



Coral responses to macroalgal reduction and fisheries closure on Caribbean patch reefs

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ABSTRACT: To determine the effects of algal reduction and fisheries closure, a crossed experimental design was undertaken over a 516 d period on the remote patch reefs of Glover's Reef Atoll, Belize. We investigated (1) the effects on health, growth, and survivorship of 2 transplanted coral species, *Porites asteroides* and *Siderastrea siderea*, and (2) the changes in the benthic and fish communities. Algal reduction (98% reduction by physical removal kept low by monthly removal) increased the abundance of all fish and slightly elevated herbivore bite rates. *P. asteroides* showed a temporal response to environmental conditions opposite of predictions, with higher bleaching and mortality in the unfished reefs cleared of algae. This may be due to reduced water flow at these sites as the growth rate of *P. asteroides* was positively related to water flow ($R^2 = 0.35$, $p = 0.04$). *S. siderea* growth showed no relationship with water flow and bleached slightly more in the control reefs. Nevertheless, there were no patterns in mortality, and growth rates were twice as high in the fished than unfished reefs for this species. This reef-scale study contrasts with results of small-scale experiments that found rapid, indirect coral mortality from erect algae. Rather, our results suggest that environmental conditions, notably reef location in relation to water flow, can be a considerably stronger factor influencing coral health than erect algae.

KEY WORDS: Marine reserve · Fishing effects · Coral growth · Algal–coral interactions · Bleaching · Management · Phase shifts

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INTRODUCTION

Understanding and promoting the factors that influence the recovery of corals is of considerable concern to Caribbean people dependent on reef resources, and reef managers tasked with conserving these resources. Reef ecosystems in the Caribbean are experiencing multiple human and natural disturbances that have caused major basin-wide changes in their ecology. Many Caribbean reefs have lost 90% of their hard coral cover since the 1970s and are now dominated by various algae associated with reductions in calcium carbonate deposition and reef growth (Gardner et al. 2003, Alvarez-Filip et al. 2009, Schutte et al. 2010). If this process continues, natural

bioerosion rates will exceed the growth processes of calcium carbonate and cause reefs to decay (Alvarez-Filip et al. 2009). As reefs decay, their ecological services including habitat for fish and fisheries productivity will decline (Paddack et al. 2009).

Losses of coral have been attributed to a series of diseases that killed the key foundation coral taxa, *Acropora* in 1981, and a key herbivore, *Diadema antillarum* in 1983 (Hughes 1994, Lessios 1988). Bleaching events and smaller-scale coral diseases since that period have either caused further declines or slowed the recovery of corals (Aronson & Precht 2001). Poor water quality may have exacerbated these impacts or further reduced the recovery potential of Caribbean reefs (Kuntz et al. 2005). Short-term

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experimental evidence suggests that algae, in general, may cause the bleaching and mortality of corals indirectly (Kline et al. 2006, Nugues & Bak 2006, Smith et al. 2006) or directly through contact (River & Edmunds 2001, Nugues & Bak 2006, Box & Mumby 2007). Some specific algae contain allelopathic chemicals that can directly poison corals under experimental conditions (Rasher & Hay 2010). Studies have also found negative effects of algae on coral reproduction (Foster et al. 2008) and recruitment (Box & Mumby 2007, Diaz-Pulido et al. 2010, Kuffner et al. 2006) or direct competition (Jompa & McCook 2002, 2003). Consequently, once algae are established, it may be difficult for corals to grow, complete their life cycle, and recover if patterns observed in these experiments are good analogues for natural field conditions.

Algae on Caribbean reefs have been remarkably persistent and possibly a good example of ecological hysteresis where recovery of corals is difficult once algae are established (Hughes et al. 2010). Experimental efforts to reduce algae in order to promote coral recovery found that algae return quickly, within 6 mo, and this is not sufficient time to facilitate coral recovery (McClanahan et al. 2001). There is some evidence that the recovery of herbivorous sea urchins and fishes facilitate coral recovery, but these changes have often been small or on a small spatial scale (Carpenter & Edmunds 2006, Mumby et al. 2006, Maciá et al. 2007, Idjadi et al. 2010). Fisheries closures have been promoted as a way to increase herbivorous fish abundances, creating high grazing conditions required of corals. Nevertheless, reserve responses have been variable and possibly only effective in old closures with low initial levels of algae (Mumby & Harborne 2010, Selig & Bruno 2010, McClanahan & Karnauskas 2011, McClanahan et al. in press). Consequently, knowledge of these coral reef ecological dynamics is not simple and there is much to learn in terms of the factors that influence coral–algal interactions and how to manage Caribbean reefs for the resilience and recovery of corals (McCook et al. 2001, Hughes et al. 2010).

The experiment described here is an attempt to evaluate 2 potential management strategies: (1) removal of algae and (2) fisheries closure on the health, growth, and survivorship of corals. This experiment was established on patch reefs in a remote field site where the field conditions and time scale used were more representative of current Caribbean reef conditions than previous small-scale manipulative experiments. Consequently, we undertook a crossed 2-factor design where 16 patch reefs located on the sand apron of Glover's Reef Atoll and patch reefs divided

equally between a young fisheries closure (~8 yr) and non-closure and where half of the reefs had their algae removed monthly over a 590 d period. We predicted higher coral mortality and decreased coral health and growth on patch reefs exposed to high levels of algae and those not protected from fishing.

MATERIALS AND METHODS

Study sites and experimental design

Glover's Reef Atoll is a coral-rimmed atoll 32 km long and 12 km wide located ~45 km off the coast of mainland Belize (Fig. 1). There are nearly 850 patch reefs in this atoll's lagoon, and most of them have lost hard coral cover and become dominated by various erect algae since baseline measurements in the early 1970s (McClanahan & Muthiga 1998). Brown algae in the genera *Turbinaria*, *Sargassum*, *Lobophora*, and *Padina* were the dominant algae and less abundant red and green genera can be found on most reef patches (McClanahan et al. 2001, McClanahan & Karnauskas 2011). In 1993 the atoll was declared a marine reserve, subdivided into 3 management zones, and has been managed by the Belize Fisheries Department. The research was undertaken in the conservation zone (CZ) where fishing is prohibited and general use zone (GUZ) where spearguns are the dominant gear in use and the largest proportion of the catch is parrotfish followed by a variety of common carnivores, including snappers, jacks, groupers, angelfish, and barracuda (McClanahan et al. in press).

The study was undertaken on 16 shallow (<2 m deep), small, and generally round-shaped patches (<100 m²) located on the sand apron of the windward side of the atoll (Fig. 1). The size of patch reefs was estimated from maximum and minimum diameter measurements, and the surface areas were calculated for placing fish abundance on a per area basis. The distance between the patch reefs in and out of the CZ was ~5 km. The windward side of the atoll is expected to have the cleanest water, due to prevailing water flow patterns across the atoll lagoon, but also not exposed to waves and storm surge. Additionally, seagrass and algae do not colonize the sand apron, and therefore influences from the surrounding biota are expected to be minimal. Consequently, these patch reefs were chosen to have the fewest external influences and disturbances while having what are expected to be good environmental conditions for coral health.

