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Life and Death of Coral Reefs

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Editor

University of Guam

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10

Effects of Reef Fishes on Corals and Algae

Mark A. Hixon

Fishes are among the most conspicuous and beautiful inhabitants of coral reefs. Their diversity is amazing. It has been estimated that nearly half of the 20,000–30,000 species of fishes worldwide inhabit such shallow tropical marine habitats (Cohen, 1970), and locally, hundreds of species can coexist on the same reef. For example, Smith and Tyler (1972) found 75 species occupying a 3-meter-diameter patch reef in the Caribbean, which is not a particularly speciose region compared to the Indo-Pacific (Chapter 14).

The variety of sizes and shapes of reef fishes is as remarkable as their species diversity. The smallest vertebrate is a goby less than 10 mm long that inhabits Indian Ocean reefs (Winterbottom and Emery, 1981), whereas at the other extreme, groupers, barracuda, and reef sharks can reach startling sizes. Fishes exploit virtually every conceivable microhabitat and food source on reefs, from incoming oceanic plankton, to a wide variety of benthic organisms, to other fishes. Moreover, they often occur in high-standing stocks, with about 2,000 kg ha⁻¹ being the presumed maximum (Goldman and Talbot, 1976). Not surprisingly, reef fishes are an important food source for many tropical third-world nations (reviews by Russ, 1991; section 1.1 in Chapter 1).

It seems almost a foregone conclusion, then, to assert that fishes have strong effects on the dominant benthos of reefs: corals and macroalgae. In fact, herbivorous fishes do substantially affect the distribution and abundance of reef algae. Surprisingly, however, the evidence for major direct effects on corals is relatively scant. Nevertheless, the effects of herbivores, especially territorial damselfishes, can cascade through the system, indirectly affecting corals and a variety of other reef organisms. Moreover, there is substantial evidence that various fishes affect

I dedicate this chapter to my son, Sean Wolf, who was born the day I completed the manuscript. I thank the National Science Foundation and the University of Hawaii for supporting my research on herbivorous reef fishes.

the distribution and abundance of invertebrate corallivores and herbivores, thereby indirectly affecting corals and algae. This complex variety of direct and indirect effects has definite ramifications for understanding and managing reef systems (Chapter 11).

This chapter focuses on (1) the effects of herbivorous fishes on the distribution and abundance of reef algae, and indirectly, corals; (2) the effects of corallivorous fishes on the relative dominance of reef-building corals; and (3) the indirect effects of fishes consuming and competing with invertebrate herbivores and corallivores. This summary is by no means exhaustive; recent reviews detailing various effects of fishes on reef corals and algae include Hixon (1986), Hutchings (1986), Glynn (1988, 1990), Steneck (1988), Horn (1989), Hay (1991), and Jones et al. (1991).

The focus of this chapter is mostly on the one-way effects of fishes upon reefs, emphasizing the mechanisms and constraints under which fishes cause switches in the relative dominance of benthic organisms. However, it is important to realize that this limited perspective ignores most of the complex interactions between fishes and the reefs they inhabit. Indeed, the reciprocal effects of reefs upon fishes is a matter of life and death for many species; reef fishes are often obligatory denizens of this habitat and derive all their food and shelter from the reef. The demise of a reef certainly has repercussions for reef fishes. For example, Reese (1981) has proposed that obligate coral-feeding fishes can be used as bioindicators of the general health of a reef, an idea that has stirred considerable controversy (Bell et al., 1985; Bouchon-Navaro et al., 1985; Williams, 1986; Roberts et al., 1988; Sano et al., 1987; White, 1988a; Bouchon-Navaro and Bouchon, 1989). The link between fishes and corals has been further documented by Harmelin-Vivien (1989), who noted a significant linear relationship between the number of fish species and the number of coral species among reefs across the Indo-Pacific region, but no such relationship with the number of algal species.

Other potentially important interactions between fishes and reefs that will not be covered are assessment of the relative effects of fishes versus invertebrate herbivores (Hay, 1984; Carpenter, 1986a; Foster, 1987; Morrison, 1988; Klumpp and Pulfrich, 1989; see Chapter 9) and the role of fish feces fertilizing the reef (Meyer et al., 1983; Meyer and Schultz, 1985a, b; Polunin and Koike, 1987; Polunin, 1988; Harmelin-Vivien et al., 1992; Chapter 13). Finally, space limitations prevent summarizing the many fascinating and ecologically important interactions among fishes and the community structure of reef fishes per se. Fortunately, Peter Sale's (1991) edited volume on these topics is unparalleled and recommended for those desiring a detailed introduction to reef-fish ecology.

10.1. The Players: Corallivorous and Herbivorous Reef Fishes

Only a handful of families of fishes have been documented to have obvious direct effects on reef corals (Fig. 10–1). Although about 10 families of fishes

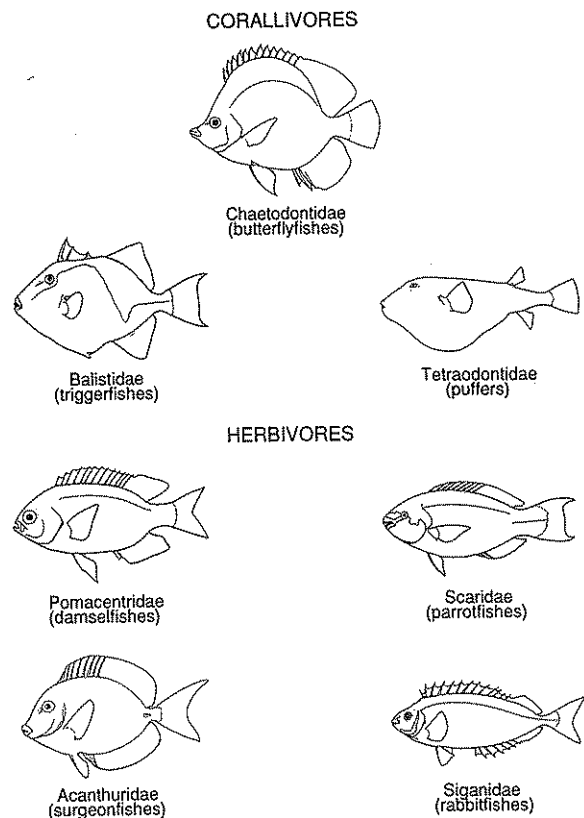


Figure 10-1. Families of larger-bodied reef fishes that include the most corallivorous and herbivorous species. Note that members of all the listed corallivore families include species that do not consume corals, and about half the species of pomacentrids are not herbivorous. Similarly, certain species in numerous other families consume corals and/or algae (drawings from Nelson, 1984).

