

## A Complex Triangle

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### Abstract

The coral-seaweed-herbivore triangle is an accepted generalization embedded within a highly complex web of biotic interactions and abiotic conditions that bring exceptions. The pattern is confirmed by observations that herbivorous fishes and urchins can have very strong effects on the standing crop of reef macroalgae, thereby opening space for corals to thrive. However, other factors, such as the abundance and distribution of territorial damselfishes, shelter for schooling herbivores, water motion, and nutrient flux, as well as multiple stressors on corals, can modify this basic pattern, sometimes strongly. High levels of herbivory lead to dominance by low-lying algae, including crustose corallines that may foster coral settlement. The intensity of herbivory by schooling fishes often varies unimodally with depth: low in very shallow water due to wave stress and other factors limiting accessibility by fishes, high at moderate depths, and low in deeper water where coral growth that provides shelter for fishes declines. Dense stands of macroalgae tend to thrive where herbivores are rare due to lack of habitat complexity that provides refuges from predation. Herbivorous damselfishes can act as natural cages by inhibiting schooling grazers and maintaining a high diversity of mid-successional algae within their territories via moderate grazing (intermediate-predation effect). These algal mats not only inhibit coral growth, but also serve as localized refugia for small invertebrates and newly settled fishes. Nutrients also play a pivotal role in structuring benthic algal productivity, standing crops, and species assemblages. Besides directly consuming corals or algae, reef fishes can also affect invertebrate corallivores and herbivores, causing subsequent indirect effects on reef benthos. Examples include predation on the corallivorous crown-of-thorns seastar and herbivorous sea urchins, the latter causing halos around patch reefs where urchins remain near cover. From a management perspective, conserving herbivores is clearly important for keeping reef algae in check. Maintaining both the abundance and species diversity of herbivores of a variety of sizes, especially via marine reserves, is likely the best means of ensuring that macroalgae do not displace corals. Such rules of thumb are likely essential for fostering the ecological resilience of coral reefs, especially in the context of a warming and acidifying ocean.

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### Keywords

Herbivore • Corallivore • Territorial damselfish • Phase shift • Trophic cascade

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## 10.1 Introduction

### 10.1.1 Fishes and Coral Reefs

Besides the corals themselves, fishes are perhaps the most conspicuous and beautiful inhabitants of coral reefs. Their diversity is amazing. It has been estimated that over 5,000 species of fish inhabit coral reefs worldwide (Cowman and Bellwood 2013), and locally, hundreds of species can coexist on the same reef. For example, Smith and Tyler (1972) found 75 species occupying a 3-m diameter patch reef in the Caribbean, which is not a particularly speciose region compared to the Indo-Pacific (Paulay 1997).

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, reef sharks, groupers, barracudas, and even wrasses and parrotfishes can reach startling sizes measured in meters. 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 (see reviews in Sale 1991, 2002). Moreover, reef fishes often occur in high standing stocks, with 8 mT/ha being near the likely present maximum, observed on uninhabited Jarvis Atoll in the Pacific (Sandin et al. 2008). Not surprisingly, reef fishes are an important food source for many tropical nations (reviews by Russ 1991; Polunin and Roberts 1996).

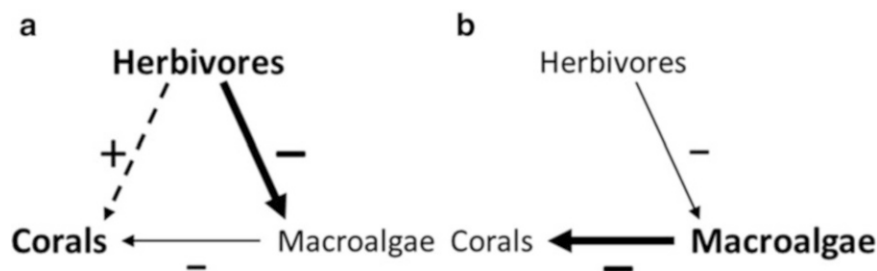
It seems almost a foregone conclusion, then, to assert that fishes have strong effects on the dominant benthos of reefs: corals and macroalgae. As reviewed below, herbivorous fishes normally do substantially affect the distribution and abundance of algae on reefs that are not overfished. Although relatively few major direct effects of corallivorous fishes on corals have been found, newly reported cases of corallivory are increasing, and the indirect effects of herbivorous fishes on corals can be substantial and perhaps essential for the ecological resilience of reefs. Additionally, there

is evidence that various fishes affect the distribution and abundance of invertebrate herbivores and corallivores, further affecting reef algae and corals indirectly.

### 10.1.2 Coral-Seaweed-Herbivore Triangle

A popular yet somewhat controversial hypothesis is that herbivorous fishes (and some macroinvertebrates, especially sea urchins) facilitate dominance by corals on reefs by preventing macroalgae (or equivalently, “seaweeds”, with apologies to phycologists) from outcompeting or otherwise hindering corals (e.g., Hughes 1989, 1994; Carpenter 1990; Done 1992; Knowlton 1992; Tanner 1995; McClanahan et al. 1996; Lirman 2001; Burkepille and Hay 2008, 2010; Barott et al. 2012). Indeed, there is some evidence that the evolution of modern herbivorous reef fishes may have been a prerequisite for dominance by reef-building corals. Bellwood and Wainwright (2002: 30) conclude from the fossil record that “the inferred scenario is one of increased herbivory, both in intensity and excavation depth, with a concomitant decrease in the abundance of macrophytes. This results in a system dominated by close-cropped turfs, where decreased competition between algae and corals permits coralline algae and corals to proliferate.” Thus, herbivores, seaweeds, and corals can be viewed as an important interaction web on healthy reefs, whereby predators (herbivores) control the dominant competitors for space (macroalgae), allowing subordinate competitors (reef-building corals) to thrive (Fig. 10.1a).

At the risk of proliferating ecological jargon, let us call this concept the **coral-seaweed-herbivore triangle**. Overfishing of herbivorous fishes combined with the loss of herbivorous macroinvertebrates can degrade this triangle, facilitating the replacement of corals by macroalgae as the dominant benthos (Fig. 10.1b). This change is often characterized as a “**phase shift**” that contributes to the demise of coral reefs (reviews by McCook 1999; McManus



**Fig. 10.1** The coral-seaweed-herbivore triangle as a simple interaction web, showing positive (+) and negative (–) direct effects (solid arrows) and indirect effects (dashed arrows). Arrow thickness depicts the relative strength of interactions, and font size represents relative biomass between scenarios. (a) The triangle on a reef that is relatively

healthy from a human perspective: many herbivores indirectly cause high live coral cover. (b) The triangle on a reef that is relatively degraded from a human perspective: macroalgae overgrow corals in the absence of substantial herbivory

et al. 2000; Nyström et al. 2000, 2008, 2012; McManus and Polsenberg 2004; Pandolfi et al. 2005; Ledlie et al. 2007; Mumby et al. 2007b, 2013; Mumby and Steneck 2008; Bruno et al. 2009; Cheal et al. 2010; Hughes et al. 2010; Roff and Mumby 2012; Graham et al. 2013). Such phase shifts may represent “alternative stable states” in that a positive feedback loop can develop following the loss of herbivores in which more algae and less coral means less shelter for fishes and macroinvertebrates, which inhibits further recruitment of herbivores, which means continuing low herbivory, high algal growth, and less coral (review by Petraitis 2013). Of course, degradation of the triangle is only one of a multitude of threats to coral reefs, as detailed elsewhere in this volume.

