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Effects of fish predation and seaweed competition on the survival and growth of corals

Abstract On Caribbean coral reefs, high rates of grazing by herbivorous fishes are thought to benefit corals because fishes consume competing seaweeds. We conducted field experiments in the Florida Keys, USA, to examine the effects of grazing fishes on coral/seaweed competition. Initially, fragments of *Porites divaracata* from an inshore habitat were transplanted into full-cage, half-cage, and no-cage treatments on a fore-reef. Within 48 h, 56% of the unprotected corals in half-cage and no-cage treatments (62 of 111) were completely consumed. Stoplight parrotfish (*Sparisoma viride*) were the major coral predators, with redband parrotfish (*S. aurofrenatum*) also commonly attacking this coral. Next, we transplanted fragments of *P. porites* collected from the fore-reef habitat where our caging experiments were being conducted into the three cage treatments, half in the presence of transplanted seaweeds, and half onto initially clean substrates. The corals were allowed to grow in these conditions, with concurrent development of competing seaweeds, for 14 weeks. Although seaweed cover and biomass were both significantly greater in the full-cage treatment, coral growth did not differ significantly between cage treatments even though corals placed with pre-planted seaweeds grew significantly less than corals placed on initially clean substrate. This surprising result occurred because parrotfishes not only grazed algae from accessible treatments, but also fed directly on our coral transplants. Parrotfish feeding scars were significantly more abundant on *P. porites* from the half and no-cage treatments than on corals in the full cages. On this Florida reef, direct fish predation on some coral species (*P. divaracata*) can exclude them from fore-reef areas, as has previously been shown for certain seaweeds and sponges. For other corals that live on the fore-reef (*P. porites*), the benefits of fishes removing seaweeds can be counterbalanced by the detrimental effects of fishes directly consuming corals.

Key words Coral · Corallivory · Florida · Predation · Seaweed competition

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Introduction

Invertebrate corallivores are widely recognized as having important effects on reef development and reef coral populations in both the Caribbean (e.g., the gastropod *Coralliophila*: Ott and Lewis 1972; Brawley and Adey 1982; Knowlton et al. 1990) and Pacific (e.g., *Acanthaster* and other echinoderms: Endean 1973; Glynn et al. 1979; Glynn and Krupp 1986). In contrast, much of the literature on corallivory by reef fishes refers to specialized Pacific butterflyfishes (Reese 1977; Neudecker 1979; Cox 1986). Most research in the Caribbean and temperate Atlantic has focused on how grazing fishes indirectly benefit corals by consuming seaweeds and thus reducing competitive pressure (Birkeland 1977; Lewis 1986; Steneck 1988; Hughes 1994; Miller and Hay 1996). These studies suggest that a significant reduction of fish grazing can result in the overgrowth of juvenile and adult corals by other benthic life forms, especially fleshy macroalgae. Observations by Birkeland (1977) in the tropical eastern Pacific indicate that herbivorous fishes actively avoid consuming juvenile corals greater than a few millimeters in size. A similar result was reported by Brock (1979) for Hawaiian parrotfish. In his laboratory study, field densities of parrotfish were determined to be "optimal" in promoting coral recruitment and benthic community development.

The exceptions to this rule are an anecdotal account from Barbados of substantial direct predation on corals by parrotfishes (Frydl 1979) and a careful experimental study by Littler et al. (1989) showing that direct predation by parrotfishes on *Porites porites*, but not *P. astreoides*, is a primary factor controlling the distinct zonation of these two coral species on the protected side of a Belizean reef flat.

Long-term overfishing of grazers as well as piscivores in many areas of the Caribbean (Hay 1984a; Hughes 1994), in combination with the loss of the echinoderm grazer *Diadema antillarum* in a pandemic die-off in 1982–1983 (Lessios 1988), is implicated in the proliferation of macroalgae and the loss of live coral from many Caribbean reefs (Liddell and Ohlhorst 1986; de Ruyter van Steveninck and Bak 1986; Hughes et al. 1987; Carpenter 1990a; Hughes 1994). Though many reef fisheries in the Florida Keys are also classified as overfished (J. Ault and J. Bohnsack, personal communication), these fisheries are primarily of a recreational rather than a subsistence nature, and the overfished stocks are primarily carnivores, such as grouper and snapper, rather than grazing scarids and acanthurids.

