks after settlement, and in most cases, mortality is quite high during this period (Doherty and Sale, 1986; Victor, 1986b; Meekan, 1988; Sale and Ferrell, 1988). However, for the type III survivorship model to be tested adequately, survival must be monitored into adulthood. I am aware of

seven studies that have followed survivorship for at least the first year of postsettlement life.

Four of these studies, all conducted on the Great Barrier Reef, did not report sufficient data to construct lifelong survivorship curves. Doherty (1982) found that approximately 20% of transplanted recruits of *Pomacentrus flavicauda* survived a year at One Tree Island. At the same site, Doherty (1983a) estimated 75% survival of transplanted *P. wardi* recruits after one year. This is by far the highest survivorship yet documented, yet this value may be somewhat inflated because Doherty transplanted as many fish as necessary to establish a set stable number over the first few days of each experiment (P. F. Sale, personal communication). Thus, while the pattern of *P. flavicauda* is difficult to categorize, *P. wardi* apparently exhibited either type I or II survivorship (Fig. 4A).

Aldenhoven (1986b) monitored harems of the angelfish *Centropyge bicolor* over three years at four sites at Lizard Island. She found 10-fold differences in mortality between two sites, but did not investigate causation. Although she found that mortality did not vary significantly with size, she noted that "a significant decreasing trend in mortality with increasing size may have been found in each area had more data been available" (p. 239). Such a pattern would have indicated type III survivorship. Finally, Eckert (1987) monitored survival of various wrasses on ten patch reefs at One Tree Island. She followed multiple cohorts of new recruits of 11 species for one year. Of 27 cohorts that included at least five fish initially, 24 showed monthly mortality better described statistically as declining exponentially rather than linearly, indicating type III survivorship. Moreover, in comparing 9 species for which Eckert gathered data on both new recruits and adults, I calculated that the weighted average annual mortality for recruits was 78.0%, while that of adults was 20.6%, again indicating type III survivorship.

Three more complete data sets also support the prediction of type III survivorship. Shulman and Ogden (1987) estimated the survival of French grunt (*Haemulon flavolineatum*) from settlement to about one year of age at St. Croix, U.S. Virgin Islands (Fig. 4B). Warner and Hughes (1988) summarized postsettlement, size-based survivorship data from Warner (1984) and Victor (1986b) on bluehead wrasse (*Thalassoma bifasciatum*) at the San Blas Islands off the Caribbean coast of Panama (Fig. 4C). In this case, size was approximately linearly related to age for fish up to 75 mm TL (at least one year past settlement). Finally, J. P. Beets and I are following the survivorship of cohorts of various species on isolated artificial reefs at St. Thomas, U.S. Virgin Islands. Figure 4D is a typical pattern from our study, showing the fate of a single cohort of about 100 blackbar soldierfish (*Myripristis jacobus*) on one such reef. Logarithmic plots of the three data sets in Fig. 4 are still hyperbolic, indicating that cohorts of all three species exhibited type III survivorship and

suffered disproportionally high mortality early in life (Deevey, 1947). While mortality can have several sources, the investigators in all of these studies could detect no source other than predation. At the same time, virtually all studies to date have equated disappearance with mortality. The role of juvenile emigration remains largely unknown (Robertson, 1988a), indicating a need for monitoring tagged or otherwise recognizable individuals.

C. Prey-Fish Density versus Refuge Availability

Consistent with the prediction developed in Section III,A,2, there is considerable circumstantial evidence that reef fishes compete for shelter holes as refuges from predation. First, observations and experiments indicate that fish select shelter holes closely matching their body sizes, which would minimize the risk of predation within those holes (Robertson and Sheldon, 1979; Shulman, 1984; Hixon and Beets, 1989). Second, fish often defend shelter sites, suggesting that suitable holes are in short supply (Low, 1971; Hobson, 1972; Ebersole, 1977; McFarland and Hillis, 1982; Shulman, 1985a). Third, settlement (by postlarvae) and/or colonization (by juveniles and adults) is often more rapid to empty sites than to similar sites already occupied by fish, consistent with there being competition for shelter [Sale, 1976; Talbot *et al.*, 1978; Sweatman, 1985a (one of two species)]. Fourth, juveniles and adults (in addition to postlarvae) rapidly colonize artificial reefs or denuded natural reefs, suggesting that nearby natural reefs are crowded (Randall, 1963; Sale and Dybdahl, 1975; Molles, 1978; Talbot *et al.*, 1978; Bohnsack and Talbot, 1980; Shulman *et al.*, 1983; Walsh, 1985; Hixon and Beets, 1989; Bohnsack, 1990).

There have been a considerable number of community-level studies relevant to the prediction of a positive correlation between refuge availability and prey-fish densities. Unfortunately, all but one of these studies examined fishes in general, including predators and prey, as well as habitat complexity in general, which is not necessarily equivalent to refuge availability. Perhaps as a consequence, the evidence has been mixed. On one hand, both Luckhurst and Luckhurst (1978c) and Carpenter *et al.* (1981) found significant correlations between reef-substrate complexity and fish abundance in the Caribbean and the Philippines, respectively. Temporally, the abundance of resident fishes decreased dramatically following the collapse of a Japanese reef caused by the coral-eating seastar *Acanthaster planci* (Sano *et al.*, 1987). The authors associated this decline to the associated decrease in shelter availability, although food abundance was also undoubtedly affected. On the other hand, both Risk (1972) and Sale and Douglas (1984) detected no correlation between habitat complexity and fish abundance when comparing reefs in the Caribbean and

the Great Barrier Reef, respectively. In a study examining a single guild, Thresher (1983a,b) similarly found no correlation between an index of topographical relief and the abundance of planktivorous fishes at the Great Barrier Reef. However, in the most thorough such study to date, Roberts and Ormond (1987) examined both structural complexity in general and hole density per se in Red Sea reefs. A stepwise multiple regression of these and other habitat variables showed that the density of holes in the reefs accounted for 77% of the variance in fish abundance.