are known to eat coral polyps, there are few groups that feed strictly on corals (reviews by Robertson, 1970; Randall, 1974). This pattern may be due to coral polyps being relatively unpalatable compared to other prey, in terms of their chemical composition, their protective nematocysts, and their calcium-carbonate skeletons. The predominant corallivores are butterflyfishes (family Chaetodontidae); about half of the over 100 species eat corals (Allen, 1981). The only other large fishes whose members regularly consume corals are some triggerfishes (Balistidae) and puffers (Tetraodontidae). Whereas the butterflyfishes delicately extract individual polyps from the coral skeleton, the triggerfishes and puffers tend to scrape and chew pieces they break off the coral colony with their beaklike mouths. Smaller corallivores include at least one goby (Gobiidae; Patton, 1974).

Among the coral eaters, the social systems of the butterflyfishes are best documented, often comprising territories defended by male-female pairs (Reese, 1975; Hourigan, 1989; Roberts and Ormond, 1992).

In contrast to the corallivores, herbivorous reef fishes are relatively speciose. As collated by Choat (1991) and Allen (1991), the predominant consumers of benthic algae are most of the approximately 75 species of surgeonfishes (Acanthuridae), all 27 species of rabbitfishes (Siganidae), all 79 species of parrotfishes (Scaridae), and over half of the approximately 320 species of damselfishes (Pomacentridae). Other herbivorous families include smaller fishes, such as the combtooth blennies (Blenniidae).

The feeding modes of these herbivores are highly variable (reviews by Ogden and Lobel, 1978; Horn, 1989; Glynn, 1990; Choat, 1991). Surgeonfishes and rabbitfishes tend to crop seaweeds in a browsing mode that leaves algal holdfasts intact. Parrotfishes, on the other hand, have highly modified jaws and teeth. With these beaks (which inspired their name) they scrape the bottom and remove algal holdfasts along with the dead coral substratum to which the algae attach. This activity makes parrotfishes the major source of bioerosion among reef fishes (reviews by Hutchings, 1986; Choat, 1991; Chapter 4). All three of these families exhibit variable social systems, from individual territories to transient foraging aggregations (e.g., Ogden and Buckman, 1973; Robertson et al., 1979; Robertson and Gaines, 1986).

Most herbivorous (actually, omnivorous) damselfishes maintain permanent individual territories, measuring about a square meter in area, which they defend vigorously against other herbivores (e.g., Low, 1971). This defense, combined with moderate browsing and even "weeding" behavior (sensu Lassuy, 1980), often maintains a distinctive mat of erect algae within the territory. By forming large schools, parrotfishes and surgeonfishes can sometimes overwhelm and denude damselfish territories (Jones, 1968; Barlow, 1974; Vine, 1974; Robertson et al., 1976; Foster, 1985; Reinthal and Lewis, 1986).

Overall, both corallivorous and herbivorous fishes display a wide variety of feeding modes and behaviors, suggesting that the ecological effects of these consumers are bound to vary widely from species to species and from reef to reef. What follows, then, are summaries of specific studies that can be generalized only with caution.

10.2. Fish Effects on Algae

10.2.1. Schooling Herbivores

Parrotfishes, surgeonfishes, and rabbitfishes often occur in dense aggregations that have obvious effects on reef macroalgae. Densities can average well over 10,000 herbivorous fish per hectare (review by Horn, 1989), standing stocks on unfished reefs in the Great Barrier Reef can reach 45 metric tons per km² (Williams

and Hatcher, 1983), and secondary productivity can approach 3 metric tons per km² per year (review by Russ and St. John, 1988). In the Caribbean, parrotfishes can graze at rates of over 150,000 bites per m² per day (Carpenter, 1986a). In some systems, such intense grazing enhances local primary productivity by maintaining algae at an early successional stage (Montgomery, 1980; Birkeland et al., 1985; Carpenter, 1986a). Hatcher (1981) estimated that about half the net algal production on One Tree Reef, Australia, was consumed by fishes. At the same site, Hatcher and Larkum (1983) demonstrated that algal standing crops were controlled by grazing fishes all year (autumn and spring) on the reef slope (10 m depth), but only during spring in the lagoon (2 m depth). In autumn, inorganic nitrogen limited the standing crop of lagoon algae despite the continued presence of fishes (Chapter 7).

In addition to seasonal variations, an apparently general trend is that the spatial distribution of fish grazing varies inversely with tidal exposure and/or wave action (Van den Hoek et al., 1975, 1978) and directly with the availability of shelter for the herbivores from predatory fishes (Hay, 1981a; Lewis, 1986), with both turbulence and shelter decreasing with depth. Thus, as documented in Guam (Nelson and Tsutsui, 1982), the Caribbean (Hay et al., 1983; Lewis and Wainwright, 1985), and the Great Barrier Reef (Russ, 1984b), the depth distribution of herbivores and grazing intensity may often be unimodal: low in very shallow water due to limited accessibility by fishes, high at intermediate depths due to high accessibility and shelter, and low in deep reef areas (greater than about 10 m), where the abundance of coral shelter for fishes typically decreases. However, in areas where intense fishing has greatly reduced the abundance of piscivores, herbivorous fishes may be active at greater depths, with algal standing stocks consequently being lower than usual at those depths (Hay, 1984). The unimodal depth distribution of herbivorous fishes may explain the bimodal zonation of erect algal cover found on reefs such as those in Curaçao (Van den Hoek et al., 1978): high cover in the eulittoral zone (0–1 m depth), low on the upper reef slope (1–30 m), and high again on the lower slope (30–50 m).

The lack of shelter for grazing fishes probably also explains the existence of extensive algal plains occurring on sand bottoms below and between reefs, as well as high algal densities on very shallow reef flats lacking adequate shelter (Van den Hoek et al., 1978; Hay, 1981b). Overall, it appears that the risk of predation limits the grazing activities of smaller reef fishes to areas providing structural refuges (reviews by Hixon, 1991; Hixon and Beets, 1993).

