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Effects of nutrients versus herbivores on reef algae: A new method for manipulating nutrients on coral reefs

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Abstract

There has been much discussion and some controversy regarding the role of nutrient enrichment versus other factors, such as altered rates of herbivory, in the degradation of coral reef ecosystems. The resolution of this controversy has been hampered by the lack of manipulative field studies testing the effects of ecologically relevant levels of nutrient enrichment on coral reef communities. We present a new method for adding ecologically relevant levels of nutrients to experimental substrates on coral reefs. The method elevates nutrients for sustained periods of time (>41 d without replenishment of nutrients) and allows for testing interactions of nutrients and altered levels of herbivory. Results from an offshore reef in Key Largo, Florida, show strong effects of excluding large herbivorous fishes, negligible effects of nutrient enrichment—or effects that are opposite of predictions, and no interaction between nutrient levels and herbivory in affecting algal abundance. Patterns observed for this reef did not confirm predictions of previously proposed models that frondose macroalgal or crustose algal abundance would be enhanced with nutrient enrichment or that dominance of filamentous turfs would be greater in unenriched conditions. In contrast to previous predictions, the abundance of larger macroalgae at this site was not increased by elevating nutrients above predicted threshold response levels of 1.0 μM for total inorganic nitrogen or 0.10 μM for soluble reactive phosphate. Also conflicting with some models, filamentous, nitrogen-fixing cyanobacteria were enhanced, rather than suppressed, by nutrient enrichment.

There is considerable concern among scientists and conservationists regarding the degradation of coral reef com-

munities, supposedly attributable to anthropogenic nutrient enrichment (e.g., Bell 1992; Dubinsky and Stambler 1996; Lapointe 1997). However, most of the studies addressing nutrient effects on coral reefs are observational, comparing sites that are apparently more versus less impacted or a single site observed over a time course of nutrient disturbance (e.g., Tomascik and Sander 1987; Littler et al. 1991; Wittenberg and Hunte 1992; Genin et al. 1995). Observational studies of such sites are valuable but run the risk of being confounded by other factors that vary between the sites being compared or by multiple types of anthropogenic and natural disturbances. The best-known case study of macroalgal blooms killing reefs, presumably due to eutrophication, is that of Kaneohe Bay, Hawaii in the 1970s and early 1980s (Smith

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et al. 1981). However, even in this case, there have been multiple and persistent modes of human impact other than nutrient addition (Hunter and Evans 1994). The potential role of other ecological factors such as grazing in controlling macroalgal standing stock in Kaneohe Bay had not been addressed until recently (Stimson et al. 1996). Recent transplant studies (McCook 1996) provide a good example of how reasonable suppositions that remain untested can lead to incomplete understanding. Although the striking cross-shelf gradients in macroalgal distribution on Australia's Great Barrier Reef had long been presumed to result from differences in nutrient levels and other aspects of water quality, McCook's investigation indicated that they could instead be explained by variation in herbivory and macroalgal recruitment rates.

There are few manipulative field studies testing the effects of nutrient enrichment on coral reef communities (notable exceptions include Hatcher and Larkum [1983] and the ENCORE studies discussed below). The ambiguity of most correlative studies and the rarity of controlled field manipulations have led to considerable controversy regarding the actual degree of reef degradation attributable to nutrient enrichment in many regions, including the Florida Keys. For example, from review of these observational studies, some authors have hypothesized that there are threshold levels of nutrient concentrations (proposed to be 1 μM dissolved inorganic nitrogen and 0.1 μM soluble reactive phosphorus) for tropical coral reefs that, if exceeded, will yield macroalgal blooms and the loss of a coral-dominated reef (Bell 1992; Lapointe 1997). Other authors have suggested that, given the great diversity of nutrient regimes in which tropical coral reefs have developed and the importance of other ecological factors in structuring coral reefs, the notion of a universal nutrient threshold for tropical coral reefs is untenable (Szmant 1997; Hughes et al. 1999).

Degradation of reefs in the Florida Keys has been documented by several recent studies (Dustan and Halas 1987; Porter and Meier 1992). Some studies suggested that water column nutrients were elevated along the Florida reef tract due to anthropogenic inputs from sewage contamination of groundwater and phosphate mining in western Florida and argued that these nutrient inputs were coincident with eutrophic reef degradation (Lapointe et al. 1990, 1993). However, other studies found no evidence that anthropogenic nutrients reached the offshore areas where reef degradation has been observed (Szmant and Forrester 1996). The presence of a variety of other disturbances on Florida reefs resulting from a latitudinally marginal climate (Walker et al. 1982; Burns 1985), repeated incidence of coral diseases and bleaching (e.g., Fitt et al. 1993; Richardson et al. 1998; M. W. Miller pers. obs.), and a trophic structure disrupted by fishing (Ault et al. 1998) make nutrification unlikely as a univariate, independent cause of reef decline.

The overall lack of experimental evidence regarding nutrient effects on reef communities is largely due to the significant logistical challenge of performing sustained nutrient manipulations in the open ocean. One high-tech solution to this challenge has been implemented by the ENCORE project underway at One Tree Island in Australia's Great Barrier Reef (Larkum and Steven 1994). The presence of natural

mini-atoll reef structures in the lagoon allowed daily enrichment of the water column inside these atolls during low tide periods via computer-controlled addition of nutrient stock solutions by robots. Preliminary reports indicate that no effects of enrichment have been found on epilithic algal communities (Larkum and Koop 1997). These investigators suggest that the paradigm of nutrient limitation of reef algal communities may need adjustment and that inorganic carbon limitation may be more important to algal turf communities in highly productive reef environments. Other ENCORE results include significant nutrient inhibition of coral larval settlement (Ward and Harrison 1997), and variable nutrient effects on coral calcification with some species showing phosphorus inhibition (Hoegh-Guldberg et al. 1997) while others display enhanced skeletal growth in treatments with elevated phosphorus (Steven and Broadbent 1997). The overall weakness of responses to nutrient enrichment has prompted a doubling of the treatment intensities in the later stages of the ENCORE project.

Other, less expensive means for conducting nutrient enrichment treatments in the field have included less extensive nutrient pulse treatments (e.g., Lapointe 1987; Miller and Hay 1996) and various types of nutrient-leaching substrates such as porous clay flower pots containing commercial fertilizer (Hatcher and Larkum 1983), agar-based nutrient suspensions (Fairchild et al. 1985; Tate 1990), or coated time-release commercial fertilizer (M. M. Littler, D. S. Littler, and J. S. Feingold, pers. comm.). While pulsed delivery of nutrients may be an ecologically relevant method of delivery (as via episodic upwelling or excretion by passing fish), the time scales and intensities of such natural phenomena are often neither known nor duplicable. Also, human-delivered pulse treatments can be labor intensive and difficult to maintain over extended periods of time or during periods of rough weather. Diffusing methods have the advantage of operating in the experimenter's absence but also have proven problematic in that treatment levels (i.e., nutrients emitted from the diffusing substrate) may decline exponentially over time (Tate 1990; M. W. Miller pers. obs.).

The major community-level mechanism by which nutrient enrichment degrades coral reefs involves alteration of competition between slow-growing corals and potentially faster-growing seaweeds (Lewis 1986; Hughes 1994). The growth rates of reef seaweeds are believed to be constrained by nutrient limitation, thereby preventing seaweeds from overgrowing and killing corals under oligotrophic conditions typical of tropical reefs (Birkeland 1988; Littler et al. 1991; Lapointe 1997). Another important factor in this balance of coral/seaweed competition is the high rate at which seaweeds are consumed by abundant and diverse coral reef herbivores (Carpenter 1986; Lewis 1986; Hay 1991). More than a decade ago, Littler and Littler (1984) recognized the interdependence, complexity and context-specific nature of factors determining coral reef community structure and proposed the relative dominance model to predict changes in reef communities as a function of interactions between herbivory and nutrient levels. Despite the potential importance of this model for reef conservation, management, and ecology, its clear predictions (Fig. 1) remain largely untested by controlled experiments.