Concerning ontogenetic niche shifts involving prey refuges, Shulman (1985b) documented that juvenile grunts in the Caribbean refuge effectively in seagrass beds, where piscivores are relatively rare. The grunts shift to sheltering in nearby reefs only when they become too large to hide among seagrass blades. This spatiotemporal correlation is more consistent with the predation hypothesis than with other explanations, especially given that adult grunts continue to forage in seagrass beds nocturnally (see Section II,C,3).

D. Prey-Fish Density versus Piscivore Density

Several studies provide correlative evidence testing the predicted negative relationship between the densities of piscivores and their prey (Section III,A,3). At One Tree Island on the Great Barrier Reef, Thresher (1983a) compared 26 patch reefs and documented a significant inverse relationship between the abundance of the piscivorous serranid *Plectropomus leopardus* and the abundances of both the diurnal planktivorous pomacentrid *Acanthochromis polyacanthus* and a group of four nocturnally planktivorous cardinalfishes. Interestingly, there was no correlation between the abundance of these potential prey and the total abundance of all piscivores on the reefs. There was also no correlation involving a group of 12 diurnally planktivorous species. In the same study, Thresher (1983b) noted that, over a year-long period, adult *Acanthochromis* disappeared on 3 of 4 reefs where *Plectropomus* occurred, but on only 1 of 20 reefs where the piscivore was absent. He also noted that the percentage mortality of 27 broods of juvenile *Acanthochromis* over 30 days was positively correlated with the mean total of all fish present, but was not correlated with the number of piscivores per se. Overall, such contradictory patterns are difficult to interpret.

At St. Croix in the Caribbean, Shulman *et al.* (1983) examined colonization and recruitment patterns on 30 concrete-block reefs (11 blocks per reef) over two months. On reefs with early immigration by small snappers (*Lutjanus* spp.), subsequent recruitment and/or survival of grunts (*Haemulon* and *Equetus* spp.) was significantly lower than on reefs where grunts settled without such piscivores. Off Miami, Florida, Bohnsack (1990) observed a similar

pattern with respect to immigration by the apparently piscivorous serranid *Diplectrum formosum* and recruitment and/or survival of various species on larger artificial reefs.

In another study at St. Croix, Shulman (1985b) followed recruitment to meter-square plots of conch shells placed various distances from a reef. She found increasing rates of recruitment with increasing distance from the reef. Typical of the Caribbean, the reef was surrounded by a grazed bare "halo zone" that gave way to a seagrass bed farther from the reef. In a series of experiments, Shulman manipulated natural and artificial seagrass, which provided shelter for new recruits, and followed the fates of juvenile grunts tethered at various distances from the reef. Her results suggested that the risk of predation facing new recruits decreased with increasing distance from the reef, following the predicted pattern.

Finally, Hixon and Beets (1989) examined fish assemblages that developed on isolated, cubic-meter, concrete-block reefs (48–72 blocks per reef) at St. Thomas in the Caribbean. Over the 30-month duration of their study, they detected a highly significant negative regression between the number of resident piscivores (moray eels, squirrelfishes, and groupers) and the maximum number of potential prey fish (defined as fishes small enough to be consumed by the piscivores, mostly juvenile grunts) occupying a reef (Fig. 5A).

At the level of individual species, Hixon and Beets (unpublished data) followed the fates of recruit cohorts of the damselfish *Chromis cyaneus,* which settled simultaneously and in nearly equal abundance among three adjacent reefs. Survivorship of these cohorts over the first 3 months following settlement was inversely correlated with the abundance of piscivores on these reefs. Taken together, these correlative studies support the idea that piscivores do affect the density of their prey.

E. Prey-Fish Diversity versus Piscivore Density

If predation structures reef fish assemblages, then local prey-fish diversity should respond to broad ranges in predation intensity (Section III,A,4). An ongoing study by J. P. Beets and myself on fish assemblages occupying artificial and natural reefs at St. Thomas provides the only relevant data of which I am aware. Figure 5B illustrates the same reef censuses as Fig. 5A (see above), showing the number of potential prey species as a function of the number of resident piscivores occupying a reef. Assuming that predation intensity increased with piscivore density, this statistically significant pattern suggests that predation negatively affected local prey species richness. While there are a number of possible mechanisms that could produce this pattern (reviewed by Hixon, 1986; Ebeling and Hixon, Chapter 18), it appears that piscivores in this system simply extirpated locally rare species.