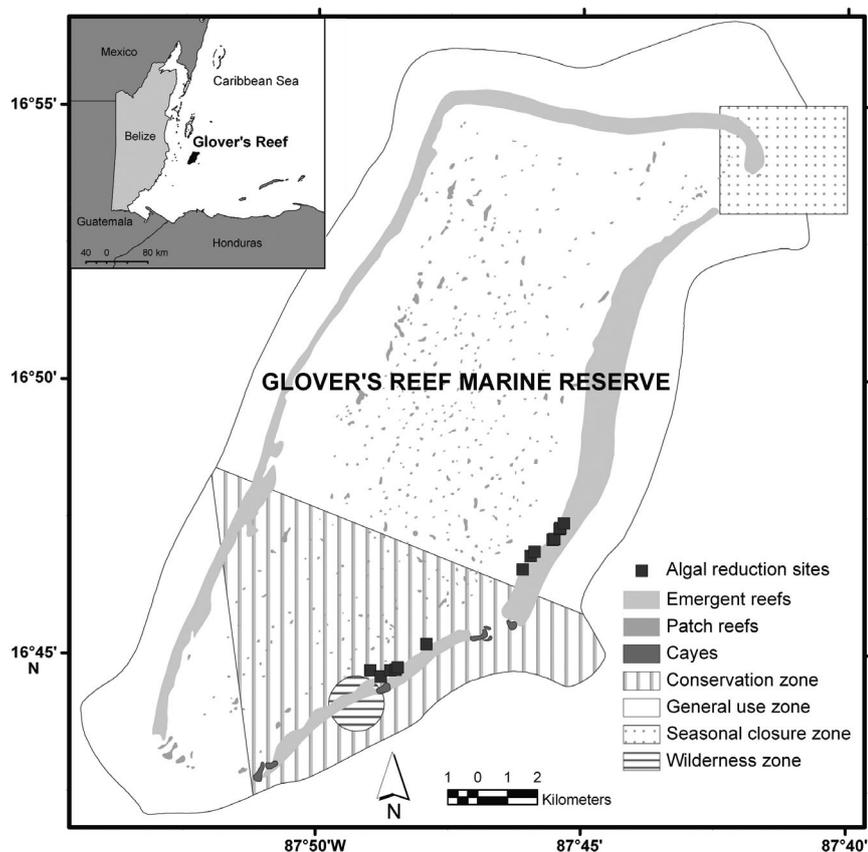


Fig. 1. Glover's Atoll, Belize, and location of experimental patch reefs on the sand apron of the conservation and general use zones

In January 2003, 16 of these patch reefs were selected based on having similar sizes (~25 to 50 m²) such that half were in and out of the CZ. After initial measurements of benthic cover and fish abundance, half were haphazardly chosen for the experimental treatment of algal reduction, such that both the CZ and GUZ had 4 unmanipulated controls and 4 experimental patches. Field measurements were repeated on the experimental patch reefs 1 or 2 d after the algal reductions.

To perform the initial algal reduction, hedge clippers were used to clear the large fronds, and wire brushes with metal scrapers and wire brushes were used to remove smaller algae and, where possible, the holdfasts. Extreme care was taken to minimize the damage to surrounding corals and other benthic invertebrates. Approximately 30 person hours (5 individuals × 6 h in the water) were necessary for the initial algal reduction on each patch reef. The experimental patches averaged 4.2 kg m⁻² of algal wet wt prior to cleaning, and after the reduction the mean wet wt per patch was reduced to 0.088 kg m⁻². This is equivalent of ~1 to 2 tons of algae removed per patch,

and this value was further reduced by the monthly removals. The algae that remained were largely holdfasts and algae that were not easily removed with these tools. Following this initial reduction, the 8 experimental patches were cleared of all re-growth using wire brushes and metal scrapers every month for a year (January–December 2003). Care was taken not to interfere with experimental coral transplants or any existing corals or coral recruits on the patch reefs.

To facilitate evaluating treatment effects on corals, 6 corals of similar size and initial condition were attached, or 'planted', with masonry cement on all 16 patches shortly after the algal reduction and field measurements. Collections of 96 fist-size corals from 2 taxa, *Siderastrea siderea* and *Porites asteroides*, were made from the adjacent back reef area with minimal erect algae. These species were chosen because they shared similar hemispherical shapes that would allow for easy measurements. Additionally, *S. siderea* was more likely to represent a stress-resistant (Muthiga & Szmant 1987) and *P. aster-*

oides a faster-growing and opportunistic life history (Lirman et al. 2003). Collection locations were just windward of the experimental patch reefs but on the leeward side of the reef rim in areas of good water flow. Colonies were removed from the bottom with a chisel, placed in buckets, and transported ~1 to 3 km to the patch reefs. One sample of each species was fastened to the reef with masonry cement on the windward, middle, and leeward side of the patch reefs. These transplanted corals were checked 2 d later to determine if they had survived and if they were securely attached to the bottom. Transplant mortality or loss was very low, but any coral that had either come loose or died immediately following transplantation was replaced, rechecked 2 d later, and found to be secure and alive. After this transplantation period, all 96 corals were measured for initial size and assessed through time for changes in survival, health, and growth. Although algae were initially cleared in a small area before placing the masonry cement and for the planting process, erect algae growing alongside or over a planted coral were not removed in the control patches. Following these

baseline assessments, sampling of the benthos and fish was done on either a monthly or quarterly basis, depending on the type of measurement.

Monthly field sampling

Seawater analyses. Seawater samples were collected in plastic and acid-rinsed Nalgene bottles from the experimental patches monthly for assessments of inorganic nitrogen, phosphorous, and suspended solids concentrations. The concentration of nitrates, nitrites, and ammonia were determined separately and the values added to determine total nitrogen. From each patch, a single 500 ml sample was taken from the leeward edge ~10 to 20 cm from the bottom. Although only 15 ml of each sample was used for any given test, large samples were taken from the patches to eliminate the risk of analyzing contaminated water. Samples were analyzed immediately using the Middle Key spectrophotometer (Hach Company model DR/2500; 2.5 cm cell length). Nitrates were analyzed using the cadmium reduction and phosphorus by the ascorbic acid methods. This method has a detection limit of 0.2 mg l⁻¹ for nitrate, 0.002 mg l⁻¹ for nitrite and a 0.02 mg l⁻¹ limit for phosphorous. Water was sampled for the control patches on a quarterly basis as these patches were assumed to remain relatively stable.