There is some controversy regarding the generality of the coral-seaweed-herbivore triangle. First, it has been debated whether macroalgal standing crops on reefs are controlled more from the top-down by herbivory or more from the bottom-up by nutrient flux (Lapointe 1997, 1999; Hughes et al. 1999; McCook 1999; Miller et al. 1999; Aronson and Precht 2000; Belliveau and Paul 2002; Jompa and McCook 2002; McClanahan et al. 2002; Diaz-Pulido and McCook 2003; Lapointe et al. 2004; Sotka and Hay 2009), although meta-analyses have indicated that herbivores are typically more important than nutrients (Burkepile and Hay 2006). Nonetheless, there are reef systems where both top-down and bottom-up factors are simultaneously important (e.g., Smith et al. 2001, 2010; Stimson et al. 2001; Thacker et al. 2001), a pattern that is also evident in meta-analyses (Gruner et al. 2008).

Second, the extent to which macroalgae outcompete or otherwise inhibit corals is also somewhat controversial (Miller 1998; McCook 1999; McCook et al. 2001; Williams et al. 2001; Birrell et al. 2008), with lab and field experiments both demonstrating such effects (Hughes 1989; Tanner 1995; Lirman 2001; Birrell et al. 2005, 2008; Kuffner et al. 2006; Box and Mumby 2007; Arnold et al. 2010) and failing to do so (Jompa and McCook 1998; McCook 2001). Dominance in competitive interactions between turf algae and corals varies with human presence, likely due to effects of fishing on herbivores (Barott et al. 2012). The effects of parrotfish consuming both seaweeds and corals can make it difficult to detect seaweed-coral competition (Miller and Hay 1998), and competition between sea urchins and herbivorous fishes further complicates these interactions (McClanahan 1992; McClanahan et al. 1996). Rather than extending such debates, my intent is to examine the complex role of reef fishes in structuring coral-reef benthos.

It is important at the outset to stress that the coral-seaweed-herbivore triangle may often not be as simple as depicted in Fig. 10.1 because this triad does not occur in isolation from the remainder of the reef ecosystem. All three

groups of organisms are affected by a variety of other organisms and abiotic factors that act in concert with interactions inside the triangle. Indeed, the coral-seaweed-herbivore triangle is part of the vastly complex interaction web that we call a coral reef ecosystem, involving a variety of direct and indirect effects among herbivores, seaweeds, corals, and their biotic and abiotic environment in ways that defy simplistic explanations (as detailed below). For example, herbivorous fishes can actually aid the dispersal of macroalgae, fragments of which may survive gut passage and reattach to the reef (Vermeij et al. 2013). Unfortunately for present-day scientists, much of what we know of reef ecosystems is a recent remnant of far richer systems that included numerous mega herbivores, including sea turtles, manatees, etc. (Jackson 1997).

Given this context, this chapter focuses on the myriad effects of (1) herbivorous fishes on the distribution and abundance of reef algae, and indirectly, corals, (2) corallivorous fishes that directly consume reef-building corals, and (3) fishes that consume and compete with invertebrate herbivores and corallivores, thereby indirectly affecting macroalgae and corals. The overall conclusion is that, beyond useful yet not quite universal concepts like the coral-seaweed-herbivore triangle, the immense complexity of coral reefs – combined with numerous synergistic threats to these ecosystems – makes explicitly detailed guidelines for conservation and management difficult. Nonetheless, there is sufficient generality that rules of thumb – such as maintaining high diversity and large populations of herbivores of a variety of body sizes – should be widely implemented to bolster the ecological resilience of coral reefs.

### 10.1.3 Scope of Review

This chapter focuses on the one-way effects of fishes upon reefs, emphasizing the mechanisms and constraints under which fishes cause shifts 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 (e.g., interaction arrows that would flow in the opposite directions as those in Fig. 10.1) are a matter of life and death for many species; many fishes are obligatory denizens of coral reefs and derive all their food and shelter from this habitat. The demise of a reef certainly has repercussions for reef fishes (review by Sale and Hixon 2014). For example, macroalgal overgrowth of reefs may reduce the density of both herbivorous and carnivorous fishes in Kenya (McClanahan et al. 1999). Indeed, Reese (1981) proposed that the density of obligate coral-feeding fishes can be used as a bioindicator of the general

health of a reef, yet this idea stirred considerable controversy (Bell et al. 1985; Bouchon-Navarro et al. 1985; Williams 1986; Roberts et al. 1988; Sano et al. 1987; White 1988; Bouchon-Navarro and Bouchon 1989; Clarke 1996; Kokita and Nakazono 2001). The close association of fishes and corals was 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. In any case, the death and collapse of a coral reef reduces living space for fishes, which in turn may reduce local populations of herbivores, thereby inhibiting reef recovery (Mumby and Steneck 2008; Nyström et al. 2012; Sale and Hixon 2014).

Other potentially important interactions between fishes and reefs that will not be covered here are, first, assessment of the relative effects of fishes vs invertebrate herbivores (Hay 1984; Carpenter 1986; Foster 1987; Morrison 1988; Klumpp and Pulfrich 1989), and second, the role of fish defecation and excretion fertilizing reef benthos (Meyer et al. 1983; Meyer and Schultz 1985a, b; Polunin and Koike 1987; Polunin 1988; Harmelin-Vivien et al. 1992; Burkepile et al. 2013). Finally, space limitations preclude exploration of the many fascinating and ecologically important interactions among fishes and the community structure of reef fishes per se. For example, changes in the abundance of predatory fishes could result in reciprocal shifts in the density of herbivorous fishes, with ramifications for the benthos (Graham et al. 2003; Mumby et al. 2006, 2012). Fortunately, volumes on these topics edited by Sale (1991, 2002) and Mora (2014) are unparalleled and recommended for those desiring a detailed introduction to reef-fish ecology, just as Polunin and Robert's (1996) edited volume covers reef fisheries.

This review, then, is by no means exhaustive. Previous reviews detailing interactions among reef fishes, seaweeds, and corals include Hixon (1986), Hutchings (1986), Glynn (1988, 1990), Steneck (1988), Horn (1989), Hay (1991, 1997), Jones et al. (1991), and McCook (1999). This review summarizes relevant literature published through 2013, emphasizing earlier foundational studies that are not always readily available on-line.

