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REPORT

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Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth

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Abstract Recent declines in coral abundance accompanied by increases in macroalgal cover on Florida reefs highlight the importance of competition for space between these groups. This paper documents the frequency of coral–algal interactions on the Northern Florida Reef Tract and evaluates the effects of grazer exclusions and experimental algal addition on growth and tissue mortality of three coral species, *Siderastrea siderea*, *Porites astreoides*, and *Montastraea faveolata*. The frequency of interactions between corals and macroalgae was high as more than 50% of the basal perimeter of colonies was in contact with macroalgae; turf forms, *Halimeda* spp., and *Dictyota* spp. were the most common groups in contact with corals. Decreased grazing pressure resulted in significant increases in algal biomass within cages, and caged corals showed species-specific susceptibility to increased algal biomass. While no effects were detected for *S. siderea*, significant decreases in growth rates were documented for caged *P. astreoides* which had growth rates three to four times lower than uncaged colonies. When an algal addition treatment was included to duplicate maximum algal biomass levels documented for reefs in the area, colonies of *P. astreoides* in the algal addition treatment had growth rates up to ten times lower than uncaged colonies. High susceptibility to algal overgrowth was also found for the reef-building coral *M. faveolata*, which experienced significant tissue mortality under both uncaged (5.2% decrease in live tissue area per month) and caged (10.2% per month) conditions. The documented effects of increased algal biomass on coral growth and tissue mortality suggest a potential threat for the long-term survivorship and growth of corals in the Florida Reef Tract if present rates of algal growth and space utilization are maintained.

Key words Coral–algal competition · Caging · Grazer exclusion · Algal overgrowth · Florida Reef Tract

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Introduction

In the recent past, reports of rapidly declining reef health and localized phase shifts towards macroalgal-dominated systems have highlighted the importance of competition for space between corals and macroalgae, the outcome of which can have significant implications for the long-term survivorship and growth of corals (e.g., Smith et al. 1981; Lessios 1988; Hughes 1989, 1994; Done 1992; Knowlton 1992; Lapointe et al. 1997; McClanahan and Muthiga 1998). The main objective of the present study was to document the intensity of coral–algal interactions on the Northern Florida Reef Tract and to evaluate the effects of reduced herbivory and algal competition on coral growth and tissue mortality.

Several studies have reported decreases in coral cover and diversity along the Florida Reef Tract in the recent past (Dustan and Halas 1987; Jaap et al. 1988). Just as in many other places in the Caribbean, declines in coral cover in Florida have been accompanied by corresponding increases in the percent cover of macroalgae (Porter and Meier 1992). Although the actual causes of coral decline are being debated, changes in water quality and trophic structure linked to human activities as well as natural stressors such as elevated temperatures, storms, and epizootic diseases have all been proposed as potential causal agents (Hughes 1994; Lapointe 1997; Lirman and Fong 1997; Hughes et al. 1999; Porter et al. 1999).

Even though macroalgae are important components of Florida reef communities, only limited information is available on their abundance, distribution, and community dynamics (Chiappone and Sullivan 1997; Lapointe 1997). In the Northern Florida Reef Tract, the study

area for this project, macroalgal cover fluctuates seasonally, reaching up to 56% during the summer (Lirman and Biber 2000). During the time of peak algal abundance, small coral colonies can become completely covered by dense macroalgal mats. Similarly, large massive colonies can experience intense competition from algae growing along colony margins or on dead portions of colonies.

A limited number of studies have examined experimentally the effects of coral–algal competition on coral growth and survivorship. These studies have shown consistently that coral colonies in direct contact with macroalgae can experience reduced growth and fecundity, as well as increased tissue mortality (Potts 1977; Lewis 1986; Hughes 1989; Coyer et al. 1993; Tanner 1995; Miller and Hay 1996, 1998). The present study quantifies the frequency of interactions between corals and macroalgae at the peak time of algal abundance and determines experimentally the effects of reduced herbivory and increased algal biomass on the growth and tissue mortality of three common coral species on Florida reefs, *Siderastrea siderea*, *Porites astreoides*, and *Montastraea faveolata*.

Methods

Coral–algal contact interaction surveys

Photographic surveys were performed on reefs within Biscayne National Park, Florida (Fig. 1) to document the frequency of contact interactions between corals and macroalgae. These surveys were carried out on two inshore patch reefs, Bache Shoals (25°29.187′N, 80°08.880′W, depth = 4 m) and Elkhorn Reef (25°21.782′N, 80°09.841′W, depth = 4 m), and two offshore bank reefs, Triumph Reef (25°28.333′N, 80°06.704′W, depth = 6 m) and Pacific Reef (25°22.186′N, 80°08.360′W, depth = 6 m) during July–August 1998, at the seasonal peak of algal abundance when mean percent cover of macroalgae on these reefs was 56.7% (Lirman and Biber 2000). A belt transect (25 × 2 m) was haphazardly placed at each site, and all coral colonies (5–50 cm in diameter) found within the transect were photographed. The resulting images were scanned and the percentage of each colony's basal perimeter in direct contact with macroalgae was determined using NIH Image. Smaller colonies were not detected by this photographic method.

