

Effects of herbivores, nutrient enrichment, and their interactions on macroalgal proliferation and coral growth

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Received: 12 February 2009 / Accepted: 15 June 2009 / Published online: 4 July 2009
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Abstract We conducted a 20-week manipulative field experiment on shallow forereefs of the Florida Keys to assess the separate and interactive effects of herbivory and nutrient enrichment on the development of macroalgal communities and the fitness of the corals *Porites porites* and *Siderastrea siderea*. Excluding large herbivorous fishes produced macrophyte blooms both with and without nutrient enrichment. In contrast, there were no direct effects of nutrient enrichment. There were, however, small, but significant, interactive effects of herbivory and enrichment on macroalgal cover. Following nutrient enrichment, total macroalgae and the common seaweeds *Dictyota* spp. were suppressed in the presence, but not in the absence, of large herbivorous fishes—suggesting that fishes were selectively feeding on nutrient-enriched macrophytes. Access by large herbivores prevented algal overgrowth of corals, but these large fishes also directly grazed both corals. Excluding fishes did not alter survivorship of either coral species, but did decrease parrotfish grazing scars on both corals and increased the net growth of *P. porites*. Nutrient additions had no direct effects on the survivorship of corals, but there was a trend ($P = 0.097$) for nutrients to stimulate the growth of *P. porites*. The preponderance of experiments available to date indicates that loss of key herbivores is a major factor driving

macroalgal blooms on coral reefs; anthropogenic nutrient pollution generally plays a more minor role.

Keywords Herbivory · Herbivore–nutrient interactions · Seaweed–coral interactions · Threats to corals · Nutrifaction

Introduction

Since the mid 1970s, corals on Caribbean reefs have declined from about 50% to about 10% cover (Gardner et al. 2003), a rate of decline unprecedented within the Holocene for at least some coral groups (e.g., *Acropora* spp.: Aronson and Precht 2001; Aronson et al. 2002). Macroalgae now dominate Caribbean reefs (Knowlton 1992; Hughes 1994; Jackson et al. 2001), where they sometimes overgrow corals (Lewis 1986; Jompa and McCook 2002) and commonly impede coral recruitment (Edmunds and Carpenter 2001, Birrell et al. 2008). The relative role of seaweeds as a cause versus a consequence of coral decline is uncertain (Jackson et al. 2001, McCook et al. 2001, Aronson and Precht 2006, Mumby and Steneck 2008), but they clearly suppress coral recovery once they become established (Birrell et al. 2008), making a ‘phase-shift’ back toward coral-dominated reefs unlikely unless some process suppresses seaweeds (Knowlton 1992; Hughes 1994; Mumby et al. 2007; Jackson 2008).

Stressors associated with macroalgal proliferation or coral loss on Caribbean reefs include hurricane damage (Gardner et al. 2005), coral disease (Richardson 1998), global warming and ocean acidification (Hoegh-Guldberg 1999; Hoegh-Guldberg et al. 2007), sedimentation (Rogers 1990), predation (Baums et al. 2003; Rotjan and Lewis 2005), algal competition following herbivore declines

Communicated by Ecology Editor Prof. Peter Mumby

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(Hughes 1994; Jackson et al. 2001), nutrient additions (LaPointe 1997), and interactions of the above factors. While all stressors appear to play some role in reef decline, overfishing of herbivores and nutrient pollution are the most commonly cited and most amenable to human management. Observational and experimental evidence indicates that the harvesting of herbivorous reef fishes (Hay 1984; Jackson et al. 2001; Mumby et al. 2006) and the ecological extinction of *Diadema antillarum* urchins (Lessios 1988) are responsible for much of the recent Caribbean explosion in macroalgal cover (Jackson 2008). These top-down mechanisms (cf. Hairston et al. 1960) are supported by dozens of studies that show experimental removal of large herbivores consistently results in a proliferation of reef macrophytes (see reviews by Hay 1997; Hughes et al. 1999; McCook 1999; Bellwood et al. 2004; Burkepile and Hay 2006; Heck and Valentine 2007). Moreover, in marine reserves where natural assemblages of fishes persist or have recovered, macroalgal cover is significantly decreased (e.g., Mumby et al. 2006; Jackson 2008).

During the years of coral decline, there has been an increase in anthropogenic nutrient pollution in nearshore environments worldwide which could drive proliferation of seaweeds in some habitats (Smith et al. 1999). In response, a relative dominance model (RDM) was first proposed in the 1980s (e.g., Littler and Littler 1984; Littler et al. 2006a) to explain how nutrients and herbivory might interact to determine reef community structure and to cause declines in coral cover via macroalgal overgrowth. Its primary assertion is that natural coral reef seaweeds are nutrient limited and that organism types dominating a reef will be determined by interactions between nutrient levels and rates of herbivory. The model predicts that corals dominate when reefs have low nutrients and high rates of herbivory, crustose corallines dominate with high nutrients and high rates of herbivory, and turf algae dominate when reefs have low rates of herbivory and low nutrients. An important prediction is that macroalgae will proliferate only with both elevated nutrients and reduced herbivory.

Since the RDM was proposed, considerable evidence has amassed showing that herbivore loss allows macroalgal proliferation on coral reefs either with or without elevated nutrients. A recent survey of 15 fully factorial field experiments (Burkepile and Hay 2006) indicated that herbivore removal has a strong positive effect on macroalgal abundance on coral reefs while empirical support for the direct effects of nutrients or nutrient interactions with herbivores is relatively weak (see also Hughes et al. 1999; Szmant 2002; Heck and Valentine 2007, but see counter arguments by Littler et al. 2006b). These studies suggest that potentially stimulatory effects of nutrients on algal populations are buffered by natural rates of herbivory.

Despite the evidence, the relative importance of herbivore removal versus anthropogenic nutrient pollution in advantaging seaweeds over corals continues to be debated (e.g., Hughes et al. 1999; Szmant 2002; Lapointe et al. 2004; Littler et al. 2006a; Heck and Valentine 2007). This is due in part to a small number of studies that report significant direct effects of nutrient additions alone on some reefs (Smith et al. 2001; Littler et al. 2006a), suggesting that more investigations at more sites and over longer temporal scales may be useful.

Here, we report results from a factorial manipulation of herbivores and nutrients over a period of 142 days on two reefs in the Florida Keys. We factorially manipulated local nutrient levels and access by large herbivorous fishes to assess the direct and interactive effects of herbivore removal and nutrient enrichment on macroalgal proliferation and on the survival and growth of the corals *Porites porites* and *Siderastrea siderea*. Despite differences in years, spatial locations, and duration, our results largely support the findings of other experiments in the Florida Keys (Miller et al. 1999; Furman and Heck 2008) and elsewhere (see Miller and Hay 1996; Szmant 2002; Burkepile and Hay 2006; Heck and Valentine 2007) and document the primacy of herbivore removal over anthropogenic eutrophication in facilitating macroalgal blooms under field conditions.

