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Nutrient versus herbivore control of macroalgal community development and coral growth on a Caribbean reef

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ABSTRACT: Coral reefs are in global decline, with seaweeds replacing corals as spatial dominants. Overfishing of herbivores, anthropogenic eutrophication, and interactions between these factors have been postulated as causes, but long-term tests of these factors are uncommon. We factorially manipulated herbivorous fishes and nutrients at a depth of 16 to 18 m for 7 to 10 mo in 2 experiments over 2 yr. Herbivore exclusion increased algal cover by about 4 to 10×, algal biomass by 4 to 6×, and suppressed cover of crustose coralline algae by 80 to 100%. Nutrient enrichment had no effect on the cover or mass of upright algae, but altered species composition by suppressing cyanobacteria and facilitating red macroalgae in the absence of herbivores. Nutrient addition increased macroalgal species richness in the absence, but not the presence of herbivores. Feeding by herbivorous fishes increased by 3 to 13× on nutrient-enriched vs. control plots. This herbivory facilitated cover of crustose coralline algae, demonstrated that herbivores selectively target more nutritional prey, and suggested that herbivores could suppress macrophyte accumulation at sites with increased nutrient availability. Effects of fishes and nutrients on corals varied as a function of coral species. For the branching coral *Porites porites*, 56% of individuals exposed to fishes were completely consumed; however, individuals that survived grew 60 to 80% more in the presence of fishes. For *Porites astreoides*, exposure to fishes did not affect mortality, but increased net growth by 3 to 4 times. For this coral, nutrient addition decreased growth when exposed to fishes but not when protected from fishes, suggesting that fishes may have fed more on nutrient-enriched corals.

KEY WORDS: Eutrophication · Overfishing · Parrotfish · Selective grazing · Surgeonfish · Plant–herbivore interactions

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INTRODUCTION

Anthropogenic impacts to natural communities are pervasive in marine ecosystems, where humans alter consumer pressure by selectively harvesting higher trophic levels (Jackson et al. 2001) and alter productivity by increasing nutrients (Smith et al. 1999). Dramatic changes in community structure often follow alterations of top-down and bottom-up forces (Valiela et al. 1997, Steneck et al. 2004, Myers et al. 2007), making it critical to understand how changes to these forces cascade through marine ecosystems. Because changes to biotic and abiotic forces may not have equivalent effects, are not mutually exclusive, and can act synergistically (Worm et al. 2002, Burkepile & Hay 2006), it is important to identify the relative effects of decreasing consumers and increasing nutrients, as well as when and where these impacts interact to affect community organization.

Coral reefs are at high risk to anthropogenic impacts and are undergoing unprecedented declines due to stressors such as climate change, overfishing, disease,

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and eutrophication (Hughes et al. 2003, Jackson 2008). These stressors appear particularly acute on reefs in the Caribbean Sea where corals have undergone dramatic declines in recent decades (Gardner et al. 2003, Mora 2008). Increases in nutrients and decreases in herbivory are often emphasized as primary drivers of changes in community structure and ecosystem function on reefs (Littler & Littler 1984, Lapointe 1997, Hughes et al. 1999). Altering these top-down and bottom-up forces can lead to increased macroalgal growth (Burkepile & Hay 2006) which can negatively impact the survival, growth, and recruitment of corals as well as increase the prevalence of coral diseases (Lewis 1986, Nugues et al. 2004, Hughes et al. 2007). Ultimately, alterations to consumer pressure and primary productivity may act synergistically to reduce reef resilience and increase the probability that global-scale forces such as climate change and ocean acidification will drive reefs to alternate states, such as algal domination (Bellwood et al. 2004, Anthony et al. 2008).

Although a number of experiments have addressed the interactions of herbivory and nutrient availability in determining algal abundance on coral reefs (reviewed by Burkepile & Hay 2006), few experiments were conducted for more than a few weeks or months, few were conducted on deeper reefs, and fewer still addressed how alterations to herbivore pressure and nutrient availability cascaded to affect coral survivorship and growth. Additionally, few experiments to date have addressed how changes in local nutrient levels may affect herbivore feeding patterns and, thus, the benthic community. Here, we report the results of two 7 to 10 mo experiments addressing how herbivore exclusion and nutrient addition interact to affect primary succession of the algal community and growth of the corals *Porites porites* and *P. astreoides* on reefs at a depth of 16 to 18 m in the Florida Keys, Florida, USA.

MATERIALS AND METHODS

Experimental setup and maintenance. We tested the effects of herbivore exclusion, nutrient enrichment, and their interaction on algal community development at a depth of 16 to 18 m on Conch Reef (24° 57′ N, 80° 27′ W) in the Florida Keys. Conch Reef is a fringing reef approximately 8 km southeast of Key Largo. It is located within a Special Protection Area within the Florida Keys National Marine Sanctuary where all fishing has been prohibited since 1997. The reef is a spur and groove formation that is dominated by upright macroalgae (30 to 40% cover, mostly *Dictyota* spp. with lesser amounts of *Lobophora variegata* and *Halimeda* spp.), filamentous turf algae (~25% cover), and crustose coralline algae (20 to 25% cover) (Table A1). Live coral cover is 6 to 7%, with sponges and gorgonians each occupying 5 to 7% cover.

As part of a larger experiment, we excluded large herbivorous fishes by constructing 2 × 2 × 1 m tall cages (n = 8) using 2.5 cm wire mesh (see Burkepile & Hay 2008 for details of cage construction and placement). Mesh of this size has little impact on algal community development, coral growth, sedimentation rates, or bulk water flow (Miller et al. 1999, Smith et al. 2001, Burkepile & Hay 2007). Adjacent uncaged areas of 4 m^2 (n = 8) served as controls. We did not include open-sided control cages because previous experiments indicated that these produced artifacts by attracting predators (e.g. jacks, grouper, snapper) that sheltered in or among the open-sided cages and may have altered the density or behavior of herbivorous fishes using these treatments (M. E. Hay pers. obs.). Larger herbivores at this site were parrotfishes in the genera *Sparisoma* and *Scarus* and surgeonfishes in the genus *Acanthurus*. We quantified the abundance of parrotfishes and surgeonfishes within seven 50 × 2 m belt transects. Transects were laid out on the reef parallel to the spur and groove reef formation. As we slowly swam each transect, we counted all parrotfish and surgeonfish that were >5 cm in total length. The abundance of the sea urchin *Diadema antillarum* was not quantified, but in 2 yr of extensive day and night diving we saw <10 individuals at the study site and never observed *D. antillarum* in our uncaged experimental plots.

Cinderblocks (~10 × 20 × 40 cm) were used as substrate for the development of algal communities because they are easily anchored to the reef with metal spikes, are readily colonized by the same algae that colonize quarried coral blocks, and can be used to provide a slow diffusion of nutrients onto their surface (Miller et al. 1999). The 2 parallel chambers that run the length of each cinderblock were sealed on one end with cement; the other end was sealed with a removable plug of closed cell foam. Fertilizer was placed in each of the chambers where it diffused through the block and became available to algae on the block surface (Miller et al. 1999). Cinderblocks were placed in opposite corners on one side of each caged or uncaged replicate and randomly assigned to either the nutrient enrichment or control treatment. For the enrichment treatment, 100 ± 10 g of Osmocote® (19:6:12, N:P:K) slow-release garden fertilizer in a mesh pouch (L'eggs Knee Highs©) was placed in each of the 2 chambers. Osmocote was replaced every 23 to 40 d to ensure continuous delivery of nutrients. Our enrichment treatment was not intended to achieve a specific level of nutrients around the cinderblock as nutrients vary depending on changes in flow and turbulence (Miller et al. 1999); the treatment was instead intended to pro-

duce local increases in nutrients in order to evaluate the effects of elevated nutrients on algal growth under field conditions.