Our study was designed to test the direct effect of large grazing fishes on the accumulation of seaweed standing stock, as well as the indirect effect of fish grazing on coral growth and survivorship on a fore-reef in the Florida Keys. Our a priori hypothesis, based on our own and others' previous results (Lewis 1986; Morrison 1988; Hughes 1994; Miller and Hay 1996), was that the exclusion of large grazing fishes would result in a proliferation of seaweeds and a decrease in coral growth and/or survivorship due to competition from these seaweeds. This is not what we found.

Materials and methods

Field experiments were conducted in the relict spur and groove zone at Pickles Reef, Key Largo, Fl, USA (24°59.200′ N, 80°25.133′ W). We used flat cinder blocks (20 × 41 × 5 cm) as our experimental units. A 2-cm hole was drilled in the center of each cinder block and a large galvanized steel stake was hammered through the hole and driven into the reef substrate to secure the blocks in place. Forty-five blocks were arranged in 15 groups of three ($n = 15$, each with three treatments) in an approximately linear arrangement running northeast to southwest at a depth of 6–8 m. Each group of three blocks was separated from adjacent groups by at least 2–3 m. One of each group of three blocks was left bare (no cage), one was completely enclosed in plastic mesh (full-cage treatment), and one was partially enclosed (two walls and a top, half-cage control; see Fig. 1). A large mesh size (2-cm openings) was used to exclude large grazing fishes while allowing access to smaller predatory fishes such as wrasses and blennies. Access by these smaller fishes should minimize potential artifacts resulting from cages providing predation refuges for mesograzers (Lewis 1986).

A second factor was also used in the experiments. Because we were starting with clean substrates, we chose to preplant seaweeds into one end of every cinder block. Clumps of *Dictyota* spp. and of *Halimeda opuntia* were attached with cable ties to a 5-cm wide strip of mesh cut from a seine. This mesh was cable-tied around one end of each cinder block so that it held the algae firmly against the block and allowed them to attach to the block and grow up
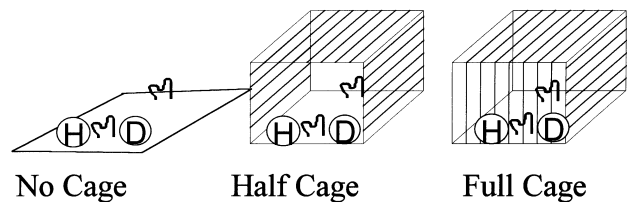
Fig. 1 Schematic design of one replicate of the field experiment. *H* and *D* represent preplanted clumps of the seaweeds *Halimeda opuntia* and *Dictyota* spp., respectively. In the experiment with *Porites divaracata*, two coral transplants were placed on each end of each cinder block

through the mesh. A bare strip of mesh was cable-tied around the other end of the block as a control. One or two corals (depending on the experiment, see below) were then attached through slits in the mesh onto each end of each block (i.e., attached between the clumps of preplanted algae on one end and through the mesh onto the bare block on the other end; see Fig. 1). Because each experimental unit (cinder block) received both levels of the preplanting factor but only one level of the caging factor, we had a two-factor split-plot experiment for which we used an ANOVA design suggested by Milliken and Johnson (1984) with the error mean square term associated with the cinder block used to test significance of the cage treatment. Over the course of the experiment, a few of our cages were lost due to rough weather, yielding a sample size for analysis of 12 or 13. Due to this imbalance, we report statistical results of type III sum-of-squares calculated by PROC GLM of SAS (Shaw and Mitchell-Olds 1993).