Methods

Manipulating large herbivores and nutrient enrichment

We evaluated the effects of nutrient addition, herbivore removal, and interactions of these factors in a fully factorial block design at two coral reefs separated by ~2 km near Pickles Reef, Florida (25°00'05"N 80°17'34"W and 24°39'38"N 80°24'22"W). Identical experiments on two reefs allowed an assessment of between-site variation in responses to our treatments. These shallow spur-and-groove reefs are dominated by upright macroalgae (30–40% cover, mostly *Dictyota* spp. with lesser amounts of *Lobophora variegata* and *Halimeda* spp.), filamentous turf algae (~25% cover), and crustose coralline algae (20–25% cover), with cover of live corals being only 5–7%. We placed the experiment at a depth of 6–7 m where periodic input of cold, nutrient-rich waters is uncommon (Leichter et al. 1996, 2003).

Each experimental unit was composed of a slab of quarried coral rock (~15 cm × 30 cm × 2 cm) that sat on a cinder block (~10 cm × 20 cm × 40 cm) and was secured to the reef with a single galvanized spike (~20 cm long) fitted through a hole drilled in the center of the slab and block and pounded into the reef (see Fig. 2 in Miller

et al. 1999). The coral slab provided a natural substrate for the development of seaweed and macroinvertebrate communities. Although our spikes were galvanized, seaweeds grew directly on the spikes and there was no indication of community development differing near versus at a distance from the spikes. In order to exclude large consumers, galvanized chicken wire (2.5 cm mesh size) coated with PVC was wrapped around each block and its carbonate slab to form a tube with a height of ~ 40 cm and a length of ~ 44 cm. The ends of these tubes were either left open (partial cages) to allow grazing by larger herbivores or closed (full cage) to prevent access by larger fishes. Small fishes (wrasses, small parrotfishes and surgeonfishes, some damselfishes, etc.) could, and did, enter and feed in all cages. The full cages thus excluded grazing by larger fishes only. Previous caging studies using this design demonstrated that these partial cages yielded algal cover not statistically different from blocks with no cage structure (Miller 1998); thus, they impart minimal cage artifact.

To deliver nutrients, we placed commercial fertilizer spikes within the three parallel chambers that ran the width of the cinder block base. One end of each chamber was cemented shut while the other end could be sealed with a fitted plug of dense, closed cell foam. New fertilizer spikes (Jobes tree spikes, Weatherly Consumer Products, Inc.), 80% of whose surface was coated with paraffin wax to reduce dissolution rates, were added into each chamber and the chamber plugged shut. Spikes were replaced every 15–39 days (Table 1). We attempted to generate three nutrient levels: ambient, medium, and high levels. Medium nutrient treatments held three spikes per block while high-nutrient treatments held six spikes per block. This design allowed the passive seepage of nutrients through the cinder and coral blocks substrate with the aid of six 9.5-mm holes drilled through the top

surface of each cinder block chamber. Our procedures mirror those of Miller et al. (1999) and those suggested by Worm et al. (2000).

We spatially blocked our treatments into groups of six experimental units per block (two herbivore removal levels and three nutrient enrichment levels). Five complete blocks of the six experimental treatments were attached to hard-substratum across a 250 m² area at each reef site. The experimental units within a block were separated by 1–3 m, and each block was separated from others by ≥ 6 m.

Nutrient analysis

Previous experiments using our block design demonstrated that nutrients were enriched on the block surface [total inorganic nitrogen (TIN) and soluble reactive phosphorus (SRP) were 1.1–4.1 μM and 0.11–0.33 μM , respectively], but rapidly diluted to ambient levels (0.3–0.9 μM TIN and <0.01 –0.03 μM SRP) within ~ 1 cm of the block surface (Miller et al. 1999). In order to see if medium and high-nutrient treatment levels differed in the dissolved nutrients leaching from the blocks, we measured nutrient levels within the experimental chambers of each treatment type at day 1, 16, and 32 after nutrient replacement (see Table 1). We reasoned that assessing nutrient levels still available within block chambers would allow an assessment of nutrient delivery rate unconfounded by variable patterns of flow outside the blocks when we were collecting samples. At each sampling period, SCUBA divers rinsed 140-ml syringes three times in ambient seawater, placed the tip of the syringe into a small length of tubing and slid the tubing inside each block to be sampled and slowly drew out water samples that were immediately returned to the boat, filtered (GF/F) into new 60-ml sample bottles, stored on ice, returned to the laboratory, and frozen until they were

Table 1 Timeline of events and ambient seawater nutrient levels (in $\mu\text{mol l}^{-1}$)

	Date	Experimental day	Census	Fertilizer added	Water DIN in μM (Mean \pm SD)	Water SRP in μM (Mean \pm SD)
	April 20, 1998	0	X	X		
	May 15, 1998	25	X	X		
	May 18, 1998	28			0.43 \pm 0.20	0.01 \pm 0.02
	June 14, 1998	55	X			
	June 16, 1998	57			0.74 \pm 0.39	0.02 \pm 0.05
	June 23, 1998	64		X		
Coral slabs were submerged on March 1, 1998, ~ 50 days before experimental treatments were applied	July 9, 1998	80			0.33 \pm 0.09	0.17 \pm 0.02
	July 14, 1998	85	X			
	July 23, 1998	94		X		
DIN dissolved inorganic nitrogen; SRP soluble reactive phosphate; SD standard deviation	August 7, 1998	109		X	0.34 \pm 0.08	0.22 \pm 0.04
	August 14, 1998	116	X			
	September 9, 1998	142	X			

analyzed for total inorganic nitrogen (TIN = ammonium and nitrate + nitrite) and SRP. We used a similar protocol to assess nutrient levels of ambient seawater by sampling ~1 m above the reef.

Despite the above procedures, it is not the nutrients in, or near blocks, that is critical; rather, it is whether nutrients diffuse from the blocks in a manner that seaweeds can encounter and use. In order to test for this, we collected the green seaweed *Dasycladus vermicularis* and the brown seaweed *Dictyota* spp. from the edges of blocks in full cages after 9 weeks of treatments, dried these to a constant weight, and had their tissues analyzed for % nitrogen and % carbon at the University of Georgia's Center for Applied Isotope Studies. These species were chosen because they occurred on most replicates in full cages and represented both a rapidly and more slowly growing species (*Dictyota* and *Dasycladus*, respectively). Individuals were collected from closed cages because macrophytes were not consistently available within half cages exposed to large herbivores. As the water and tissue nutrient data were non-normal and heteroscedastic, they were analyzed by a series of non-parametric Wilcoxon exact tests. Because of initial uncertainty on their taxonomic status, we collected two individuals of *Dictyota* from some experimental units. These did not prove to be identifiably different and so were pooled to generate a mean value for that unit. As the high- and mid-fertilization treatments were statistically indistinguishable for macrophyte N and C content and for seawater TIN and SRP, we concluded that our attempt to generate a nutrient gradient had been unsuccessful (i.e., we had enriched and unenriched treatments, but both of our enrichment treatments experienced similar levels of enrichment). We thus averaged values from the two nutrient addition treatments within our blocks of treatments into a single enriched treatment when analyzing the responses of the biotic community.