## 10.2 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. 10.2). Although about 10 families and over 100 species of fish are known to eat coral polyps, there are relatively few groups that feed strictly on corals (reviews by Robertson 1970; Randall 1974; Cole et al. 2008; Rotjan and Lewis 2008). This pattern may be due to coral polyps being relatively

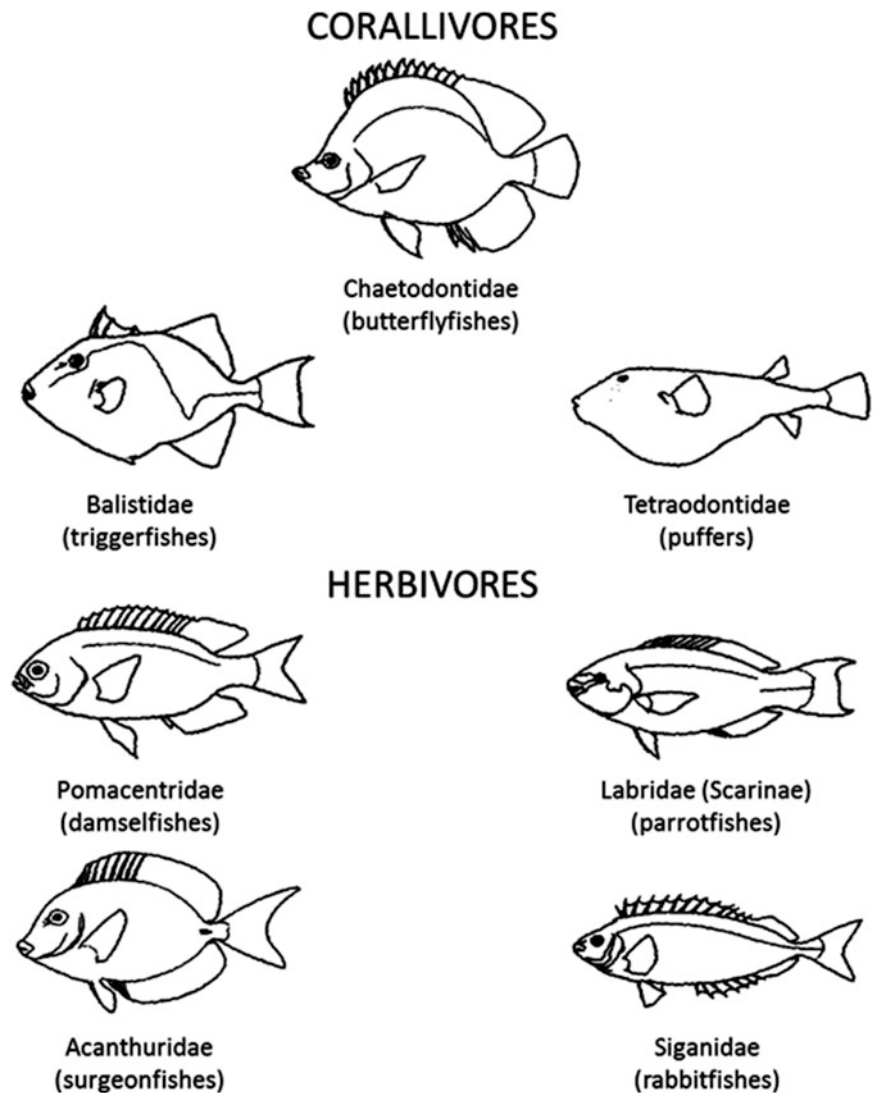
unpalatable compared to other prey in terms of their chemical composition, their protective nematocysts, and their calcium-carbonate skeletons. The predominant **corallivores** are butterflyfishes (Family Chaetodontidae, Cole et al. 2011); about half of the over 100 species eat corals (Allen 1981; Cole et al. 2008; Rotjan and Lewis 2008). Other relatively large fishes that regularly consume corals are triggerfishes (Balistidae), filefishes (Monacanthidae), and puffers (Tetraodontidae) (e.g., Jayewardene et al. 2009). Whereas the butterflyfishes delicately extract individual polyps from the coral skeleton, triggerfishes and puffers tend to scrape or excavate pieces of the coral colony with their beak-like mouths. Smaller corallivores include at least one goby (Gobiidae; Patton 1974).

Among the corallivores, 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). About 8 species of wrasse and about 20 species of parrotfish (both Labridae) also consume living coral tissue (Bruckner et al. 2000; Rotjan and Lewis 2006, 2008; Cole et al. 2008, 2010; Mumby 2009; Rotjan and Dimond 2010; Bonaldo and Bellwood 2011; Cole and Pratchett 2011a; Burkepile 2012), especially the largest species, the endangered bumphead parrotfish *Bolbometopon muricatum* (Randall 1974; Choat 1991; Bellwood et al. 2003). About a third of the species of corallivorous reef fish feed almost exclusively on corals (Cole et al. 2008).

In contrast to the corallivores, **herbivores** are relatively speciose (Fig. 10.2). As collated by Allen (1991) and Choat (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 (formerly Scaridae, now the Subfamily Scarinae of the Family Labridae), and over half of the approximately 320 species of damselfishes (Pomacentridae). Other herbivorous families include smaller fishes, such as combtooth blennies (Blenniidae), and even batfish (*Platax pinnatus*, Bellwood et al. 2006). The geographic distribution of herbivorous reef fishes is likely limited by temperature-related feeding and digestive processes (Floeter et al. 2005).

The feeding modes of herbivorous reef fishes are highly variable (reviews by Ogden and Lobel 1978; Horn 1989; Glynn 1990; Choat 1991; Wainwright and Bellwood 2002; Choat et al. 2002, 2004). 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 fused teeth. With these beaks (which inspired their name) and depending upon the species, parrotfishes superficially scrape or deeply excavate the substratum and remove algal holdfasts along with the dead coral to which the algae attach, and occasionally, live coral

**Fig. 10.2** 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 damselfish are not herbivorous. Certain species in numerous other families also consume corals and/or algae. Note that parrotfishes are increasingly documented to consume live coral as well as algae (Modified from Hixon 1997)



(Bellwood and Choat 1990; Bruckner et al. 2000; Rotjan and Lewis 2006; Bonaldo and Bellwood 2009; Mumby 2009; Rotjan and Dimond 2010; Burkepile 2012). This activity makes parrotfishes the major source of bioerosion (and producer of coral sand) among reef fishes (reviews by Hutchings 1986; Choat 1991, Chapter 4). Different species of algae are differentially consumed by different species of herbivore, indicating that herbivore diversity is important in controlling the overall standing crop of seaweeds (Mantyka and Bellwood 2007a, b; Burkepile and Hay 2008). Surgeonfishes, rabbitfishes, and parrotfishes 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. This immense functional diversity indicates likely complementary, synergistic, and redundant roles of multiple species in maintaining the resilience of what humans consider to be healthy coral reefs. What follows, then, are summaries of specific studies that can be generalized only with caution.

## 10.3 Effects of Fishes on Seaweeds

### 10.3.1 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 km<sup>2</sup> (Williams and Hatcher 1983), and secondary productivity can approach 3 metric tons per km<sup>2</sup> per year (review by Russ and St. John 1988). At Orpheus Island on the Great Barrier Reef, the entire area of the reef crest can be grazed by the parrotfish *Scarus rivulatus* monthly (Fox and Bellwood 2007, 2008). In the Caribbean, parrotfishes can graze at rates of over 150,000 bites per m<sup>2</sup> per day (Carpenter 1986), although it has been estimated that these fish can maintain only 10–30 % of a structurally complex fore-reef in a grazed state (Mumby 2006). At lower algal productivities on reefs in the Florida Keys, herbivorous fishes may consume up to 100 % of the entire daily production, ranging as low as about 30 % in some microhabitats (Paddack et al. 2006). 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 crop was controlled by grazing fishes during both 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 (Hatcher 1997). In some systems, such intense herbivory enhances local primary productivity by maintaining algae at an early-successional stage (Montgomery 1980; Birkeland et al. 1985; Carpenter 1986).