Algal scrapings. To estimate algal biomass, a haphazardly tossed 25 × 25 cm thin-wire quadrat was thrown on each patch, and all erect algae were scraped with a chisel. To reduce variability and need for replication, if the quadrat landed in an unrepresentative place (i.e. sand) or close to a planted coral, then it was thrown again until landed in a place that was hard bottom or more typical of the entire patch. All scraped algae other than benthic turf and encrusting coralline algae were collected in a plastic bag and taken back to the station's laboratory for weighing with a triple-beam balance (0.1 g accuracy). Due to noted differential water absorption and desiccation rates of various genera, all samples were left to dry for ~4 h before weighing. Scrapings were taken once before the monthly cleaning and again afterwards selecting spots as described earlier in this paragraph, but insuring the same location was not sampled twice. By taking pre- and post-scrubbing samples, we were able to determine the monthly algal growth rates at each patch.

Coral health and mortality assessment. Visual evaluations were made to assess the health of the planted corals. Observations were divided into 3 cat-

egories based on the initial, healthy coloration of the coral. Corals with no signs of lost coloration were recorded as 'healthy', corals with lost coloration were recorded as 'paling', and corals with white tissue exposed were recorded as 'bleached'. Corals that died during this period were also recorded, and the % of corals in each category were calculated monthly.

Fish population counts. Monthly total counts of all the fish were made to species level on each patch by visual assessment. Species were counted by discrete group method based on their taxonomy, position in the reef or water column, and behavior. Groups were counted in a specific order, for example, snappers (Lutjanidae), which were wary of the observer, were counted first while territorial damselfishes (Pomacentridae) were counted last. The investigator approached and circumscribed the patches slowly so as not to scare away fish. One group was sampled during each pass around the outer edge of the reef. Fish <3 cm were not counted. A final pass across the patch reef was made to insure that fishes in the center or hidden from view were counted. The count procedure lasted 30 to 45 min and included an average of ~25 different species. Surgeonfish and parrotfish were pooled together for some statistical analyses and referred to as herbivorous fish, although detritus is a part of their diet. Fish densities per patch reef were converted to a per area basis, based on estimates of the surface area of each patch reef, prior to statistical comparisons.

Quarterly field sampling

Additional measurements were made on both the experimental and control patches 5x over the 590 d period.

Water flow. Calcium-sulphate 'clods' were used to measure current strength on each patch reef and reef location on calm days (wind < 15 knots) (Doty 1971, McClanahan & Karnauskas 2011). The dissolution rate of clods can be used to approximately measure integrated water motion and converted to current-strength estimates from weight-loss experiments in controlled flumes (Thompson & Glenn 1994). Clods were made from plaster of Paris poured into ice cube trays, allowed to set and dry in the sun, sanded to a uniform shape, and glued with waterproof epoxy to plastic 10 × 10 cm squares bases. Holes were drilled in the corners of the plastic squares so they could be attached to the reef using thin copper wire in the 3 reef locations. Time of deployment and original weight of the clod card were recorded, and clods were retrieved 48 h later. Clods were sun-dried for 2 d and then reweighed. The loss in clod weight

(g d^{-1}) was converted to flow rate (cm s^{-1}) using $([x - 0.932]/2.357)$, where x is clod loss per day (Anzai 2001).

Benthic cover and algal biomass. Benthic cover on each patch was assessed by three 10 m line-intercept transects per patch reef (McClanahan 1999). Transects were haphazardly draped over each patch so that they followed the contours of 3 zones (windward, middle, and leeward). All substrate cover >3 cm under the line was measured and recorded to species for stony corals and to the genus for fleshy and calcareous algae. Other taxa were also pooled into gross functional groups, including encrusting coral-line algae, branching coralline algae, algal turf, sponge, and soft corals.

Herbivory assays. Assays of the seagrass *Thalassia testudinum* were used to estimate herbivory (Hay 1981, McClanahan et al. 1994). Seagrass blades were collected from the seagrass beds in the Wilderness Zone, inspected to avoid using pre-bitten or epiphyte covered samples, and cut to a standard length of 10 cm. Clippings were held in weighted clothespins attached at ~ 2 m intervals along a thin nylon line draped around the shoulder of each patch such that it was never resting on sand or lying across gaps. Assays were left for 24 h before recovering and examining for bites. The observer recorded whether or not the samples had been bitten, the amount bitten (to the closest 0.5 cm) and, based on bite scar characteristics, which herbivores were responsible for the bites: finfish or sea urchins (Hay et al. 1983, McClanahan et al. 1994). The mean number of bites by fish and urchins, and the percentage of seagrass lost to grazing were calculated. This herbivory assay method is biased towards macroalgal feeding species and underestimates herbivory by some groups such as scraping and excavating parrotfish and sea urchins, and does not measure herbivory by some sucking and scraping species such as most grazing surgeonfish (McClanahan et al. 1994). The combination of herbivores counts and the assay was expected to reflect herbivory differences between treatments.

Coral size measurements. Planted coral sizes were measured with Vernier caliper to the nearest mm, where each coral colony's length and width was measured using the longest and shortest edges of the coral as the standard for length and width measurements. These 2 measurements were used to determine the coral's approximate area (oval assumption $A = L \times W \times 0.8$) and change over the 4 mo period. Percent change in colony size (cm^{-2}) from initials was calculated over the 590 d interval (13 January 2003 to 5 August 2004) for transplanted *Siderastrea*

siderea and *Porites asteroides* colonies. The small number of corals that exhibited 100% mortality was excluded from coral growth analysis.

Data analyses

Initial effects of the algal reduction on the benthic and fish community composition of experimental patch reefs were explored using 2-way fixed factor ANOVAs (Management \times Time). The effects of the repeated reduction of algae over time were tested with 3-way fixed factor ANOVAs with 4 replicate patch reefs in each of the experimental treatments (algae reduction and fishing reduction) with Time as the third factor. A repeated measures ANOVA was not an appropriate statistical test as sampling was conducted on haphazardly placed rather than fixed transects or quadrats. This analysis was applied to the benthic cover, fish abundance, and herbivory data. Data were tested for normality and homogenous variances using the Shapiro-Wilks' and Cochran's tests, respectively. Square root and $\log_{10}(x + 1)$ transformations were applied to meet the assumption of normality and equal variance when necessary. For the analysis of fish abundance, all species with <30 individual total sightings throughout the entire sampling period were excluded from the analyses. Only the abundance of one species, *Chromis viridis*, differed significantly between treatments before the algal removal (Tukey's HSD post hoc analysis, $p < 0.05$).