Macrophyte community response

Before initiating the experimental treatments, coral slabs were submerged for 50 days on a back reef near Pickles Reef to allow natural colonization. At the end of this 50-day period, we initiated our experimental treatments and followed the development and maintenance of the biotic community for an additional 142 days, or about 5 months (Table 1). The community composition was sampled every 25–31 days by identifying algae at each of 60 randomly positioned points within a 15 cm × 30 cm quadrat placed over each slab. We were unable to identify all algae to the species-level in the field and grouped several species into genera or morphological groups [e.g., short (<0.5 cm) or tall (>0.5 cm) filamentous algae]. If more than one species were present at each point (e.g., crustose coralline

overgrown by an upright macrophyte), then both species were counted.

Initial analyses detected no statistical differences between the responses of the biotic communities from the two separate reef sites, so data from the separate reefs were pooled. As nutrient concentrations in mid- and high-nutrient treatments did not differ, we also averaged the algal cover data from high- and mid-nutrient coral slabs and used this mean value for our enrichment treatment effect.

Percent cover data for broad categories of the biotic community [i.e., total upright macrophytes, algal filaments (i.e., short and tall turfs), crustose corallines, and cyanobacteria] were analyzed by a series of blocked, repeated measures ANOVAs, which delineate the mean effect over time (between subjects) and the change in effect over time (within subjects). When a significant interaction between factors of interest was detected (i.e., cage type or nutrient levels), we performed Tukey–Kramer post hoc tests within each sampling period. We also analyzed the percent cover of the five genera of seaweeds that represented 95% or more of the total macrophyte community during the final census (i.e., *Dictyota*, *Dasycladus*, *Hypnea*, *Jania*, and *Amphiroa*). As *Dictyota* spp. occurred in all experimental treatments, we analyzed these data using a blocked, two-way ANOVA followed by Tukey–Kramer post hoc tests. Other seaweed genera occurred only on blocks protected from herbivores. For these seaweeds, we used a series of non-parametric Wilcoxon tests to test for the effect of nutrient enrichment within the closed cages. As neither *Amphiroa* nor *Jania* demonstrated a significant nutrient effect, but both tended in that direction, we also pooled these structurally similar and taxonomically related seaweeds and tested for a nutrient effect on this pooled group.

Nearly all percent cover data were heteroscedastic and non-normal. However, the potential bias imposed by these violations of parametric ANOVAs is modest because the experimental design is completely balanced ($n = 10$ for all treatments) and we log-transformed all data to minimize violations of ANOVA.

Mortality and growth of corals

In addition to the responses of the seaweed community, we tested the response of the common corals *P. porites* and *S. siderea* to our treatments by cementing small portions of each coral (≤ 30 cm³) onto each coral slab and measuring their mortality, growth rate, and whether they were overgrown by algae or exhibited fish feeding scars at the end of the experiment. Before being affixed to the blocks with small dabs of concrete, each coral piece was stained by enclosing corals in clear plastic bags with a 15 mg l⁻¹ solution of Alizarin red for 6 h in full sunlight at

a depth of 3 m on the reef (Dodge 1984). At the end of the field experiment, we inferred growth rates from the amount of tissue that was distal to this alizarin red stain when corals were sectioned with a diamond saw and viewed in cross section. Growth of *P. porites* was measured from the tips of several distal branches and averaged within a colony. We attempted to measure growth of *S. siderea* from the top of the hemispherical colonies, but growth of this species was too low for reliable measurements over this time period. Growth of *P. porites* was analyzed by a series of two-way parametric ANOVAs because these data were normally distributed and homoscedastic. Among treatment differences in survivorship, numbers of corals overgrown by algae and numbers of corals with fish grazing scars on day 142 (the termination of the experiment) were analyzed by χ^2 tests. A χ^2 test assessed the interaction between the two factors (cage and nutrients) when data were parsed into four categories (i.e., full cage enriched, full cage ambient, half cage enriched, and half cage ambient). Separate χ^2 tests assessed the effect of each factor individually (e.g., full cage vs. half cage).

Results

Effectiveness of the nutrient enrichment treatment

Nutrient levels inside enrichment blocks were several orders of magnitude greater than inside control blocks shortly after replacement of the fertilizer and declined over time (compare absolute values at days 1, 16 and 32; Fig. 1). However, even after 32 days, dissolved inorganic nitrogen (DIN) and SRP levels within experimental blocks were still 6–16 \times greater than control levels. Thus, we replenished fertilizer with enough regularity (15, 25, 30, 33, and 39 days intervals) to maintain elevated nutrients throughout the experiment. These enriched waters were delivered to seaweeds on our slab surfaces as evidenced by N being 36% higher in *Dasycladus vermicularis* from enriched blocks than from control blocks (Fig. 2). This same pattern was not detectable for *Dictyota* spp. despite both seaweeds being from the same blocks (Fig. 2).

The dissolved inorganic nitrogen (DIN) level in ambient reef seawater was always below 1 μM , while the SRP level was below 0.1 μM on 2 of 4 days (Table 1). The DIN levels are below thresholds hypothesized to be necessary for macroalgal proliferation (LaPointe 1997). The elevated phosphorus on two sample dates is consistent with the influence of upwelled, cold, and nutrient-rich waters that periodically inundate Florida Keys forereefs (Szmant and Forrester 1996; Leichter et al. 2003), but if this was the source of the elevated P, then one might expect elevated DIN as well.

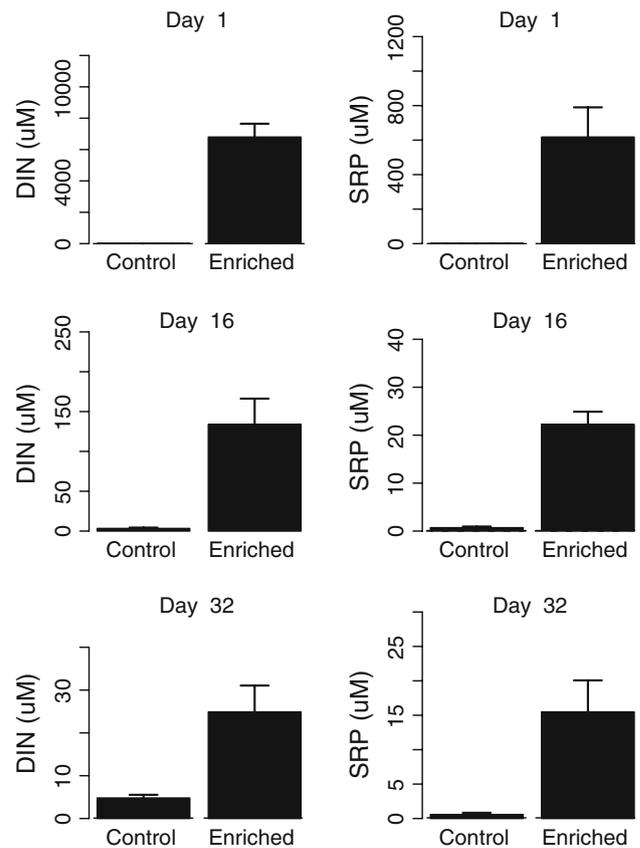


Fig. 1 Concentrations ($\mu\text{mol l}^{-1}$) of dissolved inorganic nitrogen (DIN) and soluble reactive phosphate (SRP) in seawater within the chambers of experimental cinder blocks as a function of treatment and of time since fertilizer replenishment (1, 16, or 32 days after replacement). Blocks contained 0 (control) versus 3 or 6 stakes of tree fertilizer (enriched) at all times. As nutrient levels within blocks holding 3 versus 6 fertilizer stakes did not differ, these were pooled into one “enriched” treatment. Nutrient levels were significantly greater within enriched than control blocks across all time periods ($P < 0.001$; Wilcoxon exact test; $n = 10$)