In addition to seasonal variation, an apparently general trend is that the spatial distribution of herbivory by fishes 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 often decreasing with depth. Thus, as documented in Guam (Nelson and Tsutsui 1981), the Caribbean (Hay et al. 1983; Lewis and Wainwright 1985), the Great Barrier Reef (Russ 1984a, b), and the Indian Ocean (Sluka and Miller 2001), 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 Curacao (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).

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 for fishes (Van den Hoek et al. 1978; Hay 1981b; McCook 1997). 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, 2015).

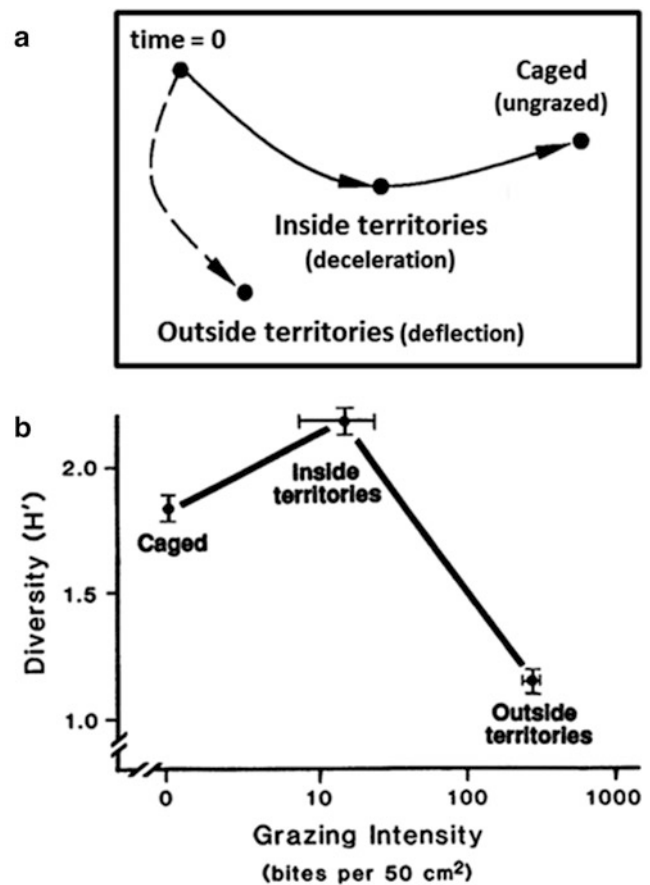
At the microhabitat scale, schooling herbivores may invade territories of damselfish, which harbor higher standing crops of seaweeds than the surrounding seascape (Jones 1968; Barlow 1974; Vine 1974; Robertson et al. 1976; Foster 1985; Reinthal and Lewis 1986). However, herbivores may spend less time foraging where macroalgal stands are particularly dense (Hoey and Bellwood 2011). At broader regional scales, on the Great Barrier Reef, inner-shelf reefs support both high macroalgal cover and high densities yet low biomass of parrotfishes, whereas outer-shelf reefs support the opposite patterns (Hoey and Bellwood 2008; Wismer et al. 2009), although other schooling herbivores are more abundant on the outer reef than inshore (Williams and Hatcher 1983; Russ 1984a, b). The mechanisms underlying these patterns appear to be related to between-region differences in the palatability and productivity of reef algae (Roff and Mumby 2012). (Chap. 9 provides a general review of regional variation in coral-reef processes.)

Regionally, comparisons among reefs have shown clear inverse correlations between the biomass of herbivorous fishes and the percent cover of macroalgae in the Caribbean (Williams and Polunin 2001) and the Great Barrier Reef (Wismer et al. 2009). Locally, herbivores can be more abundant inside marine reserves, with consequent declines in macroalgal abundance relative to fished areas, as documented in the Bahamas (Mumby et al. 2006), but not in Belize (McClanahan et al. 2011b). In the Bahamas, this pattern can lead to a trophic cascade that benefits corals (Mumby et al. 2007a). 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 such correlations are a case of cause and effect. 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 1986; Lewis 1986; Morrison 1988; Scott and Russ 1987; McCauley et al. 2010). 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 Hawai'i 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, 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 trajectory over the year (Fig. 10.3a). Intense herbivory by parrotfishes and surgeonfishes outside damselfish territories caused succession to follow a very different path, where the early filaments were replaced immediately by grazer-resistant crustose species, including the red coralline *Hydrolithon* (Fig. 10.3a). This result suggests that heavy grazing deflected the normal trajectory of succession toward herbivore-resistant algae (Hixon and Brostoff 1996). Other experiments showing the important role of herbivores in benthic algal succession include McClanahan (1997) in Kenya, Ceccarelli et al. (2005) in Papua New Guinea, and Burkepille and Hay (2010) in Florida.

In summary, intense herbivory, especially where an abundance and variety of herbivore species are present, strongly influences the standing crop, productivity, and community structure of reef algae. It also appears that selection for resistance to such herbivory may compromise competitive ability among algal species (Littler and Littler 1980; Hay 1981b; Lewis 1986; Morrison 1988). Off the Caribbean coast of Panamá, fishes may prevent competitively dominant (but highly palatable) sand-plain species from displacing 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).



**Fig. 10.3** Patterns of macroalgal succession and local species diversity on a Hawaiian coral reef under three levels of grazing by macroherbivores: caged (none), inside damselfish territories (moderate), and outside territories (intense). (a) Succession as a stylized ordination of macroalgal communities through time in species space (i.e., each curve shows community change in species composition and relative abundance through time). The pattern of ungrazed succession (caged) is decelerated within damselfish territories, whereas succession is deflected onto a new trajectory toward crustose algae outside territories. (b) Macroalgal species diversity after 1 year, indicating an intermediate-predation effect within damselfish territories, such that the damselfish is locally a keystone species (Modified from Hixon and Brostoff 1983, 1996)

### 10.3.2 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; Hata and Kato 2003). 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 on some reefs (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 damselfish (possibly combined with localized fecal fertilization) strongly affect the local species diversity of reef algae. This general effect has been demonstrated by three similar experiments in Guam (Lassuy 1980), Hawai'i (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 he studied (*Stegastes lividus* and *Hemiglyphidodon plagiometopon*), Lassuy (1980) found that caged surfaces exhibited the greatest algal diversity after 2 months. Both 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 relatively early successional stages.

In the Hawai'i study, Hixon and Brostoff (1996) showed that moderate grazing by the damselfish *Stegastes fasciolatus* (now *S. marginatus*) slowed and appeared to stop succession at a high-diversity middle stage dominated by red filaments (Fig. 10.3a). Thus, rather than deflecting the successional trajectory like more intensive grazers (see above), damselfish appeared to simply decelerate algal succession. Territorial fish may maintain the mid-successional 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, whereas local species diversity was at its maximum. These results thus corroborated the **intermediate-predation hypothesis** (review by Hixon 1986). At low levels of grazing 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. 10.3b).