Experiment with *P. divaracata*

On 28 July 1996, we collected fragments of the slender branching coral *P. divaracata* from the grass flats around Rodriguez Key, approximately 3 km inshore from the fore-reef site at Pickles Reef. The fragments were returned to the National Undersea Research Center in Key Largo and kept in flowing seawater until the buoyant weight of each fragment was determined (Davies 1989). On 29 July, each fragment was placed in an individually numbered plastic bag, transported back to Pickles Reef, and attached to a numbered cinder block using Petit Polypoxy Underwater Patching Compound. In this experiment, two small fragments were glued to each end of each cinder block (i.e., four coral pieces/cinder block).

Two days later (31 July), we found that many of the corals in the no-cage and half-cage treatments were missing, apparently bitten off at the base which remained embedded in the epoxy. At this time, each of the four corals in each cage was scored as undamaged, one-quarter, one-half, three-quarters, or completely eaten. These scores were averaged to obtain the percentage of corals remaining for each cage. We had 12 excess corals that had not been used in the initial experiment, so these were affixed to the blocks at 1100 hours. We observed several of these corals for the next hour (to see if they were attacked by fishes) and then revisited them 4 h later. At this time, the experiment was ended because all of the corals had been completely consumed.

Because of the short duration of this experiment, the preplanted seaweed factor was ignored and a Kruskal-Wallis nonparametric one-way ANOVA followed by Dunn's pairwise comparisons was used to detect significant differences in coral survival between the cage treatments.

Video assay

To determine which fishes were consuming corals, four underwater video cameras were set up at haphazard positions in the vicinity of the experimental cages on 31 July 1996. Fist-sized aggregations of four species of corals collected from grassbeds near Rodriguez Key

(*P. divaracata, Cladocora arbuscula, Siderastrea radians*, and *Manicina* sp.) were placed at the corners of a 50-cm square in view of each camera and filmed for 2 h. The number of bites of each coral species taken and the identity of fishes attacking the corals were quantified.

Experiment with *P. porites*

We repeated the above experiment using *P. porites* collected from the fore-reef near our cages. On 1 August 1996, these corals were weighed and one piece of coral was transplanted onto each end of each cinder block as described above. This experiment ran for 14 weeks at which time (20 November 1996), the corals were harvested and seaweed cover was estimated on each half of each cinder block using a 50-point grid to determine the number of points intersecting macroalgae. Corals were returned to the laboratory at the Rosenstiel School of Marine and Atmospheric Science at the University of Miami where they were buoyant-weighed and examined carefully to quantify the number of bite scars. Number of bite scars, seaweed cover, and coral growth were analyzed by the ANOVA design described above.
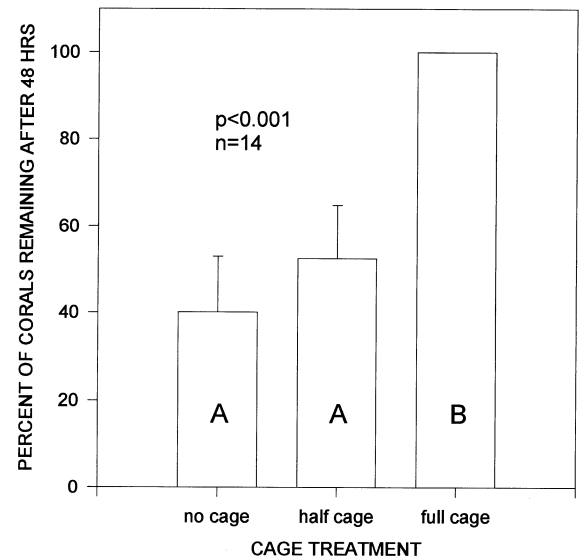
Results

Experiment with *P. divaracata*

When we first monitored the *P. divaracata* transplants, 48 h after placing them in the field, we found that 56% of the corals (62 of the 111) in no-cage and half-cage treatments were missing. In most cases, it appeared that they had been bitten off at the base, leaving what looked like parrotfish feeding scars in the bit of skeleton remaining embedded in the epoxy. All corals in full cages remained intact. New corals transplanted onto the cinder blocks at 1100 hours were immediately attacked and completely consumed by stoplight parrotfish (*Sparisoma viride*). All of these transplants were consumed within 4 h. Stoplight parrotfish were also observed nosing against the full cages, apparently trying to access the corals they protected.