Direct effects of nutrient enrichment and herbivore removal on seaweed communities

Herbivores strongly and significantly affected four of the five algal types we monitored. Excluding large herbivores allowed macrophytes to dominate both control and enriched treatments (Fig. 3). Throughout the 142 days of the experiment, coral slabs exposed to natural densities of large herbivorous fishes were dominated by crustose corallines and short (<0.5 cm) filamentous turf algae. Upright macrophytes never exceeded about 15% cover when herbivores were present, but comprised 80–100% cover when herbivores were excluded. Coral slabs within herbivore-exclusion cages were initially dominated by tall (>0.5 cm) filamentous turfs, but these were soon replaced by macrophytes. Between day 85–146, the cover of upright macrophytes ranged from 75 to 100%. Cyanobacteria were

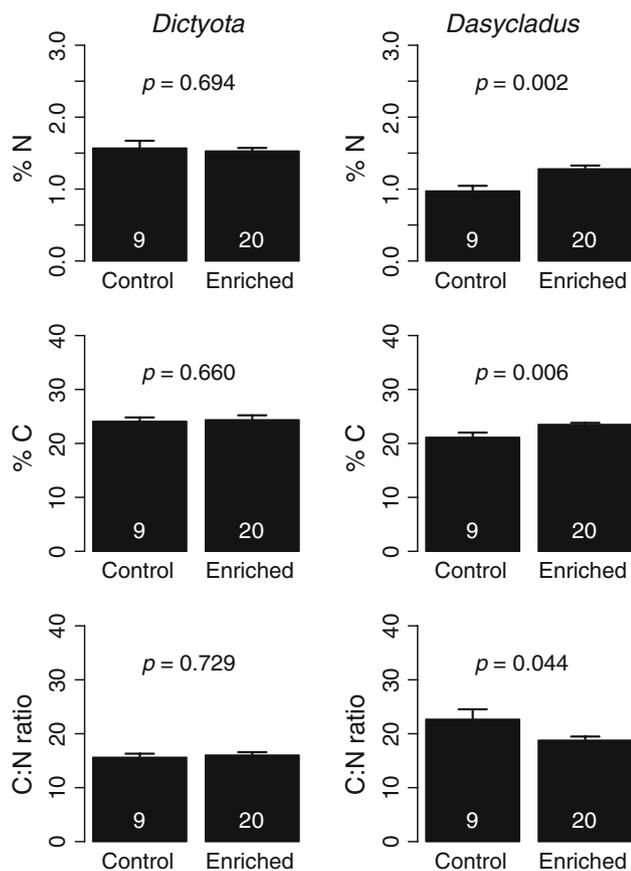


Fig. 2 The mean concentrations (\pm SE) of nitrogen and carbon (as a percentage of algal dry mass) and the mean C:N ratios for tissues from the seaweeds *Dasycladus vermicularis* and *Dictyota* spp. collected from coral slabs within closed cages where nutrients had (enriched) or had not (control) been added. Sample sizes are indicated within bars. *P*-values are from Wilcoxon exact tests. As nutrient levels within blocks holding 3 versus 6 fertilizer stakes did not differ, and because the tissue N of seaweeds from those blocks did not differ, those treatments were pooled into one “enriched” treatment

patchily distributed and rarely accounted for more than ~10% cover. Sessile invertebrates never represented more than about 2% cover, except for one slab with ~25% ascidian cover.

In contrast to the direct effects of excluding large herbivores, there were no direct effects of nutrient enrichment on any metric of community structure (Fig. 3). A series of repeated measures ANOVAs of the mean effect over time (i.e., between subject comparison) and the change in effect over time (i.e., within subject comparison) reveal a consistent effect of cage treatment on the percent cover of nearly all datasets (i.e., total macrophytes, short and tall algal filaments, and crustose corallines) and no significant direct effect of nutrients or the interaction of nutrients \times time for any dataset (Table 2); however, we note that these analyses required running many ANOVAs, so marginally significant *P*-values should be interpreted

cautiously due to the potential for a type I error. Only cyanobacteria failed to show a significant cage effect.

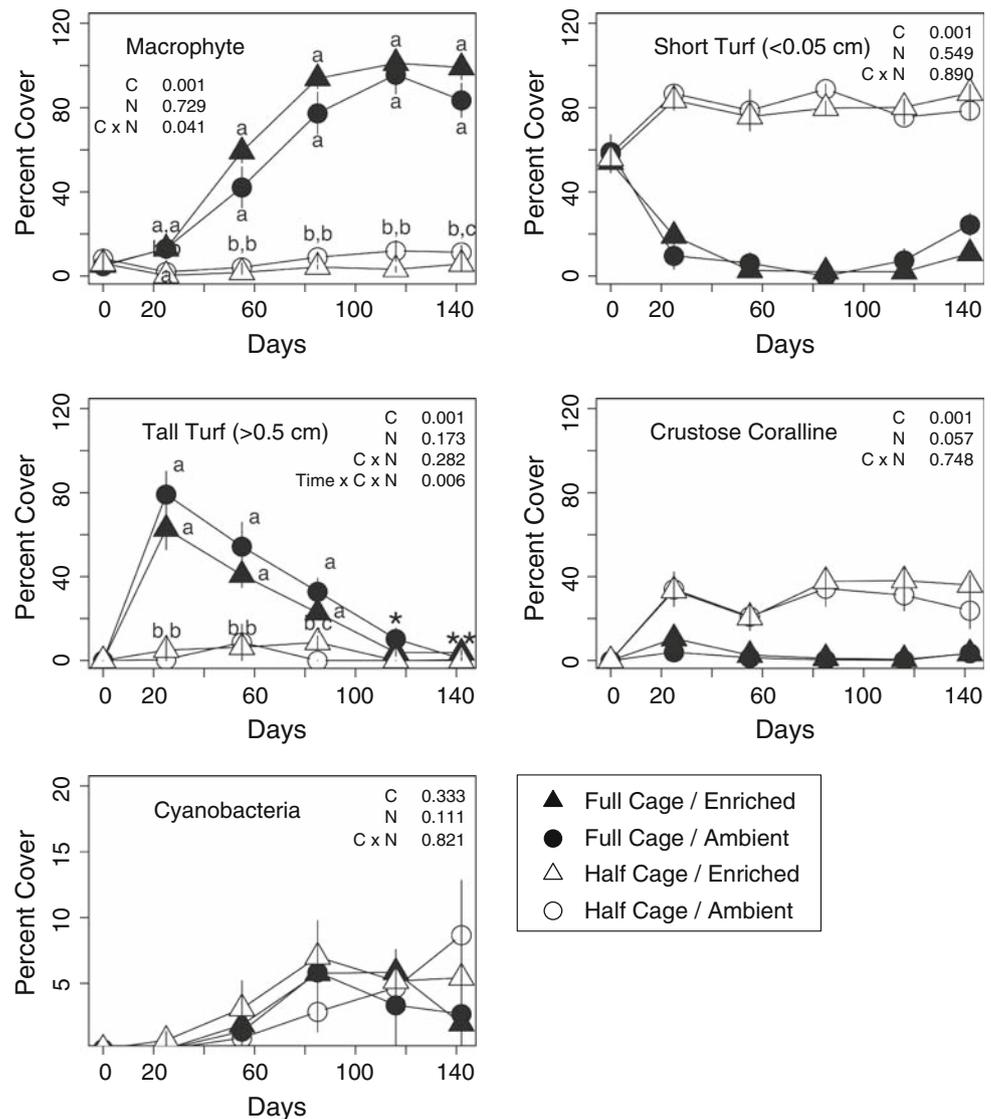
Interactive effects of nutrient enrichment and herbivore removal