Given that territorial damselfish can locally enhance species diversity, they can be considered "**keystone species**" (sensu Paine 1966, see also Williams 1980). However, unlike the normal kind 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 herbivory.

There is evidence that this pattern documented in Hawai'i 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). It has also been found that species diversity of macroalgae in territories of other damselfish, including *Stegastes planifrons* off Puerto Rico (Hinds and Ballantine 1987) and *Stegastes fuscus* off Brazil (Ferreira et al. 1998), decline in 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) and/or weeding (Hata and Kato 2002; Hata et al. 2002). Although *Stegastes nigricans* maintains strong dominance by *Womersleyella setacea* in its territories in Okinawa, the abundance and species diversity of benthic foraminifera is greater inside territories than outside (Hata and Nishihira 2002).

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), as well as newly settled fishes (Green 1992, 1998). 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). Crustose corallines also provide settlement substratum for some reef-building corals (Morse et al. 1988; Heyward and Negri 1999), so damselfish territories may additionally inhibit coral settlement.



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 (unpublished) found considerably more blue-green algae inside than outside territories in Hawai'i. 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 distribution and abundance of blue-green algae.

### 10.3.3 Conclusions Regarding Effects of Fishes on Seaweeds

Herbivorous fishes can strongly affect the distribution and abundance of reef macroalgae. Where there is ample shelter from predation and protection from strong turbulence, schooling herbivores can consume 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. Describing the coral-seaweed-herbivore triangle, Glynn (1990: 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." Nonetheless, it is important to realize that a myriad of factors are involved in these and other switches in dominance among algal growth forms and between algae and corals. For example, Littler and Littler (1984) saw nutrient levels as pivotal in determining whether and how herbivory will determine the dominant benthos on reefs, and subsequent experimental work showed that nutrient levels may or may not affect these interactions (Smith et al. 2001; Stimson et al. 2001; Thacker et al. 2001). Thus, a synergistic combination of "top-down" factors (herbivory) and "bottom-up" factors (nutrients) likely determine whether corals or seaweeds dominate reef benthos (Hatcher 1990; Szmant 2001; McClanahan et al. 2002). Additionally, by providing spatial refuges from predation for both corals and seaweeds, the physical structure of the habitat (holes and crevices) affects local grazing rates, with further ramifications for benthic community structure (Littler et al. 1989; Hixon and Menge 1991).

Besides schooling herbivores, territorial damselfishes have particularly strong local effects on shallow reef algae, effects which 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 accretion, nitrogen fixation, epiphytes and small invertebrates that inhabit the algae, and, as will be seen in the next section, corallivores (Fig. 10.4). Clearly, herbivorous fishes are major players determining the character of shallow coral-reef communities, and territorial damselfishes in particular can act as keystone species.

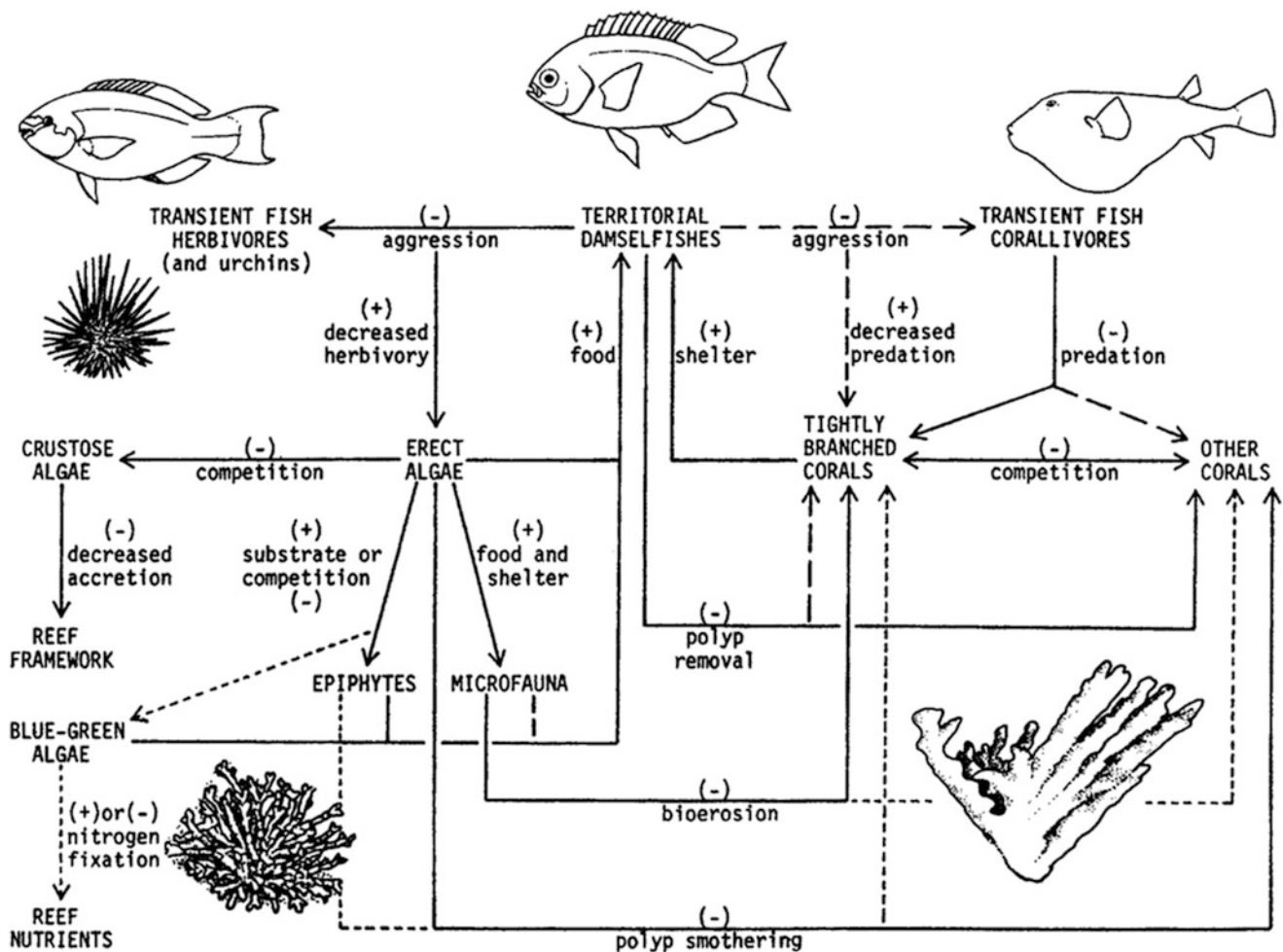
## 10.4 Effects of Fishes on Corals

### 10.4.1 Direct Consumption

The genera of corals most commonly grazed by reef fishes are *Acropora*, *Pocillopora*, *Montipora*, and *Porites* (reviews by Cole et al. 2008; Rotjan and Lewis 2008). 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 originally appeared to have a negligible effect on coral standing crops (Harmelin-Vivien and Bouchon-Navarro 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 m<sup>2</sup>, yet consumed an average of only about 10 and 28 g of coral polyps per 1,000 m<sup>2</sup> 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. 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). More recently, however, it has been documented that butterflyfishes on the Great Barrier Reef can consume up to 79 % of the annual productivity of tabular acroporid corals (Cole et al. 2012).