At larger spatial scales, there is a trend for schooling herbivores to be more abundant on the outer Great Barrier Reef than inshore (Williams and Hatcher, 1983; Russ, 1984b). The mechanisms underlying this pattern appear to be related to between-region differences in the palatability and productivity of reef algae. (Chapter 12 gives a general review of regional variation in coral-reef processes.)

Field experiments pioneered by Stephenson and Searles (1960) and Randall

(1961), in which herbivorous fishes are excluded from reef plots by cages, have shown that these fishes strongly affect the species composition and relative abundances of algae. Typically, heavily grazed dead coral surfaces become dominated by grazer-resistant algal crusts or turfs, whereas caged but otherwise identical surfaces become covered by high-standing crops of erect algae (Vine, 1974; Wanders, 1977; Lassuy, 1980; Sammarco, 1983; Hixon and Brostoff, 1985; Carpenter, 1986b; Lewis, 1986; Morrison, 1988; Scott and Russ, 1987). Essentially, erect algae competitively exclude crusts in the absence of grazing, but crusts are more resistant to grazing (Littler et al., 1983; Steneck, 1983). Overall, the local species diversity of algae on exposed flat surfaces declines with increasing density of schooling herbivores (Day, 1977; Brock, 1979), an effect that is ameliorated on surfaces where algae can grow in crevices (Brock, 1979; Hixon and Brostoff, 1985; Hixon and Menge, 1991).

A yearlong experiment off Hawaii examined the benthic successional sequences and mechanisms that cause these general patterns (Hixon and Brostoff, 1996). Succession was followed on dead coral surfaces subjected to each of three grazing treatments: protected within grazer-exclusion cages, exposed to moderate grazing inside damselfish territories (see below), and exposed to intense parrotfish and surgeonfish grazing outside territories. The ungrazed successional sequence inside cages was an early assemblage of filamentous green and brown algae (including *Enteromorpha* and *Ectocarpus*) replaced by a high-diversity assemblage of mostly red filaments (including *Centroceras* and *Ceramium*), which in turn was replaced by a low-diversity assemblage of mostly coarsely branched species (including *Hypnea* and *Tolypocladia*).

Plotted in a multispecies ordination (detrended correspondence analysis), ungrazed succession followed a distinct left-to-right trajectory over the year (Fig. 10–2). Intense grazing by parrotfishes and surgeonfishes caused succession to follow a completely opposite path, where the early filaments were replaced immediately by grazer-resistant crustose species, including the red coralline *Hydroolithon* (Fig. 10–2). This result suggests that heavy grazing “derailed” the normal trajectory of succession (Hixon and Brostoff, 1996).

In summary, intense grazing by schooling herbivores strongly influences the standing crop, productivity, and community structure of reef algae. It also appears that selection for resistance to such grazing may compromise competitive ability among algal species (Littler and Littler, 1980; Hay, 1981b; Lewis, 1986; Morrison, 1988). Off the Caribbean coast of Panama, fishes may prevent competitively subordinate (but grazer-resistant) reef algae (Hay, 1981b; Hay et al., 1983). This dichotomy may act to maintain between-habitat diversity in algae (Hay, 1981b; see also Lewis, 1986). In any case, intense grazing appears to have selected for strong chemical defenses and morphological plasticity in some reef algae (reviews by Hay and Fenical, 1988; Steneck, 1988; Hay, 1991).

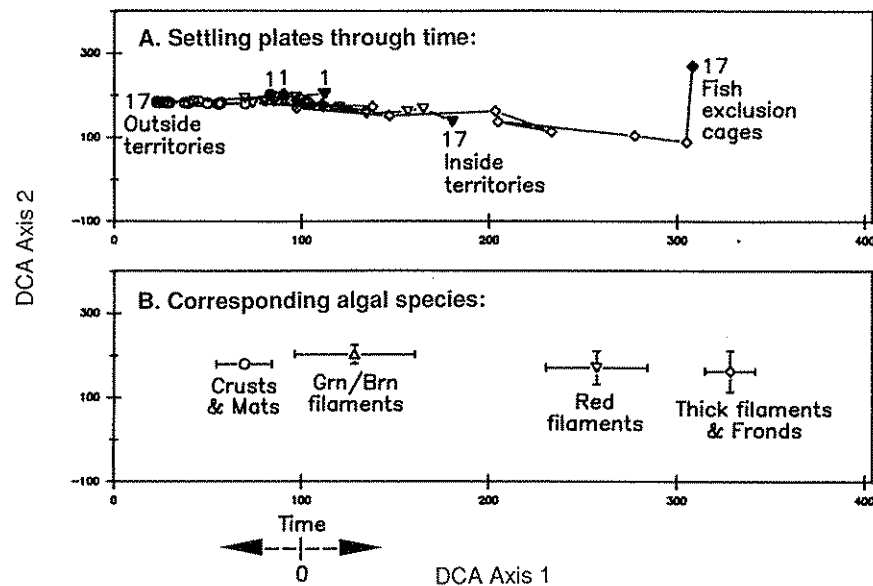


Figure 10-2. Effects of differential fish grazing on algal succession on a Hawaiian reef, illustrated by a multivariate ordination (detrended correspondence analysis, DCA) of algae growing on settling plates of different ages. (A) Each point represents the mean score values for a sample of about 21 settling plates; points closer together indicate more similar species compositions and relative abundances. There are 17 such samples for each of the three treatments indicated; sample 1 was after 7 days into the experiment (indicated as "time 0" along the x-axis), and sample 17 was at the end of one year. (B) Each point represents the mean (±SE) score values for groups of algal species corresponding to the samples in plot A. Thus, dominance during succession within cages proceeded from green and brown filaments to red filaments to thick filamentous and frondose species, whereas succession inside damselfish territories proceeded only to a mixture of red, green, and brown filaments. Succession outside territories proceeded from green and brown filaments directly to grazer-resistant crusts and mats (modified from Hixon and Brostoff, 1996).

10.2.2. Territorial Damselfishes

By defending small patches of dead coral, and grazing or "weeding" the algae in these patches in a particular way, territorial damselfishes often establish and maintain visually distinct mats of macroalgae on reefs (Vine, 1974; Brawley and Adey, 1977; Lassuy, 1980; Montgomery, 1980; Hixon and Brostoff, 1996). In general, these mats are sites of greater primary productivity than comparable areas outside territories (Montgomery, 1980; Russ, 1987; Klumpp et al., 1987). This production is an important food source for not only the resident damselfish, but also small invertebrate herbivores inhabiting the mat and larger intruding herbivores (Russ, 1987; Klumpp and Polunin, 1989).