There was a significant interaction of large herbivore exclusion and nutrient enrichment treatments that affected total macrophyte cover (Fig. 3, Table 2). A Tukey–Kramer post hoc examination indicated that nutrient enrichment suppressed macrophytes in the presence of herbivores, but not when herbivores were excluded (Fig. 3). Closer examination of the macrophyte community reveals that the interaction between nutrient enrichment and herbivore exclusion was largely driven by the response of *Dictyota*, the dominant member of these algal communities. Among blocks exposed to herbivores, cover of *Dictyota* spp. was significantly suppressed when nutrients were added (Fig. 4). In contrast, among blocks protected from herbivores, there was slightly greater cover when nutrients were added, though this increase was not significant for either *Dictyota*, upright corallines (Fig. 4), or total macrophytes (Fig. 3).

There were mixed responses to nutrients among the other members of the macrophyte community. At least four seaweed genera were absent from cages exposed to large herbivores but present where herbivores were excluded (i.e., the green seaweed *Dasycladus vermicularis* and red seaweeds in the genera *Hypnea*, *Jania*, and *Amphiroa*; Fig. 4). Thus, access by large herbivores strongly decreased cover of all common upright macrophytes (Figs. 3, 4). Of these seaweeds, cover of neither *Dasycladus* nor *Hypnea* was stimulated by nutrient enrichment within full cages. The percent cover of the erect corallines *Jania* and *Amphiroa* were more than doubled with enrichment, but this increase was not statistically significant ($P = 0.067$; Fig. 4).

Macrophytes were not the only group of algae that displayed a significant interaction between factors. There is an interaction between time, cage, and nutrient enrichment on the percent cover of tall (>0.5 cm) algal filaments (Table 2), indicating that the interaction between cage and nutrient enrichment shifts over time. Specifically, during all but the last two sampling periods (Fig. 3), tall algal filaments were more abundant when herbivores were excluded, and they tended to be more abundant in ambient than in enriched full cages, but this pattern for nutrient effects was not significant. On the final census (day 142), these previous patterns had reversed; there was a significant interaction between factors, with tall algal filaments being significantly more abundant on nutrient-enriched, herbivore-exclusion slabs relative to all other treatments.

Fig. 3 The percent cover of algal types on experimental slabs. Statistical results are from repeated measures ANOVAs (Table 2). Post hoc analyses by Tukey–Kramer post hoc tests ($\alpha = 0.05$) were performed only when there was a significant nutrient (N) enrichment by cage (C) interaction (i.e., only for total macrophytes) or when there was a time \times cage \times nutrient interaction (i.e., tall algal filaments). *The post hoc analyses of tall turf on day 116 are: full/ambient (a), full/enriched (ab), half/ambient (b), and half/enriched (b), and on day 142 are: full/enriched (a), full/ambient (b), half/ambient (b), and half/enriched (b)



The effects of herbivore removal and nutrient enrichment on corals

Both *P. porites* and *S. siderea* were more frequently overgrown by seaweeds when large herbivores were excluded than when they were present (Fig. 5). However, these corals also suffered significantly more grazing scars in treatments available to large herbivores. Although there were no significant differences in coral mortality among treatments as a consequence of this higher grazing rate, access by large herbivores significantly suppressed the net growth of *P. porites* (Fig. 5; $P = 0.021$). We did not detect significant direct effects of nutrient enrichment on growth of *P. porites*, but the trend in both full and half-cages was for nutrient additions to slightly enhance growth ($P = 0.097$). There was no nutrient \times cage interaction

($P = 0.670$). Though *S. siderea* did take up the Alizarin red dye, its slow growth rate precluded our ability to measure its growth with confidence.

Discussion

On two reefs, excluding herbivores dramatically affected algal community development, while adding nutrients had no direct effects (Table 2; Figs. 3, 4). Herbivore removal and nutrient enrichment occasionally interacted to affect macrophyte communities, as when nutrient additions suppressed total macrophyte cover and cover of *Dictyota* spp. in the presence, but not in the absence, of herbivores (Table 2; Figs. 3, 4). The effect size of this interaction was small compared to the effect size of herbivore exclusion,

Table 2 Repeated measures ANOVA of percent cover data (log-transformed) as a function of herbivore removal cages and nutrient treatments (see Fig. 3)