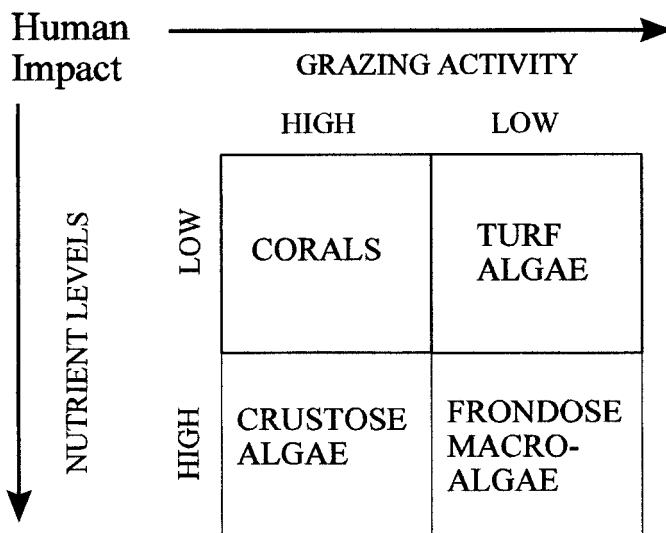


Fig. 1. Depiction of the relative dominance model of Littler et al. (1991; modified from Littler and Littler 1984). "Potentially predominant space-occupying groups of photosynthetic reef organisms are emphasized as a function of long-term nutrient levels and disturbance by herbivores. . . (M)acroalgae are posited as potential dominants on reefs where macronutrient levels are elevated. Grazing is considered the more important direct controller of algal standing stocks on undisturbed reefs, whereas nutrients set the potential upper limits to biomass" (Littler et al. 1991).

In this paper, we describe a new adaptation of the nutrient-diffusing substrate approach to achieve experimental nutrient enrichment in the field. We also give results of a 4-month application of this method in a two-way factorial field experiment examining the interactive effects of nutrient enrichment and grazing reduction on a coral reef algal community in Key Largo, Florida. Specifically, we assessed the effects of ecologically relevant levels of nutrient enrichment on the abundance of benthic algae subjected to different grazing regimes. We compare our findings with those predicted by the relative dominance model (Littler and Littler 1984; Fig. 1) and the threshold model (Bell 1992; Lapointe 1997).

Methods

Enrichment methods and documentation—Cinder blocks were used as the experimental unit and as the substrate from which nutrients would be diffused (see Fig. 2). The cinder blocks (~10 cm × 20 cm × 40 cm) had three openings running the width of the block. Quick-setting concrete was used to plug one end of each opening, creating a chamber with one open end. One commercial fertilizer spike, 80% of whose surface was coated with parafin to slow dissolution, was placed in each of the two outermost chambers. A removable piece of dense, open cell foam was used to plug the open end of each chamber. Two 9.5-mm holes were drilled through the upper surface of each outer block chamber to facilitate diffusion of nutrients from the chambers to an experimental substrate that was attached to the top of each cinder block. This experimental substrate consisted of a slab

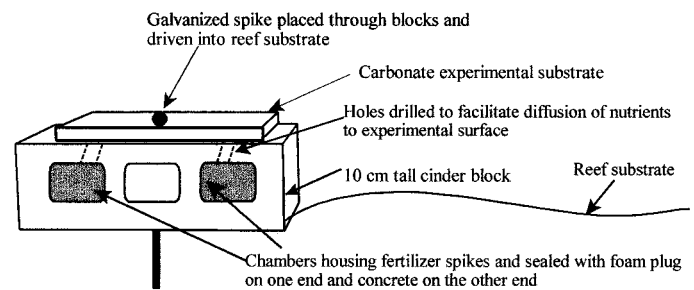


Fig. 2. Illustration of a nutrient addition experimental unit. Un-enriched (nutrient control) treatments were identical but did not have fertilizer spikes placed in the two outer chambers of the cinder block. In each group of four treatments, one enriched and one control block was completely caged by 2.5-cm mesh while one enriched and one control block were enclosed in a similar tubular cage with the two ends left open to allow access by larger herbivores.

of quarried pleistocene coral rock (15.3 cm wide × 30 cm long × 2.3 cm tall) placed on the top of each cinder block. We monitored algal recruitment and growth on this slab. We used this coral rock in order to mimic natural reef substrates more closely than the cinder block material. This same sort of quarried reef rock is used in coral reef restoration projects (e.g., following ship groundings) by the Florida Keys National Marine Sanctuary. Evaluation of these substrates at the grounding site of the *M/V Elpis* (about 10 km from the study site) at 3 yr after deployment shows a well-developed algal community including turf, macroalgal, and crustose components, and a high (relative to natural reef substrates) density of scleractinian coral recruits (Miller and Barimo, submitted).

Thus, the added nutrients were diffusing through the cinder block chamber with the aid of holes drilled in the top of the cinder block, but nutrients then had to diffuse around or through the 2-cm thickness of the calcium carbonate substrate. The block-slab unit was fastened to the reef with a large galvanized spike driven through a 1.3-cm hole drilled through the center of the cinder block and the carbonate slab.

New fertilizer spikes (either Jobes tree spikes, Weatherly Consumer Products; or tree food stakes, Domestic Fertilizer) were added to the enrichment chambers approximately monthly (see Table 1). The potassium in these fertilizer stakes was in the form of a chloride salt, so chloride ions would also have been added with our treatment. However, the salt that gives seawater its taste is sodium chloride, so chloride ions normally constitute more than 50% of natural seawater ions (Gross 1987). We assume that the small amount added with the fertilizer stakes would have had no detectable effects on community development.

A total of four sets of water samples (on days 1, 9, 24, and 41 after replacement of fertilizer spikes) were collected and analyzed to assess the degree and persistence of nutrient enrichment at the surface of the experimental substrates. Divers collected samples in the field using a 140-ml syringes rinsed three times underwater before sample collection. Collections were made by slowly drawing 140 ml of water as the syringe tip was moved along the surface of the experimental slab. Immediately after collection, the syringes were taken to a boat and filtered (GF/F) into new 60-ml sample

Table 1. Time course for elements of the experiment.

Date (1997)	Cumulative days	Fertilizer replacement	% cover	Water samples (days since fertilizer replaced)	Other events
27 July	1	✓			Initial set-up
21 Aug	26	✓	✓		
17 Sept	53	✓	✓		
18 Sept	54			✓ (day 1)	
15–22 Oct	81–88				Cage treatments lost
24 Oct	90		✓		
28 Oct	94	✓		✓ (day 41)	
7 Nov	104			✓ (day 9)	
21–22 Nov	118–119		✓	✓ (day 24)	Algal biomass samples

bottles that were rinsed with sample water several times before final sample collection. Samples were kept on ice until their return to the laboratory where they were frozen until analyzed for inorganic nutrient concentrations. Nutrient concentrations were determined via autoanalyzer analysis for total inorganic nitrogen (TIN = ammonium and nitrate + nitrite) and soluble reactive phosphorus (SRP).

At each sampling date, several types of water samples were collected to compare enriched, control, and background nutrient levels. Ambient water samples were drawn from the water column 1–2 m above the reef surface. Top samples were collected by using the syringe to suck water directly from the surface of the experimental substrate. Such samples were collected both from enriched treatment units and from control units identical to treatment units but with no fertilizer spikes in the chambers. To avoid dislodging large masses of macroalgae (that occurred only in the full cages) from the carbonate slabs and to minimize the effects that masses of algae might have on nutrients (via either rapid uptake or trapping of nutrients in spaces between fronds), we collected only from the grazed slabs in partial cages. Frondose macroalgae were largely absent from these treatments. Lastly, water samples were collected from inside the chambers of enriched and control units with a 5-cm length of tubing fitted to the end of the syringe. This was achieved by twisting the carbonate substrate by 45° in order to access the drilled holes in the top of the cinder block. The timing of fertilizer additions and nutrient samplings, as well as percent cover estimates and other activities associated with the experiment are given in Table 1.

Additional sampling was performed on day 41 to assess the degree and spatial extent of enrichment after a long period without fertilizer replacement. In addition to the ambient, top, and inside samples described above, we also collected samples from enriched blocks at 1 cm and 3 cm height above the experimental substrate to assess the extent to which elevated nutrients were detectable at these distances from the treatments. This was accomplished by placing a 1-cm tall or 3-cm tall spacer on the front of the sampling syringe while running it over the surface of the enriched block and collecting the water sample.

To test whether the nutrient concentrations on the surfaces of the enriched blocks were significantly higher than the control blocks, the TIN and the SRP concentrations in the “top” sampling for each date were compared using a paired-sample

statistical test. The day 1 samples were normally distributed and so a paired *t*-test was used. The day 9, day 24, and day 41 samples were not normally distributed and so paired Wilcoxon signed ranks tests were used. For the additional day 41 samples, a one-way analysis of variance (ANOVA) with Tukey–Kramer posthoc pairwise comparisons was performed to detect if enrichment occurred 1 and 3 cm away from the experimental surface.