Kruskal-Wallis one-way ANOVA followed by Dunn's test showed that survivorship in closed cages was significantly greater than in either half-cage or no-cage treatments; these last two treatments did not differ from each other (Fig. 2). One striking aspect of these results was that the corals consumed were not evenly distributed among replicates (Fig. 3). Replicates were arranged approximately linearly from southwest to northeast; all of the corals consumed were from the southwest end. None of the corals that were in replicates on the extreme northeast end were consumed (Fig. 3).

Video assays

The video-taped assays documented rapid consumption of *P. divaracata* by stoplight parrotfish (*S. viride*) and redband parrotfish (*Sparisoma aurofrenatum*). Our field observations and these videos both suggested that large stoplight parrotfish were responsible for the majority of


Fig. 2 Results of the experiment with *P. divaracata. Bars* represent means + 1 SE. *P*-value from Kruskal-Wallis one-way ANOVA. Treatments with the *same letter* are not significantly different ($P > 0.05$) by Dunn's post hoc pairwise comparisons
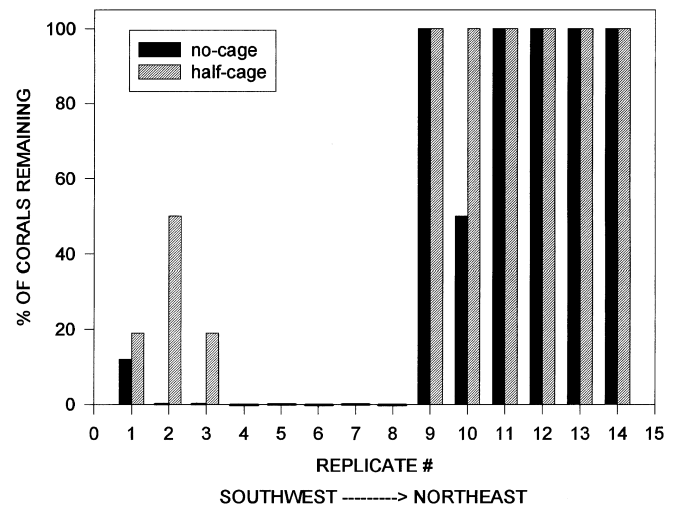
Fig. 3 Forty-eight-hour *P. divaracata* survival in individual replicates of the no-cage and half-cage treatments. Virtually all the corals consumed were at the southwest end of the experimental array

damage to these corals. They bit off large portions of whole branches, while redband parrotfish appeared to scrape only the surface of the corals. *P. divaracata* was much more attractive to both species of parrotfish than were any of the other three species of corals tested. This experiment also suggested considerable small-scale spatial variation in the intensity of coral predation. Corals at two of our four video stations received a large number of bites from the beginning of our filming, while two other stations showed very low activity until just before filming ended (Fig. 4).
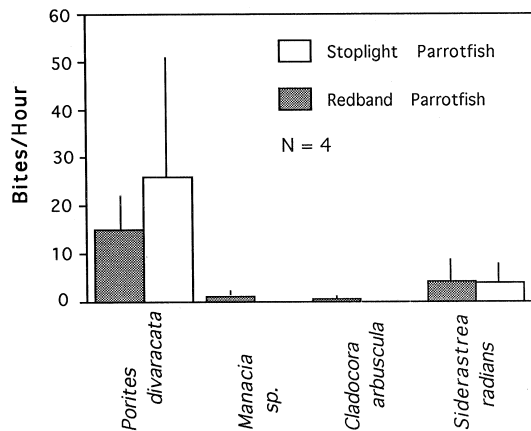
Fig. 4 Number of bites/h (mean + 1 SE) on approximately equal sized clumps of four species of corals transplanted from a seagrass bed to a fore-reef habitat. All bites were by the two species of parrotfishes indicated. The large SE is due to two sites being rapidly found and attacked by fishes while two other sites were found only near the end of the 2-h filming period