Source	df	Macrophytes			Short Turf (<0.5 cm)					
		Wilks λ	<i>F</i>	<i>P</i>	Wilks λ	<i>F</i>	<i>P</i>			
Between subjects (mean effect over time)										
Cage	1,27	0.169	132.3	<0.001	0.041	636.1	<0.001			
Nutrient	1,27	0.996	0.1	0.729	0.987	0.4	0.549			
Cage × Nutrient	1,27	0.854	4.6	0.041	1.000	0.0	0.890			
Block	9,27	0.76	0.9	0.502	0.727	1.1	0.378			
Within subjects (change in effect over time)										
Time	5,23	0.197	18.8	<0.001	0.092	45.4	<0.001			
Time × Cage	5,23	0.248	13.9	<0.001	0.058	74.3	<0.001			
Time × Nutrient	5,23	0.703	2	0.125	0.86	0.8	0.596			
Time × Cage × Nutrient	5,23	0.871	0.684	0.640	0.744	1.6	0.204			
Time × Block	45,106.0	0.093	1.7	0.019	0.226	0.9	0.600			
Source	df	Tall Turf (>0.5 cm)			Crustose Corallines			Cyanobacteria		
		Wilks λ	<i>F</i>	<i>P</i>	Wilks λ	<i>F</i>	<i>P</i>	Wilks λ	<i>F</i>	<i>P</i>
Between subjects (mean effect over time)										
Cage	1,27	0.127	185.9	<0.001	0.152	151.1	<0.001	0.965	1.0	0.333
Nutrient	1,27	0.933	2.0	0.173	0.872	4.0	0.057	0.909	2.7	0.111
Cage × Nutrient	1,27	0.957	1.2	0.282	0.996	0.1	0.748	0.998	0.1	0.821
Block	9,27	0.761	0.943	0.506	0.846	0.6	0.827	0.649	1.6	0.158
Within subjects (change in effect over time)										
Time	4,24	0.153	33.4	<0.001	0.547	5.0	0.0046	0.353	11.0	<0.001
Time × Cage	4,24	0.295	14.3	<0.001	0.455	7.2	<0.001	0.731	2.2	0.099
Time × Nutrient	4,24	0.769	1.8	0.162	0.916	0.6	0.698	0.695	2.6	0.059
Time × Cage × Nutrient	4,24	0.561	4.7	0.006	0.814	1.4	0.274	0.774	1.8	0.172
Time × Block	36,91.7	0.292	1.0	0.498	0.336	0.9	0.689	0.254	1.1	0.322

Notes: Within each block, “enriched” replicates represent an average between “mid-” and “high-” nutrient enrichment replicates; log-transformation was undertaken for all data to minimize heteroscedasticity and non-normality; any significant interactions are italicized. If interactions included both cage and nutrients, then Tukey–Kramer post hoc tests were performed and results are presented on Fig. 1; rmANOVAs in the top panel utilized data from 6 sampling periods (April–September). rmANOVAs in the bottom panel exclude April data because they were not available

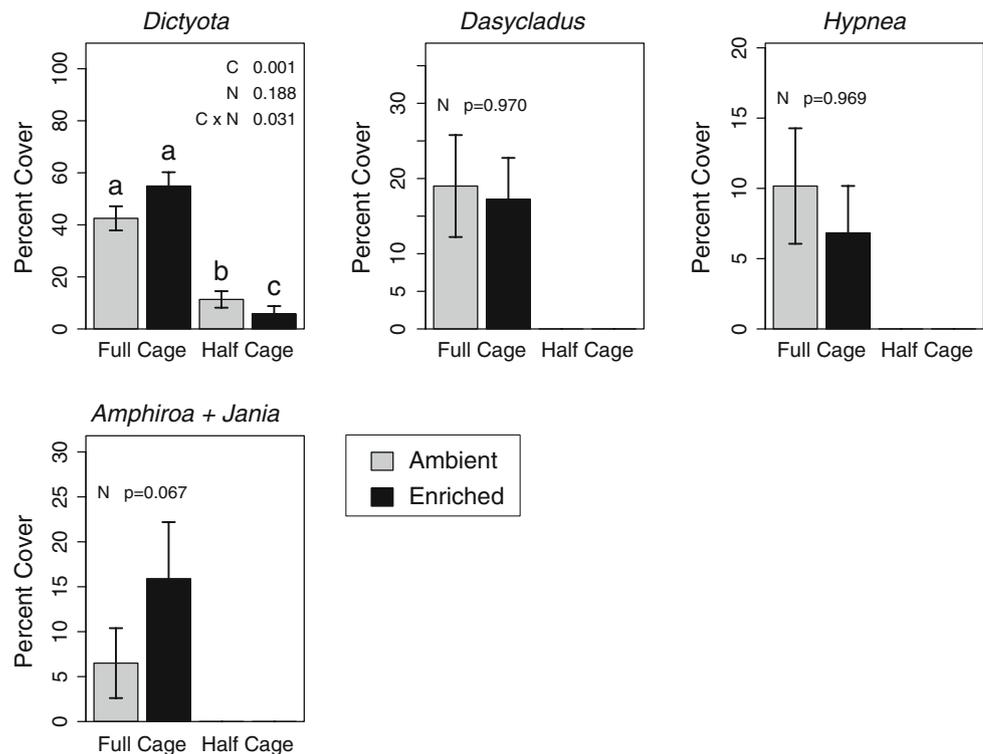
and the direction of the effect (suppression rather than stimulation of macrophytes) was opposite to the change predicted by the RDM (Littler and Littler 1984; Littler et al. 2006a). Our findings of large herbivore effects and only small and interactive nutrient effects on seaweeds is similar to the findings of the majority of other factorial studies conducted on both similar and very different reefs (see reviews by Szmant 2002; Burkepile and Hay 2006; Heck and Valentine 2007), but is at variance with a few studies that detected significant nutrient effects (Smith et al. 2001; Littler et al. 2006a).

Effectiveness of experimental manipulations

This field experiment addresses several of the criticisms (Littler et al. 2006a, 2006b) that have been levied against

several manipulative experiments (e.g., Miller et al. 1999; Thacker et al. 2001; Belliveau and Paul 2002) that detected no direct effect of enrichment on macroalgal proliferation. First, the duration of the experiment was double that of Miller et al. (1999), 9× longer than Littler et al. (2006b), only 25% as long as Littler et al. (2006a), but longer than most studies of this kind. Importantly, it was long enough to detect the competitive transition from thick turfs to macrophytes and for macrophytes to reach about 100% cover in our herbivore exclusion treatments (Fig. 3). Second, we successfully maintained elevated nutrient levels within the experimental unit (Fig. 1) and these nutrients reached macrophytes as indicated by elevated nitrogen levels and lowered C:N ratio within the green seaweed *Dasycladus vermicularis* (Fig. 2). *Dictyota* spp. did not show changes in tissue nutrient content with enrichment.

Fig. 4 The final percent cover (day 142) of common genera of macrophytes that when combined represent 95% of total upright algal cover. As *Dictyota* spp. occurred on all treatment blocks, these were analyzed by a blocked two-way ANOVA. Letters indicate treatments that differed statistically by Tukey–Kramer post hoc tests ($\alpha = 0.05$). Other macrophytes occurred only in full cages and were analyzed using non-parametric Wilcoxon paired sample for the effect of nutrient enrichment in cages only



However, *Dictyota* has shown complex, and sometimes contradictory, responses to nutrients in other experiments as well. When exposed to increased nutrients, it is sometimes unaffected (Delgado and Lapointe 1994), sometimes stimulated (Littler et al. 2006a), and can respond differently depending on its recent physiological history (Beach et al. 2006). Experiments available to date suggest that growth of *Dictyota*, as well as other brown macrophytes, are rarely enhanced by nutrient additions under field conditions (Miller and Hay 1996; Miller et al. 1999; Thacker et al. 2001; McClanahan et al. 2002, 2003, 2007). A lack of response in *Dictyota* could be due to a limited storage capacity characteristic of fast-growing seaweeds (Larned 1998), its tendency in herbivore removal blocks to grow up into the water column where much of its thallus may be beyond the influence of surface-associated nutrient enrichment, or other unknown reasons. Although we did not find a significant direct effect of nutrients on abundance of *Dictyota* or other macrophytes, our nutrient additions did in some way affect these seaweeds as evidenced by a significant ecological interaction between herbivory and nutrients in affecting total macrophytes and cover of *Dictyota* (Figs. 3, 4). This interaction suggests that despite our inability to detect effects of nutrient enrichment on the N or C content of *Dictyota* spp. that the herbivores do detect some effect and appear to feed more heavily on *Dictyota* from enriched than from control treatments.