Given that territory mats can cover well over 50% of shallow reef tracts (Sammarco and Williams, 1982; Klumpp et al., 1987), the local effects of damselfishes on the benthic community can be substantial. In particular, the defense, grazing, and weeding activities of these fish (possibly combined with localized fecal fertilization) strongly affect the local species diversity of reef algae. This effect has been demonstrated by three similar experiments in Guam (Lassuy, 1980), Hawaii (Hixon and Brostoff, 1983), and the Great Barrier Reef (Sammarco, 1983). Each experiment compared algal diversity on dead coral surfaces exposed to each of three different treatments: accessible to mostly damselfish grazing inside territories, accessible to intense grazing by other herbivores outside territories, and protected within fish-exclusion cages outside territories.

Although strict comparisons are precluded by differences in experimental design and laboratory analyses, some general patterns do emerge. For both damselfish species that Lassuy (1980) studied (*Stegastes lividus* and *Hemiglyphidodon plagiometopon*), he found caged surfaces exhibited the greatest algal diversity after 2 months. Hixon and Brostoff (1983) and Sammarco (1983) obtained the same result from samples taken after 2–6 months and 3 months, respectively. However, after a year, both the latter studies found that algal diversity was greatest inside damselfish territories. These data, combined with the fact that Sammarco studied one of the same species as Lassuy (*H. plagiometopon*), suggest that Lassuy's (1980) samples may have represented early successional stages.

In the Hawaii study, Hixon and Brostoff (1996) showed that moderate grazing by the damselfish *Stegastes fasciolatus* slowed and appeared to stop succession at a high-diversity middle stage dominated by red filaments (Fig. 10-2). Thus, rather than altering the successional trajectory like more intensive grazers (see above), damselfish appeared to simply decelerate algal succession. Territorial fish may maintain the midsuccessional algal community because these species provide a superior food source for the damselfish (Montgomery and Gerking, 1980) and/or a source of invertebrate prey and palatable epiphytes (Lobel, 1980).

Hixon and Brostoff (1983, 1996) further showed that grazing by damselfish inside their territories was of intermediate intensity relative to that within cages and outside territories. Correspondingly, the standing crop of algae was also at intermediate levels inside territories, while local species diversity was at its maximum. These results thus corroborated the intermediate-disturbance hypothesis (sensu Connell, 1978; Chapter 15). At low levels of grazing disturbance within cages, a few dominant competitors (coarsely branching species such as *Hypnea* and *Tolypocladia*) were capable of locally excluding most other species. At high levels outside territories, only a few crustose species persisted. Inside damselfish territories, the coexistence of many algal species was maintained because their densities were apparently kept below levels where resources (presumably mediated by living space) became severely limiting (Fig. 10-3A).

Given that territorial damselfish can locally enhance species diversity, they can be considered a "keystone" species (sensu Paine, 1966; see also Williams,

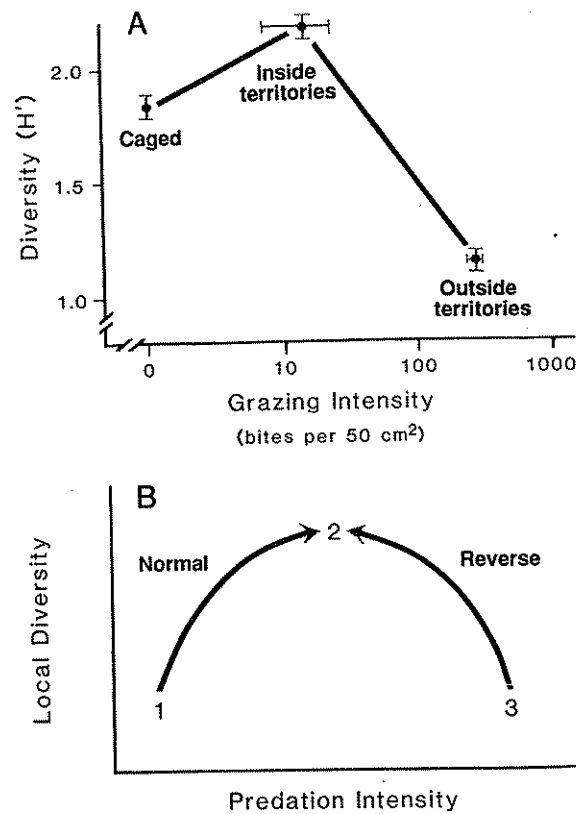


Figure 10-3. (A) Algal species diversity (measured by the Shannon-Wiener index, H') on settling plates exposed off Hawaii for one year to each of three grazing treatments: caged, exposed but defended inside damselfish territories, and exposed outside territories to parrotfishes and surgeonfishes. Each vertical bar represents 2 standard errors for mean diversity from 21 settling plates sampled at the end of one year; each horizontal bar represents the 95% confidence interval for mean grazing intensity, measured as the "standing crop" of fish bite marks per plate, from 63 settling plates sampled earlier in the year. (B) Graph of the intermediate-disturbance hypothesis, showing that a keystone species can enhance local species diversity either by increasing predation intensity from point 1 toward point 2 ("normal"), or by decreasing overall predation intensity by territorial defense from point 3 toward point 2 ("reverse"), as demonstrated by territorial damselfish (modified from Hixon and Brostoff, 1983).

1980). However, unlike the normal kinds of keystone species, which enhance diversity by increasing predation intensity on a prey assemblage, the territorial behavior of damselfish enhances diversity by decreasing predation overall (Fig. 10-3B). That is, in the absence of a normal keystone species, predation is low and diversity is low because a few prey species competitively exclude most others from the local system (e.g., Paine, 1966). However, in the absence of damselfish (keystone species in reverse), predation is high (due to schooling herbivores) and diversity is low because few prey are able to survive intense grazing.