Effectiveness of the nutrient enrichment was assessed by (1) measuring dissolved inorganic nitrogen (DIN) and soluble reactive phosphorous (SRP) in water collected from the tops of enriched versus control blocks, and (2) measuring C, N, and P content of the macroalga *Dasycladus vermicularis* collected from enriched versus control blocks in exclusion cages. For water samples, divers used 60 ml syringes to slowly draw water from the surface of either the control or enriched cinderblock. Water samples were also taken from inside block chambers to determine if the fertilizer was still releasing nutrients. Immediately after collection, samples were filtered (GF/F) into acid-washed bottles, placed on ice, returned to the laboratory, and frozen until analyzed for inorganic nutrient concentrations (Miller et al. 1999). DIN (ammonium and nitrite + nitrate) and SRP concentrations were determined via an autoanalyzer. The data were analyzed using a paired *t*-test. We also sampled ambient water column nutrients from 1 m off the benthos using the same methods. For the green macroalga *D. vermicularis* collected at the end of the experiment, concentrations of C, N, and P were analyzed at the Stable Isotope/Soil Biology Laboratory at the University of Georgia Institute of Ecology (www.uga.edu/~sisbl/). We then calculated C:N and C:P ratios and compared these for enriched and control treatments via *t*-tests.

The Year 1 experiment ran from November 2003 until August 2004 when all cinderblocks were brought to the surface, scraped of all algae, and all algal mass sorted and weighed. Cinderblocks were then soaked in a chlorine bleach solution for ~30 min, scrubbed with a brush to remove any remaining organisms, soaked in fresh water, and then stored dry for 10 wk before reuse in Year 2. The cage mesh was also removed to allow herbivorous fishes to graze the benthic areas and remove any treatment artifacts from the experiment in Year 1. In November 2004, we set up the Year 2 experiment using the same design and cage locations as in Year 1. This experiment ran from November 2004 until July 2005 when surge from Hurricane Dennis destroyed the cages. However, all data presented for Year 2 were collected in June 2005 while the treatments were intact.

Quantifying algal community development. Every 11 to 14 wk, we identified the algae under each of 100 points within a 15 × 30 cm quadrat that was placed over each cinderblock. Algae were identified to the lowest taxonomic level possible in the field, but we lumped algae into genera or morphological groups when species-level identification was problematic (e.g. short [<0.5 cm] algal turf, tall [>0.5 cm] algal turf, crustose coralline algae) or when individual species were relatively rare but could be placed into algal functional groups (i.e. Littler & Littler 1980, Steneck & Dethier 1994). At the end of the Year 1 experiment, cinderblocks were wrapped individually in plastic bags, brought to the surface, and lightly scraped with a paint scraper to remove algal biomass (except for crustose coralline algae). Algae were sorted to species or genus and then dried at 60°C to a constant weight. Hurricane Charley passed within 150 km of our field site 2 wk before biomass data were gathered so some poorly attached algae such as mats of tall filamentous algae were dislodged from the cinderblocks via wave action. Thus these data on biomass primarily represent the mass of better-attached upright macroalgae. Data on biomass from Year 2 were not gathered due to Hurricane Dennis destroying our cages.

To determine how larger herbivores and nutrient enrichment affected percent cover of algae, data were analyzed by repeated measures, split-plot, 2-factor ANOVA for total cover of upright algae and for cover of different algal groups on cinderblocks in the uncaged versus exclosure treatments. For Year 1, we performed statistical analyses on percent cover data from July 2004 (8 mo after initiation, before Hurricane Charley passed near our site) because cover data from the final sampling period in August 2004, after Hurricane Charley, may have underrepresented algal species and functional groups that were susceptible to dislodgment by wave motion. Total upright algal cover was defined as the cover of all upright macroalgae, cyanobacteria, and tall (>0.5 cm) filamentous algae because these growth forms can competitively suppress coral growth and increase coral mortality (Nugues & Roberts 2003, Box & Mumby 2007). We excluded crustose coralline algae and short (<0.5 cm) turfs from total upright algal cover because these low-growing forms were unlikely to affect corals in the size classes used in our experiment even though they can harm newly settled coral larvae and juvenile corals (Birrell et al. 2008). Total upright algae differs than upright macroalgae, which includes the cover of only larger macrophytes (e.g. *Dictyota* spp., *Dasycladus vermicularis*, *Kallymenia westii*) and not small, filamentous turf algae. To test for nutrient enrichment effects, cover or biomass of algae at the final sampling period of Year 1 was analyzed using either split-plot, 2-factor ANOVA (for macroalgae like *Dictyota* spp. that occurred in all treatments) or paired *t*-tests (for macroalgae such as *Dasycladus vermicularis* that occurred only in herbivore exclusion cages). To analyze macroalgal species richness from final percent cover data, we used split-plot, 2-factor ANOVA. Macroalgal species richness data include only those species that were identifiable in the field and do not include algal turf or crustose coralline species that

require careful laboratory analyses for species identification. Data were rank or log transformed when necessary to alleviate heterogeneity of variance.

Fish feeding on cinderblock treatments. To determine if nutrient enrichment affected feeding by herbivorous fishes, we videotaped each pair of uncaged cinderblocks to quantify feeding on enrichment versus control treatments. Two video cameras were set up simultaneously at each treatment pair. One camera taped the control and one the enriched block within that pair. The cameras were cycled through each of the 8 treatment–control pairs, videotaping each block pair for 1.25 to 2 h between 10:00 and 15:00 h when herbivory is typically the most intense. Videotapes were scored for the identity of fish and number of bites each fish took from the cinderblocks. These assessments were conducted in May 2004 (Year 1) and May and June 2005 (Year 2). Feeding assessments were conducted 6 wk after the last nutrient addition in Year 1 and 5 wk after the last nutrient addition in Year 2. We tested for differences in overall bite rates and bites per feeding foray between control and enriched cinderblocks using paired *t*-tests. We defined a feeding foray as a fish entering the frame of the videotape and taking at least one bite from the cinderblock. The foray ended when the fish left the video frame.

Effects of treatments on coral growth. To evaluate the effect of nutrient enrichment and herbivory on coral growth, one small individual of the massive coral *Porites astreoides* (~70 to 80 mm diameter individual) and one individual of the branching coral *P. porites* (~80 to 90 mm branches) were attached to each cinderblock using underwater epoxy at the initiation of Year 1. *P. astreoides* individuals were collected whole from the benthos while *P. porites* branches were removed from larger colonies. To create a benchmark from which to measure coral growth at the end of the experiment, coral pieces were incubated in clear plastic bags *in situ* for 7 h per day over 2 d with seawater and alizarin red (~20 mg l^{-1}). During incubation, alizarin red is incorporated into the coral skeleton and produces a band of color from which to measure growth. At the conclusion of the experiment, remaining corals were collected and sectioned with a diamond saw. *P. porites* was sectioned down the growth axis (i.e. from base to tip of the branch), and we measured linear extension of the skeleton (i.e. increase in branch length) as the length of coral skeleton distal to the alizarin red band. *P. astreoides* was sectioned down the vertical axis of the midpoint of each colony, and we measured the increase in thickness of the skeleton at the apex of the skeleton. Corals were not transplanted to cinderblocks in Year 2. Corals, particularly *P. porites*, were frequently missing from the uncaged cinderblocks (apparently consumed by fishes); we used Fisher's exact test to determine whether mortality differed between control and herbivore exclusion treatments. We used a 2-factor ANOVA to assess treatment effects on the growth of corals that survived until the end of the experiment. Unlike previous analyses, we did not use a split-plot ANOVA, as corals often remained on only one block out of a pair of blocks making the split-plot analysis inappropriate.

RESULTS

Abundance of herbivorous fishes

Larger herbivorous fishes averaged 15.5 ± 4.3 individuals 100 m^{-2} on Conch Reef. *Sparisoma aurofrenatum* was the most abundant parrotfish with *Sparisoma viride* being the other common species from the genus (Fig. 1). *Scarus taeniopterus* and *Scarus iserti* were similar in abundance while large *Scarus* spp. (*S. guacamaia*, *S. vetula*, *S. coeruleus*, and *S. colestinus*) were rare. *Acanthurus bahianus* was the dominant surgeonfish with *A. coeruleus* and *A. chirurgus* being less common.