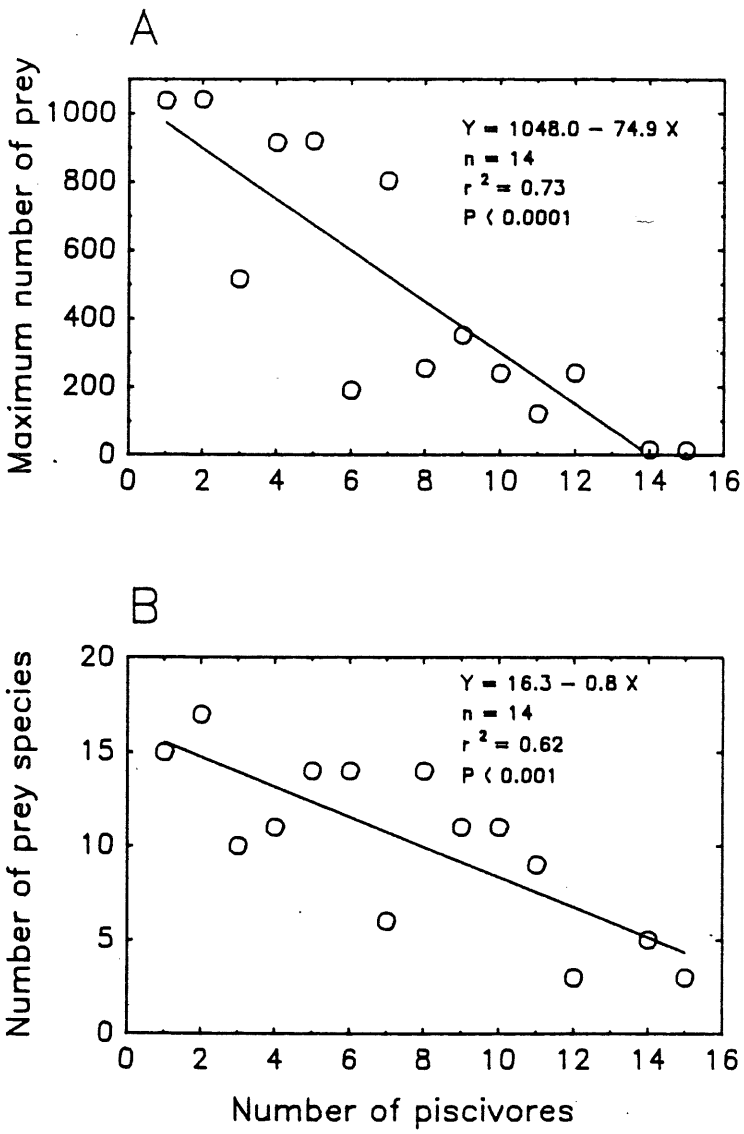


Figure 5 (*A*) Maximum observed number of potential prey fish as a function of the number of piscivorous fish occupying artificial reefs at St. Thomas, U.S. Virgin Islands. (Modified from Hixon and Beets, 1989.) (*B*) Same censuses as the previous graph, examining the number of potential prey species as a function of piscivore abundance (M. A. Hixon and J. P. Beets, previously unpublished information).

IV. Experimental Evidence

Two predictions developed in Section III,A have been evaluated experimentally. With suitable controls, the relatively indirect prediction of a positive relationship between refuge availability and prey-fish densities can be tested by

manipulating shelter holes or fish densities. Similarly, the more direct prediction of a negative relationship between piscivore and prey-fish densities can be tested by population manipulations of either predators or prey. Unfortunately, few such experiments have been attempted, and those manipulating piscivore densities have encountered problems in design or implementation.

A. Prey-Fish Density versus Refuge Availability

Five separate studies have manipulated refuge availability with suitable controls, three involving natural shelters and two involving artificial reefs.

1. Natural Refuges

At the San Blas Islands in the Caribbean, Robertson and Sheldon (1979) investigated possible nocturnal shelter limitation for bluehead wrasse. When natural shelter holes were removed, displaced fish found unoccupied shelters nearby. When fish were removed, few of the vacated shelters were used by other fish. When fish were added to a reef, the immigrants readily found unoccupied shelters and survived for the 2-month duration of the study. At the same site, Robertson *et al.* (1981) manipulated territory sites, including shelter holes, of the damselfish *Eupomacentrus* (now *Stegastes*) *planifrons* by, first, removing all substrate within territories (leaving bare sand) and, second, removing half of three entire patch reefs (originally measuring 5–11 m in diameter). These manipulations effectively increased local population densities by 50%, yet the displaced fish readily reestablished territories near their old sites and persisted through the 3-month duration of the former experiment and the year-long duration of the latter. Clearly, refuge availability did not limit local population size for either the wrasse or the damselfish.

At the Red Sea, Fricke (1980) manipulated shelter for social groups of the damselfish *Dascyllus marginatus*, which permanently occupy distinct coral heads. Translocating equal-sized heads that normally supported about three to four fish, he established isolated "blocks" of one, three, and six heads and seeded each with various combinations of six fish. Following the prediction, subsequent survival was significantly greater on the larger blocks. Fricke noted that more fish were aggressively expelled from the smaller, crowded blocks by dominant group members, and that many of those expelled were eaten by lizardfish and groupers.

2. Artificial Refuges

At St. Croix, Shulman (1984) monitored recruitment to small arrays of conch shells modified to provide zero, one, or two holes per shell. Over periods ranging between 3 and 8 weeks, she found greater recruitment to shells providing more holes. Similarly, comparing arrays of two concrete blocks to

meter-square arrays of conch shells or branching coral, thus providing a gradient of increasing shelter, Shulman found the predicted positive relationship between the abundance of recruits and shelter availability.

Only one study of larger artificial reefs has included adequate controls for testing shelter limitation. Previous studies (e.g., Talbot *et al.,* 1978) sometimes included holeless control reefs, but invariably confounded hole size and hole number (i.e., reefs with more holes had larger holes). At St. Thomas, Hixon and Beets (1989) compared fish assemblages occupying isolated concrete-block reefs of identical size (about 1 m^3) varying only in the number (0, 12, or 24) of identically sized holes (12 × 14 cm). We found that, as predicted, reefs with more holes supported more fish of that size over a 30-month period. The fact that the 24-hole reefs provided more (yet less variable) refuges than comparably sized natural reefs near this site indicated that experimental refuge limitation at this scale was realistic.

B. Prey-Fish Density versus Piscivore Density

The most direct test for a causal relationship between predator and prey abundances is to manipulate experimentally either the predator or the prey populations, including both controls and replication (Connell, 1974, 1975). To my knowledge, only predator manipulations have been attempted for reef fishes, and only four such studies have been published. The first of these was more a correlative study than an experiment (Bohnsack, 1982); the second lacked replication and failed to document a significant manipulation (Stimson *et al.,* 1982); the third lacked sufficient replication (Thresher, 1983b); and the fourth included a variety of artifacts (Doherty and Sale, 1986). Because two of these studies appeared in publications that were not widely circulated (Bohnsack, 1982; Stimson *et al.,* 1982), I provide detailed summaries.

1. Removal by Spearfishing

Bohnsack (1982) compared piscivore and potential prey-fish abundances on heavily fished versus relatively unfished reefs in the Florida Keys from 1979 to 1981. Looe Key Reef ("removal") had been spearfished by sports divers for years, while some 100 km to the northeast, Molasses and French reefs ("controls") had been protected from spearfishing since 1960. Bohnsack used 20-min random-point censuses to estimate abundances of all fishes, mostly potential prey ($n=130$ censuses at the removal site, 63 and 40 at the controls), and 15-min searches to estimate only piscivore abundances ($n=33$ searches at the removal site, 17 and 12 at the controls).