There is evidence that this pattern documented in Hawaii is common. Assuming that grazing intensity was intermediate inside damselfish territories in Sammarco's (1983) study, *Hemiglyphidodon plagiometopon* is a keystone species where it is abundant at the Great Barrier Reef, and possibly Guam (Lassuy, 1980). More recently, Hinds and Ballantine (1987) found that the algal mats in territories of *Stegastes planifrons* off Puerto Rico decline in diversity when caged, also suggesting a keystone-species effect. Note, however, that not all damselfishes enhance local algal diversity; some species maintain near monocultures within their territories by intense nonselective grazing (Montgomery, 1980).

Regardless of whether damselfishes enhance local algal diversity, the greatly increased standing crop of erect algae inside their territories (compared to more heavily grazed surfaces outside) has important secondary effects on reef benthos. The algal mat serves as a refuge for invertebrate microfauna and/or various epiphytes (Lobel, 1980; Hixon and Brostoff, 1985; Zeller, 1988). Also, because accretion by crustose coralline algae adds to the reef framework, and such algae are overgrown by the algal mat, damselfish territories may be sites of weakened reef structure (Vine, 1974; Lobel, 1980).

Damselfish territories may also indirectly affect nitrogen fixation on reefs, although available data are somewhat contradictory. During the same study as Sammarco (1983) described above, Wilkinson and Sammarco (1983) found that nitrogen fixation by blue-green algae (cyanobacteria) was positively correlated with grazing intensity on the Great Barrier Reef, being lowest within cages, intermediate inside damselfish territories, and greatest outside territories. However, both Lobel (1980) and Hixon and Brostoff (1996) found considerably more blue-green algae inside than outside territories in Hawaii. Finally, Ruyter Van Steveninck (1984) found no differences in the abundance of filamentous blue-green algae inside and outside damselfish territories in the Florida Keys. These discrepancies suggest possible regional differences in local distributions of blue-green algae.

10.2.3. Conclusion

Herbivorous fishes strongly affect the distribution and abundance of reef macroalgae. Where there is ample shelter from predation and protection from strong

turbulence, schooling herbivores can crop reef algae to very low-standing crops, leaving mostly grazer-resistant forms such as crusts, compact turfs, or chemically defended species. Such intense herbivory may be essential for reef-building corals to flourish. Indeed, Glynn (1990, p. 391) concluded that the "maintenance of modern coral reefs may be due largely to the activities of fish and invertebrate herbivores that prevent competitively superior algal populations from dominating open, sunlit substrates." In any case, it is important to realize that a myriad of factors are involved in these and other switches in dominance among algae and between algae and corals. For example, Littler and Littler (1984) see nutrient levels as pivotal in determining how herbivore activity will affect the dominant benthos on reefs (Fig. 10-4).

Besides the schooling herbivores, territorial damselfishes have particularly strong local effects on shallow-reef algae, effects that can cascade through the entire benthic community. The defensive and grazing activities of damselfishes and the resulting dense algal mats they defend can substantially affect reef

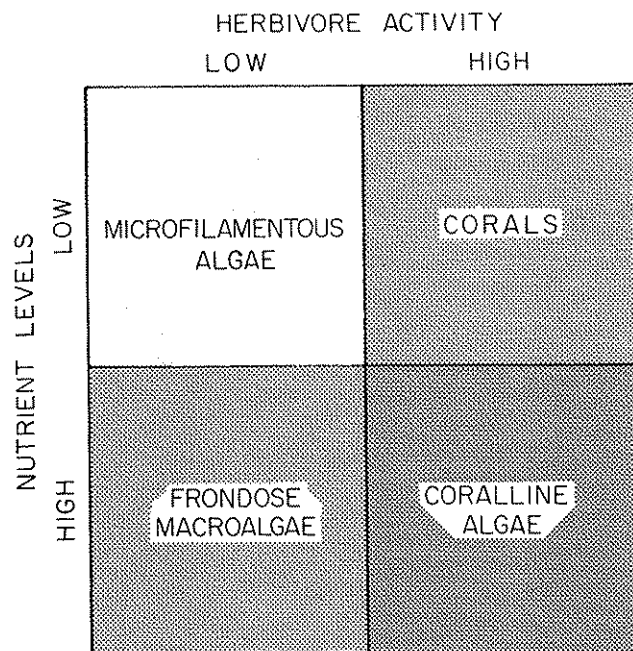


Figure 10-4. Predicted interaction of herbivore activity and long-term nutrient levels in determining the dominant benthos on shallow coral reefs. By consuming erect algae, herbivores shift the benthic community from filamentous or frondose algae (left) toward corals or grazer-resistant coralline algae (right). Secondly, nutrient levels are predicted to shift dominance between different kinds of erect algae (left) or between corals and coralline algae (right) (from Littler and Littler, 1984).

accretion, nitrogen fixation, epiphytes and small invertebrates that inhabit the algae, and, as will be seen in the next section, corals. Clearly, herbivorous fishes are major players determining the character of shallow coral-reef communities, and territorial damselfishes in particular can act as a keystone species.

10.3. Fish Effects on Corals

10.3.1. Direct Consumption

Compared to the effects of herbivores on algae, surprisingly few studies have demonstrated that corallivorous fishes influence the distribution and abundance of reef-building corals. For example, although butterflyfishes are among the most obligatory of corallivores (Reese, 1977), these fishes appear to have a negligible effect on coral standing crops (Harmelin-Vivien and Bouchan-Navaro, 1981, 1983). At Aqaba in the Red Sea and Moorea in the South Pacific, butterflyfishes occurred at average densities of 69 and 51 fish per 1,000 m², yet consumed an average of only about 10 and 28 grams of coral polyps per 1,000 m² per day, respectively. It appears that corals often retract all their polyps in response to predation by butterflyfish, making polyps locally unavailable to predators for considerable periods (D. W. Meadows, personal communication). Such factors may preclude high densities of large-bodied obligate corallivores, perhaps necessitating the large feeding territories defended by butterflyfishes (see Tricas, 1989; Roberts and Ormond, 1992).

Nevertheless, the local distributions of several coral genera are strongly affected by coral-feeding fishes. Neudecker (1979) provided one of the first experimental demonstrations that fishes can potentially affect the depth zonation of corals. Off Guam, he transplanted small colonies of *Pocillopora damicornis* from a relatively fish-free lagoon (1–2 m depth) to reef slopes (15–30 m depth) where this coral was naturally absent and corallivorous fishes were common. Coral transplants survived well when caged, but exposed colonies were partially consumed by butterflyfishes and triggerfishes within one week.