Frequency of coral bleaching, paling, and mortality for *Siderastrea siderea* and *Porites asteroides* were compared across management zone and treatment using likelihood ratio chi-squared tests. Coral growth was calculated as % change in colony size from initial (January 2003) to final (August 2004) sampling periods and analyzed using 3-factor ANOVAs (Management zone \times Treatment \times Patch reef location) by coral species. Regression analyses were performed to evaluate relationships between coral growth rates and water flow estimates. Regression analysis matched both absolute change and proportional change in colony size from initial measurements over the entire study period to mean water flow for a given patch reef location (leeward, middle, or windward) grouped by management zone and algal treatment (as these factors were significant in 3-factor ANOVA analysis of flow across all study reefs. This created 12 different 'levels' of water flow rates for the regression analysis (3 patch reef locations \times 2 management zones \times 2 algal treatments). Presented graphs are based on pooled data such that only those treatments effects

that were statistically significant are shown. Statistical tests were undertaken using the JMP 8.0 software package.

RESULTS

Initial treatment effects

The initial physical removal of macroalgae resulted in significant differences in estimates of benthic cover of 3 substrate categories: an increase in turf algae and hard coral and a decrease in erect fleshy algae (2-way ANOVAs: Time \times Zone). As anticipated, the cover of fleshy algae declined regardless of management zone from a (mean \pm SE) pre-treatment level of $63.4 \pm 3.7\%$ to a post-treatment level of $14.0 \pm 4.3\%$ ($F = 36.01$, $p < 0.0001$). A larger drop was observed when algal abundance was estimated by scraping by biomass from a (mean \pm SE) pre-treatment level of $4226 \pm 632 \text{ g m}^{-2}$ to a post-treatment level of $88 \pm 32 \text{ g m}^{-2}$ (2-way ANOVA, $F = 47.11$, $p < 0.0001$).

Analysis of initial total fish density and herbivore density found that, while herbivore density did not vary significantly between management zones nor before or after the initial algal removal treatment, a significant fisheries closure effect was found for total fish density (2-way ANOVA, $F = 6.72$, $p = 0.02$), in which the GUZ zone had greater total numbers of fish (mean \pm SE = $3.02 \pm 0.35 \text{ ind. m}^{-2}$) than the CZ zone ($1.83 \pm 0.34 \text{ ind. m}^{-2}$; Student's t -test, $t = 2.18$).

Changes over time

Water quality and flow. Both total N and P varied significantly over time (3-way ANOVA; total N: $F = 6.81$, $p = 0.003$; total P: $F = 30.18$, $p < 0.0001$) but not by treatment or management zone. Additionally, no significant effects of Time, Treatment, or Zone were detected for suspended solids. Seawater flow was determined to be significant and 23% greater in the GUZ compared to the CZ (Table 1; 3-way ANOVA, Zone \times Treatment \times Transplant location, $F = 29.06$, $p < 0.0001$). Control reefs exhibited 13% higher flow rates than algal removal reefs ($F = 7.99$, $p = 0.005$), and windward and middle transplant locations on individual reefs exhibited higher flow than the leeward edge of the reef ($F = 4.41$, $p = 0.012$). None of the interaction terms between Zone, Treatment, and Transplant location for the 3-factor ANOVA were significant.

Table 1. Seawater flow rates (cm s^{-1}) pooled across all sampling intervals and ANOVA results. Means (\pm SE) are shown for the significant factors of management zone, treatment, and reef location following 3-way ANOVA analysis (* $p < 0.05$, **bold**)

Treatment	Location	Mean	SE
Conservation zone (CZ)			
Control	Leeward	3.65	0.39
	Middle	3.99	0.39
	Windward	3.96	0.33
Experiment	Leeward	2.74	0.34
	Middle	3.48	0.27
	Windward	3.90	0.42
General use zone (GUZ)			
Control	Leeward	4.69	0.24
	Middle	5.12	0.37
	Windward	5.27	0.33
Experiment	Leeward	3.92	0.34
	Middle	4.57	0.37
	Windward	4.66	0.34
Factor		<i>F</i>	<i>p</i>
Management Treatment		29.05	0.0001*
Management \times Treatment		7.99	0.005*
0.72			0.13
Location		4.41	0.014*
Management \times Location		0.01	0.99
Treatment \times Location		0.52	0.59
Management \times Treatment \times Location		0.25	0.77

Treatment effects over time. Benthic cover changed significantly from February 2003 to May 2004, based on 3-way ANOVA (Zone \times Treatment \times Time) analyses (Table 2). Benthic cover did not vary across management zone for any of the benthic substratum measures. However, 4 benthic substrates did show changes across time and treatment (Fig. 2). Unsurprisingly, fleshy algae were consistently greater on control patches than experimental patches across the sampling intervals. However, fleshy algae cover did increase over time, with greater increases on experimental than control patches. The opposite pattern was observed for turf and encrusting coralline algae, which showed consistently greater cover in experimental removal patches versus control patches over time. Coral cover, while greater on experimental patches, declined significantly over time, regardless of patch reef treatment.

Measuring change in patch reef substrate from algal biomass scrapings over time also revealed a significant treatment effect with greater algal bio-

Table 2. ANOVA table of results showing p-values from algal removal treatment on benthic substrate (3-factor ANOVA: Management zone \times Algal removal treatment \times Time) and transformation used to improve normality for each benthic category. Initial (pre-treatment) data excluded as well as sampling from period 2 in which only treatment patch reefs were sampled. E-coralline: encrusting coralline algae; B-coralline: branching coralline algae; Calcareous: green calcareous algae; ns = not significant

Benthic substrate	Zone	Treatment	Time	Time \times Zone	Time \times Treatment	Zone \times Treatment	Time \times Zone \times Treatment	Transformations applied
Hard coral	ns	ns	0.027	ns	ns	ns	ns	None
Algal turf	ns	<0.0001	ns	ns	ns	ns	ns	Square root ^a
Fleshy erect algae	ns	<0.0001	0.005	0.016	ns	0.009	ns	None ^a
E-coralline	ns	<0.0001	<0.0001	0.001	ns	0.005	ns	Square root ^a
B-coralline	ns	ns	ns	ns	ns	ns	ns	log(x + 1)
Sponge	ns	ns	ns	ns	ns	ns	ns	log
Gorgonian	ns	ns	ns	ns	ns	ns	ns	log
Calcareous	ns	ns	ns	ns	ns	0.003	0.007	log(x + 1)

^aFailed Shapiro-Wilks test for normal distribution, cautionary results

mass on control patches compared to experimental patches (3-way ANOVA, $F = 2523.38$, $p < 0.0001$). In addition, the overall algal biomass was significantly greater on CZ versus GUZ patches ($F = 15.88$, $p < 0.0001$) and showed significant temporal variation with the greatest biomass values during the summer months ($F = 3.06$, $p = 0.001$). When algal biomass was averaged across all time periods, control reefs from the CZ and GUZ showed similar levels of algal biomass. However, removal resulted in significantly less algal biomass on GUZ compared to CZ patch reefs (Tukey's HSD post hoc analysis, $p < 0.05$).