The removal reef supported significantly fewer (and smaller) piscivorous fishes ($\bar{X}$ per census = 124 piscivores at the removal site, 757 and 204 at the controls), especially snappers, which accounted for over 75% of the total

piscivores. However, there was no significant difference among reefs in the total number of fish censused ($\bar{X}$ per census=273 at the removal site, 309 and 212 at the controls). Examining the 25 most abundant species, Bohnsack (1982) noted six species that were both significantly different in abundance between the removal and control reefs and not significantly different between the control reefs. In four of these cases, including the most abundant species overall (bluehead wrasse), the removal reef supported significantly more fish than the control reefs. (The other three species were the grunt *Haemulon aurolineatum*, the damselfish *Eupomacentrus planifrons*, and the wrasse *Halichoeres garnoti*.) Bohnsack concluded forthrightly: "stating that piscivorous predation is an important factor controlling community structure of reef fishes based on present evidence would be premature" (1982, p. 266). On the basis of a similar study involving various fishing methods in the Philippines, Russ (1985) reached the same conclusion (see also Russ and Alcala, 1989).

More recently, R. E. Schroeder (personal communication) attempted an experimental spearfishing removal at Midway Lagoon, Hawaii. Following one year of baseline observations, more than 2500 piscivores were removed from four of eight patch reefs over a three-year period. Despite this marathon effort, virtually no change in the prey-fish fauna could be detected; continuous immigration resulted in no net change in piscivore abundance or biomass. M. J. Shulman (personal communication) had encountered the same problem in attempting to remove moray eels from Randall's (1963) artificial reef in the Virgin Islands.

2. *Removal by Trapping*

Stimson *et al.* (1982) attempted an eel removal experiment in Kaneohe Bay, Oahu, Hawaii. Muraenids and congrids were trapped throughout the one-year study on two isolated 30-m-diameter patch reefs separated by 0.5 km. Eels captured at the control reef were tagged, measured, and released, while those captured at the removal reef were translocated to nonexperimental reefs. The gut contents of the eels were not examined. Unfortunately, the "catch per trap night" of eels did not decline appreciably on the removal reef throughout the study, bringing into question whether or not this study actually manipulated piscivore densities significantly. The abundances of potential prey fishes were estimated by counting the number of fish swimming over fixed 6-m lines per unit time. This method conceivably resulted in fish whose home ranges overlapped the lines being counted repeatedly, yet such biases were at least consistent between the reefs. Eels were not censused visually.

The results of this experiment were presented somewhat obscurely. Data on changes in the abundance of only one species (the butterflyfish *Chaetodon miliaris*) were reported, this being the third most abundant species at the beginning of the experiment (326 "line crossings"). [Note that this species is

mislabeled as *Dascyllus albisella* in the second figure of the publication (J. Stimson, personal communication).] For the two most abundant taxa (initially 735 and 834 line crossings, respectively), Stimson *et al.* (1982) simply stated that "no obvious differences in relative densities or size distributions were found for *Thalassoma duperrey* [a wrasse] and *Scarus* sp. [parrotfish] between reefs over time" (p. 3). There was no appreciable change in the density of *C. miliaris* throughout the experiment at the control reef. At the removal reef, there was no change until the very last census of the experiment, when a sudden immigration of adult *C. miliaris* (>10 cm TL) occurred. Stimson *et al.* examined their census data with a discriminant function analysis, which indicated that the similarity of the two fish assemblages had diverged through time. The authors concluded that "eels alone can evidently alter community structure of reef fishes" (p. 5). Given the results as presented in this paper, this conclusion seems unwarranted.

3. *Removal by Poisoning*

Thresher (1983b) examined the effects of other fishes on the survivorship of juvenile *Acanthochromis* at One Tree Island, Great Barrier Reef. Unlike other reef fishes, the larvae and juveniles of this species remain with their parents. In June 1980 (between spawning seasons), Thresher subjected small patch reefs to one of three treatments, each of which left the resident pair of *Acanthochromis* in place: (1) unmanipulated controls (three reefs); (2) removal of all fishes, that is, all potential predators and competitors (four reefs); and (3) removal of all planktivores, presumably only competitors for food (three reefs, but only one was subsequently studied because the *Acanthochromis* disappeared). The reefs he selected had exhibited comparable juvenile survivorships the previous spawning season. The manipulations were accomplished by capturing the resident *Acanthochromis* with an anesthetic and holding them upstream while either all the remaining fish were poisoned or only planktivores were collected with anesthetic. From October 1980 to January 1981, Thresher recensused these reefs an unreported number of times. The small sample sizes did not allow meaningful statistical comparisons.

Thresher predicted that the survivorship of juvenile *Acanthochromis* over 30 days would be highest on the reefs where all other fishes were removed, intermediate on the planktivore-cleared reefs, and lowest on the control reefs. While average survivorship was indeed greatest on the completely denuded reefs, there was little difference between the planktivore-cleared and control reefs (Fig. 6). However, the patterns on the denuded reefs were similar to those on the same reefs the year before the experiment, when no manipulations were made. Thus, these results are suggestive of a predation effect, yet somewhat equivocal.