The effects of fish-consuming corals can have ramifications for interactions among corals. Off Hawaii, Cox (1986) showed that the feeding preference of the butterflyfish *Chaetodon unimaculatus* for the coral *Montipora verrucosa* can reverse the competitive dominance of this coral over another species, *Porites compressa*. Inside fish-exclusion cages, *Montipora* overgrew *Porites*, yet outside cages, this dominance sometimes reversed due to differential grazing of *Montipora* by the butterflyfish.

Besides the strict corallivores, herbivorous fishes may also directly affect corals by occasionally consuming or otherwise killing them. Territorial damselfishes are known to remove polyps, thereby killing patches of coral on which the damselfish establish their algal mats. In the Caribbean, the damselfish *Stegastes planifrons* was observed killing *Montastrea annularis* and *Acropora cervicornis*

(Kaufman, 1977). Knowlton et al. (1990) suggested that such predation dramatically slowed the recovery of *A. cervicornis* off Jamaica following Hurricane Allen, inhibiting the usual dominance of this species. Similarly, off the Pacific coast of Panama, *Stegastes acapulcoensis* killed patches of *Pavona gigantea* (Wellington, 1982). Wellington's study demonstrated how this direct effect, combined with various indirect effects, strongly affected coral zonation (see below).

Outside damselfish territories, the reported direct effects of herbivorous fishes on corals are contradictory. On one hand, field observations have noted grazing fishes damaging juvenile corals (Randall, 1974; Bak and Engel, 1979). Littler et al. (1989) suggested that parrotfishes (*Scarus* spp. and *Sparisoma* spp.) substantially influence the local distribution of *Porites porites* off Belize by eliminating this delicately branching species from areas where these fish are abundant. They proposed that a combination of differential consumption of *P. porites* by parrotfishes and the relative availability of refuge holes for grazing fishes of different sizes among different microhabitats determined whether backreef bottoms were dominated by macroalgae, *P. porites*, or the relatively mound-shaped and grazer-resistant *P. astreoides* (Fig. 10-5). Similarly, recently recruited coral colonies survived intense parrotfish grazing in laboratory mesocosms in Hawaii only when structural refuges from grazing were provided (Brock, 1979).

On the other hand, there is evidence that herbivorous fishes avoid consuming living corals in the field, including recently recruited colonies (Birkeland, 1977), and only the largest species of parrotfish, the Indo-Pacific *Bolbometopon muricatum*, is reported to consume substantial amounts of live coral (Choat, 1991; see also Randall, 1974). Such differential grazing may moderate competition between algae and corals, preventing algae from excluding corals. Indeed, Lewis (1986) noted that macroalgae overgrew corals of the genus *Porites* when herbivorous fishes were excluded by fencing from a shallow reef off Belize for 10 weeks. However, given such contradictory evidence, whether nonterritorial herbivorous fishes have negative or positive effects on corals appears to depend on the particular system.

Finally, a poorly documented yet possibly substantial source of coral mortality is consumption of coral spawn by planktivorous reef fishes. At the Great Barrier Reef, Westneat and Resing (1988) noted that the guts of the planktivorous damselfishes *Abudefduf bengalensis* and *Acanthochromis polyacanthus* were packed with coral gametes during the annual mass spawning of corals.

10.3.2. Indirect Effects

Available experimental evidence suggests that indirect effects of territorial damselfishes influence the local distribution and abundance of corals more extensively than direct consumption by corallivores. By defending and maintaining their algal mats, damselfish produce patches in which juvenile corals are often smoth-

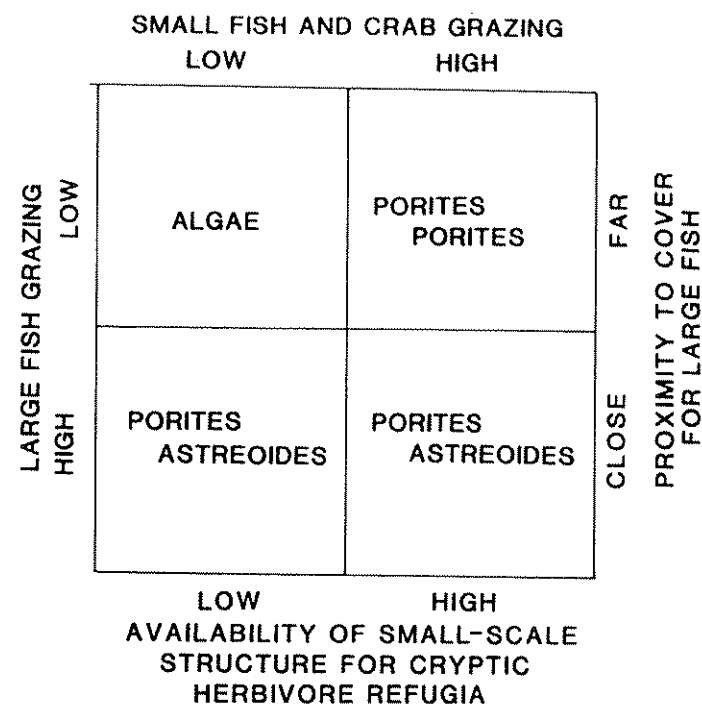


Figure 10-5. The direct influence of physical shelter from predation on the local abundance of grazing fishes, and subsequent indirect effects on the dominant backreef benthos in Belize. When large shelters are nearby, large fishes will be locally abundant and reduce both macroalgae and the delicately branching coral, *Porites porites*, leaving the relatively invulnerable mound-shaped *P. astreoides* to dominate (lower left and right). Where large shelters are rare and small shelters are abundant, small grazers will reduce algae, allowing the competitively subordinate *P. porites* to dominate (upper right). Only where all refuges for grazers are absent will algae dominate (upper left) (from Littler et al., 1989).

ered (Vine, 1974; Potts, 1977). Additionally, the algal mat provides microhabitats facilitating various boring organisms, which enhance bioerosion of the coral framework (reviews by Hutchings, 1986; Chapter 4). However, some coral species seem to recruit more successfully to damselfish territories than to adjacent undefended areas, suggesting that the territories may provide at least a temporary refuge from corallivores (Sammarco and Carleton, 1981; Sammarco and Williams, 1982; see below). If for any reason coral heads manage to reach a certain size, they may become invulnerable to algal overgrowth (Birkeland, 1977).