Measuring effectiveness of nutrient enrichment

Nutrient concentrations at the surface of enriched cinderblocks were significantly higher than those above control blocks on Day 23 but not on Day 40 fol-

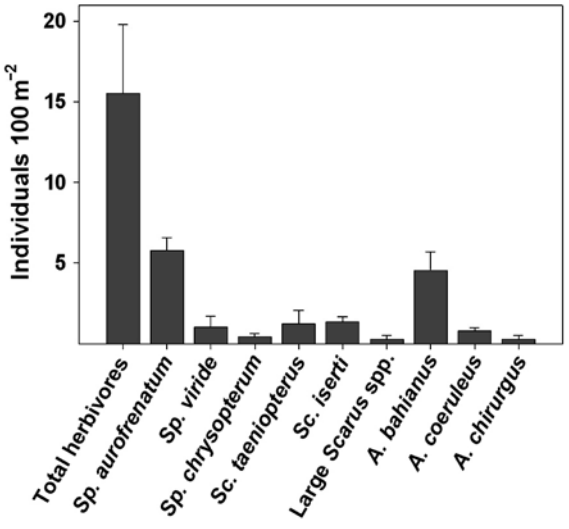

Fig. 1. Abundance of adult parrotfishes and surgeonfishes (mean ± SE) at Conch Reef. *Sp.* = *Sparisoma*, *Sc.* = *Scarus*, *A.* = *Acanthurus*. Large *Scarus* spp. include *Scarus guacamaia*, *Sc. vetula*, *Sc. coeruleus*, and *Sc. colestinus*. n = 7, 50 × 2 m transects

lowing fertilizer addition (Fig. 2). On Day 40 the DIN levels of enrichment blocks were about the same as those from Day 23, but the DIN levels of control blocks had risen by about 4× compared to Day 23. SRP levels above enriched blocks were somewhat lower on Day 40 than Day 23, but levels above control blocks appeared to have risen slightly. The smaller sample sizes of measurements on Day 40 (5 as opposed to 8, due to a laboratory mishap) may have constrained our statistical power to detect a difference. Nutrients had not been depleted by Day 40 as they were still high within the block chambers; mean SRP and DIN within treatment blocks were 275.1 ± 127.3 and 7928.0 ± 3272.9 µM, respectively, while levels in control blocks were 0.03 ± 0.02 and 4.6 ± 0.5 µM. Ambient water column nutrients (1 m above the benthos) were similar to those from the control blocks for both SRP (0.01 ± 0.01 µM and 0.02 ± 0.01 µM for post-23 day and post-40 day sampling periods, respectively) and DIN (0.53 ± 0.16 µM and 2.37 ± 0.44 µM for post-23 day and post-40 day sampling periods, respectively). Further, *Dasycladus vermicularis* growing on enriched blocks were encountering and incorporating these elevated nutrients. When collected at the end of the experiment, individuals from enrichment blocks inside herbivore exclosures were significantly enriched in N and P relative to those from control blocks (C:N for control vs. enriched was 23.1 ± 0.8 vs. 21.5 ± 0.9, respectively, df = 7, p = 0.035; C:P ratios were 224.0 ± 10.2 vs. 173.6 ± 10.2, respectively, df = 7, p < 0.001; *t*-tests).

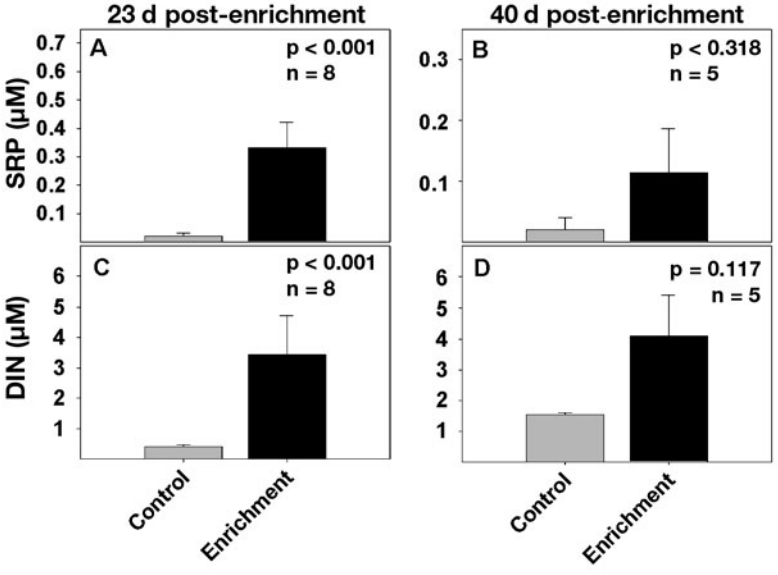

Fig. 2. Nutrient concentrations (mean ± SE) in seawater at the surface of nutrient enrichment and control cinderblocks for (A, B) soluble reactive phosphorus (SRP) and (C, D) dissolved inorganic nitrogen (DIN) at Days 23 and 40 after addition of nutrients to the interior of cinderblocks. p-values are from paired *t*-tests. Note differences in n between Days 23 and 40

Effects of herbivore removal vs. nutrient enrichment

In Year 1, herbivore exclusion enhanced the abundance of total upright algae, tall (>0.5 cm) turfs, and upright macrophytes, decreased the abundance of crustose coralline alga and short turfs, and had no effect on cyanobacteria (see Figs. 3 & 5, Table 1). Nutrient enrichment suppressed cyanobacterial abundance but increased the cover of crustose corallines, and did so dramatically in the presence of herbivores (Fig. 3). Most upright macroalgae, particularly *Dasycladus vermicularis*, *Codium* spp., and red macroalgal species (mainly *Kallymenia westii* and *Laurencia* spp.) were present only in the absence of herbivores (Figs. 3D & 4, Table A2). In herbivore exclosures, nutrient enrichment enhanced red macroalgae but had no effect on other macrophytes (Fig. 4). There ap-

Table 1. Results from split-plot, repeated measures, 2-factor ANOVAs for algal percent cover values from Year 1. Significant effects (p < 0.05) are highlighted in **bold**

Effect	df	Total algal cover		Algal turf >0.5 cm		Cyanobacteria		Upright macroalgae		Algal turf <0.5 cm		Crustose coralline algae	
		F	p	*F*	p	*F*	p	*F*	p	*F*	p	*F*	p
Herbivore (H)	1,14	396.81	**<0.001**	45.48	**<0.001**	0.04	0.854	24.59	**<0.001**	252.81	**<0.001**	29.55	**<0.001**
Enrichment (E)	1,70	3.48	0.066	0.36	0.55	4.71	**0.033**	0.02	0.888	0.05	0.829	35.92	**<0.001**
H × E	1,70	0.04	0.84	0.32	0.574	1.38	0.244	0.01	0.99	2.46	0.122	26.16	**<0.001**
Time (T)	2,70	33.27	**<0.001**	1.65	0.199	17.63	**<0.001**	18.84	**<0.001**	27.31	**<0.001**	1.73	0.185
T × H	2,70	5.23	**0.008**	1.69	0.192	2.96	0.058	16.6	**<0.001**	1.95	0.15	3.31	**0.042**
T × E	2,70	0.42	0.66	1.48	0.235	2.91	0.061	2.76	0.071	0.58	0.565	5.16	**0.008**
T × H × E	2,70	0.66	0.521	1.99	0.145	1.52	0.225	1.99	0.145	0.24	0.788	3.8	**0.027**