Effects of enrichment and herbivory on algae—The nutrient diffusion units described above were used in a two-way factorial experiment to test for the effects of nutrient addition (enriched versus control) and grazing (ambient versus reduced by grazer exclusion cages) on coral reef algae. The experiment was placed at a depth of 6–7 m, with replicates scattered over an area of ~3,000 m² (24°59.672'N, 80°24.420'W) near Pickles Reef in the Key Largo area of the Florida Keys National Marine Sanctuary. An offshore reef site (as opposed to nearshore) was chosen because levels of water column nutrients were expected to be lower offshore, further from potential anthropogenic inputs, and thus, the degree of nutrient limitation and response to enrichment should be maximized and easiest to detect. This site had low live coral cover (estimated about 5%) and moderate levels of physical relief and is typical of many areas in the Florida Keys reef tract. Of 20 offshore reef sites spanning the entire Florida Keys characterized by Chiappone and Sullivan (1997), all are reported to be dominated by benthic algae (range 48–84% cover) and at least half of the sites had coral cover less than or equal to 5%.

The two levels of grazing treatment were obtained using cages. Galvanized chicken wire (2.5-cm hole size) was wrapped around each block and its associated carbonate slab to form a tube with a diameter (height) of ~39 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 resulted in a diminution of grazing by larger fishes only. Previous caging studies at nearby Pickles Reef had demonstrated that partial cages of this design yielded algal cover not statistically different from blocks with no cage structure (Miller and Hay 1998); thus, no-cage controls were not performed.

The carbonate experimental slabs used in this experiment were preconditioned for approximately 10 weeks prior to the experiment by placing them, uncaged, on the back reef at nearby Pickles Reef on 15 May 1997. On 27 July 1997 when the experiment was begun, they contained visible algal turf, including tufts of the filamentous cyanobacteria *Scytonema* sp. and small germlings of frondose macroalgae that appeared to be species of *Laurencia* and *Chondria*. Fifteen replicate groups of four units each (fertilizer and control \times caged and partial-caged) were placed haphazardly on the reef such that each replicate group was at least 3 m from adjacent groups and each unit within the group was 1–2 m from the other three units in that group.

Percent cover of each identifiable benthic alga was estimated twice during the duration of the cage treatments (Table 1), after approximately 1 and 2 months of treatment. Percent cover estimates were obtained using a chain that had 20 randomly chosen links (~ 2 mm diameter) painted red. This chain was placed three times across the experimental substrate (across the slab near its upper edge, across the slab near its lower edge, and along the diagonal) and the algal taxa under each painted link were recorded (i.e., 60 points counted for each substrate). Percent cover for each algal taxa was calculated as the number of links divided by 60.

For this first segment of the experiment (at the 1- and 2-month censuses), there were two experimental factors in effect (caging and enrichment), each with two levels. A separate analysis was performed for each of four algal categories; frondose macroalgae (mostly *Dictyota* sp. and *Laurencia* sp.), the prominent filamentous cyanobacteria *Scytonema* sp., smaller turf algae, and a category referred to as bare + crustose algae. During the first half of the experiment, colonizing crustose algae and very sparse microfilamentous algae were difficult to distinguish clearly from bare substrate so they were lumped with the bare category. For each of the four algal categories, a multivariate repeated-measures ANOVA (SAS Institute 1995) was conducted with the JMP statistical software package using percent cover at each of the first two censuses as the multiple response variables to test for significant responses to the main effects (caging, enrichment, and time) and possible interactions.

Approximately 10 weeks into the experiment, the galvanized cage material rusted, lost integrity, and the caging treatments ended. When this loss was discovered in mid-October, only 5 of the original 30 full cages remained intact (2 enriched and 3 control). Percent cover was censused on all blocks including these five remaining full cages. All remaining cage material was then removed from all cages. Forty-eight hours after removing mesh from the five intact full cages, percent cover was recensused on these slabs to determine if herbivores would rapidly alter algal cover on these replicates. Although our caging treatments had been lost, enrichment treatments were continued for an additional 8 weeks and percent cover estimates made after approximately 3 and 4 months of nutrient enrichment (Table 1).

In order to assure that crustose algae or other diminutive organisms that could be obscured by larger seaweeds were not underestimated, one half of each block was cleaned with a scrub brush after the final (4-month) census. An additional percent cover estimate (60 random points) was then made

for this half of the block for crustose algae and other remaining forms. This second estimate of crustose algal cover was significantly higher than the one made before scrubbing (paired *t*-test, $P < 0.001$), so this second estimate of crustose algal cover was considered more accurate and used for analysis. Small fronds of macroalgae became visible on a few blocks after scrubbing removed taller bluegreen filaments; the presence or absence of the macroalgae on each slab was noted. Lastly, algal biomass for each slab was determined by using a chisel to excavate the top 2 mm from a 39-cm² area (two 1.3-cm-wide strips across the 15.7-cm width of the unscrubbed half of each carbonate slab) of each replicate. All organic material and calcareous debris were harvested, placed in numbered plastic bags, and frozen. Later, each sample was thawed, dried to a constant weight, and ashed to obtain ash free dry mass (AFDM).

During the second half of the experiment (i.e., following failure of the cages), frondose macroalgae were largely absent from the experimental slabs. The algal percent cover categories analyzed for this segment of the experiment were thus turf, cyanobacteria, and crustose algae. The total cover for these groups was in most cases greater (sometimes substantially greater) than 100% because turf was ubiquitous and often grew over crustose forms. Despite the loss of cages, we chose to analyze these data from the latter half of the experiment in a two-factor analysis in case there was some persistent effect of historical cage treatments on algal community components. Thus, we performed similar two-factor multivariate repeated-measures ANOVA, as described above, on the 3- and 4-month percent cover estimates for each algal group.

Macroalgae that became visible only after scrubbing the blocks were too rare to be evaluated using percent cover data. For this algal group, the frequency of occurrence on different treatments was analyzed by a Fisher's exact test. For the algal biomass data, we performed a 2×2 factorial ANOVA to test for historical cage effects and/or effects of nutrient enrichment. Because no historical cage effect was found, we pooled the blocks from the historical caging treatments and conducted a one-factor nonparametric analysis (Wilcoxon signed rank test) with higher (pooled) sample size as a more powerful test for nutrient impacts on algal biomass.

Results

Did we achieve nutrient enrichment?—Inorganic nutrient concentrations drawn from the surface of fertilized blocks at 1, 9, and even 41 d after fertilizer placement were significantly enriched in both TIN and SRP (1.1–3.1 μM and 0.11–0.14 μM , respectively; Fig. 3) compared to samples from the control blocks (0.3–0.9 μM TIN and <0.01 –0.03 μM SRP; Fig. 3). Nutrient levels on control blocks were similar to those of ambient seawater collected about 2 m away from the blocks (0.4–0.8 μM TIN and <0.01 –0.04 μM SRP; Fig. 3). For the day 24 sampling, ambient nutrient levels were elevated (1.2 μM TIN and 0.13 μM SRP) and there were no among-treatment differences in nutrient concentrations against this elevated background level. For TIN, there is a