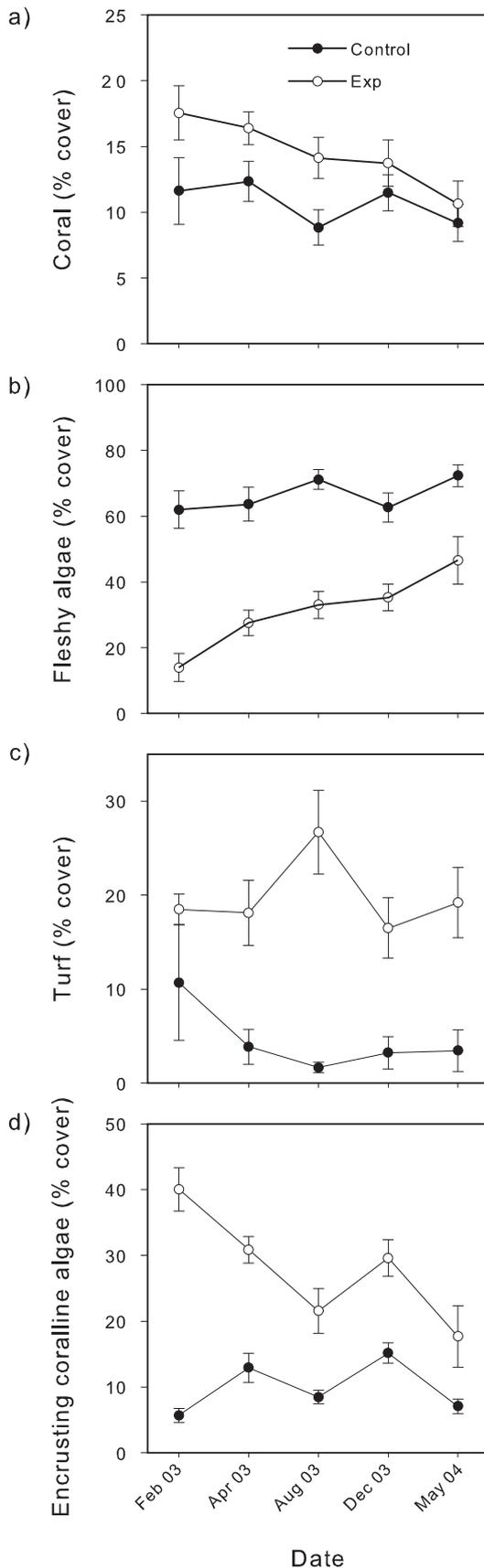
Numbers of fish and grazing. Time was the most frequently statistically significant factor in the fish data, significant for 7 of the 9 tests, suggesting a strong seasonal pattern or summer usage of the patch reefs by herbivores (Table 3, Fig. 3). Management was significant for 6 tests, and the algal removal was significant for 3 of the 9 tests. Three of the 4 larger herbivores were more abundant in the CZ, namely the blue tang, and the stoplight and redband parrotfish, whereas there were no differences in the small striped parrotfish and doctorfish between management zones. The doctorfish and damsselfish had interactive Treatment \times Management effects but in the opposite directions — damsselfish abundance increased and doctorfish decreased in the CZ after the algal removal and vice versa for the GUZ. Total fish numbers increased in the removal reefs immediately after the removal, and this difference was maintained until the October–November sampling.

Fish grazing on the experimental *Thalassia testudinum* assays greatly exceeded urchin grazing in both control and experimental patches for both management zones regardless of the time interval (Table 3). Fish grazing, measured as numbers of bites

min^{-1} , was low overall but significant and only slightly greater on experimental (mean \pm SE = 3.41 ± 0.45) compared to control patches (mean \pm SE = 2.72 ± 0.47 , $p < 0.05$) and probably driven by the low fish grazing on the GUZ control patches. Urchin grazing was considerably higher in the GUZ, $\sim 10\times$ greater than in the CZ ($p < 0.033$). Estimates of *T. testudinum* tissue loss were low ($< 16\%$), and no statistical differences between treatments were found.

Coral health and growth. To assess coral health, the frequency of observed full mortality, paling, and bleaching of coral tissue by management zone and algal removal treatment were examined. For *Porites asteroides*, low but significantly higher rates of mortality and bleaching were found in the CZ than the GUZ (likelihood ratio of mortality, chi-squared 26.7, $p < 0.05$; bleaching, chi-squared 27.3, $p = 0.04$) (Fig. 4a,b). Additionally, higher rates of mortality occurred in the experimental algal removal than the controls reefs (chi-squared 28.3, $p = 0.03$). For *Siderastrea siderea*, mortality and paling did not show any patterns with Management and Treatment. However, greater bleaching was observed in control reefs versus experimental reefs (chi-squared 12.2, $p = 0.03$) (Fig. 4b).

Analyses of the coral growth indicated high variation, no algal reduction treatment effects, but significant management zone effects for both species (Table 4, Fig. 4c). *Siderastrea siderea* growth averaged a $12.8 \pm 3.5\%$ (mean \pm SE) increase in colony size within the CZ, but growth was twice as high in the GUZ (mean \pm SE: $27.8 \pm 4.0\%$). The difference in *Porites asteroides* growth across zones was even greater, though more variable. Inside the CZ, transplanted *P. asteroides* colonies averaged a $1.7 \pm 6.5\%$ (mean \pm SE) increase in colony size, compared to a $24.3 \pm 6.5\%$ (mean \pm SE) increase in the GUZ.



Seawater flow rate was explored, using regression analysis, as a possible explanatory mechanism behind what could be driving rates of growth due to differences between management zones. Total coral growth as % change from initial over the entire study period (January 2003–August 2004) was regressed against mean flow for a given transplant location (leeward, middle, or windward) grouped by zone and algal treatment (as these factors were significant in 3-factor ANOVA analysis of flow across all study reefs). A significant positive relationship between % change in coral growth and increasing flow was detected for *Porites asteroides* ($r^2 = 0.35$, $p = 0.04$, $n = 12$) but not for *Siderastrea siderea*.

DISCUSSION

Our results suggest that these 2 hard coral species can coexist with very abundant erect algae without a strong response in their condition for more than one year. Consequently, other factors such as recruitment limits, temperature anomalies, disease, and predation pressure could be more important than macroalgae in determining these species' health and survival (Vu et al. 2009, Venera-Ponton et al. 2011). Many of the small-scale experimental manipulations show immediate responses on the order of days to weeks (Smith et al. 2006, Liu et al. 2009), which we suggest are largely a result of experimental conditions that are atypical of field conditions. The reef-scale field study reported here emulates the treatments of smaller laboratory experiments, but under conditions of natural water flow, nutrients, sunlight, spacing, and fish communities at much larger spatial and temporal scales. Consequently, the lack of agreement between our results and some previous investigation of algal-coral interaction suggests that experimental investigations exploring this complex algal-coral relationship should be conducted across longer temporal and large spatial scales that mimic natural systems. Macroalgae and corals have co-existed over long periods of evolutionary history, occupying the same habitat, and it is unexpected that algae would quickly kill corals at a distance under natural conditions.