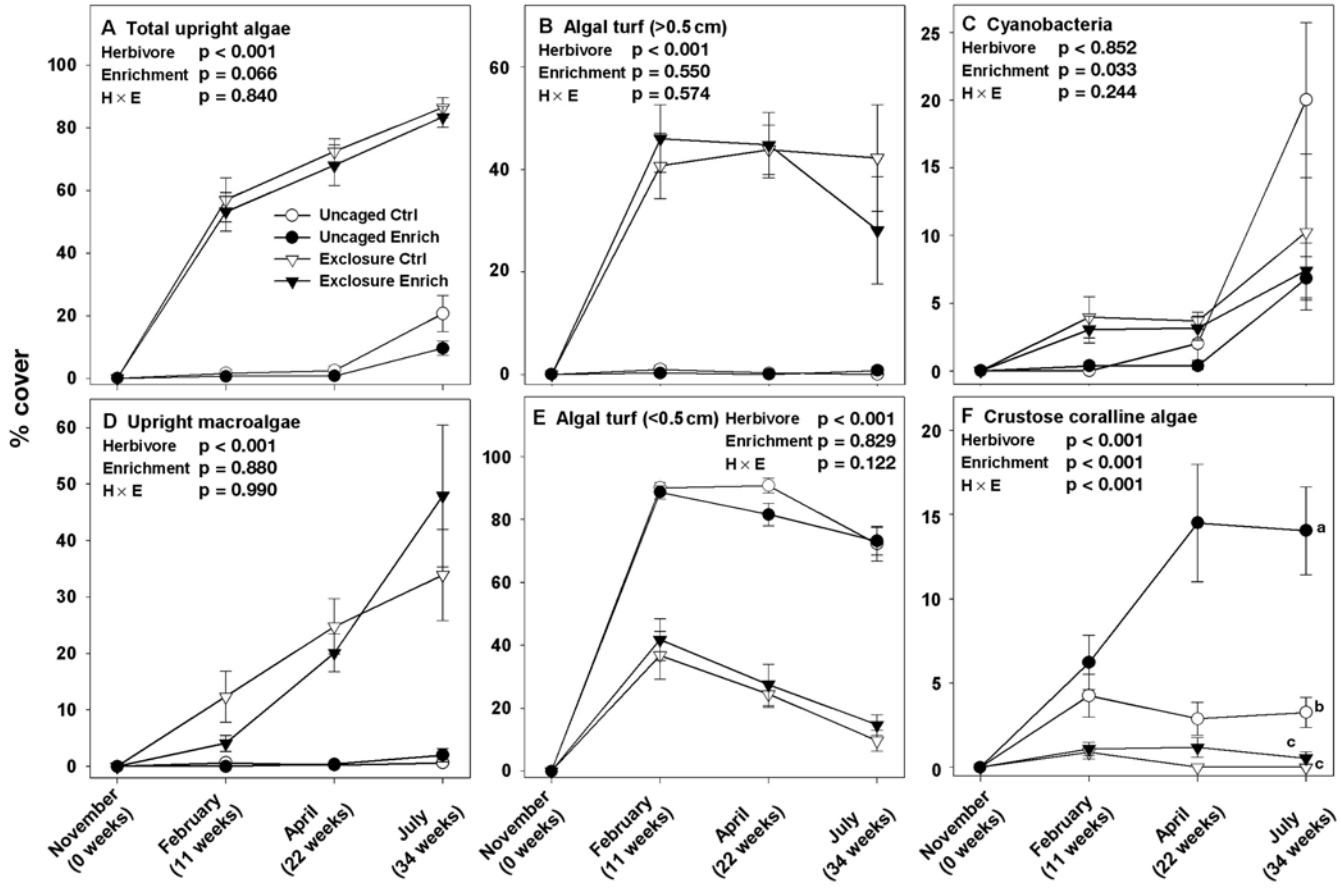

Fig. 3. Percent cover (mean ± SE) of (A) total upright algae and (B–F) common algal types on control and enriched cinderblocks in uncaged and exclosure treatments over the course of Year 1 (duration was 10 mo; n = 8). p-values are from split-plot, repeated-measures ANOVA. See Table 1 for full ANOVA table. Letters in F designate significant groupings via Tukey's multiple comparison test for final sampling period. Note different scales on y-axes

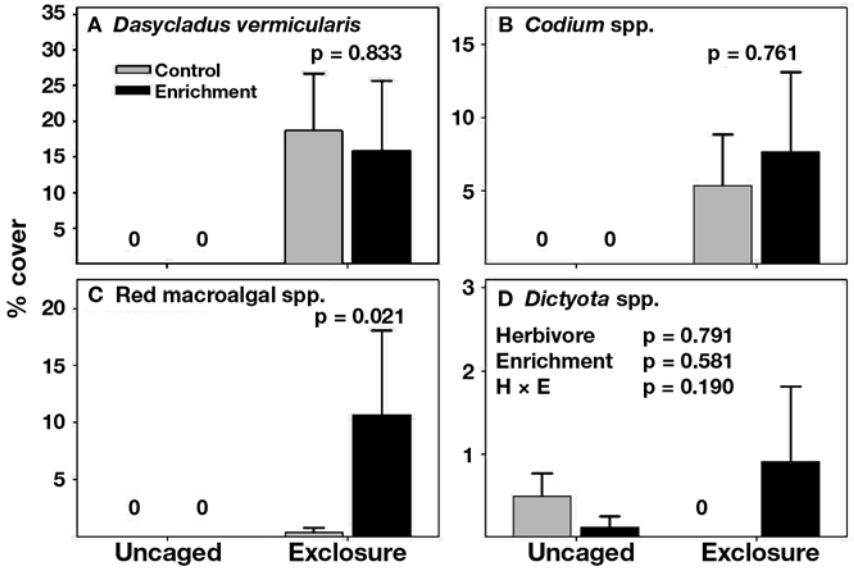

Fig. 4. Percent cover (mean ± SE) of macroalgal species or groups comprising >1% cover on some treatments during July 2004 of Year 1 on control and enriched cinderblocks in uncaged and exclosure treatments (n = 8). *Dictyota* spp. data were analyzed by a split-plot, 2-factor ANOVA. The remaining 3 macroalgae were found only in herbivore exclusion cages, so data from within cages were analyzed for the effect of nutrient enrichment only using paired *t*-tests. 0: zero cover

peared to be little seasonality in the algal communities as the patterns in the experimental treatments developed early and maintained similar trajectories over the course of the experiment. At the end of the experiment, total algal biomass had increased by 4 times due to herbivore exclusion (p = 0.001), but nutrient addition had no effect on algal biomass (p = 0.572; Fig. 5). Data on biomass for *D. vermicularis*, *Codium* spp., and red macroalgae showed similar patterns to data for percent cover: all 3 algae were absent in the presence of herbivores and red macroalgae was facilitated by nutrients in the absence, but not in the presence of herbivores (Fig. 5). For macroalgal species richness, there were significant herbivore exclusion (p < 0.001) and herbivore exclusion × nutrient enrichment effects (p = 0.05), with nutrients increasing species richness in the absence of her-

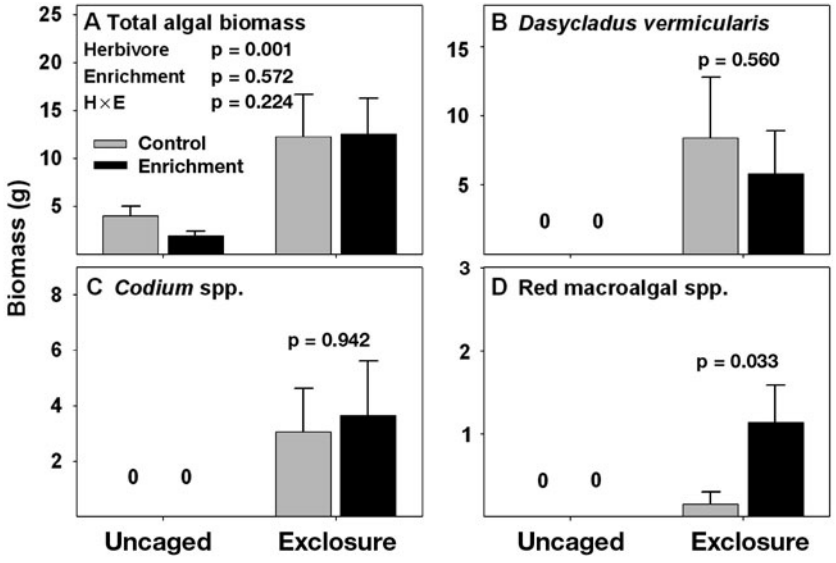

Fig. 5. Biomass (mean ± SE) of (A) total algae or (B–D) macroalgal species or groups for Year 1 in August 2004 after 10 mo comparing control and enriched cinderblocks in uncaged and exclosure treatments (n = 8). p-values are from (A) split-plot, 2-factor ANOVA or (B–D) paired *t*-tests as in Fig. 4. 0: zero biomass

bivores but not in the presence of herbivores (Fig. 6A). There was also a significant herbivore × nutrient interaction for crustose corallines (Fig. 3F) due to nutrients dramatically increasing coralline cover in the presence of herbivores, but only slightly, if at all, when herbivores were excluded.