Given that damselfishes may have both positive and negative effects on corals, complex interactions can result. An example is provided by a study of coral zonation on the Pacific coast of Panama by Wellington (1982). In this system, branching *Pocillopora* corals dominated shallow areas (0-6 m depth), while the

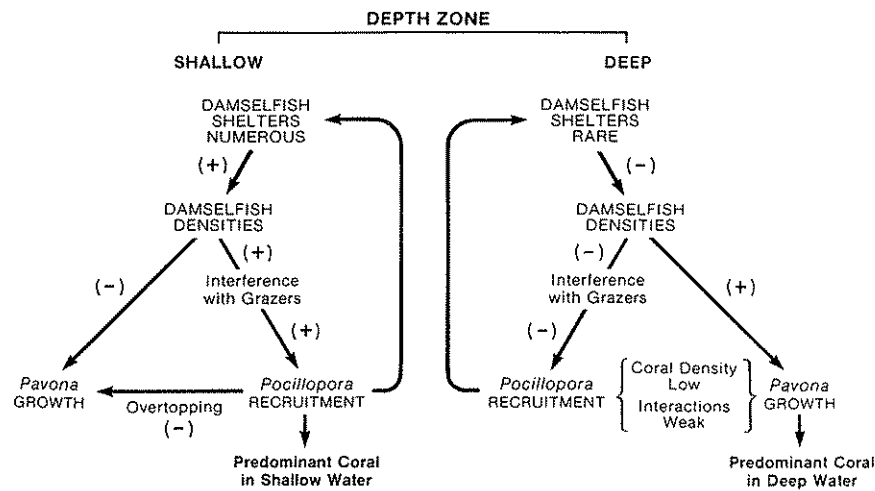


Figure 10-6. Interactive feedback loops influencing the depth zonation of *Pocillopora* and *Pavona* corals off the Pacific coast of Panama. Arrows indicate the direction of each effect; "+" and "-" indicate positive and negative effects, respectively. The direct negative effect of damselfish on *Pavona* in shallow water is due to polyp removal; the "direct" positive effect in deep water is actually an indirect effect mediated by the scarcity of damselfish shelters (from Wellington, 1982).

massive *Pavona gigantea* dominated deeper areas (6–10 m depth). Using a clever series of observations and experiments, Wellington discovered an interactive feedback loop whereby the damselfish *Stegastes acapulcoensis* may directly and indirectly cause this zonation (Fig. 10-6). When establishing territories in the shallow zone, damselfish differentially kill *Pavona* by polyp removal and maintain their algal mats on the exposed substrata; *Pocillopora* is apparently protected by its tightly branched morphology and rapid polyp regeneration. Moreover, *Pocillopora* colonies within the periphery of territories are protected from corallivores by the defensive behavior of the damselfish. These factors enhance the ability of *Pocillopora* to competitively dominate *Pavona* in shallow areas. The *Pocillopora* framework, in turn, provides the damselfish with shelter, a necessary requisite for a territory. In the deep zone, shelter sites and thus damselfish densities are low because overall coral cover (and thus intercoral competition) is low, apparently due to physical factors (attenuated light, reduced water motion, etc.). Here, transient fish corallivores (mostly puffers) differentially eat *Pocillopora*, whose branches they can ingest and masticate, leaving *Pavona* as the dominant coral.

10.3.3. Conclusion

Truly corallivorous fishes have been shown to affect the local distribution and abundance of some corals. However, the territorial activities of herbivorous

damselfishes appear to have more substantial effects on corals in shallow water. This difference appears to be a function of the wide variety of direct and indirect effects manifested by damselfishes. In any case, interactions between fishes and corals seem to be largely indeterminate. It appears that, on exposed reef surfaces, coral recruits may initially experience enhanced survival where they are protected from extensive fish grazing, such as within damselfish territories, but will often be overgrown by algae eventually. Those coral larvae settling on surfaces exposed to grazing by herbivorous fishes outside territories may or may not initially suffer high mortality, depending on whether they are consumed along with other fish prey, but some colonies will eventually reach an invulnerable size where they are both immune to incidental predation and freed from competition with algae.

10.4. Fish Effects on Invertebrate Corallivores and Herbivores

Besides directly consuming corals or algae, reef fishes can also affect invertebrate corallivores and herbivores, causing subsequent indirect effects on the dominant reef benthos. Most obviously, some fishes consume these organisms, including the major invertebrate corallivore, the crown-of-thorns seastar (*Acanthaster planci*), and the major invertebrate herbivores, sea urchins (Chapters 9 and 11). At the Great Barrier Reef, Pearson and Endean (1969) noted planktivorous damselfish consuming early developmental stages of *Acanthaster*. In the Red Sea, Ormond et al. (1973) documented that triggerfishes and puffers killed 1,000 to 4,000 *Acanthaster* per hectare each year, a rate that accounted for an observed decline in the *Acanthaster* population.

Triggerfishes and puffers also consume sea urchins, as do large wrasses (Labridae) and porcupinefishes (Diodontidae; e.g., Randall, 1967). Field experiments have demonstrated that such predation can be intense (Glynn et al., 1979) and can force urchins to remain near shelter (Carpenter, 1984). Thus, the risk of predation by fishes limits the area over which urchins can overgraze algae and seagrass, resulting in discrete barren zones or "halos" around Caribbean reefs (Ogden et al., 1973). Hay (1984) suggested that overfishing of large wrasses and triggerfishes has resulted in unusually high urchin densities in populated regions of the Caribbean.

Besides the mechanism of direct consumption, fishes may negatively affect invertebrate corallivores and herbivores by competitive interactions. In defending their territories, several damselfish species in the South Pacific exclude *Acanthaster*, as first noted by Weber and Woodhead (1970). This exclusion apparently results in the preferred prey of the seastar (mostly acroporid corals) being more abundant and more diverse inside territories than outside (Glynn and Colgan, 1988). In contrast, the species diversity of new coral recruits on the Great Barrier Reef was smaller inside territories of the damselfish *Hemiglyphidodon plagiometopon*, although the density of coral spat (mostly acroporids) was greater there (Sammarco and Carleton, 1981).