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 1 week (see also Hixon and Brostoff 1996). Additionally, butterflyfishes may negatively affect corals indirectly by being vectors for diseases (Raymundo et al. 2009).

Locally high densities of corallivorous fishes can clearly stress their particular host corals (Cole and Pratchett 2011b), and these predators may selectively target colonies with high



**Fig. 10.4** Flowchart synthesizing the interactions between fishes and benthos on a shallow coral reef where territorial damselfishes are abundant. Arrows indicate positive (+) and negative (-) effects. Dashed lines indicate relatively weak effects, and dotted lines indicate effects that are poorly documented and/or controversial. Where

territorial damselfishes are rare, some of these effects reverse. In particular, erect algae and their associates are often replaced by grazer-resistant crustose algae (which may serve as settlement habitat for corals) due to intense grazing by transient herbivores (Modified from Hixon 1983)

densities of macroboring organisms (Rotjan and Lewis 2005). Such differential effects can have ramifications for interactions among corals. For example, off Hawai'i, 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 coral, *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 *Orbicella* (formerly *Montastraea*) *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 Panamá, *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, there can be direct consumptive effects of herbivorous fishes on corals. Field observations have noted grazing fishes damaging juvenile corals (Randall 1974; Bak and Engel 1979), although Birkeland (1977) documented herbivores avoiding coral recruits. 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 back-reef bottoms were dominated by macroalgae, *P. porites*, or the relatively mound-shaped and grazer-resistant *P. astreoides*. Similarly, recently recruited coral colonies survived intense parrotfish grazing in laboratory mesocosms in Hawai'i only when structural refuges from grazing were provided (Brock 1979). Indeed, although it was long believed that only the largest species of parrotfish, the Indo-Pacific *Bolbometopon muricatum*, consumes substantial amounts of live coral (Randall 1974; Choat 1991), individually consuming about 2.5 metric tons of living coral per year (Belwood et al. 2003), there is increasing evidence that smaller parrotfishes may also negatively affect corals (Bruckner and Bruckner 1998; Bonaldo and Bellwood 2011; Burkepile 2012, but see Mumby 2009).

A poorly documented yet possibly substantial source of coral mortality is consumption of coral spawn by planktivorous reef fishes, especially on the Great Barrier Reef (Westneat and Resing 1988; Pratchett et al. 2001). Less directly, parrotfish of the genus *Sparisoma* may differentially target gravid polyps of *Orbicella* in the Caribbean, thereby lowering the fitness of grazed coral colonies prior to spawning (Rotjan and Lewis 2009). Also poorly documented yet potentially important are the combined negative effects of corallivory and bleaching on the condition and recovery of corals. Fish may (or may not) target bleached corals (Cole et al. 2009), and bleached corals that have been previously grazed by parrotfish may show a persistent reduction in the density of endosymbiotic zooxanthellae compared to bleached colonies that have not been grazed (Rotjan et al. 2006).

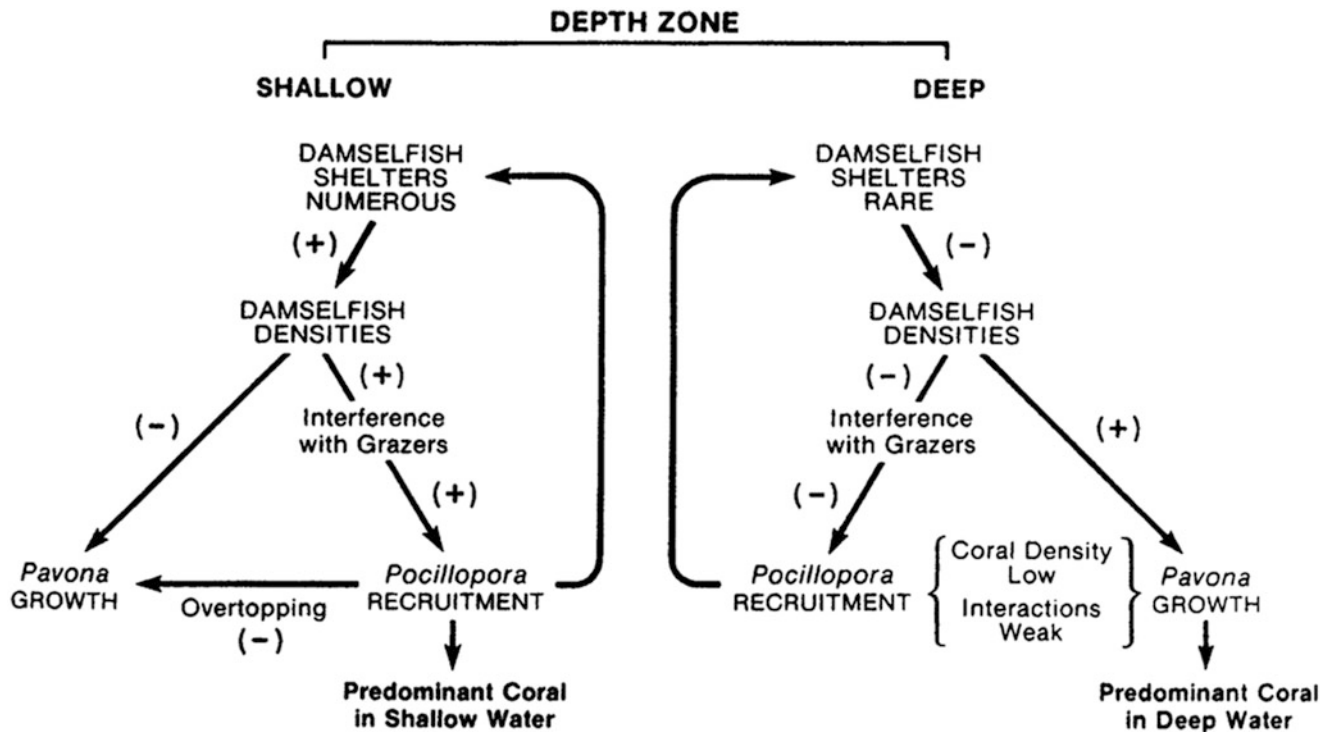
#### 10.4.2 Indirect Effects

Available experimental evidence suggests that indirect effects of herbivorous fishes influence the local distribution and abundance of corals more extensively than direct consumption by corallivores. As reviewed in the introduction to this chapter, schooling herbivores can benefit corals indirectly by reducing the standing crops of seaweeds that compete with corals via the coral-seaweed-herbivore triangle (Fig. 10.1a). For example, 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. Lirman (2001) documented that more than 50 % of the basal perimeter of *Siderastrea siderea*, *Porites astreoides*, and *Orbicella faveolata* in the Florida Keys was in contact with macroalgae. Excluding

herbivores by caging these perimeters resulted in increased algal biomass, accompanied by decreased growth rates of *Porites* and increased mortality of *Orbicella*. However, *Siderastrea* was unaffected by seaweeds. Following a coral bleaching event on the Great Barrier Reef, algal cover increased and live coral cover decreased in plots caged to exclude herbivorous fishes, indicating the important role of herbivores in fostering ecological resilience (Hughes et al. 2007). Inside a marine reserve in the Bahamas, herbivory was greater, macroalgal abundance was less, and coral recruitment was greater than in adjacent fished areas, yet overall coral community structure was no different (Mumby et al. 2006, 2007a). Following the massive coral bleaching event in 1998, which shifted benthic dominance from corals to seaweeds on many reefs, a marine reserve harboring herbivorous fishes recovered at a rate no greater than fished reefs (McClanahan 2008).