Fishes increased their grazing on blocks enriched with nutrients. In Year 1, bite rates on nutrient-enriched blocks were 3 times those on control blocks (Fig. 7A); in Year 2, grazing increased by 9.8× in May (Fig. 7B) and 1.9× in June (372.7 ± 187.0 vs. 198.9 ± 88.5 bites min^{-1} on enriched vs. unenriched blocks, respectively; n = 8, p = 0.038). In both years, much of this grazing was due to bites by parrotfishes in the genus *Scarus*.

Nine of the 16 *Porites porites* and 3 of the *P. astreoides* were missing from open blocks. Basal portions of *P. porites* remained in the epoxy on the cinderblocks, suggesting that these corals had been consumed by parrotfishes—a common occurrence for some species of *Porites* (Miller & Hay 1998, Rotjan & Lewis 2005). Inside cages, there were only 3 coral deaths (all *P. astreoides*), and these individuals were all still in place on the blocks. Mortality was significantly higher (p = 0.006) in the open than in fish exclosures for *P. porites* but not for *P. astreoides* (Fig. 8A,B). Considering only corals surviving on cinderblocks at the end of the experiment, herbivore exclusion suppressed growth of *P. porites* by 40%, while nutrient enrichment had no effect (Fig. 8C). For *P. astreoides*, there were significant effects of herbivores, nutrients, and the interaction between herbivory and nutrient enrichment on *P. astreoides* growth (Fig. 8D). Growth of individuals in herbivore exclusions was suppressed by 60 to 80% relative to those in uncaged areas. Nutrient effects were not detectable with fishes excluded, but nutrients suppressed net coral growth with fishes present (Fig. 8D).

In Year 2, herbivore exclusion significantly enhanced cover of total upright algae and tall turfs, but suppressed short turfs and crustose coralline algae; cover of upright macroalgae and cyanobacteria were not significantly affected (Fig. 9, Table 2). Nutrient enrichment had no effect on most algae but did enhance crustose coralline algae, with the effect being large in the presence of herbivores (cover increased from about 7 to 18%) but undetectable in their absence. There was a significant herbivore × enrichment interaction for the cover of short turf algae (Fig. 9E), with nutrient addition tending to increase cover in herbivore exclusions and decrease cover where fishes could graze. Neither herbivory nor

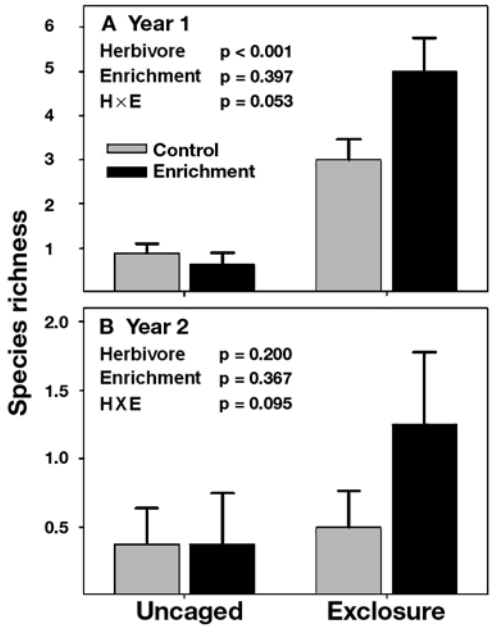

Fig. 6. Macroalgal species richness for (A) Year 1 in July 2004 and (B) Year 2 in June 2005 (n = 8). p-values are from split-plot, 2-factor ANOVA

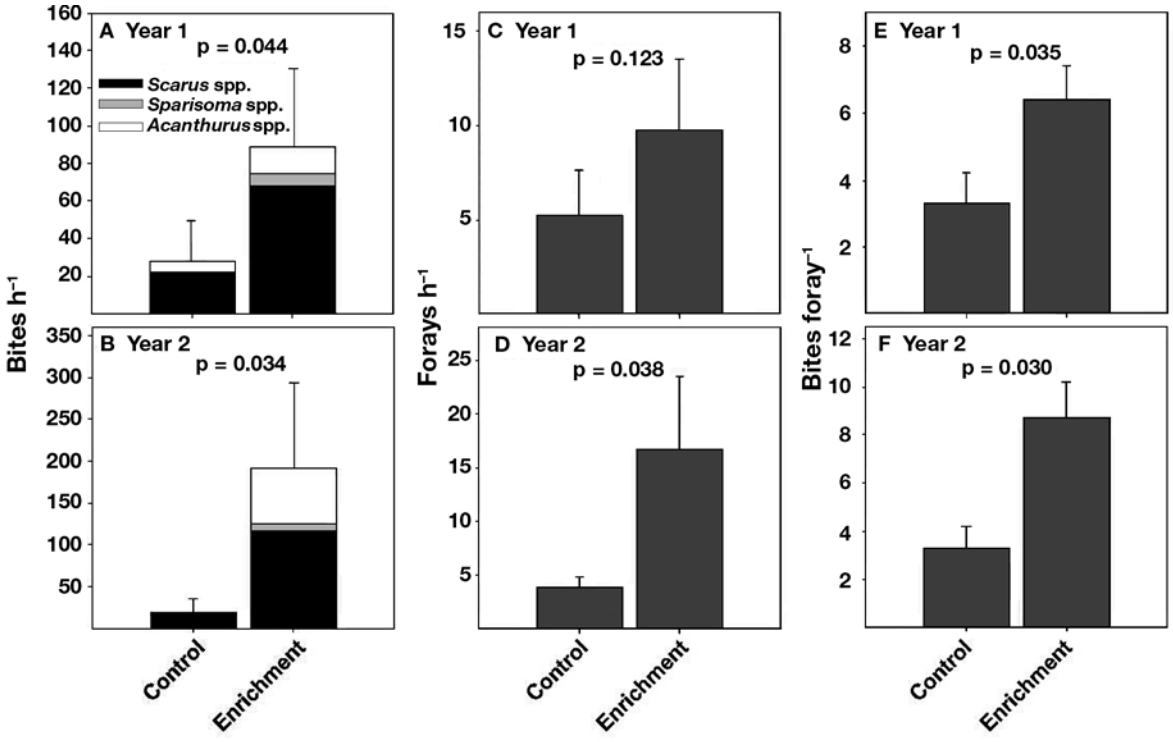

Fig. 7. Bites per hour, forays per hour, and bites per foray by herbivorous fishes (mean + SE) on control and enriched cinderblocks in (A,C,E) Year 1 during May 2004 and (B,D,F) Year 2 during May 2005. (A, B) bars represent SE for overall mean bite rates; p-values are from paired *t*-tests; tests for A & B are on overall bite rates (n = 8). (C–F) represents combined results for all fishes