Fig. 2. Change in benthic cover over time. Mean %cover (\pm SE) by treatment for each benthic substrate category exhibiting a significant change in cover over time or treatment is shown for experimental (○) and control patch reefs (●). No differences across management zones were detected (3-factor ANOVA), so results are pooled across zone

Table 3. (A) Fish densities and (B) grazing rates per patch. Mean values, SE in parentheses. Fish densities (m^{-2}) include the 6 most abundant herbivore species, damselfish, total fish, and total herbivorous fish pooled across post-treatment sampling intervals. Grazing rates were calculated as number of bites min^{-1} for fish and urchins, and % loss of experimental *Thalassia testudinum* assays. Significant factors and interactions from 3-factor ANOVA (Zone \times Treatment \times Time) are shown at right: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Insignificant interactions are not shown

Fish species	Common name	Conservation zone		General use zone		Zone	Treatment	Time	Zone \times Treatment
		Control	Expt	Control	Expt				
(A) Fish density									
<i>Acanthurus coeruleus</i> ^a	Blue tang	4.75 (0.35)	4.94 (0.49)	2.49 (0.24)	2.78 (0.3)	***		***	
<i>A. chirurgus</i> ^a	Doctorfish	3.56 (0.48)	3.65 (0.52)	3.71 (0.43)	2.88 (0.36)				
<i>A. bahianus</i> ^a	Ocean surgeon	2.15 (0.3)	1.14 (0.32)	2.12 (0.27)	2.50 (0.59)	**	*		*
<i>Scarus inserti</i> ^a	Striped parrotfish	45.40 (2.98)	45.24 (3.67)	39.94 (3.07)	37.88 (3.35)		*	***	
<i>Sparisoma viride</i> ^a	Stoplight parrotfish	8.58 (0.76)	9.02 (0.75)	6.64 (0.71)	5.44 (0.49)	***		***	
<i>Sparisoma aurofrenatum</i> ^a	Redband parrotfish	11.83 (1.53)	10.65 (1.27)	8.76 (0.76)	7.5 (0.84)	*		**	
<i>Stegastes</i> spp.	Damselfish	38.92 (2.06)	48.06 (3.08)	29.75 (1.88)	25.02 (0.94)	***		**	**
Total fish		5.07 (0.32)	5.96 (0.38)	4.52 (0.41)	5.72 (0.39)	*	***	***	
Total herbivores		1.46 (0.08)	1.49 (0.08)	1.26 (0.09)	1.52 (0.1)			***	
(B) Grazing rates									
Urchin bites		0.06 (0.06)	0.13 (0.09)	0.69 (0.18)	1.44 (0.43)	*			*
Fish bites		3.56 (0.75)	3.06 (0.59)	1.88 (0.52)	3.75 (0.7)		*		
<i>T. testudinum</i> loss		15.94 (4.6)	11.41 (3.25)	7.27 (2.49)	15.44 (5.36)				

^aDenotes 6 most abundant macroalgal herbivore species that were pooled to calculate total herbivore density ($ind. m^{-2}$)

Experimental treatment effects

Well-executed, small-scale mesocosm and aquarium experiments are often favored because environmental conditions can be controlled such that each variable can be analyzed and studied separately without confounding factors. Yet, laboratory and small-scale experiments create experimental arti-

facts and environmental conditions that do not emulate conditions experienced by the species and, therefore, need to be interpreted and extrapolated to natural systems with caution. Similarly, experiments that restrict scale or multiple realistic interactions may overlook factors critical to the health and survival of corals (Venera-Ponton et al. 2011). Many algal-coral competitive experiments that have found negative

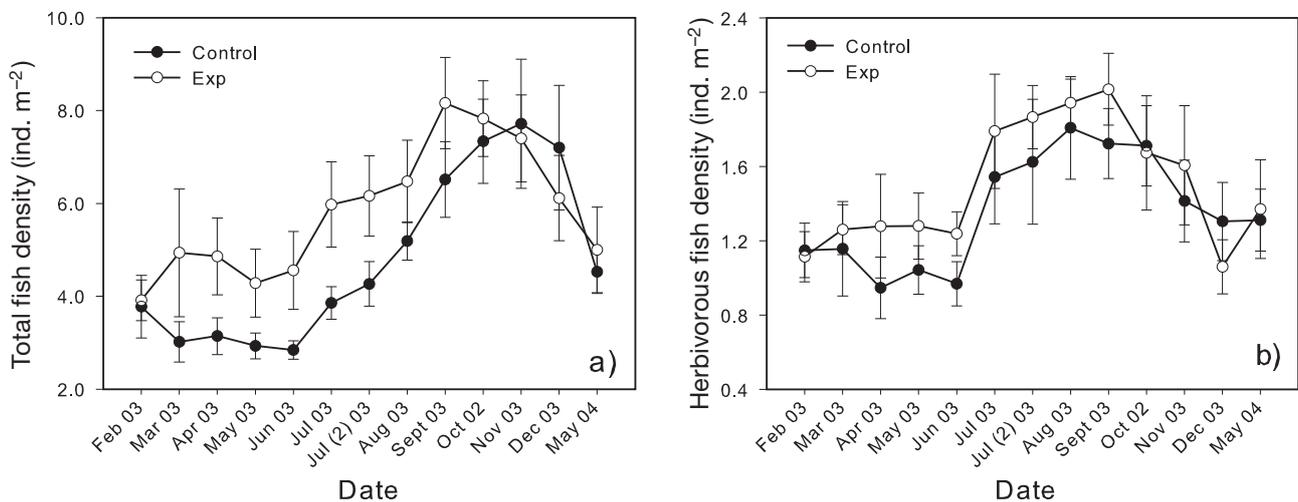


Fig. 3. (a) Total fish density ($ind. m^{-2}$) and (b) density ($ind. m^{-2}$) of herbivorous fishes (pooled densities of Scaridae and Acanthuridae species) over time and treatment. Mean \pm SE. Results of statistical tests are given in Table 3