Experiment with *P. porites*

At the end of the 14-week experiment, seaweed percent cover was significantly higher (approximately double, Fig. 5A) in full-cage treatments than in the half-cage and no-cage treatments ($P = 0.002$). In addition, seaweed cover on the preplanted side of each block remained significantly greater (by 5–10%) than on the initially bare side ($P = 0.002$). There was also a significant spatial effect of cinder block ($P < 0.002$). *Dictyota* spp. that had been preplanted were the most abundant seaweed present in all replicates of all cage treatments. *H. opuntia* was also present in all types of cage treatments, but at lower abundance that *Dictyota*. Colonizing species of seaweed (mostly reds) were largely restricted to full-cage treatments (Fig. 6).

Contrary to our a priori hypothesis, there was no significant cage effect on coral growth (Fig. 5B, $P = 0.886$) even though there was a significant effect of the initial planting of seaweeds on coral growth ($P = 0.007$). Thus, seaweed competition clearly has an important detrimental effect on coral growth based on the significant effect of preplanting of seaweeds. However, the significant difference in seaweed cover between cage treatments was not reflected in a significant effect on coral growth associated with treatments that had low algal cover due to their open access to grazers. This may be because the reduction in seaweed cover that occurred in the presence of grazers (Fig. 5A) was offset by significantly higher rates of direct predation (as measured by bite scars) on corals (Fig. 5C, $P < 0.001$). The two treatments that had the highest coral growth rates were ones that had both few grazing scars on the corals (Fig. 5C) and relatively less algal competition (Fig. 5A). The full-cage treatment without preplanted seaweeds had relatively high coral growth despite having the second highest incidence of seaweed cover, seemingly be-
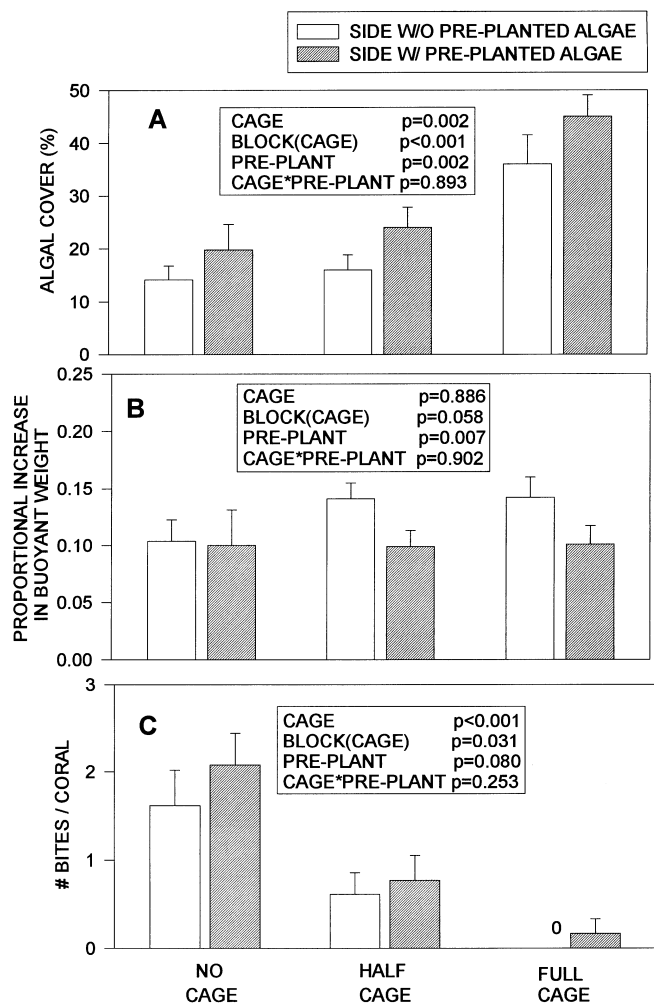
Fig. 5A–C Results of the experiment with *P. porites*. Bars represent means + 1 SE. *P*-values from two-factor split-plot ANOVA ($n = 12$–13). **A** Macroalgal percent cover in the six treatment groups after 14 weeks. **B** Coral growth as relative change in buoyant weight over the course of the experiment. **C** Grazing scars on corals in the six treatment groups