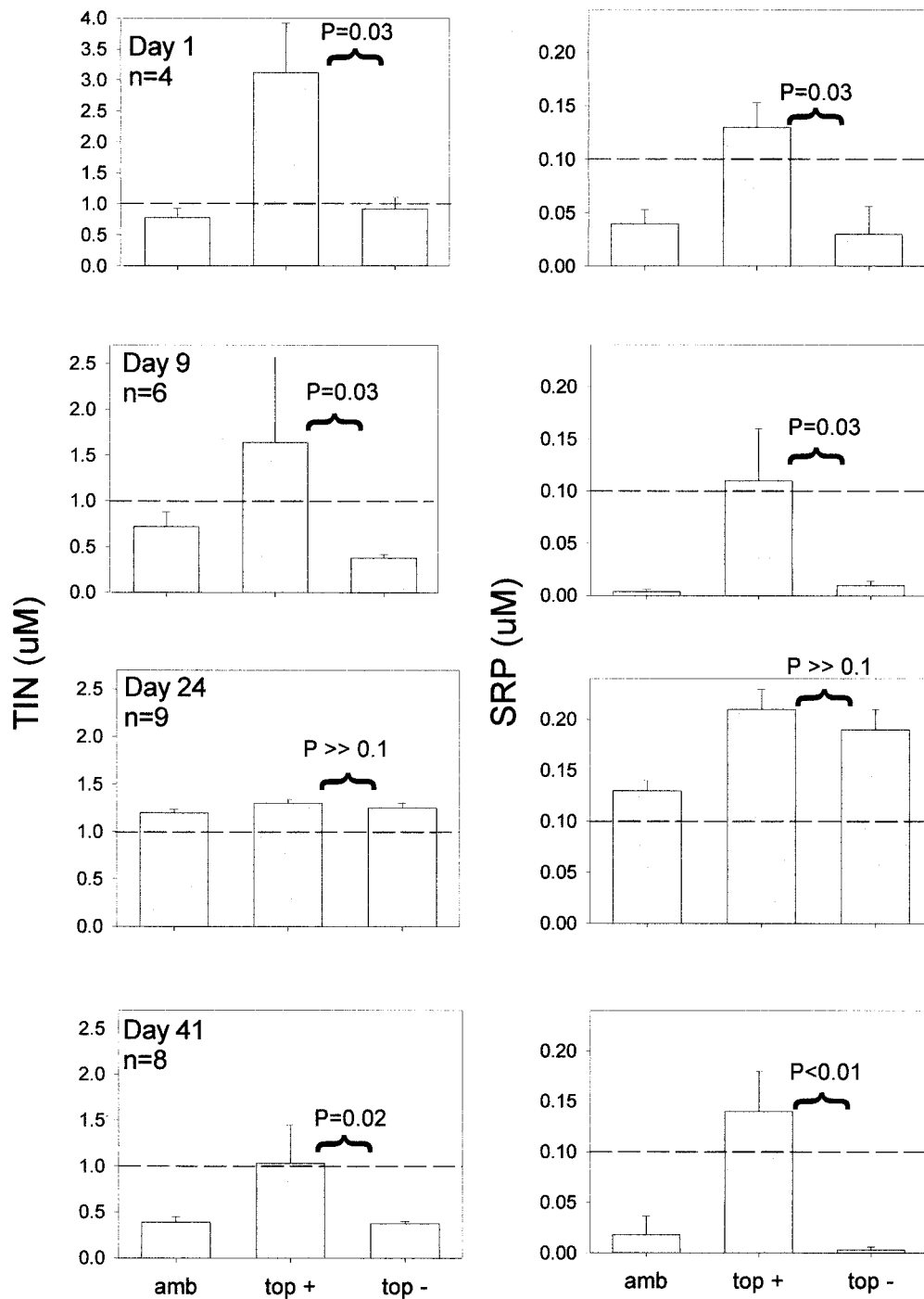


Fig. 3. Inorganic nutrient concentrations of water samples from the surface of experimentally enriched blocks (top+), control blocks (top-), and the ambient water column (amb) taken at varying lengths of time after fertilizer deployment. TIN = total inorganic nitrogen (ammonia + nitrate + nitrite), SRP = soluble reactive phosphate. P values are from paired *t*-test for day 1 (data were normal) or Wilcoxon paired signed ranks tests for days 9, 24, and 41 (data were non-normal) comparing the experimentally enriched and control blocks. The dashed line on each graph indicates proposed nutrient thresholds for eutrophic status as suggested by Bell (1992) and Lapointe (1997).

pattern suggesting that levels of enrichment may have declined with time after addition of fertilizer. For SRP, no such trend is apparent (Fig. 3).

The fertilizer placed inside the blocks was still creating elevated nutrient concentrations after 41 d without replen-

ishment. In all cases the inside samples from enriched blocks had high concentrations (ranges of 12 to >10,000 μM TIN and 6 to 200 μM SRP) while chamber samples from control blocks were slightly higher than ambient for TIN (1–2 μM) and similar to ambient for SRP (0.01–0.15 μM). Rough es-

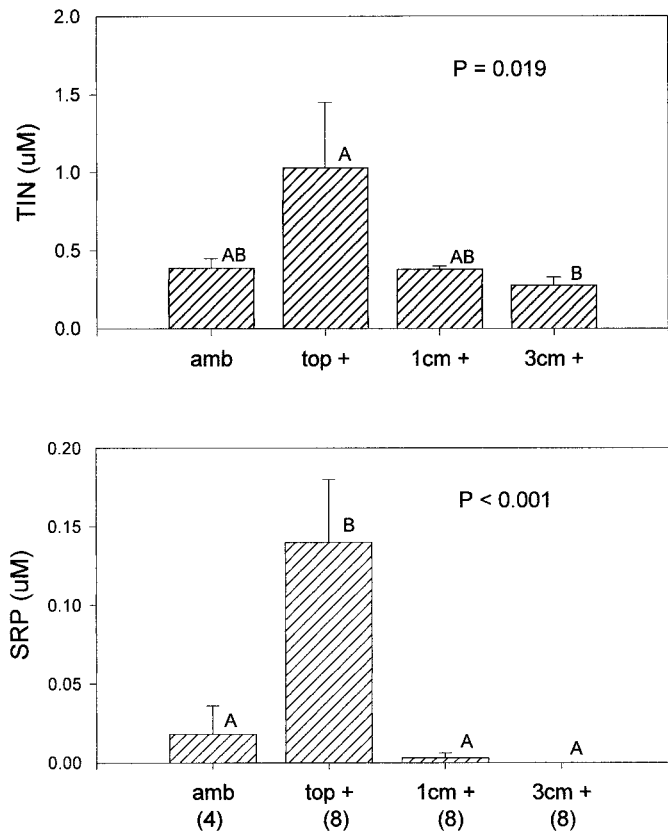


Fig. 4. Inorganic nutrient concentrations collected from enriched blocks 41 d after fertilizer placement. This period included substantial periods of rough seas that should have increased advection of nutrients away from our blocks. Ambient samples (amb) were taken 1–2 m above the blocks. Top samples (top) were taken from the block surfaces, while 1-cm and 3-cm samples were drawn from those distances above the block surface. *P* values are from one-way Kruskal–Wallis tests. Bars with the same letter do not differ significantly ($P > 0.05$, Dunn's posthoc pairwise comparisons). Number of samples for each bar is given below in parentheses.

estimates of internal nutrient concentrations (using a value of 10,000 μM TIN for samples that were still offscale after several dilutions) yield means (± 1 SE) for TIN inside the blocks on days 1, 9, 24, and 41 of 276 ± 94 , 845 ± 88 , 64 ± 13 , and 100 ± 31 μM , respectively. Similar means for

SRP were 26 ± 4 , 116 ± 23 , 14 ± 2 , and 37 ± 9 μM . These means clearly indicate that the block chambers retained high concentrations of nutrients that were available for diffusion to the carbonate slab, but we would be uncomfortable using them as a rigorous assessment of how internal nutrient concentrations varied through time due to the high error associated with serial dilutions. When internal measurements appeared to be highest (day 9), external values on the block tops were similar to days 1, 24, and 41 (Fig. 3) when internal nutrient levels appeared to be lower. The blocks thus appear to be delivering a relatively consistent addition of nutrients to the carbonate slab surfaces.

The vertical sampling on day 41 showed that samples from the slab tops were significantly enriched in SRP ($P < 0.001$) over ambient and over samples from distances of 1 cm and 3 cm away from the experimental carbonate substrates (Fig. 4). Samples drawn from 1 cm and 3 cm above the enriched surface did not differ from ambient concentrations. A similar pattern occurred for TIN ($P = 0.019$) though the posthoc pairwise comparisons were ambiguous (Fig. 4).

Algal response to nutrient enrichment and exclusion of large herbivorous fishes—Percent cover data for most algal groups were non-normal and were not improved by arcsin transformation. In most cases, the much more important assumption of homogeneous variances was met; however, there were two exceptions. Percent cover of turf for the 1-month census and percent cover of bare + crustose for the 2-month census both displayed heteroscedasticity that was not improved by the recommended arcsin square root transformation (Sokal and Rohlf 1981). Because ANOVA is fairly robust against moderate violations of the assumption of homogeneous variances (Underwood 1981), at least when sample sizes are equal amongst groups (Winer et al. 1991), we proceeded with the planned parametric analyses on untransformed percent cover data (Table 2). According to Winer et al. (1991), violation of the homogeneous variances assumption likely reduces the value of alpha by only a few hundredths when sample sizes are equal, as in these analyses. Thus, the probability of a type I error may be slightly increased for turf and bare + crustose cover.