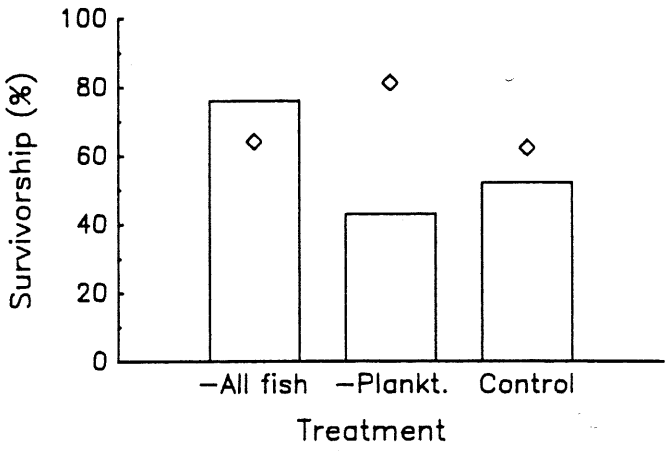


Figure 6 Mean survivorship over 30 days of juveniles of the damselfish *Acanthochromis polyacanthus* on patch reefs under three treatments: all fish except parents removed (*−All fish*; $n=4$ reefs), only planktivores removed (*−Plankt.*; $n=1$), and unmanipulated control (*Control*; $n=3$). The diamonds represent the mean values for the same reefs during the previous year, when no manipulations were made. (Modified from Thresher, 1983b.)

4. Removal by Caging

In the most carefully designed and executed study to date, Doherty and Sale (1986) monitored recruitment of fishes to caged and uncaged 3.24-m^2 plots at One Tree Island. They designed their experiment to avoid a major artifact encountered during previous unpublished and apparently unsuccessful studies: leaving piscivore-exclusion cages in place too long resulted in abundant algal growth inside (due to exclusion of herbivores), which left the results impossible to interpret accurately. In a series of four independent trials, each lasting from about 15 to 30 days and involving 7 to 11 complete visual censuses, Doherty and Sale studied 8 to 10 replicate plots subjected to one of three treatments: (1) fully caged with 10-mm wire mesh (2 m^3 per 0.6-m-high cage), which effectively excluded piscivores, but not settling postlarvae; (2) partially caged with a full roof and half of each wall; and (3) uncaged. The partial cage was designed to control for secondary cage effects, presumably allowing access by piscivores. All cages were cleaned regularly to prevent fouling.

The average outcome of all trials was that there were always more juvenile fish in the full cages than the partial cages or open plots, superficially supporting the prediction of the predation hypothesis. However, this trend was never statistically significant because of high variances; an *a posteriori* power analysis

determined that reducing the chance of a type II error to 5% would have required about 90 replicates per treatment. Moreover, some fishes showed unanticipated evidence of: partial cages providing partial protection from predation; fish settling differentially on caged plots, apparently selecting the high relief offered by the cages; postsettlement movement of fish among plots; and an apparent preference by settlers for the disturbed substrate bordering the plots.

Despite these problems, which Doherty and Sale (1986) forthrightly acknowledged, one category of fishes during one trial appeared to provide a convincing pattern. Recruits of these fishes (solitary and sedentary butterflyfishes, damselfishes, and wrasses) could be recognized and followed as individuals, and they apparently did not produce the problems listed above. As a group, these fishes settled evenly among the three treatments and remained in the plots where they settled. During the first 15 days following settlement, apparent survivorship in fully caged plots was considerably greater than that in both the partially caged and open plots (Fig. 7). Surprisingly, Doherty and Sale (1986) interpreted this pattern as not so much supporting the predation hypothesis as indicating the relative importance of the recruitment limitation hypothesis: "it seems likely that density limitation in these populations occurs before settlement ... predation on recruited individuals simply widens the gap between potential and realized densities in this system" (p. 233).

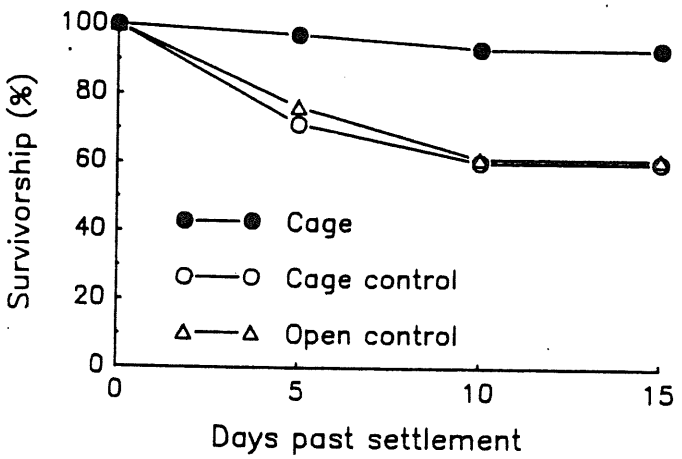


Figure 7 Survivorship of juveniles of solitary, sedentary reef fishes under three treatments: within piscivore-exclusion cages (*Cage*), within partial cages (*Cage control*), and within open plots (*Open control*). (Modified from Doherty and Sale, 1986.)

V. SYNTHESIS

A. Conclusions from the Evidence

Overall, there is insufficient evidence to conclude unequivocally that piscivores strongly affect the absolute and relative abundances and, by extension, the community structure of reef fishes in many systems. The circumstantial evidence that piscivory has been a powerful selective agent molding the morphology and behavior of reef fishes is diverse and convincing (Section II). This evidence strongly suggests that researchers should pay more attention to the possibility that piscivory is a major process structuring reef fish assemblages.

Correlative evidence evaluating the predation hypothesis has been less abundant, yet largely supportive. All species studied through adulthood suffer disproportionally high mortality shortly after settlement (type III survivorship), apparently due to severe predation on new recruits (Section III,B). Evidence for a positive correlation between shelter availability and prey-fish density, based on the hypothesis that the risk of predation forces prey fishes to compete for refuge space, has been mixed (Section III,C). This may be because all but one of these nonexperimental studies examined fishes in general (not prey fish per se) and habitat complexity in general (not shelter availability per se). Finally, several studies have documented a significant negative relationship between piscivore and prey-fish densities, the strongest correlative inference supporting the predation hypothesis to date (Section III,D). Considering piscivore effects on local prey-fish diversity, only a single study has provided relevant data: a significant inverse relationship between piscivore abundance and prey species richness (Section III,E).