By defending and maintaining their algal mats, territorial damselfish produce patches in which juvenile corals are often smothered (Vine 1974; Potts 1977). Additionally, the algal mat provides microhabitats facilitating various boring organisms, which intensifies bioerosion of the coral framework (review 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; Wellington 1982; Suefuji and van Woesik 2001). If for any reason coral colonies 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 Panamá by Wellington (1982). In this system, branching *Pocillopora* corals dominated shallow areas (0–6 m depth), while the massive *Pavona gigantea* dominated deeper areas (6–10 m depth). Combining field observations and experiments, Wellington discovered an interactive feedback loop whereby the damselfish *Stegastes acapulcoensis* may directly and indirectly cause this zonation (Fig. 10.5). When establishing territories in the shallow zone, damselfish differentially kill *Pavona* by polyp removal and maintain their algal mats on the exposed substrata. However, *Pocillopora* is apparently protected by its tightly branched morphology and rapid polyp regeneration. Additionally, *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



**Fig. 10.5** Interactive feedback loops influencing the depth zonation of *Pocillopora* and *Pavona* corals off the Pacific coast of Panamá. Arrows indicate positive (+) and negative (-) effects. The direct negative effect of territorial damselfish on *Pavona* in shallow water is due to polyp

removal, whereas the “direct” positive effect in deep water is actually an indirect effect mediated by the scarcity of damselfish shelters (From Wellington 1982)

are low because overall coral cover (and thus between-coral 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.

Finally, a variety of reef fishes have been observed feeding on diseased *Acropora* coral tissue affected by black-band and brown-band disease, which could potentially spread these diseases from head to head and/or foster recovery of infected heads (Chong-Seng et al. 2011).

### 10.4.3 Conclusions Regarding Effects of Fishes on Corals

Truly corallivorous fishes have been shown to affect the local distribution and abundance of some corals directly via consumption. However, the indirect effects of the coral-seaweed-herbivore triangle and the territorial activities of herbivorous damselfishes appear to have more substantial effects on corals in shallow water. In any case, direct 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 intensive fish grazing, such

as within damselfish territories, but will often be eventually overgrown by algae in the absence of substantial herbivory. 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 targeted prey, but some colonies normally reach an invulnerable size where they are both immune to incidental predation and freed from competition with algae. Rotjan and Lewis (2008) suggest that, as reefs continue to be degraded by various human activities, corallivory will become increasingly important as an agent of reef decline.

## 10.5 Effects of Fishes 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 directly consume these organisms, including the major invertebrate corallivore – the crown-of-thorns seastar (*Acanthaster planci*) – and the major invertebrate herbivores: sea urchins (reviews by Jackson 1994; Roberts 1995). 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 1,000–4,000 *Acanthaster* per hectare each year, a rate that accounted for an observed decline in the *Acanthaster* population. However, experiments on the Great Barrier Reef detected no effects of fish predation on juvenile *Acanthaster* (Sweatman 1995).

Triggerfishes and puffers also consume sea urchins, as do large wrasses and porcupinefishes (Diodontidae, Randall 1967). Field experiments have demonstrated that such predation can be intense (Glynn et al. 1979) and 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 caused the unusually high urchin densities in populated regions of the Caribbean before the mass mortality of *Diadema antillarum* in 1983 (Lessios 1988). Mumby (2006) calculated that, following the ecological extinction of *Diadema*, parrotfish grazing alone was insufficient to prevent macroalgae from displacing corals.

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* (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 recruits (mostly acroporids) was greater there (Sammarco and Carleton 1981).

In the Caribbean, the damselfish *Stegastes planifrons* can exclude *Diadema* urchins from their 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, that 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 1986). 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; Hixon and Beets, unpublished).

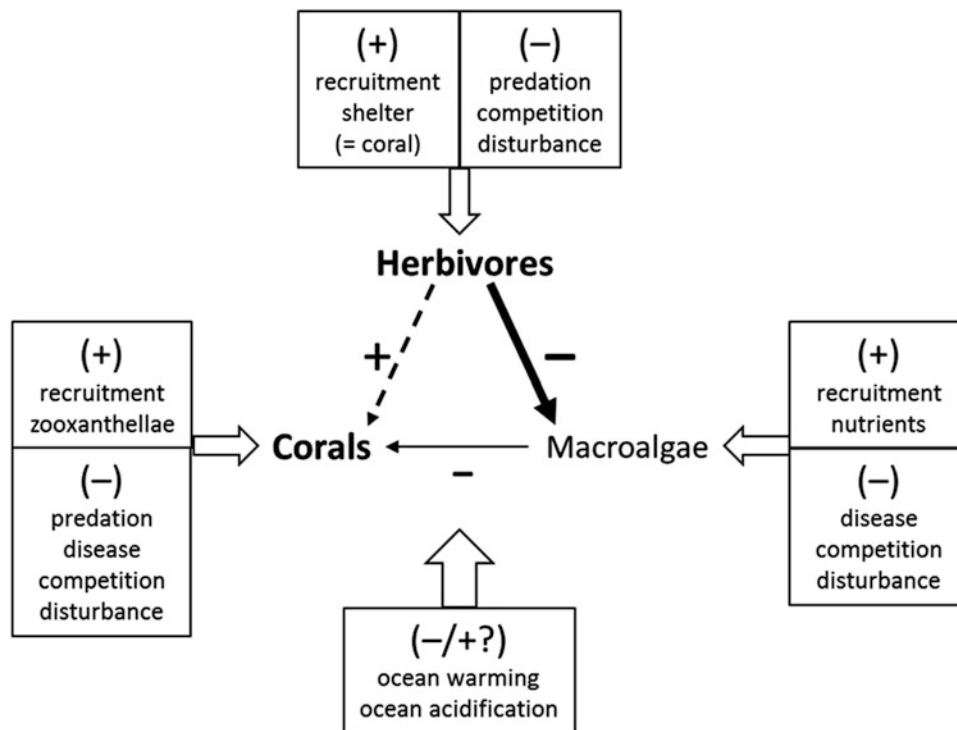
Finally, complex interactions between invertebrates and fishes can occur. Outbreaks of *Acanthaster* can kill large tracts of coral, presumably increasing the availability of substrata for macroalgal growth, which in turn may increase the local densities of herbivorous fishes and decrease densities of 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.