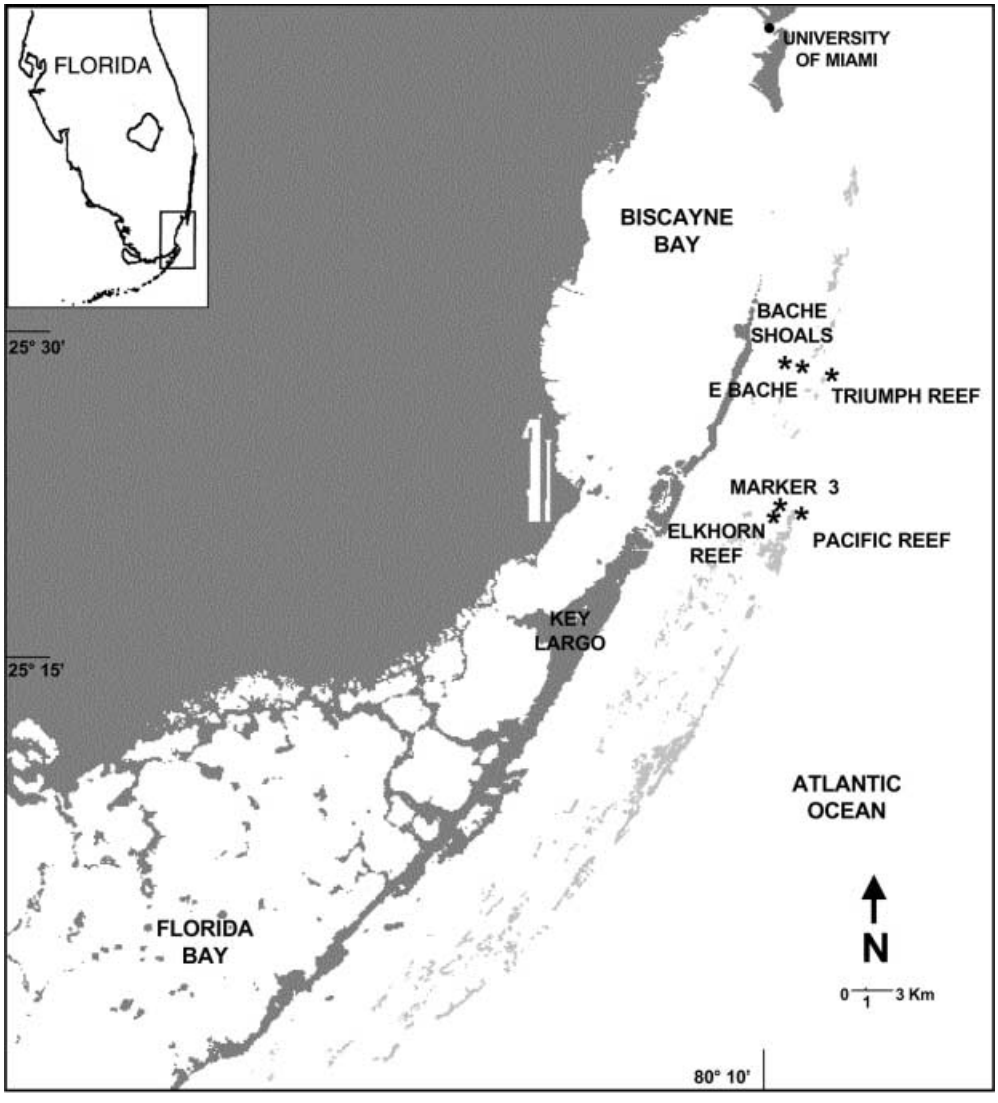

Fig. 1 Map of South Florida and the study area including location of study sites

Algae were grouped by genus if abundant (e.g., *Halimeda* and *Dictyota*) or by functional group (Steneck and Dethier 1994). The functional groups used here are: filaments (e.g., *Polysiphonia* spp., *Cladophora* spp.), corticated terete algae (CTA, e.g., *Laurencia* spp., *Acanthophora* spp.), articulated calcareous algae (ACA, e.g., *Amphiroa* spp., *Jania* spp.), and crustose coralline algae (CCA).

Herbivore exclusion experiments

Porites astreoides and *Siderastrea siderea*

In 1998, a caging study was carried out on two reefs, Triumph Reef (offshore bank reef, depth = 6 m) and East Bache Shoals (inshore patch reef, 25°29.002′N, 80°08.388′W, depth = 5 m) from 1 July–20 September (Fig. 1) to test the effects of herbivore exclusion on coral survivorship and growth. On each reef, colonies (5–15 cm in diameter) of *Porites astreoides* and *Siderastrea siderea* were labeled with metal tags and assigned to one of four treatments: caged ($n = 8$ per reef), caged-open top controls ($n = 4$), caged-open side controls ($n = 4$), and uncaged controls ($n = 8$). Cages built of galvanized steel mesh (22 cm in diameter, 15 cm in height, 1 × 1 cm opening size, Fig. 2A) were placed over colonies and secured to nails hammered onto the bottom. Cages were brushed free of colonizing organisms at bi-weekly intervals. Photographs of the coral colonies were taken at the start and at the end of the study with a Nikonos V camera equipped with a 28-mm lens and close-up lens outfit. The resulting prints were scanned and analyzed with NIH Image. Growth was estimated as the percent change in projected surface area of live coral tissue. At the end of the experiment, all algal tissue was collected by hand from caged and uncaged plots, identified, and dry weights compared among treatments.