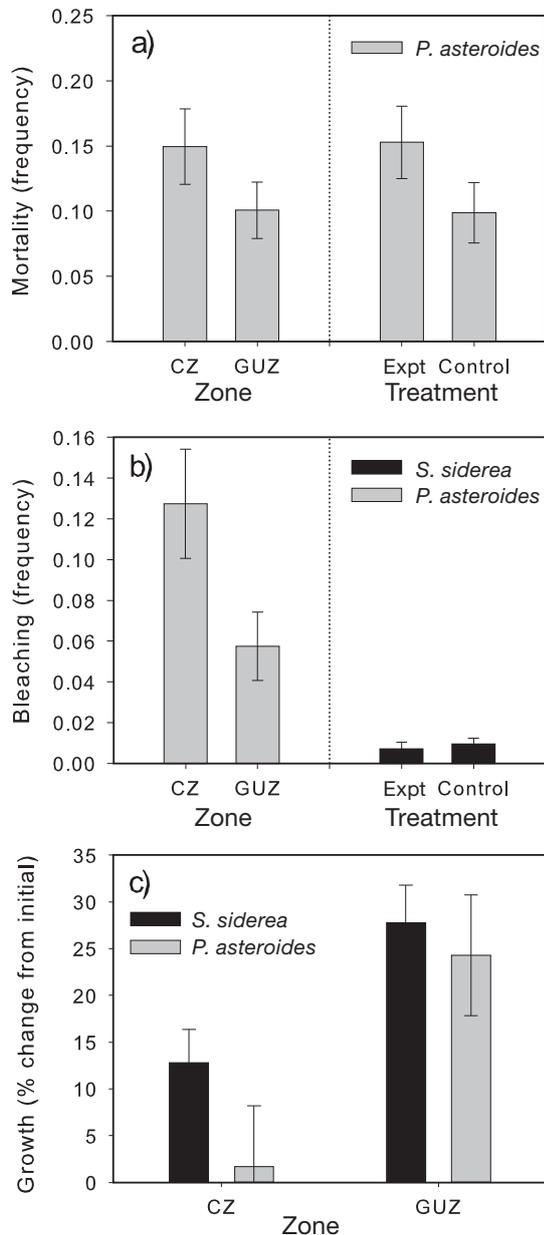


Fig. 4. *Porites asteroides* and *Siderastrea siderea*. (a) Mortality, (b) bleaching, and (c) coral growth (all in %, \pm SE) for the 2 hard coral species, showing only those factors that were statistically significant

effects have used either caging experiments, aquariums, or transplanted or placed algae in direct or close contact with corals and generally over short time periods (Jompa & McCook 2002, 2003, Nugues & Bak 2006, Smith et al. 2006, Titlyanov et al. 2007, Foster et al. 2008, Liu et al. 2009, Rasher & Hay 2010). Long-term field experiments have found fewer negative interactions (Venera-Ponton et al. 2011), and often specific to species (Nugues & Bak 2006) or limited to physical shading or abrasion rather than indirect and lethal interactions (Box & Mumby 2007).

These above studies generally suggest negative responses of coral to algal contact, but the responses can be very species-specific depending on the corals and algae used in the experiments, and sometimes corals can be unaffected or be competitively dominant to algae (McCook et al. 2001, Nugues & Bak 2006, Vu et al. 2009). Sometimes the results of short-term species interactions can be reversed when given more time or with different spatial arrangements (Chornesky 1989, Idjadi & Karlson 2007) or influenced by environmental conditions such as water quality and herbivory (Nugues & Roberts 2003, Sotka & Hay 2009). For example, if coral mesenterial filaments are part of the competitive interaction, it may take some time for corals to grow them and respond to competitors (Lapid & Chadwick 2006).

The algal taxa on these patch reefs were both very abundant and diverse (McClanahan et al. 2001) and included taxa such as *Halimeda*, *Lobophora*, and *Dicytota* in abundance, which are expected to be competitors, promote diseases, and have allelopathic effects on corals (Nugues et al. 2004, Rasher & Hay 2010). Interestingly, in this experiment, which did not promote direct contact of coral and algae but rather used natural algal abundances and conditions of water quality and flow typical of lagoonal reef conditions, the negative impacts of these algal species were not observed on transplanted corals. The corals used in the present study were expected to represent 2 of a number of life history types. They did respond differently to the environmental conditions with

Table 4. Mean coral growth (SE in parentheses) for each transplant location on the reef (windward, middle, and leeward) by management zone, irrespective of treatment. Coral growth was calculated as % change in colony size from initial (January 2003) to final (August 2004) sampling period. Significant 3-factor ANOVA results (Zone \times Treatment \times Location) for coral growth are shown at right: * $p < 0.05$, ** $p < 0.01$. Insignificant interactions are not shown

Coral species	Conservation zone			General use zone			Zone	Location \times Treatment
	Windward	Middle	Leeward	Windward	Middle	Leeward		
<i>Porites asteroides</i>	3.0 (6.2)	-1.1 (13.2)	3.0 (15.5)	33.9 (9.6)	25.7 (8.2)	13.2 (14.9)	*	
<i>Siderastrea siderea</i>	17.4 (7.2)	9.6 (2.2)	11.4 (7.8)	23.1 (7.1)	20.1 (6.3)	40.1 (6.0)	**	*

Porites asteroides, as expected, being more sensitive than the robust *Siderastrea siderea* (Muthiga & Szmant 1987). However, the lack of the predictive response to algae for these corals may reflect increased capacity to tolerate declining environmental conditions on Caribbean reefs. Both *P. asteroides* and *S. siderea* are currently common to Caribbean reefs and may even increase in abundance in recent decades (Green et al. 2008, Huntington et al. 2011).

Interestingly and unexpectedly, the experimental removal of macroalgae on the reefs seemed to result in greater incidence of bleaching. This has, however, been reported elsewhere in unpublished observations and literature (Jompa & McCook 1998) and may be due to lack of shading from macroalgal canopy or lower water quality on control reefs. We did not find any evidence for reduced light on control reefs by our turbidity measure, but there was evidence for a 13% reduced water flow on the algal reduction treatments. Changing water flow can enhance bleaching if it significantly changes conditions to which the corals have acclimated (McClanahan et al. 2005, van Woesik et al. 2005). Bleaching was expected to represent a response to poor health and possibly disease, but here it is most likely influenced by water flow and changes during the warm season. It is unclear why reducing algae would reduce water flow but perhaps algae create a slightly more turbulent flow that is detected by this clod dissolution method.

Our experimental results have several limitations to generality that can be expected from site-specific large-scale experiments. First, our results are specific to the grazing intensity, reserve efficacy, species selection, habitat, and biogeographic conditions of Glover's Atoll patch reefs and not readily generalized to the larger Caribbean. Hard corals dominated Glover's Atoll in the early 1970s, and hence the shallow, lagoonal abiotic conditions, favored high coral cover (Wallace & Schafersman 1977) prior to wide-scale mortality after 1983. The reserve effect was not large in terms of the initial conditions and response to the algal removal, but there was evidence for larger herbivores and somewhat higher herbivory in the fisheries closure. However, possible poaching in reserves and habitat-specific responses of fish to reserve protection may have prevented strong effects of fisheries closure in this manipulation (Huntington et al. 2010, Karnauskas et al. 2011). The reserve was legal for ~8 yr, but effective management was delayed by a few years, and this may explain the smaller reserve effect than reported in the oldest Caribbean reserves where reserve protection led to higher numbers of grazing fishes that reduced algal

cover and facilitated coral recovery (Mumby et al. 2006, Mumby & Harborne 2010). Nevertheless, lower water flow in the fisheries closure than in the fished reefs appeared to have a greater influence on the experimental results than macroalgae and fishing, for our conditions and scale of study.