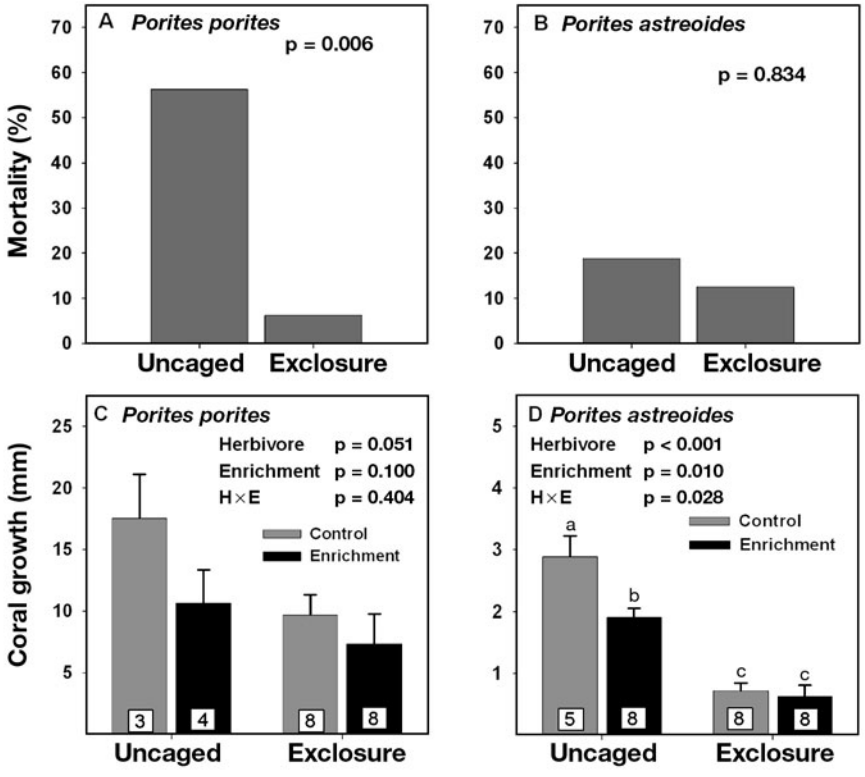

Fig. 8. *Porites porites* and *P. astreoides*. Year 1 (A,B) mortality of the corals *P. porites* and *P. astreoides* in caged vs. uncaged areas (n = 16) and (C,D) growth (mean ± SE) of *P. porites* or *P. astreoides* on control and enriched cinderblocks in uncaged or exclosure treatments for corals that remained at the end of the experiment (n given in inset). Data are from August 2004. p-values are from (A,B) Fisher's exact test and (C,D) 2-factor ANOVA. Letters in (D) designate significant groupings via Tukey's mutiple comparison test

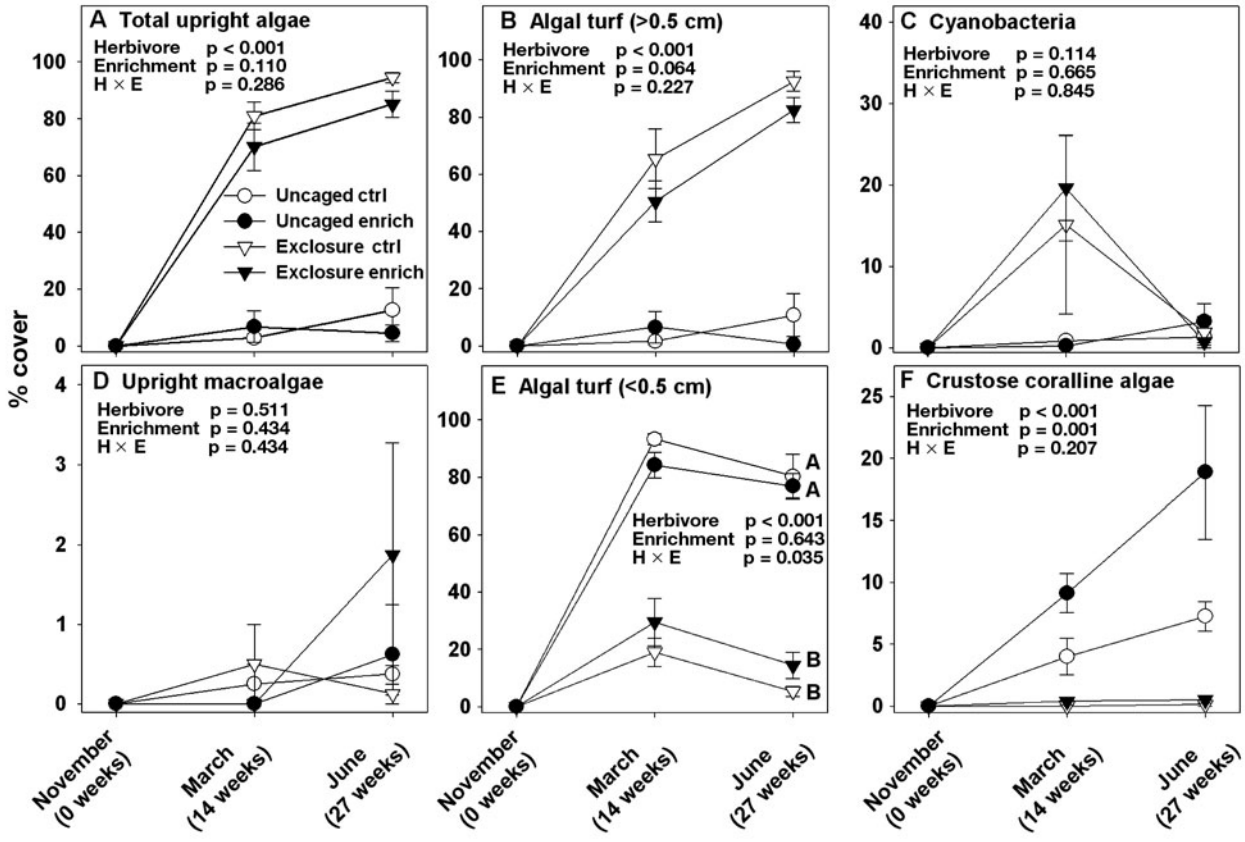

Fig. 9. Percent cover (mean ± SE) of algal groups on control and enriched cinderblocks in uncaged and exclosure treatments over the course of the experiment for Year 2 (duration was 7 mo). n = 8 for each treatment. p-values are from split-plot, repeated-measures ANOVA; see Table 2 for full ANOVA table. Letters designate significant groupings via Tukey's multiple comparison tests for final sampling period. Note different scales on y-axes

Table 2. Results from split-plot, repeated measures, 2-factor ANOVAs for algal percent cover values from Year 2. Significant effects ($p < 0.05$) are highlighted in **bold**

Effect	df	Total algal cover		Algal turf >0.5 cm		Cyanobacteria		Upright macroalgae		Algal turf <0.5 cm		Crustose coralline algae	
		F	p	*F*	p	*F*	p	*F*	p	*F*	p	*F*	p
Herbivore (H)	1,14	413.29	**<0.001**	206.43	**<0.001**	2.84	0.114	0.46	0.51	323.35	**<0.001**	158.03	**<0.001**
Enrichment (E)	1,70	2.66	0.11	3.62	0.064	0.19	0.665	0.62	0.434	0.22	0.643	12.8	**0.001**
H × E	1,70	1.17	0.286	1.5	0.227	0.04	0.845	0.62	0.434	4.73	**0.035**	1.64	0.207
Time (T)	2,70	5.76	**0.021**	15.31	**<0.001**	7.41	**0.009**	2.02	0.162	11.04	**0.002**	0.01	0.99
T × H	2,70	2	0.164	12.39	**0.001**	11.48	**0.002**	0.22	0.638	0.33	0.572	0.56	0.46
T × E	2,70	0.51	0.479	0.42	0.523	0.09	0.763	3.02	0.09	0.08	0.778	0.7	0.409
T × H × E	2,70	0.82	0.371	1.58	0.216	0.61	0.44	1.22	0.271	0.23	0.636	0.39	0.267

nutrients affected macroalgal species richness in Year 2 (Fig. 6B), but there was a trend ($p = 0.095$) towards a herbivore × enrichment interaction, with nutrients tending to increase richness in the absence of herbivores but not in their presence, as was the case for Year 1.