Only one category of algae, the filamentous cyanobacteria *Scytonema* sp., was significantly stimulated by nutrient enrichment ($P = 0.046$, Table 2), and this appeared to occur

Table 2. Results of four multivariate repeated-measures ANOVAs (one for each of the four algal categories) for the initial two-factor experiment (cage treatments still in effect). Significant effects are highlighted in bold.

Effect	Bare + crustose		Turf		Bluegreen		Frondose	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Cage	50.630	0.000	20.340	0.000	4.750	0.034	48.250	0.000
Nutrients	0.004	0.953	2.960	0.091	4.150	0.046	0.009	0.925
C × N	0.141	0.709	1.560	0.216	0.940	0.335	0.000	0.994
Time	10.520	0.002	0.001	0.977	0.660	0.420	86.240	0.000
T × C	0.144	0.705	0.091	0.764	1.440	0.235	41.770	0.000
T × N	2.980	0.090	1.150	0.288	0.310	0.580	0.420	0.518
T × N × C	1.610	0.210	0.405	0.527	0.290	0.594	0.320	0.575

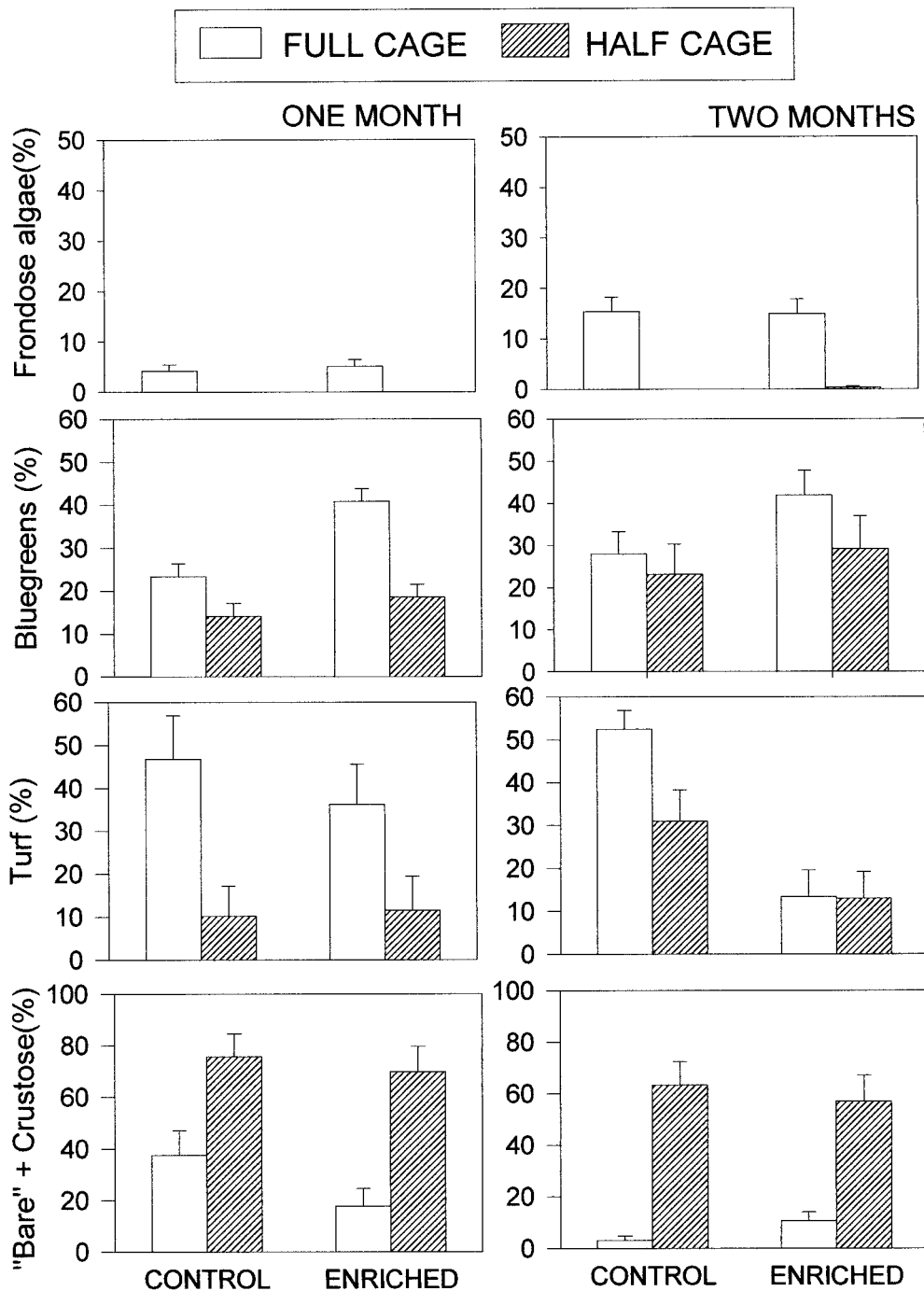


Fig. 5. Response of each of four algal categories to caging and nutrient treatments at 1 month and 2 months duration as measured by percent cover. Bars represent mean + 1 SE. Statistical results, as P values from two-way ANOVA, $n = 15$, are given in Table 2. The cage effect was significant for every algal category. Nutrients were significant ($P = 0.046$) only for bluegreens.

primarily in the full cage treatment (Fig. 5). There was a nonsignificant tendency ($P = 0.091$) for enrichment to suppress abundance of other filamentous algae (turf), and this was especially apparent during the second month of the experiment (Fig. 5). Importantly, frondose macroalgae had virtually identical cover in enriched and unenriched full cages (~5% at 1 month and ~15% at 2 months, nutrients $P =$

0.925, Fig. 5, Table 2). These algae were largely absent from the grazed treatments.

In contrast to the minimal effects of nutrient addition, all algal categories showed significant, and often large, responses to the caging treatments (Fig. 5, Table 2). Not surprisingly, frondose macroalgae, turf, and bluegreens all showed higher cover in full cages where grazing pressures were re-

duced, while bare + crustose had higher cover in partial cages where ambient grazers had access (Fig. 5). Frondose macroalgae and bare + crustose algal categories both showed significant time effects (and frondose macroalgae a significant time \times cage interaction) reflecting the longer successional period required for development of these slower-growing algae. The large effect of herbivores on macroalgae is also illustrated by the rapid change in macroalgal abundance following removal of the five full cages (two enriched and three control) that were still intact at our mid-October sampling. Before cages were removed, macroalgal cover averaged 36% (range = 15–85%); 48 h after cage removal, macroalgal cover had declined to 1% (paired *t*-test, $P = 0.008$, $n = 5$).

Incidentally, if the major component taxa of the frondose macroalgae (*Dictyota* spp., *Laurencia poitei*, and *Neomeris annulata*) for the 2-month census data are analyzed in separate two-way ANOVAs, the results are similar to those for the functional group. That is, for all three species, cage effects are significant ($P < 0.0001$ for *Dictyota* and *L. poitei*, $P = 0.006$ for *N. annulata*), but there are no significant nutrient ($P = 0.566, 0.257, 0.687$ for the three species, respectively) or interaction ($P = 0.566, 0.257, 0.990$, respectively) effects.

As in the first half of the experiment, many of the percent cover data from the second half of the experiment (after loss of the cages) violated the homogeneous variances assumption, as well as the normality assumption, of parametric ANOVA and were not improved by arcsin transformation. In this case, sample sizes were slightly unequal because some blocks were lost over time due to physical disturbance ($n = 12$ – 15 for this analysis). Winer et al. (1991) suggest that when groups with smaller sample sizes have higher variances (as is the case for turf algae), the ANOVA may be expected to yield anticonservative results. In cases where groups with smaller sample sizes have lower variances (as is the case for crustose algae and cyanobacteria), the test is expected to yield conservative results (i.e., lesser likelihood of rejecting the null hypothesis). Thus, the following statistical results may be slightly biased due to violation of homogeneous variance assumptions, but we predict that this bias is conservative in the analyses for crustose algae and cyanobacteria and anticonservative in the analysis for turf.

Nutrient addition (after the loss of cages) had no effects on algal cover (Fig. 6, Table 3). The only statistically significant treatment effect from these analyses was a persistent effect of the initial caging treatment on cover of crustose algae (which should be a conservative result). Also, there was a significant time effect on turf and on crustose algae. There was a tendency ($P = 0.099$) for slightly higher cover of turf in the enriched treatment, but this probability value is anticonservative (i.e., lower than the true value) due to nonhomogeneity of variances.