## 10.6 Implications for Reef Management and Conservation: A Complex Triangle

As a generality subject to exceptions, the coral-seaweed-herbivore triangle on healthy reefs (Fig. 10.1a) is confirmed by observations that herbivorous fishes and urchins can have very strong effects on the standing crop of reef macroalgae, thereby opening space for corals to thrive. However, other factors, such as the abundance and distribution of territorial damselfishes, shelter for schooling herbivores, water motion, and nutrient flux, as well as multiple stressors on corals, can modify this basic pattern, sometimes strongly (Szmant 2001; Cheal et al. 2010; McClanahan et al. 2011a). The degradation of the coral-seaweed-herbivore triangle (Fig. 10.1b) is also reasonable generality, in that overfishing of herbivores (or loss by other factors) can facilitate the overgrowth of corals by macroalgae. Again, however, there are exceptions and conflicting results. For example, although a negative correlation was documented between the density of herbivorous fishes and the cover of seaweeds on Caribbean reefs, the abundance of seaweeds was high even on lightly fished reefs (Williams and Polunin 2001; see also Cheal et al. 2010).

In New Caledonia and elsewhere, there may be little correlation among reef protection status (especially in lightly fished regions), coral recovery, and relative macroalgal development following severe storms and bleaching events (Carassou et al. 2013). Also problematic is determining whether seaweeds truly outcompete corals, or merely colonize dead coral surfaces after a polyp colony is killed by other factors (McCook 1999; McCook et al. 2001), including algae fostering coral disease (Smith et al. 2006). Additionally, there are sufficient differences between Caribbean and Indo-Pacific reef ecosystems and their respective stressors that extrapolating findings between ocean basins may be unwarranted (Roff and Mumby 2012).

Given the variety of factors that may modify the simple coral-seaweed-herbivore triangle (Fig. 10.1a), it may be more prudent to include the many biotic and abiotic environmental factors that can affect the outcome of the basic interaction web. Figure 10.6 is offered as an image of the



**Fig. 10.6** The coral-seaweed-herbivore triangle including some of the major complicating factors that affect each member of the triad. Note that “predation” can include disease, parasitism, carnivory, and fishing mortality, and “disturbance” can include wave surge, sand scour, sedimentation, and pollution. Ocean warming and acidification will affect all members of the triad in ways that are likely to be negative for corals (and perhaps fishes) and may be positive for

macroalgae. The relative strengths of all direct and indirect interactions among all these factors (among others) will ultimately determine whether or not the triangle is dominated by interactions illustrated among herbivores, macroalgae, and corals. Given the number of factors involved and high variation in their intensities, the simple coral-seaweed-herbivore triangle is unlikely to operate in every system, despite its broad relevance

more realistic triangle, including some of the more important complicating factors (see related figures by Mumby and Steneck 2008; Nyström et al. 2012; Burkepile et al. 2013). Recent models have attempted to address some of this complexity (Mumby 2006; Mumby et al. 2007; Ruiz Sebastián and McClanahan 2013).

From a management perspective, conserving herbivores is clearly important for keeping reef seaweeds in check (Mumby et al. 2007a, b; McClanahan et al. 2012). Given that seaweeds have evolved a variety of structural and chemical defenses that inhibit particular herbivores (reviews by Hay and Fenical 1988; Steneck 1988; Duffy and Hay 1990; Hay 1991, 1997), maintaining both the abundance and species diversity of herbivores of a variety of sizes is likely the best means of ensuring that seaweeds do not displace corals, as demonstrated experimentally by Burkepile and Hay (2008, 2010) and suggested by the modeling studies of Mumby (2006) and the correlative field studies of Cheal et al. (2010). Parrotfishes, especially larger individuals, are often seen as a particular conservation target for enhancing the ecological resilience of coral reefs (Bellwood et al. 2004, 2012; Mumby 2006, 2009; Mumby et al. 2006, 2007a, b).

Larger parrotfish are particularly important in controlling macroalgal biomass (Jayewardene 2009).

Beyond the general rule of thumb of “conserve and foster herbivores,” the complexity of interactions among fishes, seaweeds, corals, and their reef environment makes it difficult to provide explicitly detailed predictions relevant to the management and conservation of coral reefs. For example, before predicting how fishing will secondarily affect the benthic community on a reef explicitly, one must know how different fish populations will respond to exploitation, and as a prerequisite, what determines the local population sizes of fishes in the absence of fishing. Understanding of the mechanisms driving and regulating the population dynamics of coral-reef fishes is an onerous undertaking (e.g., Hixon et al. 2012). Nonetheless, it is clear that both corallivores and herbivores are often subjected to intensive overfishing (review by Russ 1991; Roberts 1995; Polunin and Roberts 1996; Bellwood et al. 2012), so rules of thumb are essential for fostering the reef resilience.

The immense complexity of coral-reef ecosystems means that the demise or outbreak of a single species or functional group of species due to human activities may have

unanticipated and possibly severe consequences for the remainder of the system (Chap. 11). Reef fishes, in particular, manifest a very complex variety of direct and indirect effects on the benthos of coral reefs (e.g., Figs. 10.4 and 10.5) – far more complicated than the simple triangle illustrated in Fig. 10.1, or even the complex triangle illustrated in Fig. 10.6. The numerous indirect interactions between 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 productivity and species diversity of seaweeds and associated fauna, including new recruits of reef fishes, but may also be sites of reduced coral growth and weakened reef framework. The multitude and complexity of these effects severely limits our ability to predict the precise outcome of active management of any particular species, let alone multiple species.

Although reef systems may be too complicated to allow us to predict explicit outcomes of human activities beyond basic concepts like the coral-seaweed-herbivore triangle, 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 reduce the abundance of any native coral-reef inhabitant. The secondary results of such alterations may be both unexpected and undesirable. Perhaps more than any other natural system, coral reefs 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." Given the widespread degradation of coral reefs occurring worldwide, perhaps the most effective approach to the conservation and management of these amazing and valuable ecosystems is to ensure that some reefs – especially those buffered from or adapted to ocean warming and acidification – are fully protected from regional human impacts (both extractive and nonextractive) in large marine reserves, thereby ensuring substantial local populations of herbivorous fishes and other resilience mechanisms (Pandolfi et al. 2005; Hughes et al. 2006; Mumby and Steneck 2008; Steneck et al. 2009; Edwards et al. 2010; Selig and Bruno 2010).

Marine reserves may harbor more coral-reef piscivores that may inhibit increases in herbivore populations (Graham et al. 2003), but there is ample evidence that piscivores also play an important role regulating and thus stabilizing the population dynamics of their prey (Hixon and Jones 2005). Of course, marine reserves are necessary but not sufficient for saving reefs; multiple sources of protection and active management are essential (Pandolfi et al. 2005; Nyström et al. 2012; Carassou et al. 2013). In any case, despite broad protections in substantial regions such as the Great Barrier Reef Marine Park in Australia and the Papahānaumokuākea Marine National Monument in Hawai'i, humankind has by-and-large been woefully slow in fostering the resilience of our

remaining coral reefs (Mora et al. 2006; Hughes et al. 2010). Time is short to reverse this dangerous trend.

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