Our results parallel a similar study conducted on deeper reefs (16–18 m) in the Florida Keys (Burkepile and Hay *in press*). In that study, fishes fed from nutrient-enriched blocks 3–13× more frequently than from control blocks, strongly suggesting that fishes were selectively targeting nutrient-enriched seaweeds. Such selective feeding could explain the significant decrease in macrophytes that occurred in the presence, but not in the absence, of large herbivorous fishes (Fig. 3). Herbivores are commonly nitrogen rather than carbon limited (Mattson 1980), so they should be selected to detect and feed from nutrient-enriched prey, as has been found for seaweeds from mangroves, seagrass beds, coral reefs, and temperate rocky reefs (Boyer et al. 2004; Fong et al. 2006; Heck et al. 2006; Russell and Connell 2007). Nutrient enrichment can also counteract the deterrent effects of algal defenses because defenses that are effective in low quality prey often become ineffective when prey increase in nutritional value (Cruz-Rivera and Hay 2003). Selective herbivory on enriched macrophytes might also explain other reef studies that found suppression, rather than enhancement, of macrophytes when they were fertilized; this seems especially common for chemically defended brown seaweeds (Diaz-Pulido and McCook 2003; McClanahan et al. 2003, 2007).

Littler et al. (2006b) argue that experiments like ours are compromised because of the use of fertilizer stakes, which in their experiments were reported to kill fleshy upright

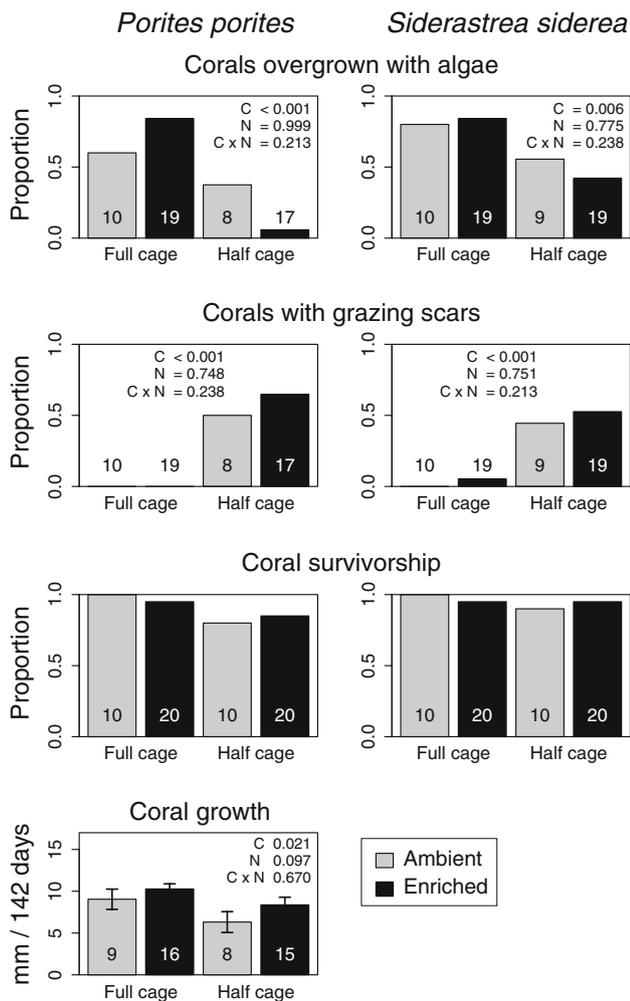


Fig. 5 The effects of herbivore removal and nutrient enrichment on small (<30 cm²) colonies of the corals, *Porites porites* and *Siderastrea siderea* after 142 days. We analyzed the frequency of grazing scars, survivorship, and overgrowth by seaweeds (i.e., seaweeds covering formerly live tissue). We analyzed the growth of *P. porites* using a two-way ANOVA. The slow growth rate of *S. siderea* precluded analysis. Sample sizes are presented within bars

algae and coralline crusts. They inferred that this was due to chlorine in the tree stakes. Our results conflict with those of Littler et al. (2006b) in that both coralline crusts and fleshy seaweeds grew well in the presence of enrichment from fertilizer stakes (Figs. 3, 4). Others using fertilizer stakes also have detected no damaging effects and sometimes have found nutrient enhancement effects (Miller et al. 1999; Smith et al. 2004; Beach et al. 2006). The mention by Littler et al. (2006b) of “chlorine” as a biocide in tree stakes that may kill macrophytes is a confusion of chemical terminology. A discussion with the producers of Jobe’s Tree Stakes (Domestic Fertilizer, Inc. in Paris, Kentucky) suggests some ambiguity of the nutrient labels on their product. The Cl on the label stands for the chloride ion (i.e., Cl⁻), not the strong oxidizing diatomic gas Cl₂ or

the hypochlorite (used in pools as sodium hypochlorite). The fertilizer does not contain these biocides. The chloride ions in the fertilizer come from potassium being added as potassium chloride (a potassium salt just like the sodium salt, sodium chloride, that makes sea water salty). In natural seawater, chloride ions make up 55.03% of total seawater ions (Millero et al. 2008), so the chloride ions in tree stakes are the same as those that dominate natural seawater. Additionally, similar experiments in the Florida Keys using slow-release fertilizer (Osmacote[®], as recommended by Littler et al. 2006b) instead of tree stakes produce similar effects on seaweed community development to those we found here. The algal die-offs reported by Littler et al. (2006b) do not occur in our experiments or those of others using fertilizer tree stakes (Burkepile and Hay in press); perhaps there is a difference between using cinderblocks versus clay pots as substrates, or perhaps their tree stakes were not coated with paraffin to slow rates of delivery.

Finally, measurement of water column nutrients at (Table 1) or near (Miller et al. 1999; Szmant 2002) our sites indicates that our site is not affected by nutrient pollution characteristic of some other Floridean reefs (e.g., eastern shelf of Florida, Lapointe et al. 2005). Nutrients were generally below levels thought to be tipping points (cf. LaPointe 1997) for enhancing macrophyte growth. Consistent with our measurements, Szmant and Forester (1996) found that inshore sources of nutrient pollution are not transported offshore in the Florida Keys.