In 1999, a second caging experiment was carried out with *P. astreoides* on Marker 3 Reef (25°22.408′N, 80°09.667′W, depth = 2–3 m, Fig. 1) from 14 May–10 September. Although grazer exclusion resulted in increased biomass within cages in 1998 (Fig. 3), algal biomass did not reach maximum levels observed for other reefs in the Northern Florida Reef Tract where mean biomass of *Dictyota* exceeded 20 g m^{-2} and small colonies of *P. astreoides* and other species were totally covered by macroalgae (Lirman and Biber 2000). Therefore, an algal addition treatment was added to duplicate observed maximum algal biomass levels. Caged corals were divided into two groups, and algal tissue was added as loose clumps to one group at bi-weekly intervals. Clumps of *Dictyota* spp. (1.5–2.5 g dry weight) were collected and introduced into the cages. The treatments used in this experiment were caged ($n = 10$), caged with algal addition ($n = 10$), caged-open top controls ($n = 10$), caged-open side controls ($n = 10$), and uncaged controls ($n = 10$). The amount of algal biomass introduced into cages approximated the maximum macroalgal biomass values recorded on reefs of the Northern Florida Reef Tract (Lirman and Biber 2000).

Montastraea faveolata

Rectangular cages were placed on large *M. faveolata* colonies (diameter > 1 m) on Elkhorn Reef (depth = 6 m, Fig. 1) from 19 May–10 September 1999. Cages (15 cm in length, 10 cm in width, 6 cm in height, 1 × 1 cm opening size, Fig. 2B) were placed so that roughly one half of the surface area enclosed was occupied by live coral tissue and the other half by macroalgae growing on dead coral skeleton. Cages were also placed over live coral tissue to document coral survivorship in the absence of direct algal competition and to determine whether algae could colonize live coral surfaces in the absence of grazing. Uncaged plots were established on coral–algal interfaces and live coral tissue without algal interaction. Each *M. faveolata* colony ($n = 10$) received one set of treatments (caged interface, caged live coral tissue without algal interaction, uncaged interface, and uncaged live coral tissue). Cages were brushed free of colonizing organisms at bi-weekly intervals and changes in percent live tissue were determined from digitized photographs of the experimental plots. In addition, the retreat rate of the live coral tissue margin was estimated by tracing the initial and final positions of the coral margin within each plot and estimating the distance between them. Distance estimates between the margins were measured at 2-cm intervals and averaged within plots. All algal tissue was collected from each plot at the end of the experiment, identified, and dry weights compared among treatments.

Statistics

The data were examined for conformity to the assumptions of each statistical test prior to analysis. Normality was tested with the Shapiro-Wilk test and homoscedasticity was tested with the Bartlett's test. As the normality assumptions were not met for percent growth of *P. astreoides* and *S. siderea*, an arcsine transformation (arcsine $\sqrt{x}$) was successfully applied prior to analysis. To evaluate potential caging artifacts, algal biomass and coral growth were compared for caged open-top controls, cage open-side controls and uncaged controls within reefs using ANOVA. Since no significant differences or patterns in algal biomass or coral growth were found