There have been very few field experiments relevant to the predation hypothesis, and these have provided mixed and ambiguous results. Tests for predation-induced competition for refuge space have demonstrated excess shelter for two local populations, yet limited shelter for three other systems (Section IV,A). Direct piscivore manipulations have faced various problems in design and implementation, and to date have produced equivocal results (Section IV,B).

B. Predation in Context: A Continuum of Processes

In this section, I offer my ideas on how we can best approach the question of what processes, including predation, structure assemblages of reef fishes. In so doing, I synthesize and extend the work of many researchers. Basically, I suggest that we stop treating different processes as being mutually exclusive,

and instead examine their relative contributions to structuring communities (see also Jones, Chapter 11).

In the introduction to this Chapter (Section I,A), I simplistically state the competition, recruitment limitation, and predation hypotheses as mutually exclusive alternatives. Unfortunately, this approach has been embraced by most reef fish ecologists, resulting in an artificial controversy that has persisted for over a decade (Sale, 1984, 1988a). Despite similar controversies among community ecologists in general (see Salt, 1984; Strong *et al.,* 1984a; Diamond and Case, 1986), various researchers have reached the conclusion that most communities are not structured by a single predominant process (e.g., Strong *et al.,* 1984a; Diamond and Case, 1986; Menge and Sutherland, 1987; Hixon and Menge, 1991). Only recently have some reef fish ecologists followed suit (e.g., Shulman and Ogden, 1987; Warner and Hughes, 1988). Even the most avid proponents of recruitment limitation have lately adopted this new attitude, and now acknowledge the potential importance of predation-induced mortality after recruitment (Victor, 1986b; Doherty and Williams, 1988a,b).

Considering only the three processes treated here, it is easy to envision a combination of low larval abundance (recruitment limitation) and high postsettlement predation precluding competition for food (Victor, 1986b), yet forcing prey fishes to compete for refuge space (Holt, 1984, 1987; Jeffries and Lawton, 1984). Clearly, such complex reality would render controversy over the predominant process meaningless. A more realistic controversy would address the relative contribution of each process. Once this determination was made for all local populations belonging to a particular guild, one could then draw cogent conclusions concerning the determinants of community structure *at a particular place and time*. I stress the last part of the previous sentence because repeated overgeneralizing from one study of one species at one site over one period has unnecessarily aggravated the ongoing controversy. Indeed, given that most of the evidence for recruitment limitation has come from damselfishes on the Great Barrier Reef (reviewed by Doherty and Williams, 1988a), while most evidence favoring the predation hypothesis has come from grunts in the Virgin Islands (Shulman, 1984, 1985a; Shulman and Ogden, 1987; Hixon and Beets, 1989), we are hardly in a position to generalize either hypothesis.

As a prelude to examining experimental designs, consider the circumstances under which presettlement mortality, postsettlement predation, and competition would each be the major process structuring a local reef fish population. Extending Victor's (1986b) graphical model, Fig. 8 illustrates a variety of hypothetical survivorship curves for an average cohort, from the time of spawning (fertilization), through settlement (S), to the death of the longest-

lived individual. The initial abundance at spawning represents the number of postlarvae that would settle on a particular reef (following dilution due to dispersal) if there was zero mortality in the plankton. I define $\mathbf{N_c}$ as the mean postsettlement population density (over the life span of the cohort) above which competition for nonrefuge resources becomes detectable through experimentation. Victor (1986b) used adult carrying capacity here, but there are problems with applying this concept (Peters, 1976; Sale, 1979a). Note that $\mathbf{N_c}$ in reality is not so much a threshold density as a range of densities, resulting in a gradient of increasing resource limitation and varying at different life stages. (Note also that the relative position of $\mathbf{N_c}$ along the ordinates and **S** along the abscissas is purely arbitrary to allow comparison between different scenarios.) In each plot on Fig. 8, the upper curve represents extreme type I postsettlement survivorship (low early-life mortality), while the lower curve represents extreme type III survivorship (high mortality, presumably due to predation; see Fig. 4A).

1. Competition

Figure 8A depicts the circumstances where either competition or predation is the predominant process determining the abundance and distribution of the cohort. As a result of relatively high recruitment, the initial density of recruits at settlement is above $\mathbf{N_c}$, setting the stage for competitive interactions. Subsequently, if the intensity of predation is low (upper curve region, **C**), then resources will remain limiting, and intraspecific (and possibly interspecific) competition will be the primary process determining resource use (niche breadth, etc.). Here I assume that competition will not be so severe as to grossly reduce survivorship to the point where the population density drops below $\mathbf{N_c}$. [In fact, studies of simple laboratory systems have demonstrated that severe competition can shift survivorship from type I to type II [see Fig. 4A], but virtually never to type III (Pearl, 1928; Deevey, 1947).]

2. Predation

If, on the other hand, postsettlement mortality due to predation is severe (lower curve region, **P**, in Fig. 8A), then piscivory has reduced the density of prey fish below $\mathbf{N_c}$, precluding competition for nonrefuge resources. This is the purest manifestation of the predation hypothesis. The possibility still exists that refuges from predation may be limiting, so that competition for shelter occurs (Holt, 1984, 1987; Jeffries and Lawton, 1984). Note that if survivorship was linear (Fig. 8A, type II), the predominant structuring process would shift from competition for nonrefuge resources early in life to predation later (perhaps including competition for refuges).