cause of protection from predation (zero bite scars in all replicates). Thus, protection of *P. porites* from direct predation in our full cages appears to counterbalance the detrimental effects of increases in competing seaweeds when fishes are excluded.

We used the half-cage treatment to control for artifacts associated with caging (e.g., water movement and shading). In the case of algal proliferation, the half-cage treatments behaved similarly to the no-cage controls, suggesting that these effects were due to grazers rather than cage artifacts. In contrast, the number of bite scars on corals in half cages was intermediate between those in the open and in the full cages. It appears that coral-eating fishes were somewhat deterred by half cages, probably because larger individuals were responsible for most of the coral predation (video observations) while all sizes of fish eat seaweeds. Thus, the half-cage treatment may more accurately be considered an intermedi-
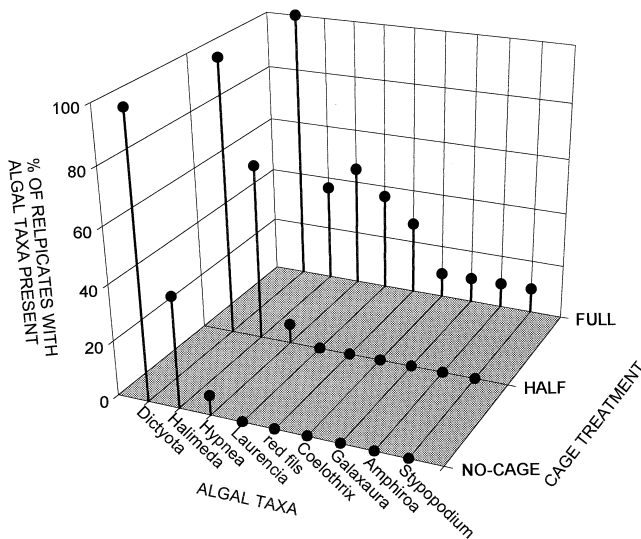
Fig. 6 Seaweed composition of each cage treatment indicated by the percent of replicates with each taxa present (*n* = 11 for full cages, *n* = 14 for half cages, and *n* = 15 for no cages) (*red fils* multiple unidentified red filamentous species)

ate treatment with regard to coral predation while it functioned more as the described control with regard to grazing on seaweeds.

Discussion

Parrotfish grazing on corals in the Caribbean is thought to be low and relatively inconsequential for both the fishes and the corals (Randall 1974; Bruggemann et al. 1996). Grazing fishes are, however, thought to be essential components of healthy reefs because they remove seaweeds, avoid eating corals, and thus prevent seaweeds from excluding corals via competition (Birkeland 1977; Brock 1979; Lewis 1986; McClanahan and Muthiga 1988; Hughes 1994). Our data suggest that the beneficial effects of fish grazing are not generalizable to all locations or all corals, but vary greatly depending on the coral species and parrotfish species involved. Stoplight and redband parrotfishes rapidly consumed most of our P. *divaracata* transplants. They completely consumed over 50% of our transplants in 48 h (Fig. 2) and systematically removed all transplants from some areas of the reef (Fig. 3). When four coral species typical of grassbed habitats were moved to the fore-reef, parrotfishes rapidly consumed P. *divaracata*, commonly bit S. *radians*, but paid minimal attention to *Manicina* sp. or C. *arbuscula* (Fig. 4). Additionally, placing P. *porites* on the same cinder blocks used in the P. *divaracata* experiment showed that, even though it was grazed, P. *porites* could persist and grow (Fig. 5) in areas where grazing fishes excluded P. *divaracata*. Thus, even within the genus *Porites*, there is considerable variation in susceptibility to parrotfish grazing, as shown previously by Littler et al. (1989). Similarly, Neudecker (1979) showed

strong intragenus variation in susceptibility of *Pocillopora* species to fish predation in Guam, even between species whose taxonomic distinctness was debated by taxonomists.