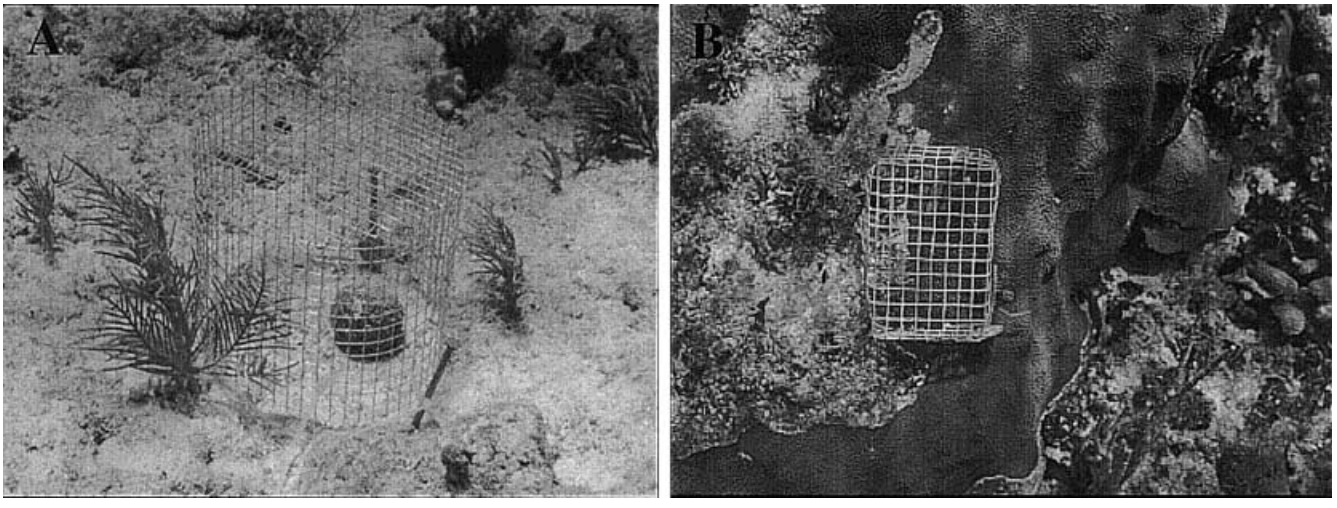

Fig. 2 Two types of herbivore exclusion cages used in this study: **A** circular cages (22 cm in diameter, 15 cm in height, 1 × 1 cm opening size) were placed over colonies of *Siderastrea siderea* and *Porites astreoides* and **B** rectangular cages (15 × 10 × 6 cm, 1 × 1 cm opening size) were placed over coral–algal interfaces on *Montastraea faveolata* colonies

(ANOVA, $p > 0.05$ for all experiments), data from these plots were pooled into a single control group for each coral species (*P. astreoides* and *S. siderea*) from each reef (Triumph Reef, East Bache, and Marker 3 Reef). Data from the 1998 caging experiment with *P. astreoides* and *S. siderea* were analyzed using a two-way ANOVA with grazing (ambient grazing–grazer exclusion cages) and reef location (inshore–offshore) as factors.

Results

Coral–algal interaction surveys

The frequency of interactions, estimated as the percentage of the basal perimeter of colonies ($n = 273$) that was in direct contact with macroalgae, was high, exceeding 50% on all four sites surveyed, reaching up to 85% on Pacific Reef (Fig. 4). Although the relative percentage of interactions varied for algal groups among sites, turf forms, *Halimeda* spp., and *Dictyota* spp. were the groups most commonly in contact with coral colonies. Cross-shelf patterns in the frequency of interactions were detected, with *Halimeda* spp. being more commonly in contact with corals at East Bache Shoals, and *Dictyota* spp. on offshore reefs (Fig. 3).

Herbivore exclusion experiments

Porites astreoides and *Siderastrea siderea*

The exclusion of grazers had significant effects on macroalgal biomass at Triumph Reef, East Bache Shoals, and Marker 3 Reef (Fig. 3). Although all groups accumulated higher biomass within cages, significant differences were not detected for all of these. Biomasses of *Dictyota* spp. and articulated calcareous algae (ACA) were significantly higher within caged plots ($n = 16$ for Triumph Reef and East Bache Shoals and 10 for Marker 3 Reef) compared to control plots ($n = 32$ for Triumph Reef and East Bache Shoals and 30 for Marker 3 Reef; t-tests, $p < 0.01$) at all three reefs. In contrast, corticated terete algae (CTA) had significantly higher biomass within cages only at Triumph Reef (t-tests, $p < 0.01$), and filamentous algae accumulated significantly higher biomass within caged plots only at East Bache Shoals (t-tests, $p < 0.01$).

In 1998, the caging experiment showed patterns of decreased coral growth rates under grazer exclusion for both *Porites astreoides* and *Siderastrea siderea* (Fig. 5); however, only the difference for *P. astreoides* was statistically significant ($n = 8$ for caged; $n = 16$ for uncaged; $p < 0.05$). No reef location or interaction effects were detected ($p > 0.1$) for either species. Colony appearance remained unchanged throughout these studies and no polyp retraction was detected.

In 1999, the loose clumps of *Dictyota* added to the cages at bi-weekly intervals remained free-floating within the cages for the first 2–3 days, but attached to the sides of the cages and to existing macroalgae after this, mimicking more natural conditions. Significant differences in the growth of *P. astreoides* were found among caged, algal addition, and control treatments (ANOVA, $p < 0.01$; Fig. 6). Although corals within cages ($n = 10$) had reduced growth rates compared to controls ($n = 30$), Tukey pairwise comparisons showed that only