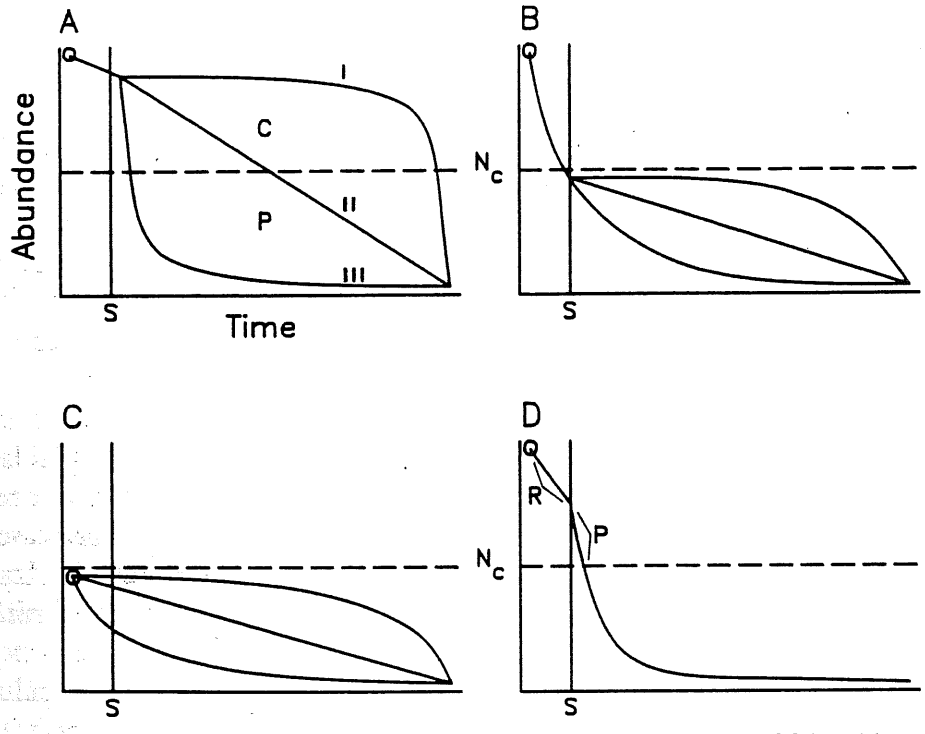


Figure 8 Hypothetical survivorship curves for a cohort of coral reef fish, with postsettlement survivorship ranging from extreme type I (upper curves) to extreme type III (lower curves). Each curve extends from the time of spawning (open circle), through planktonic larval life, postlarval settlement (**S**), juvenile, and adult life. The initial abundance (open circle) reflects the number of postlarvae that would settle on the reef if there was no mortality in the plankton. $\mathbf{N_c}$ is the mean postsettlement population size above which nonrefuge resources become limiting. The different sets of curves represent cases where the major process affecting the population is: **A,** competition (**C,** above $\mathbf{N_c}$) or predation (**P,** below $\mathbf{N_c}$); **B,** recruitment limitation; **C,** zygote limitation; or **D,** a nearly equal combination of presettlement mortality (the mechanism of recruitment limitation, **R**) and postsettlement predation (**P**). See text for discussion.

3. *Recruitment Limitation*

Figure 8B illustrates the purest manifestation of recruitment limitation [Victor's (1986b) "primary recruitment limitation"]. At settlement and subsequently independent of survivorship, the number of recruits is less than $\mathbf{N_c}$, precluding competition for nonrefuge resources. As before, if predation is severe, then the prey may still be forced to compete for refuge space. Moreover, to the extent that mortality in the plankton is caused by predation (reviewed by Frank and Leggett, 1985; Richards and Lindeman, 1987; Bailey and Houde, 1989), recruitment limitation can actually be considered a subset of a broader predation hypothesis.

4. *Zygote Limitation*

Figure 8C represents a possibility that, to my knowledge, has not been proposed for reef fishes. This is the situation where the initial number of zygotes at spawning is lower than $\mathbf{N_c}$. While some may consider this pattern simply a subset of recruitment limitation, Victor (1986b) asserted in his formulation of recruitment limitation that "the shortage of planktonic larvae certainly does not reflect the production of zygotes by spawning adults" (p. 145). Therefore, I believe that the distinction is important for separating causative mechanisms. If the initial number of zygotes is less than $\mathbf{N_c}$, which may be caused by any number of processes affecting adult abundance, spawning success, and/or larval dispersal, then subsequent mortality of eggs, larvae, juveniles, and adults is clearly irrelevant as far as competition for nonrefuge resources is concerned—such competition does not occur in any case. Of course, without data on the production and fate of zygotes, this "zygote limitation" hypothesis is indistinguishable from the recruitment limitation hypothesis, and therefore untestable.

5. *Combined Processes*

Thus far, I have considered mostly cases in which competition, predation, recruitment limitation, or zygote limitation is the predominant process structuring the population. Figure 8D represents what I hypothesize may approximate a typical pattern for reef fishes. As drawn, this survivorship curve shows presettlement mortality (the mechanism of recruitment limitation, **R**) and postsettlement mortality (predation, **P**) both contributing substantially to bringing the population density below $\mathbf{N_c}$. Victor (1986b) called such patterns "secondary recruitment limitation" when they occur before a cohort reaches sexual maturity. In fact, this pattern resembles the predation hypothesis (Fig. 8A, type III curve) more than the recruitment limitation hypothesis (Fig. 8B). Indeed, without the effect of predation or other postsettlement mortality, the population density exceeds $\mathbf{N_c}$ in this case, manifesting the competition hypothesis. Actually, arguing that one process is more important than the other is meaningless in this scenario. The point is that predation, especially on new recruits, can be every bit as important as presettlement recruitment limitation in precluding competition for nonrefuge resources (see also Talbot *et al.*, 1978).

6. *Conclusions*

The foregoing exercise provides three lessons for determining what structures reef fish assemblages. First, two or more processes may operate simultaneously in structuring a population or assemblage. Asserting that data consistent with one hypothesis falsify all alternatives is mere advocacy. For example, Doherty

and Sale's (1986) statement that predation serves only to limit population densities below levels that are already recruitment limited (see Section IV,B,4) asserts that the type III pattern in Fig. 8B is the truth. In fact, the type III patterns in Figs. 8A, C, and D are equally as viable given their data set.

Second, predation can play an important role regardless of whether it is the predominant process structuring a population or assemblage. In all cases illustrated in Fig. 8, predation may cause important secondary effects, having ramifications for community-level interactions. In particular, whether or not population densities are sufficiently high to cause competition for food or other nonrefuge resources, predation can conceivably cause prey to compete for refuge space (Holt, 1984, 1987; Jeffries and Lawton, 1984). Further, predation can reduce prey densities beyond reductions due to other factors. In particular, if two prey species are competing for food, differential predation on the dominant may tilt the effective competitive asymmetry to the otherwise subordinate species (reviewed by Sih *et al.*, 1985).