DISCUSSION

The relative roles of herbivore loss versus eutrophication in determining algal abundance on reefs comprise a long-running debate in coral reef ecology (Lapointe 1997, Hughes et al. 1999, Burkepile & Hay

2006, Littler et al. 2006). The relative dominance model (Littler & Littler 1984), which predicts the responses of coral reef communities to varying levels of herbivory and nutrient availability, suggests that lowering herbivore pressure will yield increases in turf algae but that increased nutrient inputs are required for upright macroalgae to proliferate. Although some studies support this prediction (Smith et al. 2001, Littler et al. 2006), the present study and others do not (e.g. Miller et al. 1999, Thacker et al. 2001, Diaz-Pulido & McCook 2003, McClanahan et al. 2003). Both turf algae and upright macroalgae increased due to herbivore exclusion (>50× in relative cover for each algal type), but did so without nutrient enrichment (Figs. 3B,D & 9B). Nutrient addition did increase the cover (Fig. 4C) and biomass (Fig. 5D) of red macrophytes when herbivores were excluded and tended to increase the species richness of macrophytes when herbivores were excluded ($p = 0.053$ and 0.096, respectively; Fig. 6). But enrichment did not increase overall abundance of upright algae, upright macroalgae, or either category of turf algae (Figs. 3, 5A & 9). The proliferation of algae in herbivore exclosures, either with or without nutrient additions, was associated with a 30 to 80% reduction in growth of surviving corals as compared to areas where herbivores were present. Our data reinforce the finding that herbivory is a major driver of algal abundance and coral–algal competition on reefs, with nutrient availability playing a lesser role (Burkepile & Hay 2006). However, nutrient increases can interact with herbivore pressure to change algal community composition.

Given that nutrients should enhance and herbivores suppress algal abundance, one might expect significant herbivore–nutrient interactions in determining overall primary producer abundance. However, these interactions have been surprisingly rare across diverse ecosystem types (Burkepile & Hay 2006, Gruner et al. 2008), and we could detect no interaction between nutrients and herbivores in driving overall algal abundance. One potential explanation is that nutrient limitation at our field site is reduced because internal bores periodically bring nutrient rich waters onto the reef (Leichter et al. 2003). However, internal bores likely did not suppress the effects of experimental nutrient enrichment because (1) these internal bores are seasonal, not year-round (Leichter et al. 2003); (2) algae do experience nutrient limitation at this site (Smith et al. 2004, Beach et al. 2006); (3) *Dasycladus vermicularis* from our fertilized blocks contained higher concentrations of N and P than individuals from control blocks, (4) the same pattern of minimal effects of nutrient enrichment occurred on shallower sites that would infrequently experience nutrients from internal bores (Miller et al. 1999, Sotka & Hay 2009); (5) we documented significant effects of nutrient enrichment on algal community composition, as has been seen in other studies (Miller & Hay 1996, Smith et al. 2001, Thacker et al. 2001, Worm et al. 2002, McClanahan et al. 2003); and (6) findings from the present study are consistent with those from studies conducted in many other tropical locations (Burkepile & Hay 2006).

In contrast to effects on other algal groups, nutrient enrichment consistently interacted with herbivory to facilitate cover of crustose coralline algae (Figs. 3F & 9F). In Year 1, nutrient addition increased crustose coralline algae by a significant 5 times in the presence of herbivores, but had no significant stimulatory effect when herbivores were excluded (Fig. 3F). In Year 2, there was also a significant nutrient × herbivore interaction with nutrients increasing crustose coralline algae by ~3 times in the presence of herbivores, but having little effect when they were excluded (Fig. 9F). Other experiments on coral reefs show similar effects (Smith et al. 2001, Littler et al. 2006, Furman & Heck 2008). Although increasing nutrients has been suggested to directly facilitate crustose coralline algae (Littler & Littler 1984, Smith et al. 2001), these algae should rarely experience nutrient limitation given their slow growth rates and location within the benthic boundary layer where they may be enriched by nutrients excreted from boring sponges and other benthic invertebrates. The mechanism driving increases in crustose coralline algae may be the indirect effect of nutrients increasing herbivory by 3 to 10 times (Fig. 8) rather than the direct effects of nutrients increasing algal growth. *Scarus* spp. parrotfish in particular, which focus their feeding on algal turf communities (McAfee & Morgan 1996, Burkepile & Hay 2008), appear to facilitate crustose coralline algae, as they were responsible for approximately 70% of the feeding on the enriched cinderblocks (Fig. 8). Thus, the suppression of cyanobacteria (Fig. 3C) and the trend for suppression of total upright algae (Figs. 3A & 9A) and tall algal turf (Fig. 9B) by nutrient additions could be due to increased herbivory on enriched algal tissues (Fig. 8). This intense herbivory can enhance coralline crusts by removing their less herbivore-tolerant competitors (Steneck & Dethier 1994, Littler et al. 1995). Increased herbivory on nutrient-enriched treatments is not surprising given that herbivores are commonly N- rather than energy-limited (Mattson 1980) and that other experiments with herbivorous fishes have shown more rapid feeding on macrophytes that have been nutrient-enriched (Boyer et al. 2004, Fong et al. 2006, Furman & Heck 2008). Nutrient enrichment also could counteract the deterrent effects of algal defenses; defenses that are effective in low quality prey often become ineffective when prey increase in nutritional value (Cruz-Rivera & Hay

2003). Herbivorous fishes focusing their feeding on enriched macrophytes might also explain other reef studies that found suppression, rather than enhancement, of macrophytes when they were fertilized (Diaz-Pulido & McCook 2003, McClanahan et al. 2003, Furman & Heck 2008, Sotka & Hay 2009).

Nutrient enrichment not only affected abundance of crustose coralline algae, but also suppressed cyanobacteria (especially in the presence of herbivores) and facilitated red macroalgae in the absence of herbivores, but not in their presence (Figs. 3, 4 & 9), as also occurs on temperate reefs (Miller & Hay 1996). Enrichment also increased macroalgal species richness in the absence of herbivores (Fig. 6). This result is surprising as increased nutrients in the absence of herbivores lowers species diversity in many systems (Worm et al. 2002), as has been shown in a similar experiment on a reef in Belize (McClanahan et al. 2003). One mechanism potentially driving the increase in species richness may be the presence of 3 different sources of nutrients in our fertilizer: ammonium (NH_4^+), nitrate (NO_3^-), and phosphate (PO_4^-). Different algal species have different thresholds for absorbing and utilizing different nutrient sources (Pedersen & Borum 1997). The differential abilities of algal species to uptake nutrients can increase macroalgal diversity (Bracken & Nielsen 2004), and higher algal diversity can increase the total rates of N uptake (Bracken & Stachowicz 2006).

Our experiment is the first factorial herbivore removal–nutrient addition experiment conducted on a deeper (>7 m) reef in the Caribbean. Because shallower reefs typically have more herbivorous fishes and increased grazing rates, one might expect the impact of herbivores to decrease with depth, but this will depend on the relative changes in herbivory vs. algal production over depth (see Hay 1985). However, our results for this reef at 16 to 18 m deep are consistent with those from similar experiments on shallow fore-reefs in the Florida Keys (Miller et al. 1999, Sotka & Hay 2009) and shallow back-reefs in Belize (McClanahan et al. 2003, Littler et al. 2006). Although all factorial herbivore–nutrient manipulations show consistent top-down effects of herbivores (reviewed by Burkepile & Hay 2006), there are interesting patterns among studies when comparing the effects of nutrient enrichment across depths. For experiments performed on the shallowest reefs (<2 m), many showed significant effects of nutrient enrichment on total algal abundance or on algal community structure (Hatcher & Larkum 1983, Thacker et al. 2001, McClanahan et al. 2003, Littler et al. 2006). However, with the exception of Smith et al. (2001), experiments on deeper reefs (6 to 18 m) showed minimal effects of nutrient enrichment on overall algal abundance and only moderate effects on community structure (Miller et al. 1999, Belliveau & Paul 2002, Diaz-Pulido & McCook 2003, Sotka & Hay 2009, present study). If these apparent differences are real, they could result from interactions between internal bores lessening nutrient limitation at depth (Smith et al. 2004) and high light in shallow areas allowing macrophytes to take full advantage of nutrient enrichment and grow rapidly. Given that nutrients stimulated the cover of red macroalgae (Fig. 5D) but not any other upright algal group, even *Dasycladus vermicularis* which showed significant uptake of more N and P, our experiments suggest possible interactions between light, nutrient availability, and species identity in determining how algal communities respond to these factorial herbivore removal–nutrient addition experiments.