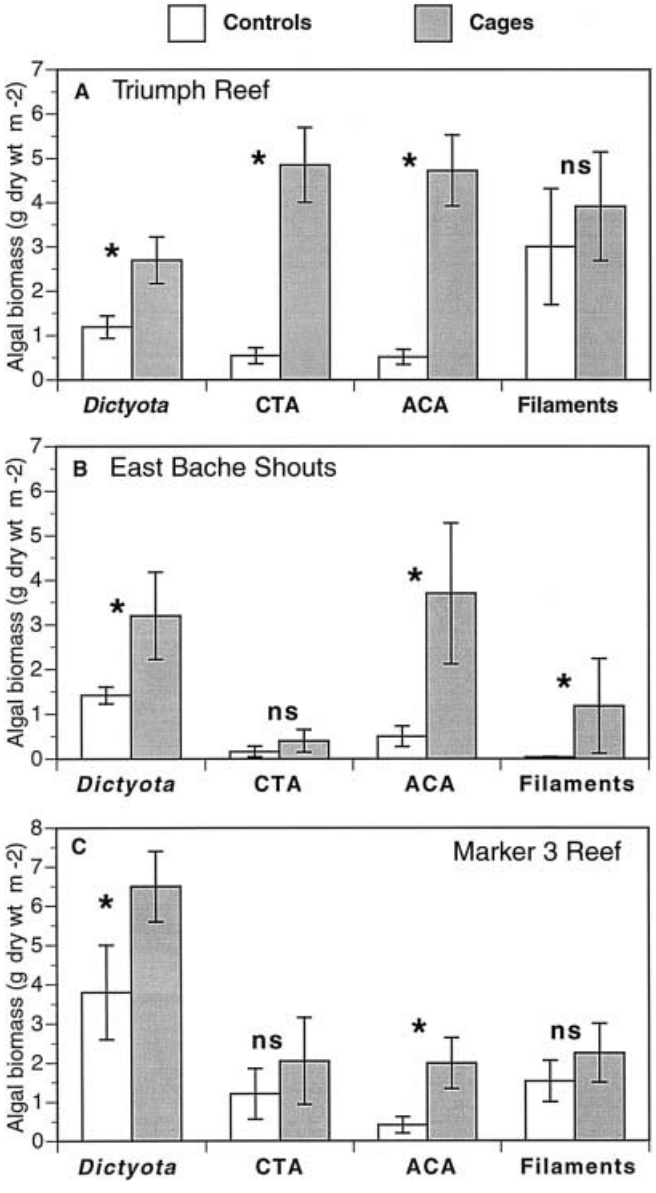

Fig. 3 Mean biomass (±1 SEM) of macroalgae (g dry wt m^{-2}) within caged ($n = 16$ for **A** and **B**, $n = 10$ for **C**) and control plots ($n = 32$ for **A** and **B**, $n = 30$ for **C**) at end of caging experiments at: **A** Triumph Reef (1 July–20 Sept 1998); **B** East Bache Shoals (1 July–20 Sept 1998); **C** Marker 3 Reef (14 May–10 Sept 1999). Functional groups represented here are: filaments (e.g., *Polysiphonia* spp., *Cladophora* spp.), corticated terete algae (*CTA*, e.g., *Laurencia* spp., *Acanthophora* spp.), and articulated calcareous algae (*ACA*, e.g., *Halimeda* spp., *Amphiroa* spp., *Jania* spp.). Data from Marker 3 do not include biomass from algal addition treatment. * Significant differences between groups (t-test, $p < 0.05$); *ns* no significant differences between groups (t-test, $p > 0.05$). Control plots combine data for caged open-top controls, caged open-side controls, and uncaged controls

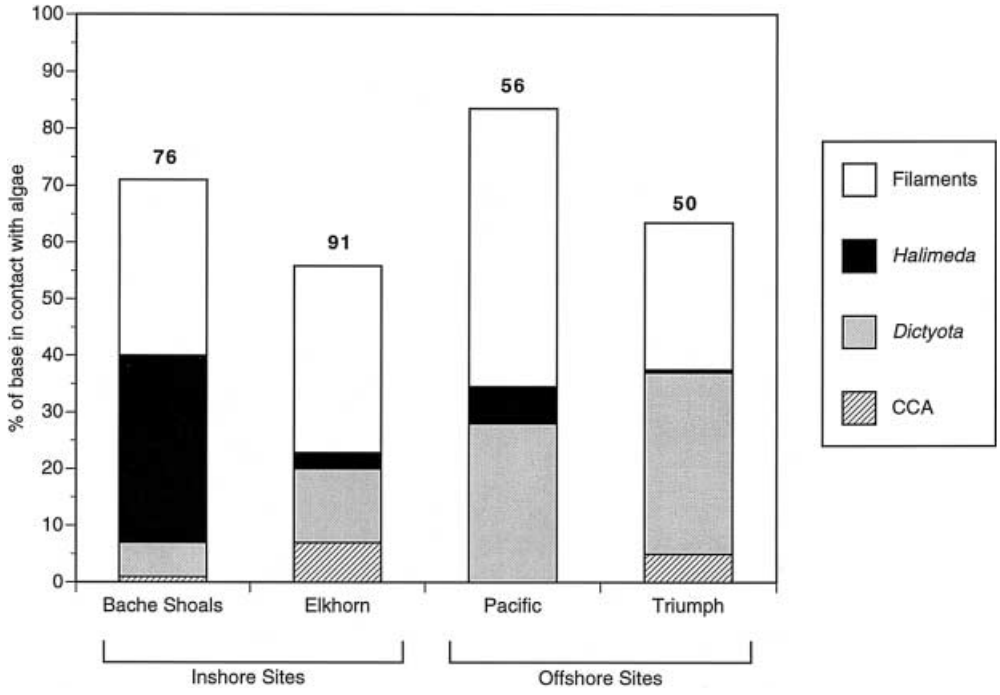

Fig. 4 Coral–algal interactions expressed as percentage of basal perimeter of colonies that was in direct contact with macroalgae on two inshore and two offshore sites within Biscayne National Park, Northern Florida Reef Tract in July–August 1998. *CCA* Crustose coralline algae. *Bold numbers* are numbers of colonies surveyed

those corals in the algal addition treatment ($n = 10$) had growth rates significantly slower than the other treatments. No net tissue losses were recorded for any of the corals, but photographic surveys showed that colonies in the algal addition treatment had retracted polyps on their upper surfaces starting 1 week after the onset of the experiment, and that this behavior was observed throughout the study.