In the Caribbean, the damselfish *Stegastes planifrons* can exclude the urchin *Diadema antillarum* from its territories (Williams, 1980, 1981), which may also serve as refuges for certain corals (Sammarco and Williams, 1982). Corals such as *Favia fragum* can apparently withstand competition with the macroalgae that dominate inside territories. Given that, first, damselfish can prevent urchins from overgrazing their territories, and second, the algae growing within the territories provide food for the damselfish, Eakin (1987) concluded that the relationship between damselfish and their algal mats is a case of mutualism.

Parrotfishes and surgeonfishes also compete with *Diadema* on Caribbean reefs, although the urchin appears to be the dominant competitor in this case (Carpenter, 1986a). In particular, increases in the local abundances of these fishes have been documented following experimental removals of, or natural declines in, populations of the urchin (Hay and Taylor, 1985; Carpenter, 1990; Robertson, 1991).

Finally, complex interactions between invertebrates and fishes can occur. Outbreaks of *Acanthaster* can kill large tracts of coral, presumably increasing the availability of substrata for macroalgal growth, which in turn may increase the local densities of herbivorous fishes and decrease those of corallivorous fishes. This sequence was documented for some fishes both at the Great Barrier Reef (Williams, 1986) and off Japan (Sano et al., 1987), although the response of herbivorous fishes was negligible. Clearly, there are many possible ecological linkages among algae, corals, invertebrate herbivores and corallivores, and reef fishes.

10.5. Ramifications for Reef Management

Even though the available evidence suggests that both corallivorous and (especially) herbivorous fishes can have strong local effects on the structure of benthic reef communities, the explicit utility of this knowledge for managing coral reefs seems limited. This is not to say that it is impossible to predict the consequences of some human activities. For example, the studies summarized here suggest that overharvesting herbivorous fishes and invertebrates can allow algae to outcompete corals, that removing fish predators of urchins can allow these herbivores to overgraze algae, and that altering the density of territorial damselfishes can drastically affect the local benthic community. However, more specific predictions may not be possible. The reasons for this less-than-optimistic view are basically twofold.

First, before predicting how harvesting fishes will secondarily affect the benthic community on a reef, we have to know what determines the local population sizes of fishes in the absence of harvesting, and subsequently, how those populations will respond to harvesting. Our knowledge of the population dynamics of unexploited reef-fish populations is rudimentary, so predicting even the direct

effects of fishing is immensely difficult (see Russ, 1991; Chapters 16, 17, and 18). For example, there is evidence that territorial damselfishes inhabiting at least one site on the Great Barrier Reef are naturally recruitment limited (review by Doherty and Williams, 1988). Assertions that this pattern is typical of reef fishes in general has fueled a controversy that has remained unresolved for over a decade (see chapters by Doherty, Ebeling and Hixon, Hixon, Jones, Sale, and Williams, in Sale, 1991). Besides damselfishes, our knowledge of the population dynamics of other reef fishes is even more limited, although it is clear that both corallivores and herbivores are subject to overfishing (review by Russ, 1991).

Second, coral-reef communities are immensely complex, so that the demise or outbreak of a single species due to human activities may have unanticipated and severe ramifications for the remainder of the system (Chapter 11). As a keystone species, territorial damselfishes can manifest a very complex variety of direct and indirect effects on shallow reef systems (Fig. 10-7). The numerous

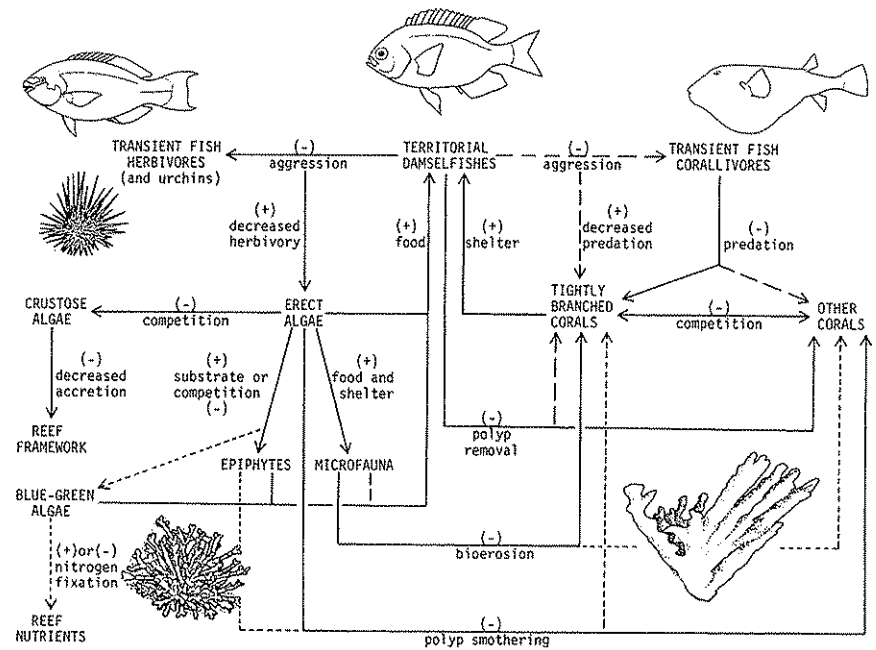


Figure 10-7. Flowchart synthesizing the interactions between fishes and benthos on a shallow coral reef where territorial damselfishes are abundant. Arrows indicate the direction of each effect; "+" and "-" indicate positive and negative effects, respectively. Dashed lines indicate relatively weak effects, and dotted lines indicate effects that are poorly documented and/or controversial. Where damselfishes are rare, some of these effects reverse. In particular, erect algae and their associates are often replaced by grazer-resistant crustose algae due to intense grazing by transient herbivores (modified from Hixon, 1983).

indirect interactions between such fishes and the reefs they inhabit may simultaneously be both positive and negative from a human perspective. For example, damselfish territories may be sites of high algal productivity and species diversity, but may also be sites of reduced coral growth and weakened reef framework. The multitude and complexity of these effects severely limit our ability to predict accurately the effects of harvesting any particular species (let alone multiple species).

Although reef systems may be too complicated to allow us to predict explicit outcomes of human activities, the patterns summarized in this and other chapters of this volume do provide an important lesson: managers should cast a skeptical and cautious eye on proposals to strongly alter the abundance of any coral-reef inhabitant. The secondary results of such alterations may be both unexpected and undesirable. More than any other natural system, coral reefs seem to verify John Muir's (1911) axiom: "When we try to pick out anything by itself, we find it hitched to everything else in the universe."