Parrotfish corallivory: do they or don't they?

Our data contribute to an ongoing debate regarding the importance of direct fish grazing on corals. A recent field study in Bonaire (Bruggemann et al. 1996) concluded, "Living coral is rarely eaten by scarids, and largely escapes erosion by grazing." A recent review by Hixon (1997) states that "outside of damselfish territories, the reported direct effects of herbivorous fishes on corals are contradictory (and) ... appear to depend on the particular system." Frydl (1979) shows photographs of extreme parrotfish grazing of coral colonies, including *Montastraea annularis* and *P. porites*, but notes that this intensity of damage is unusual. Randall (1974) and Bak and Engle (1979) reported that grazing fishes damage juvenile corals, while Birkeland (1977) reported that grazing fishes avoided damaging even very small juveniles. Other recent observations suggest that the reproductive status of the corals may also be important. Developing gonads held in coral tissue might provide a particularly rich nutritional source, and *M. annularis* in the Florida Keys appears to suffer increased predation in the weeks before the annual mass spawn (A.M. Szmant, personal communication).

In developing countries, intense overfishing often results in direct depletion of herbivore fish guilds (Hay 1984a; McClanahan and Muthiga 1988; Hughes 1994). However, in the Florida Keys, the fisheries are recreational and commercial in nature, and reef piscivores such as grouper and snapper are targeted while grazing fishes are not considered desirable. It is plausible that overfishing in the Florida Keys has reduced predation on grazers. Combined with the virtual absence of *Diadema*, which competes with grazing fishes (Hay and Taylor 1985; Carpenter 1990b; Robertson 1991), these decreases in predators and competitors could result in abnormally high intensities of parrotfish grazing on reefs in the Florida Keys. Other caging experiments in Biscayne National Park, just north of our study site, have shown that grazing fishes consume transplanted juvenile corals of many species (including *P. astreoides*, *S. radians*, and *Favia fragum*, as well as *P. divaracata*) to extinction if they are not protected in full cages (Miller et al., in preparation). At Conch Reef (adjacent to our study site in the Key Largo area), video assays have also shown that *Sparisoma* parrotfishes consume substantial amounts of sponges (Dunlap and Pawlik 1996). Dunlap and Pawlik (1996) note that numerous previous studies of parrotfish foraging have not reported parrotfishes as sponge feeders (Hanley 1984; Bellwood and Choat 1990; Bruggemann et al. 1994). It may be that Florida Keys reefs are overpopulated with *Sparisoma* parrotfishes and that their foraging has

expanded from herbivory (Bruggemann et al. 1994) to include novel foods such as sponges and corals. This hypothesis is not consistent, however, with the conventional view that reefs in the Florida Keys are overgrown with macroalgae and thus rich in algal foods relative to other reefs (Ward 1990; Torrence 1991; Hallock et al. 1993).

Does it matter?

The studies of Bruggemann et al. (1994) from Bonaire demonstrated that up to 9% of bites by the parrotfish *S. viride* were on live coral, primarily *M. annularis*. In many cases, however, bites of coral were dropped and not consumed. They speculated that coral bites may serve more of a social than a nutritional function, creating territory markers by leaving a conspicuous white spot on the live coral colony. Although they concluded that corallivory was of negligible nutritional importance for parrotfish, this would not prevent parrotfish corallivory from having a significant impact on populations of some coral species. In our study, parrotfishes were not observed dropping the corals they had bitten, and the fact that they rapidly consumed our transplants suggests that they were not biting these merely to mark territory boundaries but that some species were being targeted as desirable foods.