The Florida Keys represent one of the few areas in the Caribbean where fishing is concentrated on omnivorous and carnivorous, but not on herbivorous fishes (Ault et al. 1998). All the published factorial experiments examining herbivory–nutrient interactions on Caribbean reefs have been conducted in the Florida Keys and Belize (Miller et al. 1999, McClanahan et al. 2003, Littler et al. 2006, Sotka & Hay 2009), two Caribbean areas that have retained relatively high herbivore abundance (Newman et al. 2006). Despite the abundance of herbivores in the Florida Keys, macroalgae covered ~30 to 40% of the benthos at our field site, possibly due to recent declines in coral cover as a result of disease outbreaks, coral bleaching, and hurricanes (Aronson & Precht 2006). Thus, with declining coral cover, herbivore pressure is diluted (Williams et al. 2001) and macroalgae have more area to colonize. Yet our experiments show that herbivores still exert strong top-down control on macroalgae. Further, when we quantified changes in the natural benthic community inside herbivore exclosures vs. in open areas, cover of upright macroalgae increased by 65% and biomass by 150% when herbivores were excluded (D. E. Burkepile & M. E. Hay unpubl. data). Herbivores affected not only algal abundance but also the species present (Burkepile & Hay 2008), suggesting that herbivores still have a strong top-down influence on the abundance, community structure, and succession of macroalgae even on reefs with relatively high initial macroalgal cover.

Although herbivorous fishes can facilitate corals by removing algal competitors, parrotfishes in particular also directly prey on corals (Littler et al. 1989, Rotjan & Lewis 2006). In the present study, effects of larger fishes on corals varied as a function of *Porites* species. When exposed to fishes, 56% of our *Porties porites* transplants were consumed, as occurs on other Caribbean reefs (Miller & Hay 1998). In contrast, only 1 of 16 *P. porites* died in exclosures, and its skeleton was still in place rather than having been consumed.

However, there was a tradeoff between escaping predation and maximizing growth for *P. porites*; individuals in herbivore exclosures escaped direct predation, but grew 40% slower than those that survived in uncaged areas. This pattern is in contrast to that shown on a shallow reef in the Florida Keys where *P. porites* grew more slowly in areas exposed to herbivores than in herbivore exclosures, apparently due to direct grazing from parrotfishes (Sotka & Hay 2009), which tend to be more abundant on shallower reefs (Lewis & Wainwright 1985). In contrast to *P. porites*, the mounding coral *P. astreoides* experienced only 19% mortality when exposed to fishes, and this was not significantly higher than that for *P. astreoides* protected from fishes (12%). However, corals were missing in the open treatments and dead in-place in the caged treatments. Further, in open treatments, fishes enhanced the growth of *P. astreoides* by approximately 60 to 80% via removal of algal competitors. Nutrient enrichment suppressed growth by 34% when herbivores were present but had no effect when herbivores were absent (Fig. 8D). Littler et al. (2006) showed a similar pattern for *P. astreoides* and *Siderastrea radians* in Belize, where the corals grew slower in the enriched vs. ambient conditions in the presence of herbivores. These findings are consistent with the relative dominance model which suggests that corals are disadvantaged by high nutrient concentrations (Littler & Littler 1984). However, increased predation on the nutrient-enriched corals, rather than direct suppression of coral growth, could explain these patterns. Since parrotfishes fed more frequently on enriched cinderblocks in our experiment and most corals in uncaged areas showed grazing scars characteristic of parrotfishes (Rotjan & Lewis 2005, 2008), fishes may have been feeding more intensely from the corals on enriched blocks, thus slowing their net growth. Further, enrichment slowed coral growth in open areas but not in herbivore exclosures, suggesting that herbivores may have played a direct role in suppressing growth of corals on enriched cinderblocks. Overall, results from field experiments have been variable regarding the effects of nutrient enrichment on corals; studies have documented no effect (Jompa & McCook 2002), negative effects (Koop et al. 2001, Littler et al. 2006), and even trends of a positive effect (Sotka & Hay 2009).

Our results agree with previous studies showing that excluding herbivores consistently enhances algal abundance and indirectly suppresses coral growth via algal competition; the effect of nutrient enrichment on both seaweeds and corals is more variable but is consistently moderate compared to effects of herbivore exclusion (Miller & Hay 1996, 1998, Miller et al. 1999, Diaz-Pulido & McCook 2003, McClanahan et al. 2003). Further, selective grazing of algae growing in nutrient hot-spots suggests that herbivores can ameliorate the negative effects of eutrophication and provide resilience to marine ecosystems, supporting recent verbal models (Bellwood et al. 2004) and meta-analyses (Burkepile & Hay 2006). However, these small-scale patterns might not scale up; our enriched cinderblocks were small, enriched islands against a large, less enriched background. Fishes that have broad home ranges (Mumby & Wabnitz 2002) could amass and focus on these small, enriched areas in ways that may not be possible if enrichment occurs on the large spatial scale at which some algal blooms have been documented (Smith et al. 2005, Fong et al. 2006). Thus large-scale eutrophication of reefs (on the km^2 scale) might generate different patterns that cannot ethically be produced experimentally. As a possible example, in the tropical Eastern Pacific, upwelling of nutrient-rich waters appear to be an important contributor to algal blooms on coral reefs (Fong et al. 2006), even in the presence of fairly stable herbivore populations (Glynn 2004). However, these upwelling events lower water temperatures and this considerably decreases grazing rates of herbivorous fishes (Smith 2008), thus confounding increases in nutrients and decreases in herbivore feeding rates. One of the important future challenges for reef ecology and management is to expand the temporal and spatial scales at which herbivore–nutrient interactions are investigated so as to better predict reef trajectories and enhance reef recovery in the face of increasing anthropogenic stressors.

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Appendix 1. Table A1. Percent cover (mean ± SEM) of different groups on the benthos at Conch Reef at the beginning of the experiments for Year 1 (November 2003) and Year 2 (November 2004). Cover values were obtained by identifying organisms under 50 points in 80 haphazardly placed 1.5 × 0.75 m quadrats

Benthic group	Percent cover	
	Year 1	Year 2
Total upright macroalgae	28.0 ± 1.1	42.5 ± 1.5
Dictyota spp.	24.7 ± 1.2	34.8 ± 1.3
Halimeda tuna	0.3 ± 0.2	1.6 ± 0.2
Lobophora variegata	3.0 ± 0.4	4.3 ± 0.6
Turf algae	25.6 ± 1.0	24.6 ± 0.8
Cyanobacteria	0.2 ± 0.1	0.5 ± 0.1
Crustose coralline algae	25.0 ± 1.0	21.5 ± 0.9
Sponges	6.0 ± 0.9	5.5 ± 0.6
Gorgonians	6.8 ± 0.6	6.1 ± 0.6
Corals	6.5 ± 0.7	5.5 ± 0.5

Table A2. Species list of algae present on cinderblocks over the course of the experiment. The species list includes predominantly upright macroalgae as the majority of the filamentous turf algae and crustose coralline algae were not identified to species. +: present; –: absent

Algal species	Year 1	Year 2
Phaeophyta		
Dictyota menstrualis	+	+
Dictyota pulchella	+	+
Lobophora variegata	+	+
Sargassum hystrix	+	–
Dictyopteris sp.	+	–
Ectocarpus elachistaeformis	–	+
Chlorophyta		
Caulerpa racemosa	+	–
Codium taylorii	+	+
Codium repens	+	–
Dasycladus vermicularis	+	–
Halimeda tuna	+	–
Neomeris annulata	+	–
Rhodophyta		
Amphiroa fragillisima	+	–
Amphiroa tribulis	+	–
Coelothrix irregularis	+	+
Digenia simplex	+	+
Jania adhaerens	+	+
Kallymenia westii	+	+
Laurencia sp.	–	+
Laurencia sp. 1	+	–
Laurencia sp. 2	+	–
Unidentified red alga	+	–
Cyanobacteria		
Lyngbia sp.	+	+
Schizothrix sp.	+	+

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