Montastraea faveolata

Macrograzer exclusion influenced macroalgal biomass along coral–algal interfaces on *M. faveolata* colonies. Although biomass of CTA and filamentous algae was higher within caged interface plots ($n = 10$) compared to uncaged interface plots ($n = 10$), statistically significant differences were only found for *Dictyota* spp., the most abundant group along coral–algal interfaces (t-test, $p < 0.01$). Mean dry weight of *Dictyota* spp. was 16.8 g m^{-2} in caged interfaces compared to 12.7 g m^{-2} in uncaged interface plots. No macroalgae were found colonizing or growing within caged ($n = 10$) and uncaged ($n = 10$) live coral plots.

Both caged and uncaged interfaces on *M. faveolata* experienced a net loss of coral tissue in the presence of algal interaction (Fig. 7). Tissue mortality rates were significantly higher (t-test, $p < 0.05$) in caged plots where live tissue was lost at a rate of 10.2% per month (SEM = 2.4), compared to 5.2% (SEM = 2.2) in uncaged plots. Similarly, the rate of retreat of the coral tissue margin was faster on caged plots (0.43 cm $month^{-1}$, SEM = 0.09) compared to uncaged plots (0.25 cm $month^{-1}$, SEM = 0.09). No tissue mortality occurred within cages over entirely live tissue.

Discussion

Contact interactions between corals and macroalgae can be common along the margins of colonies. Along the Northern Florida Reef Tract, coral colonies had more than 50% of their basal perimeter in contact with macroalgae during the peak of algal abundance in the summer of 1998. Similarly, Tanner (1995) found algal interfaces for 92% of coral colonies surveyed at Heron Island, Great Barrier Reef. These results clearly highlight the importance of space competition between corals and algae.

Observations of coral overgrowth by macroalgae are numerous in the literature (e.g., Hughes 1989; Littler et al. 1989; Coyer et al. 1993; Tanner 1995; Anthony et al. 1997; Littler and Littler 1997; McClanahan and Muthiga 1998). In most cases, coral declines were mediated by drastic reductions in grazing due to trophic shifts, overexploitation, or massive die-offs of herbivores that resulted in uncontrolled algal growth (Carpenter 1990; Lessios 1988; Hughes 1994; Aronson and Precht 1999). The caging treatments, used here as a mechanism to increase algal biomass, showed that coral susceptibility to increased algal competition is species-specific and can be affected by the amount of algal biomass in contact with corals. Significant decreases in growth rates were documented for caged *Porites astreoides*, which had

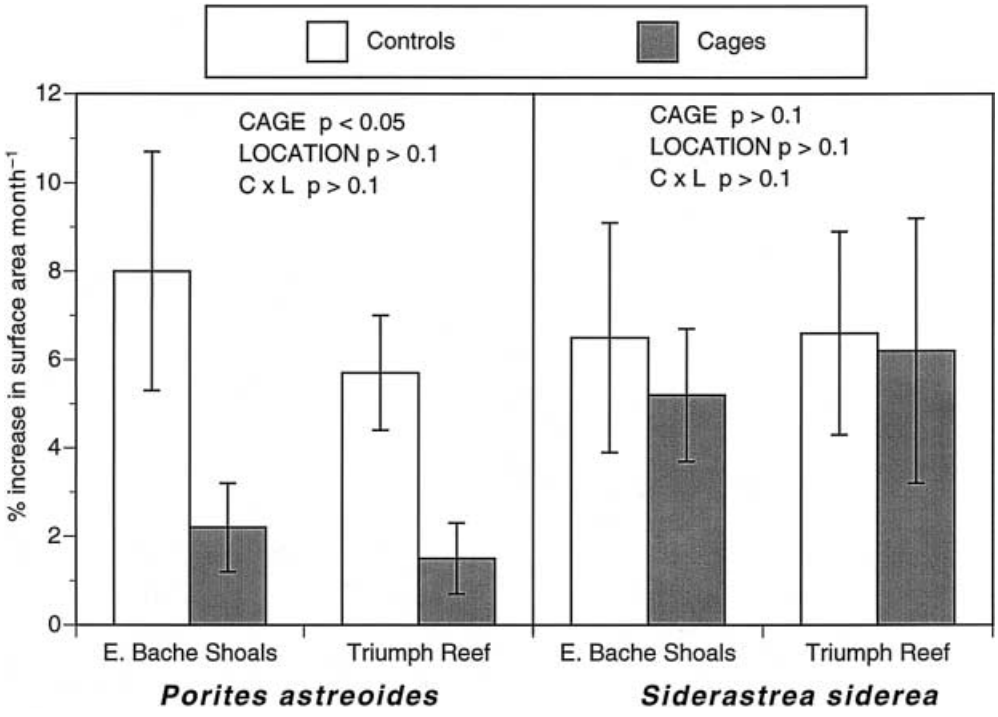

Fig. 5 Mean percent growth rates (±1 SEM) of caged ($n=8$) and control ($n=16$) *Siderastrea siderea* and *Porites astreoides* during caging studies at East Bache Shoals and Triumph Reef. Study ran from 1 July–20 Sept 1998. Control plots combine data for caged open-top controls, caged open-side controls, and uncaged controls. *P* values from two-factor ANOVA