At the end of the experiment, small individuals of *Laurencia* and *Dictyota* were recorded on 6 of 24 control blocks, but on 0 of the 24 fertilized blocks. Thus, fertilized blocks had a significantly lower, rather than higher, frequency of frondose macroalgal occurrence compared with control blocks ($P = 0.007$, Fisher's exact test). There also was no significant effect of either nutrient enrichment or initial cage

treatment on the AFDM of epilithic algae at the end of the experiment (Fig. 7a, $n = 10$ – 14). The unbalanced AFDM data violated the homogeneous variance assumption (not improved by arcsin transformation) with smaller samples coming from groups with larger variance, suggesting the possibility of anticonservative results. However, even when analyzed with a more powerful one-factor nonparametric test with $n = 22$ and 26 , there was no positive effect of nutrient enrichment on algal biomass ($P = 0.924$, Wilcoxon signed ranks test, Fig. 7b). The appropriate significant P value to control experimentwise error for this sequential test on the same data would be $P = 0.0253$ (Sokal and Rohlf 1984).

Discussion

The relative dominance model (Littler and Littler 1984; Littler et al. 1991) is a comprehensive conceptual model predicting the dominant group of benthic autotrophs in coral reef communities as a function of nutrient levels and herbivory. Our study provides one test of the predictions of this model regarding seaweeds (but not corals that are also considered in the model) at one site in the Florida Keys, a high-latitude reef system. Predictions are that algal turf should dominate when nutrients and grazing are low, that frondose macroalgae should dominate when nutrients are high and grazing is low, and that crustose algae should dominate when both nutrients and grazing are high (Fig. 1). The threshold hypothesis (Bell 1992; Lapointe 1997) predicts that coral reefs will experience macroalgal blooms at nutrient concentrations above threshold levels of $1.0 \mu\text{M}$ dissolved inorganic nitrogen (DIN) and $0.1 \mu\text{M}$ SRP. An experimental test of these models' predictions required a method for sustained in situ nutrient enrichment that could be integrated with traditional caging studies. At our field site, the effects of herbivores were consistent and strong, but the effects of nutrient enrichment to levels above the hypothesized thresholds for both DIN and SRP were nonexistent (most groups) or opposite the predictions of the models (i.e., macroalgal germ-lings and filamentous bluegreens).

Effectiveness of enrichment method—Quantification of nutrient concentrations at the surface of the experimental units indicated that treatments with fertilizer stakes were enriched considerably compared to ambient conditions or to treatments without fertilizer. This pattern was statistically significant for three of four sampling dates. The 3 d showing significant alterations of nutrients were days when ambient nutrients were at the low concentrations normally found on these reefs (see the following web site for 3 yr of data assessing nutrient levels on reefs in the Florida Keys—<http://www.fiu.edu/orgs/serp/jrpp/wqmn/datamaps/>). Our experimental enrichment was sustained above suggested threshold levels (Fig. 3) for at least 41 d after fertilizer deployment. The day 41 measurements were made following a period of rough weather when flux of nutrients away from experimental blocks should have been high (more than 13 d of sustained winds greater than 17 kt, of which more than 6 d had sustained winds greater than 20 kt; NOAA CMAN data from Molasses Reef, $25^{\circ}00'36''\text{N}$, $080^{\circ}22'48''$ —about 4 km from our study site). We felt that these conditions provided a worst

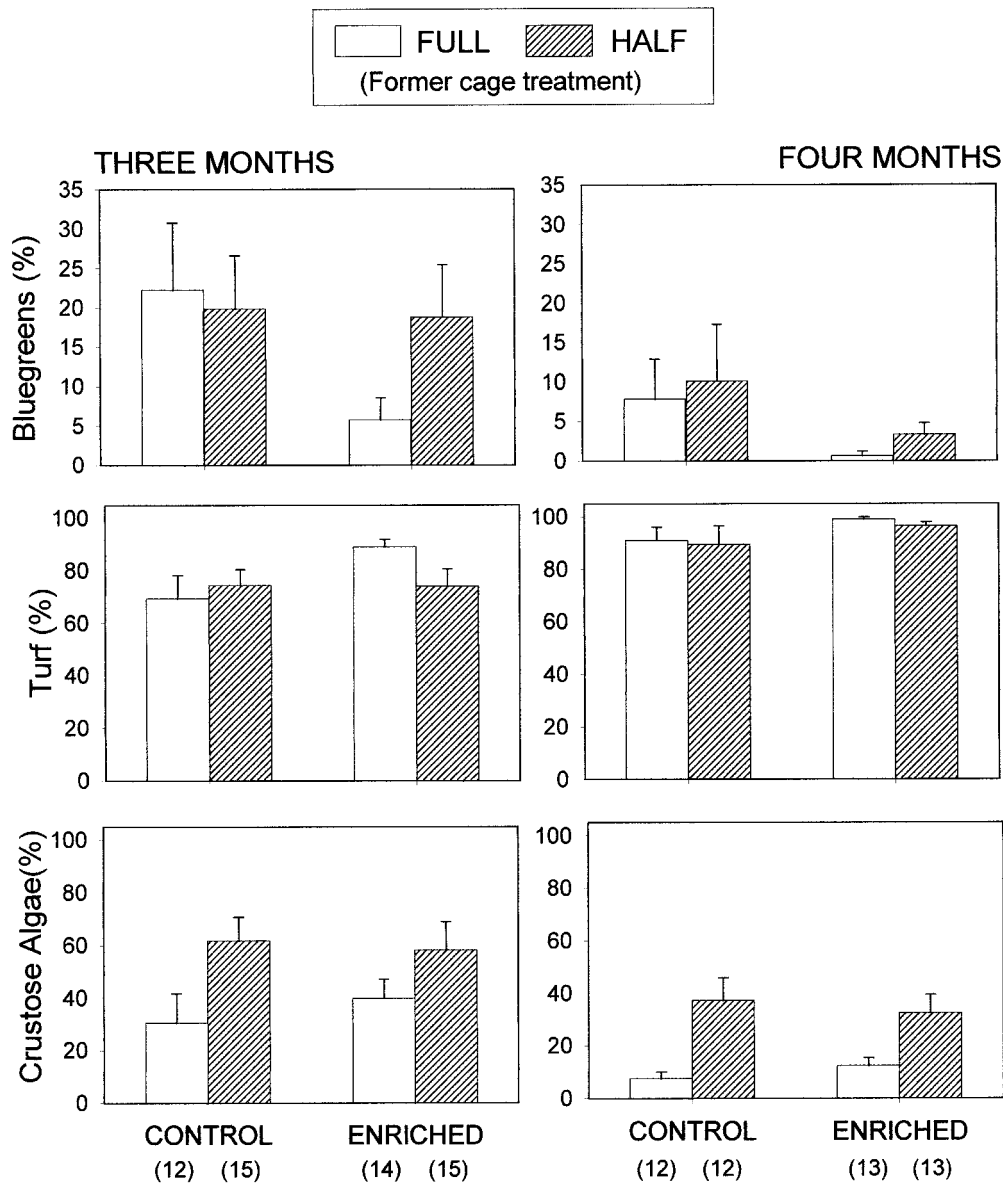


Fig. 6. Response of each of three algal forms to nutrient enrichment and former caging treatments at 3 months and 4 months duration as measured by percent cover. Bars represent mean + 1 SE and *n* is given in parentheses below the x-axis. Crustose algal cover shown for 4 months census is from estimates made after removal of occluding sediments and turf. Total cover greater than 100% results from turf growing over crustose algae. Statistical results are given in Table 3.

case for detecting duration of enrichment from a single fertilizer deployment. Also, the relatively large volume of water collected for our nutrient samples (140 ml) and the necessity of disturbing the boundary layer to collect the samples suggest that our reported concentrations probably underestimate true concentrations at the experimental surfaces.