Third, *postsettlement* survivorship patterns can suggest whether or not predation is severe, but cannot indicate the predominant process structuring a population or assemblage. That is, given that $\mathbf{N_e}$ is unknown without experimentation, the various curves in Fig. 8 are qualitatively identical to the right of the "settlement line" (**S**). What occurs before settlement remains largely an unknown "black box" (Richards and Lindeman, 1987; Doherty and Williams, 1988a). To test the models in Fig. 8 completely, one would need to document survivorship from spawning onward, which is currently an impossibility.

C. Field Experiments and Community Structure

Given the present impossibility of testing the models in Fig. 8 directly, is it possible to determine what structures assemblages of reef fishes? I believe so. If reef fish ecologists can adopt a pluralistic attitude toward community structure, then they can take advantage of multifactorial experimental designs that have proven very useful in other systems. Although all field experiments are necessarily limited in spatial and temporal scale, carefully executed experiments would provide a much more rigorous determination of structuring processes than the indirect approaches emphasized thus far. A detailed review of such experimental designs is beyond the scope of this chapter; the basic designs have been reviewed by Sih *et al.* (1985).

Given that manipulating postlarval settlement of reef fishes may be impossible in most systems, we are left with manipulating potential competitors (including new recruits) and predators by locally increasing or decreasing their densities. The simplest factorial design would involve four treatments replicated at similar yet isolated reefs: predator manipulations only; competitor manipulations only; predator and competitor manipulations; and con-

trols. The relative response of the study species among treatments would indicate the relative importance of predation versus competition in structuring the study populations (Sih *et al.*, 1985). The less the difference in responses between control and manipulated sites, especially if the responses to all four treatments were identical, the stronger the inference that recruitment limitation (or zygote limitation) was operating. Particularly valuable for determining the effects of predation would be to monitor and compare the survivorship of local recruit cohorts among different treatments, as in Doherty and Sale's (1986) pilot study (Section IV,B,4). More complex designs would provide greater resolution and allow tests of more detailed hypotheses (Sih *et al.*, 1985), including interactions between predation, competition, and refuges in determining local prey diversity (Holt, 1987; Hixon and Menge, 1991). Of course, such designs would be limited by logistic trade-offs between the number of treatments and the number of replicates.

Surprisingly few experimental manipulations of entire local populations of coral reef fishes have been attempted, none of which have included factorial manipulations of both predators and competitors. Thresher's (1983b) small pilot experiment was perhaps the closest to date (Section IV,B,3). A major task from the outset is to identify potential predators and competitors. Predators can be inferred from food-habit studies. Conspecifics are obviously potential competitors; selecting potential heterospecific competitors requires documenting relative patterns of resource use, thus identifying guilds. Of course, complications such as individuals of one species eating the juveniles of a competitor ("intraguild predation") would strain the dichotomy between predation and competition (Werner and Gilliam, 1984; Polis *et al.*, 1989).

I reviewed four approaches to removing piscivores in Section IV,B. Caging must necessarily include adequate controls against a variety of possible artifacts (Doherty and Sale, 1986). Spearfishing, trapping, or selective poisoning of piscivores is certainly feasible (Bohnsack, 1982; Stimson *et al.*, 1982; Thresher, 1983b; R. E. Schroeder, personal communication; M. J. Shulman, personal communication), although more labor-intensive. Critical to any such manipulations would be verification that piscivore densities were actually reduced. This verification emphasizes the importance of adequate isolation of experimental reefs, which was insufficient in some previous studies (Section IV,B,1 and 2). Adding rather than removing large piscivores is probably not a viable manipulation given the extreme difficulty of capturing and translocating such predators unharmed, and the tendency of these fishes to home (M. A. Hixon and J. P. Beets, unpublished observations). Smaller nonhoming piscivores would be easier to translocate.

Regardless of the method used to manipulate piscivores, it is imperative that a substantial number of the fish capable of consuming the study species be

manipulated. As reviewed in Section II,A, the impact of what can be called "diffuse predation," a prey species facing many species of predators, may be considerable for small reef fishes (including the new recruits and juveniles of any species). Analogous to the effect of "diffuse competition" (MacArthur, 1972), diffuse predation may result in the situation where the overall negative effect of all piscivore species on a prey population is substantial, even though the impact of each individual piscivore species is minor. Diffuse predation has recently been documented in the northwestern Hawaiian Islands (Parrish *et al.*, 1986; Norris and Parrish, 1988). For example, wrasses were consumed by 18 species of piscivores representing nine families. Additionally, where piscivorous species consume each other's juveniles, diffuse predation could possibly involve "predatory networks." Like "competitive networks" (Buss and Jackson, 1979), predatory networks could provide a mechanism for maintaining local diversity within a guild of piscivores. Testing such ideas will clearly require factorial experiments.

One probable reason that factorial designs have not been widely employed is that both logistic constraints imposed by working underwater and the very nature of reef fish systems inhibit their implementation. The studies reviewed here indicate two major problems. First, unless the experimental reefs are adequately isolated, immigration may negate the effects of removals, and apparent mortality may in fact be emigration. Tagging fish, including new recruits, is probably the best way to test the isolation of reefs (e.g., Hixon and Beets, 1989). Second, the reef framework inhibits a diver's ability to count, capture, or otherwise remove sheltering fish, especially piscivores like moray eels. If either or both of these problems render factorial experiments logistically impossible on natural reefs, artificial reefs could be employed to provide both sufficiently isolated replicates and shelters that are accessible to divers (M. A. Hixon and J. P. Beets, unpublished observations).

Whatever methods are used, it seems obvious that the time has come for more pluralistic experimental studies of the processes structuring assemblages of coral reef fishes. Predation is clearly one process that deserves more attention.

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