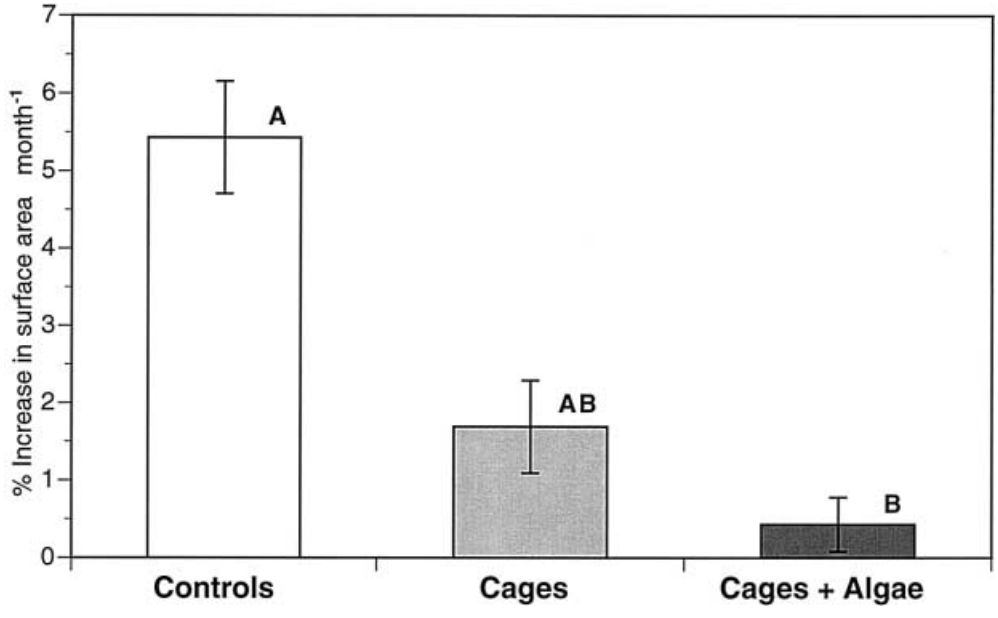

Fig. 6 Mean percent growth rates (±1 SEM) of caged ($n=10$), caged + algae ($n=10$), and uncaged ($n=30$) *Porites astreoides* during caging studies at Marker 3 Reef (14 May–10 Sept 1999). Control plots combine data for caged open-top controls, caged open-side controls, and uncaged controls. Additional algal tissue (1.5–2.5 g dry wt of *Dictyota*) was added to algal addition group at bi-weekly intervals. *Bars* with different *letters* are statistically different (ANOVA, Tukey pairwise comparisons)

growth rates three to four times lower than uncaged colonies. Similarly, caged coral–algal interfaces on *Montastraea faveolata* colonies had tissue mortality rates that were double those of uncaged interfaces.

Other studies have documented the negative effects of algal competition. Potts (1977) reported reduced coral growth within damselfish territories with high algal cover, and Tanner (1995) found decreased growth rates for two acroporid species in competition with macroalgae. In addition, Miller and Hay (1996) showed through manipulative experiments that algal competition can inhibit the growth of the temperate coral *Oculina arbuscula*. However, exceptions to these patterns were noted. In the present study, no effects of increased algal competition were detected for *Siderastrea siderea*. Also, Tanner (1995) noted no effects of macroalgal competition on growth rates of *Pocillopora damicornis*.

Even further decreases in growth rates were documented for *P. astreoides* when additional algal tissue was introduced into caged treatments to duplicate maximum levels of algal biomass documented for reefs of the Northern Florida Reef Tract (Lirman and Biber 2000). Colonies of *P. astreoides* in the algal addition treatment exhibited retracted polyps and had growth rates up to