An exception to the general pattern of experimental enrichment occurred during the day 24 sampling. On this day, ambient nutrient levels were high and above the proposed threshold level of Bell (1992) and Lapointe (1997). One possible explanation for this observation is the occurrence of an upwelling event. The possibility of upwelling is also suggested by studies of water temperature, chlorophyll *a* concentrations, zooplankton abundance, and coral growth

conducted about 6 km from our study site. These investigations indicate that subthermocline water is periodically delivered to deeper areas of reefs in the Florida Keys via internal tidal bores (Leichter et al. 1996). The intrusion of these colder waters has been detected as shallow as 15–20 m on the reef, but it is not known if they affect the shallower depths, 6–7 m, where our investigation was conducted. However, in 3 yr of quarterly nutrient sampling at the two reefs immediately adjacent to our Pickles Reef site (i.e., Molasses Reef, about 4 km NE of our study site, and Conch Reef [the site of the Leichter et al. study], about 6 km SW of our site), proposed threshold levels of DIN were detected only once for one reef (a reading of 1.0 μM), while threshold levels of SRP were never detected (South-

Table 3. Results of three multivariate repeated-measures ANOVAs (one for each of three algal categories) for the latter part of the experiment, after cage treatments ceased and ambient grazing pressure was applied to all experimental blocks. The analysis was still via a two-factor analysis in order to account for any possible historical effects of the cages. Significant effects are highlighted in bold.

Effect	Turf		Bluegreen		Crustose	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Cage	0.011	0.918	0.007	0.935	8.298	0.006
Nutrients	2.846	0.099	2.117	0.153	0.032	0.859
C × N	1.073	0.306	0.567	0.455	0.554	0.460
Time	10.619	0.002	3.254	0.078	17.413	0.000
T × C	0.110	0.741	0.086	0.771	0.056	0.815
T × N	0.008	0.931	0.038	0.846	0.135	0.715
T × N × C	1.733	0.195	1.416	0.240	0.038	0.846

east Environmental Research Program, Florida International University, Water Quality Monitoring Network, J. Boyer, pers. comm.). This suggests that the high levels of ambient nutrients we detected on day 24 may be unusual for shallow reefs in the Florida Keys. However, the low frequency of sampling in both our study and the 3-yr study is inadequate to document potential natural nutrient enrichment by intermittent upwelling events.

Although significant enrichment of nutrients occurred directly on experimental substrates at 41 d after fertilizer deployment, enrichment was not detectable in samples drawn >1 cm above the substrate (Fig. 4). We did not collect spatially explicit concentration data for shorter durations following fertilizer deployment (i.e., days 1, 9, or 24), but given that SRP shows no pattern of diminishing concentrations between days 1 and 41 (Fig. 3), it seems unlikely that other days would have differed from day 41 in this regard. Thus, the elevated nutrients at the substrate surface are rapidly diluted to ambient levels or are immediately taken up by organisms on the carbonate slabs. This method therefore produces a consistent elevation of surface-associated nutrients to ecologically relevant concentrations (i.e., similar to nutrient concentrations reported for upwelling [e.g., Genin et al. 1995] or anthropogenic pollution [e.g., Smith et al. 1981]) without altering the water column or large areas of reef. This means, however, that taller portions of macroalgal tissues, above 1 cm in height, might not be exposed to elevated nutrients (although this relationship may be altered if fronds baffle water flow and produce thicker boundary layers). Because macroalgal tissues with this height never developed in treatments open to larger herbivores (Fig. 5), this potential limitation could not have affected macroalgal growth in the half cages. In full cages, macroalgae did grow to several centimeters in height, and parts of their thalli may have exceeded the height to which enrichment occurred.

Given the crude methods we used and the turbulent field conditions that prevailed when we collected some of these samples, our data conservatively indicate that this experimental method of enrichment raises nutrient concentrations above predicted threshold levels on a small spatial scale (≤ 1

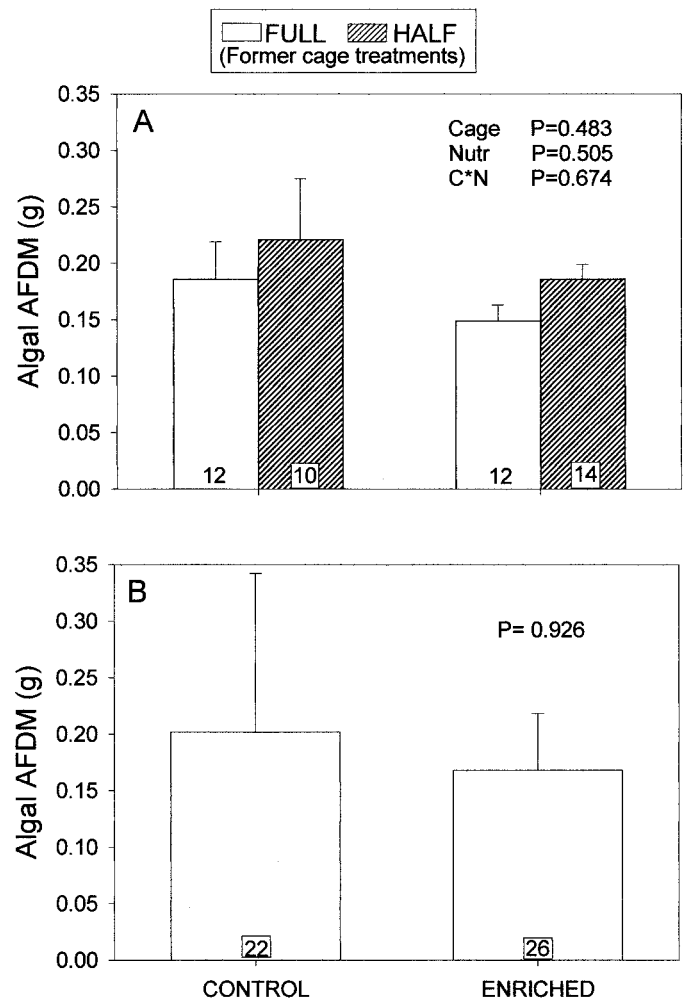


Fig. 7. Ash free dry mass of algae measured at the end of the 4-month experiment. Bars represent mean + 1 SE AFDM recovered per 39 cm² sample, *n* given in the base of each bar. (A) Initial cage treatments broken out, *P* values from two-factor ANOVA. (B) Only nutrient treatments (former cage treatments pooled), *P* value from Wilcoxon signed ranks test.

cm from the surface) and that nutrients remain elevated for at least 41 d following addition of fertilizer.

Response of reef algae to nutrient addition and caging—As predicted by the relative dominance model (Littler and Littler 1984; Littler et al. 1991), both turf algae and macroalgae increased when large herbivores were excluded while crustose algae declined. In the case of crustose algae, the response persisted 2 months after cage removal. A similarly strong response of reef seaweeds to herbivore exclusion has been shown in numerous previous investigations (e.g., Randall 1961; Ogden et al. 1973; Sammarco et al. 1974; Hatcher and Larkum 1983; Carpenter 1986; Lewis 1986; Miller and Hay 1998). These strong responses to herbivore exclusion are all consistent with some implications of the relative dominance model. However, the notion that macroalgae cannot become abundant on tropical reefs unless increased nutrients are available to support their growth (Lit-

tlar and Littler 1984; Lapointe 1997) was not supported by our data.

In contrast to predictions of both the threshold and relative dominance models, macroalgal abundance was not increased by fertilizer addition regardless of the grazing regime (Fig. 5, Table 2). When cages protected frondose macroalgae from large herbivores, percent cover was virtually identical between enriched and unenriched treatments (14.9 versus 15.4% cover, respectively, at 2 months, Fig. 5). Crustose algae also did not increase with increased nutrients. Percent cover was again almost identical in enriched and control treatments (e.g., ~22% at 4 months duration, Fig. 6, Table 3). To make sure that differences in algal thickness or mass were not obscured by considering only percent cover data, we also measured ending standing biomass (AFDM) of the community. There was no significant effect of nutrient enrichment and no trend suggesting that increased nutrients yielded increased algal mass (Fig. 7). Similarly, the numerous herbivore exclusion studies cited above all demonstrated rapid accumulation of macroalgae without any enrichment of nutrient levels. Our findings extend these previous studies by showing, for our study site, that even when nutrient levels are locally elevated above predicted threshold levels, macroalgae are not advantaged by this in either the presence or absence of large herbivores. Alternative explanations for lack of an enrichment effect include (1) that enrichment did not extend far enough into the water column to be effectively utilized by taller frondose macroalgae, or (2) that periodic upwellings coupled with excess uptake allowed seaweeds to remain nutrient saturated throughout this 4-month study. In contrast to some of our findings, a similar study by Hatcher and Larkum (1983) on an Australian reef found that nutrient additions increased algal abundance during some times and in some locations, if herbivores were excluded.