The primacy of herbivore removal over nutrient availability in macroalgal proliferation

Our data, several previous overviews (Hughes et al. 1999; Szmant 2002; Lesser 2004; Heck and Valentine 2007), and a recent meta-analysis of herbivore and nutrient effects on coral reefs (Burkepile and Hay 2006) all demonstrate the primacy of an abundant and diverse herbivore guild, rather than nutrient limitation, in controlling seaweed abundance on coral reefs. Additionally, there is a long history of virtually all caging or herbivore removal experiments on reefs producing a rapid increase in macroalgal mass following herbivore exclusion, and this happens without nutrient addition (e.g., Stephenson and Searles 1960; Randall 1961; Hay and Taylor 1985; Carpenter 1986; Lewis 1986; Hughes et al. 2007; Burkepile and Hay 2008, in press). Such experiments are necessarily small scale, however, in the very large-scale natural experiment following the ecological extinction of the sea urchin *Diadema antillarum* on Caribbean reefs in the 1980s, macroalgae often bloomed on reefs where *Diadema* had been abundant (Lessios 1988). Also consistent with herbivore control of macroalgae, macrophytes are declining or rare, and coral recruitment is increasing or high in areas where *Diadema* is

recovering (Edmunds and Carpenter 2001; Carpenter and Edmunds 2006) or areas where natural assemblages of reef fishes occur (e.g., Mumby et al. 2006; Harborne et al. 2008; Jackson 2008).

When herbivores are abundant, nutrient additions can decrease rather than increase macrophytes (Figs. 3, 4). This is not a direct effect of nutrient “poisoning” because nutrient-enriched seaweeds grew well on herbivore exclusion treatments. Other studies have also shown trends for nutrient suppression of macrophytes in the presence of herbivores (Miller et al. 1999; Diaz-Pulido and McCook 2003; McClanahan et al. 2003, 2007). This likely occurs due to herbivores selectively targeting more nutritious individuals, as has been documented in other studies (Boyer et al. 2004; Fong et al. 2006; Heck et al. 2006; Russell and Connell 2007).

We suggest that the controversy over top-down versus bottom-up regulation of tropical coral reef macroalgae occurs in part due to an assumption of nutrient limitation of algal growth within generally oligotrophic tropical waters, and due to observations of changing algal and coral abundance in human impacted areas where alterations of herbivore populations, nutrient levels, sediment input, etc. are commonly confounded. While many coral reefs occur in low-nutrient waters, benthic organisms experience naturally occurring fluxes of nutrients that are not anthropogenic in origin (e.g., upwelling; Szmant 2002; Leichter et al. 2003) or may experience nutrient fluxes from macrofaunal excretion, groundwater seeps, remineralized organic matter in reef cavities and sediment patches, and endo-upwelling (Atkinson 1988; Rougerie and Wauthy 1993; Larned and Atkinson 1997; Larned 1998; Szmant 2002). Moreover, even when water column nutrients are low, nutrient levels required for growth can be achieved as long as water motion and turbulence provide an adequate flux of nutrients (Larned and Atkinson 1997). The long history of all herbivore removal studies resulting in macroalgal blooms is a clear indication that nutrients on coral reefs are rarely, if ever, too low to sustain macroalgal growth in the absence of herbivory (e.g., Hay 1997; Hughes et al. 1999; Burkepile and Hay 2006; Heck and Valentine 2007). There are some cases of macroalgae increasing due to nutrient additions alone (Smith et al. 2001; Littler et al. 2006a), but these are unusual relative to the norm (Burkepile and Hay 2006).

Although nutrient additions rarely increase total macrophyte abundance, nutrient additions may affect macroalgal species composition. In our experiment, nutrient enrichment tended to increase the abundance of crustose corallines (mostly in the presence of grazers) and upright corallines (but only with herbivores excluded; $P = 0.057$ and 0.067 , respectively; Figs. 3, 4), suggesting nutrients impact their abundance (e.g., Smith et al. 2001; Littler et al.

2006a). However, for crustose corallines, their increased abundance with nutrient addition could be an indirect effect of enhanced grazing on nutrient-enriched blocks removing upright competitors (Figs. 3, 4) rather than a direct physiological effect of increased nutrients on encrusting corallines. A study paralleling ours but on deeper reefs documented similar patterns—a significant increase in crustose corallines and upright red algae with nutrient addition, but no overall increase in macrophytes (i.e., nutrients affected species composition but not macroalgal cover or biomass). Thus, blooms of specific macroalgal species and shifts in macroalgal community structure may be facilitated by nutrient additions, but nutrient pollution is not required for macroalgal proliferation.

Consequences for coral fitness

Grazing fishes suppressed algal overgrowth of both coral species in our experiments, but also directly grazed both corals, and significantly lowered the net growth of *P. porites* (Fig. 5). Previous investigators have shown that herbivorous fishes prevent algal overgrowth and competitive suppression of corals (Lewis 1986; Jompa and McCook 2002), but several also show that algal-consuming fishes may consume and kill some coral species (Littler et al. 1989; Miller and Hay 1998; Rotjan and Lewis 2005). The balance of these positive (removing algal competitors) and negative (direct consumption) effects of fishes on corals likely varies as a function of coral species, herbivore species, algal versus coral growth rates and competitive abilities, and the environmental context in which the interactions occur (Littler et al. 1989; Bellwood and Choat 1990; Miller and Hay 1998; Stachowicz and Hay 1999; Hay et al. 2004).

Restoration implication

There remains little doubt that for most reefs worldwide, the loss of large herbivorous fishes and urchins has allowed macroalgal blooms and impeded the recovery of coral-dominated reefs (Jackson et al. 2001; Mumby et al. 2007; Jackson 2008). Restoration of reefs depends on our ability to minimize the threats that are manageable by humans (e.g., over-fishing, habitat destruction, pollution), so that reefs develop resiliency to less manageable threats (e.g., a warmer, saltier, and more acidified ocean) (Bellwood et al. 2004; Hoegh-Guldberg et al. 2007; Hughes et al. 2007; Jackson 2008). Anthropogenic nutrient pollution is a manageable threat which should be addressed because of its detrimental effects in some locations. However, evidence to date indicates that its influence on tropical coral reefs is limited compared to the effects of overharvesting herbivores (Hughes et al. 1999; Szmant 2002; Burkepile

and Hay 2006; Heck and Valentine 2007). Given the limited resources and time afforded managers of coral reefs and given the overwhelming evidence that large herbivores limit macroalgal blooms, maintaining a healthy food web (e.g., Mumby et al. 2006; Hughes et al. 2007) and diverse herbivore guild (Mumby et al. 2007; Burkepille and Hay 2008) should be among the highest priorities for coral reef restoration.

Acknowledgements This research was supported by the Teasley Endowment to Georgia Tech with supplemental support from the University of North Carolina, Wilmington National Undersea Research Center (to MEH) and NSF grant OCE-0550245 (to ES). We thank S. Bullard, G. Cetrulo, E.H. Hay, K. Hay, A. Hollebhone, and C. Kicklighter for help with field work. This represents Grice Publication number 343.

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