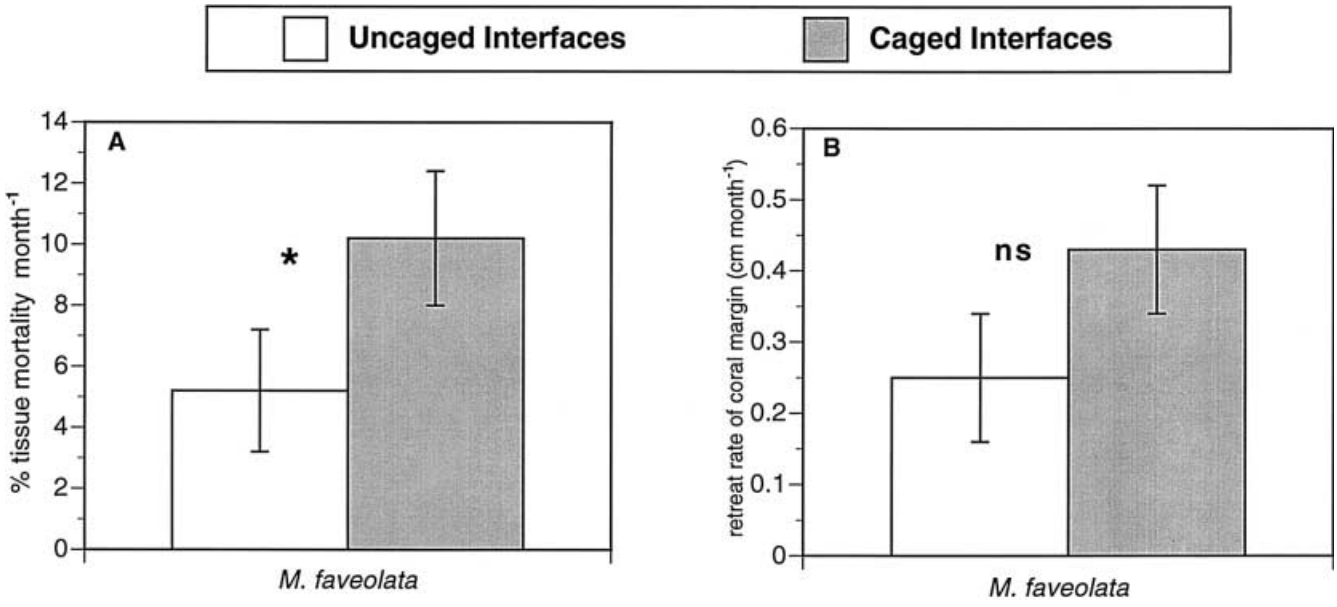

Fig. 7 **A** Mean percent tissue mortality rates (±1 SEM) and **B** mean retreat rate (±1 SEM) of coral margin of *M. faveolata* within caged ($n=10$) and uncaged ($n=10$) coral–algal interface plots at Elkhorn Reef (19 May–10 Sept 1999). * Significant differences between groups (t-test, $p<0.05$); *ns* no significant differences between groups (t-test, $p>0.05$)

ten times lower than uncaged colonies. It is important to note, however, that polyp retraction was only observed in corals in the algal addition treatments and may be a result of the potential scouring action of the clumps of algae added, which remained unattached within cages for several days. Polyp retraction and reduced growth in corals in contact with macroalgae were previously documented by Coyer et al. (1993) on a temperate rocky reef.

Coral colony morphology may have an important influence on the outcome of coral–algal competition and may partly explain the species-specific results reported here. Tanner (1995) and Hughes (1989) found encrusting colonies to be more affected by algal encroachment than branching or massive morphotypes based on the higher perimeter-to-area ratio of encrusting colonies compared to colonies with higher three-dimensionality. In agreement with these reports, growth rates of encrusting *Porites astreoides* colonies in this study were negatively affected by increased algal competition, whereas growth rates of massive *Siderastrea siderea* colonies were not affected. However, colonies of the massive *Montastraea faveolata* were found to be highly susceptible to algal overgrowth as caged tissue plots lost an average of 10% of their live tissue area per month.

For massive corals that commonly maintain live tissue cover over their whole colony surface (e.g. *Siderastrea* spp., *Diploria* spp., *Colpophyllia* spp.), algal competition would be concentrated along the colony perimeter, as few dead areas would be available for algal colonization. As colonies of these species grow, a smaller percentage of their surface area would be in direct contact with macroalgae, reducing the negative effects of competitive interactions. However, for coral species that do not normally maintain live tissue cover over their whole colony surface, dead patches provide suitable substrate where macroalgae can attach and grow. In these cases, coral–algal interfaces would be found not only along the colony base, but also at numerous points within the colony surface. Such is the case of *Montastraea annularis* where live tissue is found only at the tops of columns (Knowlton et al. 1992) or large colonies of *M. faveolata* like those surveyed in this study, which have experienced partial mortality due to the establishment of damselfish territories or other disturbances.

The present study showed that large, massive colonies like those of *M. faveolata* can experience rapid tissue losses at coral–algal interface margins. These results emphasize the importance of chronic disturbance agents such as corallivores, sedimentation, diver and boat impacts, elevated temperatures, and storms that rarely cause whole-colony mortality, but can cause numerous dead patches within coral colonies that can be subsequently colonized by algae (e.g., Bythell et al. 1993; Meesters et al. 1996; Lirman 2000). Cages placed over live tissue areas without any direct competition from algal margins experienced no tissue mortality, reinforcing the need for dead patches to be created before algae can colonize, even in the absence of grazing. Once these dead patches are colonized, the subsequent reductions in coral growth and enhanced tissue losses documented here may take place, compromising the long-term survivorship of the affected colonies.

Competition for primary space has always been considered a major structuring force within reef communities (Lang and Chornesky 1990). Increases in macroalgal cover and biomass on Caribbean reefs in response to reduced herbivory, damselfish territorial behavior, and eutrophication can result in increased

rates of coral–algal interactions. Moreover, results from the present as well as previous studies show that these interactions can have significant, species-specific, negative effects on coral growth and survivorship. The susceptibility of reef-building corals like *Montastraea faveolata* to algal overgrowth under present levels of grazing suggest long-term negative effects on reef development in the area if present rates of macroalgal space utilization are maintained.

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