Also conflicting with expectations derived from the assumption of nutrient limitation, macroalgal germlings occurred significantly more frequently on treatments without fertilizer (6 of 24 replicates, or 25%) than on treatments with fertilizer (0 of 24 replicates). There are at least two possible explanations. The inhibition of macroalgal germlings on nutrient-enriched treatments might suggest that the fertilizer used in these treatments was toxic to the germlings. This explanation can be discounted because no such inhibition of macroalgae occurred in the full cage treatments during the initial phase of the experiment (Fig. 5). Another possible explanation involves complex interactions of herbivores and algal food quality in enriched treatments. Macroalgae grown under nutrient-enriched conditions contain enhanced levels of N and P compared to unfertilized individuals (Lapointe 1997). Because herbivores are generally nitrogen limited, they commonly need to consume many times their basic carbon requirement in order to obtain sufficient nitrogen (e.g., Horn 1989; Sterner and Hessen 1994). Enriched macroalgae might therefore be preferred by herbivores and removed at a faster rate than unenriched macroalgae.

There was a tendency (anticonservative $P = 0.099$) for slightly higher cover of turf in the enriched treatment during the latter part of the experiment. It could be argued that this trend might have become significant given a longer duration of the experiment or a larger sample size. However, even if

this response had been statistically significant, the effect size was small (Fig. 6) and thus possibly of limited biological significance. More importantly for the models being assessed, the relative dominance model predicts that, other things being equal, turf dominance should be enhanced by lower rather than higher nutrient regimes. Because filamentous turf-forming algae have high growth rates, have a significant portion of their total biomass in the benthic boundary layer, and may have nutrient uptake limited due to boundary layers produced by closely spaced upright filaments (Carpenter and Williams 1993), growth of these algae may be limited by nutrients more than is the growth of larger macroalgae. If this hypothesis is correct, then portions of the relative dominance model would need revision.

During the initial phase of the experiment, the filamentous cyanobacteria *Scytonema* sp. (<2 cm tall) significantly increased in response to nutrient enrichment (Fig. 5, Table 2). Because *Scytonema* fixes nitrogen, it may be P-limited and thus expected to display a positive response to P addition. Benthic bluegreens are subject to episodic blooms on reefs in the Florida Keys (M. D. Hanisak, pers. comm.), and our results are consistent with the hypothesis that these blooms may be affected by nutrient pulses. The relative dominance paradigm (Littler and Littler 1984) does not distinguish filamentous bluegreens from other turf algae, but again, our results for both bluegreens and other filamentous turfs do not support the model's predictions that filamentous algae will be enhanced under low, rather than high, nutrients.

It might be argued that our nutrient additions were not sufficiently high to enhance algal abundance in herbivore exclusions. However, the surface enrichment levels sampled at 1, 9, 24, and 41 d after fertilizer deployment (Fig. 3) were consistently above the proposed threshold nutrient levels for both TIN ($1 \mu\text{M}$) and SRP ($0.1 \mu\text{M}$) suggested by Bell (1992) and Lapointe (1997) as criteria for classifying a coral reef system as eutrophic and for triggering rapid increases in macroalgal cover. It is possible that higher nutrient concentrations or enrichment of a greater portion of the water column would have elicited greater algal response. Alternatively, it could be argued that ambient nutrient levels at our study site were periodically high enough (due to episodic upwelling?) that no responses to increased nutrients would be expected. As discussed above, this alternative cannot be discounted given the inadequate temporal resolution of nutrient concentration data presently available for reefs in the Florida Keys; however, the limited data that are available suggest that high nutrient levels are relatively uncommon on shallow reefs. Intensive temporal samplings of nutrient concentrations coupled with physical investigations such as those of Leichter et al. (1996) are needed to quantify nutrient patterns attributable to intermittent processes such as upwelling.

Nutrient limitation from a physiological perspective is most often measured by assaying some physiological response (usually photosynthetic rates) after short (5–12-h) incubations in very high nutrient concentrations. Such macroalgal studies from several pristine tropical reef areas have shown nutrient limitation of photosynthetic rate (Lapointe 1987; Littler et al. 1991, 1993). However, Atkinson (1988) pointed out the distinction between nutrient limitation of a

physiological rate and what he termed nutrient regulation of community structure. The relative dominance and threshold models both make predictions about nutrient regulation of community structure. Evidence of physiological nutrient limitation may be inadequate to predict community-level responses given the complex community and ecosystem interactions at work in coral reefs. For example, Williams and Carpenter (1988) performed in situ enrichment of reef algal turfs with ammonia and found increased photosynthesis with enrichment (physiological limitation) but no significant difference in algal biomass between treatments.

Our study deals with community-level, not physiological-level, responses to enrichment (Atkinson's nutrient regulation). We found no enhancement of in situ macroalgal cover with nutrient enrichment. It might be argued that the duration of our experiment was too short (though 4 months of continuous nutrient elevation is certainly long compared to 5–12-h pulse treatments) to reach steady-state community structure as addressed in the relative dominance model. If the experiment had run longer, the results could have differed. However, 2 months was long enough for large and significant differences in macroalgal abundance to develop between full- and half-cage treatments. Also, many experimental studies of reef algal communities have documented dramatic community changes and, in some cases, competitive exclusions in less than 4 months (e.g., Lewis 1986 [10 weeks]; Carpenter 1986 [as little as 8 weeks]; Stachowicz and Hay 1996 [4 weeks]). If nutrients were strongly affecting algal growth or community composition, we should thus have been able to detect effects in experiments of this duration.

Why did we see so little nutrient response?—Our results suggest that seaweeds on the offshore reef that we studied are nutrient replete; addition of inorganic nitrogen and phosphorus did not increase accumulation of algae even in low-grazing conditions within full cages. There are many alternative explanations to explain nutrient repleteness of reef algae at our study site. First, it has been suggested that the waters of the Florida Keys are subject to anthropogenic nutrient enrichment (Lapointe and Clark 1993) that could account for the lack of macroalgal response to additional experimental enrichment in the current study. However, quantitative studies of nutrient distribution patterns in the Florida Keys do not support the suggestion that anthropogenic nutrients reach the offshore areas of the reef tract where the current study was conducted (Szmant and Forrester 1996). Secondly, natural external sources of nutrient enrichment such as upwelling (discussed above, Leichter et al. 1996; Szmant and Forrester 1996) could account for nutrient repleteness of reef algae at our site. However, the data are currently inadequate to prove or refute the impact of upwelled nutrients at our study site.

A third, and most simple, explanation is offered by the recent work of Larned and Atkinson (1997) showing that adequate nutrient flux for macroalgal growth can be achieved at low concentrations as long as water motion and turbulence are adequate. These investigators have measured nutrient uptake by the macroalga *Dictyosphaeria cavernosa* from Kaneohe Bay, Hawaii at different current speeds. They calcu-

late that for this nitrogen-limited species, water velocities higher than 0.5 m s^{-1} at ambient water column concentrations of nutrients ($0.4 \mu\text{M}$ DIN, substantially below the supposed threshold level) would provide adequate nutrient flux to sustain field levels of growth. This result suggests that the depletion of boundary layers surrounding algal thalli, not water column concentration, limits nutrient availability to benthic algae, and that moderate water movement and turbulence can remove this limitation.

Over the past 20 yr numerous other investigations have been devoted to discerning alternative nutrient sources (other than the water column, reviewed by D'Elia and Wiebe [1990]) that might support the high production of benthic communities on coral reefs. Known alternatives include regeneration in reef interstitial sediments (Stimson et al. 1996) and nitrogen fixation (Weibe et al. 1975). Also, studies of organism-mediated nutrient flux indicate that coral reef sponges, even at only 1–2% benthic cover, can convert vast amounts of water column microbial biomass to dissolved inorganic nutrients (Corredor et al. 1988; A. Pile et al. unpubl.). Given that boring sponges often have high abundance on coral reefs (Rutzler 1975), they may represent a vast, and relatively unrecognized, source of inorganic nutrients for reef organisms.

Overall, a general explanation for our finding of nutrient repleteness of reef macroalgae is that the nutrient limitation of tropical seaweeds has been overstated. As suggested by recent Hawaiian studies (Stimson et al. 1996; Larned and Atkinson 1997) and, explicitly, by Larkum and Koop (1997), the nutrient-limited (or nutrient-regulated) status of coral reef algae may be a paradigm in need of revision.

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