In agreement with our findings, Littler et al. (1989) documented that grazing fishes had a large impact on some corals in Belize. The distribution of *P. porites* and *P. astreoides* as a function of distance from the reef flat was controlled by differential palatability to grazing fish. In areas with sufficient structure to harbor larger fishes, *P. porites* was rapidly eaten while *P. astreoides* was largely ignored.

Our a priori hypothesis was that reduced grazing in full cages would allow macroalgae to proliferate and overgrow corals, substantially reducing their growth. While filamentous algae have been shown to compromise and/or kill corals in damselfish territories (Potts 1977) and under natural nutrient enrichment (Genin et al. 1995), Lewis (1986) found that filamentous algae decreased significantly in caged experimental treatments and noted that macroalgae, rather than filamentous algae, overgrew and killed corals. We observed no differences in filamentous algal abundance between treatments, but did observe a significant proliferation of macroalgae in the full cages (Fig. 5A). Contrary to expectation, this increased macroalgal cover in full cages had no significant cage effect on *P. porites* growth (Fig. 5B). However, our study does confirm previous results regarding the clear importance of seaweed competition to corals (when they are not eaten directly by fishes) in that the preplanted seaweeds significantly inhibited coral growth (Fig. 5B). The intensity of direct predation on corals in our manipulations, as estimated by the number of bite scars, was inverse to the proliferation of seaweeds. Thus, it appears that parrotfish

predation had a negative impact on *P. porites* growth that matched and offset the positive effects of herbivores removing competing seaweeds (Fig. 5A).

Even more dramatically, on some portions of the reef, all *P. divaracata* transplants were eaten completely in only a few hours (Fig. 3). High susceptibility to parrotfish predation may explain the restriction of this species from reef slopes to inshore habitats with lesser grazing intensity. Similar distributional restrictions due to grazing have been shown for numerous seaweeds (Hay 1981, 1985) and, more recently, for sponges (Dunlap and Pawlik 1996). Greater chemical defenses against predation have been shown in relatively unpalatable reef species versus palatable nonreef species for both seaweeds (Hay 1984b; Paul and Hay 1986) and sponges (Pawlik et al. 1995). Chemical defenses in hard corals remain largely unexplored, but given the large variance in susceptibility to fish grazing that occurs between coral species (Fig. 4) and even among species within a genus (Neudecker 1979; Littler et al. 1989; this paper), investigations of hard coral defenses seem warranted.

Another unexpected aspect of our results is the considerable small-scale (a few meters) spatial variation in corallivory (Fig. 3). In both the cage experiments and the video assays, corals transplanted to some areas were consumed rapidly while those transplanted a few meters away appear to have been found and consumed much more slowly, or not at all. Spatial variation in predation intensity, both herbivory and corallivory, is well documented between sites, habitats, and depth zones (Neudecker 1979; Hay 1981, 1985; Steneck 1988; Littler et al. 1989; reviewed in Glynn 1990). Work with seaweeds and reef herbivores has demonstrated that grazing pressure can vary dramatically over spatial scales of only centimeters to meters due to effects of territorial damselfishes or of noxious seaweeds creating microsites of associational escapes for more palatable seaweeds (Hay 1985, 1986, 1996). However, to our knowledge, there are no previously published reports of such significant variation in predation of corals on such a small scale (2–3 m) within a single habitat/depth zone (7–8 m, fore-reef relict spur and groove). The spatial pattern of coral consumption we document (Fig. 3) could have resulted from territorial behavior of parrotfishes. *S. viride* are known to be territorial (Bruggemann et al. 1994) and the video assays showed this species to be the primary feeder on *P. divaracata* with all *S. viride* that we saw feeding being large individuals that could bite off entire coral branches.

In conclusion, direct feeding by parrotfishes in the Florida Keys can substantially reduce the abundance and distribution of some coral species (*P. divaracata*) while other corals (*P. porites*) can be negatively affected by both direct fish predation and, in the absence of grazing fishes, by seaweed competition. The effects of parrotfish feeding on coral populations are not generalizable to all corals and will depend on species-specific traits of the corals and parrotfishes involved.

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