An alternative explanation for the unexpected results is that corallivory is higher in the reserve (Rotjan & Lewis 2005, 2006) and may have an interactive effect in which the presence of macroalgae deters predation on corals by herbivores (Venera-Ponton et al. 2011). Rotjan & Lewis (2005) report high corallivory of *Porites asteroides* and this species had the lowest growth rates in the reserve, which is supported by observed higher numbers of stoplight and redband parrotfishes in the CZ versus GUZ. Given that incidence of predation were not quantified in this study, these conclusions remain speculative, but studies in old non-Caribbean reserves have reported that corallivory causes retarded recovery after disturbances (McClanahan et al. 2005). Nonetheless, the patterns observed here and the findings of a recent study (Venera-Ponton et al. 2011) suggest that coral-algal interactions are considerably more complicated and that additional factors are involved than proposed by the common coral-algal competition hypotheses.

A final potential complication of the reserve effect is that we measured a 23% lower water flow in the CZ than the GUZ that could have confounded the effect of the fisheries closure. Water flow and the placement of the reserve in lower flow environment may explain the higher growth rates of corals outside of the reserve, but this difference was not found between years in a longer-term study of changes in coral cover (McClanahan et al. in press). Water temperature measurement in and out of the fisheries closures revealed slightly lower variation in the GUZ than CZ (6%) over a 2 yr period, suggesting that the temperature regimes could also have a small effect (McClanahan et al. in press). Large-scale natural experiments are expected to have some natural environmental variation that is difficult to control for and we suggest this variation may be influential but small relative to the very large algal reduction effects in this study.

A second weakness is that our experimental design used healthy-looking, larger colonies of 2 coral species not noted for their losses in recent time. Strong effects of coral-algal competition may be greater on smaller colonies or juvenile colonies (Raymundo & Maypa 2004, Box & Mumby 2007, Idjadi et al. 2010, Venera-Ponton et al. 2011). Similar to our results, Vu

et al. (2009), using small but not juvenile corals, did not detect negative effects of 3 common macroalgal species on coral growth in their short-term study. Furthermore, coral–algal competition may be greater on more susceptible species such as *Agaricia agaricites* (Nugues & Bak 2006). Perhaps the lack of a branching coral form in the experiment explains the lack of predicted responses, as branching taxa have been suggested to be most susceptible to competition with algae (Lirman 2001). Nevertheless, the present study does not support the negative indirect effects of algae on the abundant Caribbean species *Porites asteroides* and *Siderastrea siderea*.

Thirdly, the algal reduction treatment effect, while implemented consistently across all manipulated patch reef and resulting in very large decreases in algal biomass on treatment reefs, was variable across the atoll, the management zone, and over time. Erect algal biomass on treatment reefs was higher in the CZ than in their GUZ counterparts. Despite equivalent effort to remove algal biomass from all treatment reefs, the treatment effect was not uniform across management zones, but the differences were small compared to the controls but still might have resulted in more favorable conditions for coral growth in the GUZ compared to the CZ. Furthermore, all algal cover quantified at Glover's Atoll, regardless of macroalgal reduction treatment or management zone, was >20% for the majority of the study period. Erect algal cover on reduction patches exceeded the mean regional cover of macroalgae reported for the western Caribbean (mean \pm SE: 15.3 \pm 0.4%) over the same time period (Schutte et al. 2010), attesting to the abnormally high macroalgal cover at Glover's Atoll compared to other field studies in the Caribbean (Nugues & Bak 2006). The slow increase in algal cover over time in the treatment occurred due to low-lying resilient taxa that did not contribute greatly to biomass but did produce new thalli after one month, which contributed to this cover increase. Indeed, mean cover of erect algae remaining on our reduction treatment patches contrasts with the complete removal of macroalgae achieved in smaller-scale experiments and could explain the variable results among investigation (Box & Mumby 2007, Venera-Ponton et al. 2011). Nevertheless, despite these limits, the considerably higher algal biomass on the control reefs was not sufficient to kill corals over the study period, which suggests that the relatively smaller environmental variation observed within experimental treatments, space, and time were unlikely to greatly influence the conclusions.

Restoration and conservation implications

The experimental removal of algae failed to clearly improve coral health and reverse the ecological change reported on these reefs (McClanahan & Muthiga 1998, McClanahan et al. 2001). Various experimental manipulations, such as removing algae, adding the sea urchin *Diadema antillarum*, and fisheries management have failed to return these patch reefs to coral dominance (McClanahan et al. 2001). Adding sea urchins can assist in reducing algae, but they can also quickly decline within days after additions (Maciá et al. 2007, T. R. McClanahan pers. obs.). Removing algae by one-time pulses resulted in the return of algae before corals could recruit or grow (McClanahan et al. 2001), and closing the area to fishing for >15 yr did not decrease algae and increase coral cover (McClanahan et al. in press). Here, we removed algae monthly for over 1 yr, but there was no indication of a return in coral cover or improved conditions for transplanted corals. The sea urchin, *D. antillarum*, has been present in this reef for many millennia, but their body part numbers in sediments have shown large fluctuations that suggest they are not a continuous influence on these reefs (Gischler 2010) and still remain entirely absent from the majority of patch reefs within the lagoon (McClanahan 1999).

The outlook for easily and quickly reversing the observed ecological change through a return of environmental and herbivore conditions are not hopeful on the scale of the studies undertaken to date. It is possible that by manipulating multiple factors simultaneously, such as combining manual reductions in macroalgal abundances with grazer additions (i.e. *Diadema antillarum* transplants) to increase grazing pressure, will work better to increase coral cover. The costs are, however, likely to be considerable and not practical on the scale of this problem. An alternative and low-cost method may be to ban fishing of herbivores on large scales, such that fisheries closures are not the only means to restore their populations, yet this method is untested. Additionally, informed placement of fisheries closures into habitats and environments known to respond favorably to reserve protection is expected to increase their efficacy in enhancing recovery of herbivores and corals (Huntington et al. 2010, McClanahan & Karnauskas 2011). From these results, manual and continuous removal of algae does not appear to be a viable management strategy to restore degraded reefs unless this activity persists over many years or is undertaken in well-enforced fisheries reserves where grazing intensities have increased.

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