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REPORT

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An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef

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Abstract Reduced herbivory and enhanced nutrient concentrations have both been suggested as probable mechanisms driving phase shifts from coral to algal dominance on tropical reefs. While there is considerable information regarding the effects of herbivores on reefs, there is little experimental evidence of nutrient effects or the interactive effects of both of these factors. This study experimentally tested the role of these factors on benthic community structure on a coral-dominated reef in Hawaii. A randomized factorial block design was used to simultaneously investigate the effects of nutrient enrichment and herbivore exclusion on the development of benthic algal communities on artificial surfaces over a 6-month time period. Total algal biomass was greatest on settlement surfaces exposed to both nutrient enrichment and herbivore exclusion simultaneously. Fleshy algal biomass was greatest on surfaces removed from grazing whereas calcareous biomass was greatest on surfaces exposed to nutrient enrichment. Control surfaces exhibited consistently less total, fleshy and calcareous algal biomass than that on any of the experimental surfaces. Microinvertebrates were most abundant on surfaces within herbivore exclusion treatments but increased in number on all settlement surfaces over time. Sediment accumulation was positively correlated with fleshy algal biomass and was most abundant on surfaces within herbivore exclusion treatments; there was no pattern in sediment accumulation over time. This research demonstrates that on short time scales (less than 6 months), nutrient enrichment and herbivore exclusion can independently and interactively support shifts in benthic algal community structure on a Hawaiian reef.

Key words Nutrient enrichment · Herbivory · Fleshy algae · Crustose coralline algae · Eutrophication

Introduction

Although tropical coral reefs are among the most diverse and highly productive ecosystems on earth (Odum and Odum 1955; Connell 1978), phase shifts from coral to algal dominance within these ecosystems have become increasingly common (Smith et al. 1981; Hughes et al. 1987; Lapointe 1997; McClanahan et al. 1999). Identification of the factors leading to such phase shifts and the subsequent increase in algal abundance and decrease in coral cover and diversity has become a critical scientific and management issue. In single factor analyses, "top down" (herbivore pressure) and "bottom up" (nutrient availability) factors have been independently implicated as the primary causal factor leading to large shifts in community structure (Hughes et al. 1987, 1999; Lapointe 1997, 1999). However, the standing crop and productivity of any reef community is most likely the result of more complex interactions among both biological and physical controls (Hatcher 1990; Hughes and Connell 1999).

While pristine reefs typically have low concentrations of inorganic nutrients, high rates of herbivory, low algal standing crop, and high coral cover, the underlying mechanisms maintaining the balance among these constituents remain elusive. A change in the intensity of herbivore pressure or the flux of inorganic nutrients on a reef can potentially lead to substantial changes in benthic community structure (Smith et al. 1981; Littler and Littler 1984; Hughes et al. 1987) and function (Green et al. 1997). Reef algae have generally been considered to be nutrient limited, where any addition of inorganic nitrogen and/or phosphorus to the reef may lead to

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accelerated photosynthetic and growth rates and subsequent increases in primary productivity (Hatcher and Larkum 1983; Littler et al. 1991; Lapointe 1997; Larned 1998). However, the classic view that ambient nutrient levels are oligotrophic on all pristine coral reefs is no longer widely accepted (Szmant 1997).

Natural phenomena such as upwelling, natural groundwater flux and internal waves have been shown to episodically increase nutrient concentrations in reef environments (Leichter et al. 1996; Hatcher 1997). Recent studies investigating nutrient effects on reefs from the Florida Keys (Miller et al. 1999) and Australia (Larkum and Koop 1997) have demonstrated that the algal communities in these areas may be nutrient replete. Even if ambient nutrient concentrations are low, the flux within a given system may be great enough to deliver adequate levels to release the apparent nutrient limitations from the dominant algae. Yet other studies have attempted to define a threshold level of nutrient concentrations which, if exceeded, will lead to macroalgal blooms (Bell 1992; Lapointe 1997). Such thresholds likely represent static measurements and, while easily determined, do not necessarily consider pulses or flux of nutrients through a reef system (Larned and Atkinson 1997). Given the vast diversity in reef algae and the wide range of reef types in the tropics, it seems unlikely that all systems would respond equally to these threshold levels (McCook 1999; Miller et al. 1999). However, anthropogenic eutrophication has fundamentally altered nutrient dynamics in at least some reef settings (Smith et al. 1981; Hodgson 1994).

The first large-scale evidence of coastal eutrophication leading to a phase shift from coral to algal dominance on a reef occurred in the early 1970s in Kaneohe Bay, Hawaii. The green alga *Dictyosphaeria cavernosa* proliferated in this semi-enclosed embayment following the placement of two urban sewage outfall pipes in the south end of the bay. The rapid growth of this alga led to reductions in coral cover along a nitrogen and silica gradient (Hunter and Evans 1995). Following the diversion of the sewage outfalls from Kaneohe Bay, recent surveys have demonstrated that the alga has decreased in percent cover and abundance in some areas, but continues to increase in other parts of the bay (Hunter and Evans 1995). Evidence suggests that nutrients in the bay's sediments remain elevated as a result of the original water column enrichment more than 28 years ago (Stimson et al. 1996; Larned 1998). This suggests that bottom-up factors may have been influential in driving long-term changes in ecosystem structure (Smith et al. 1981). However, abundance of *D. cavernosa* as measured by percent cover was also inversely proportional to herbivore pressure (Stimson et al. 1996). Although *D. cavernosa* did not become a dominant component of the ecosystem until the enrichment event occurred, reduced herbivory could have also favored increases in abundance at specific sites (Stimson et al. 1996). Thus, the mechanistic bases for such phase shifts remain unclear in Kaneohe Bay.

Herbivory, or lack thereof, is clearly one of the most important biotic factors structuring benthic community composition and species diversity on coral reefs (Carpenter 1986; Lewis 1986; Hay 1997). Herbivores can affect algal assemblages in several ways, both negatively and positively, including: (1) physical disturbance that removes plant biomass and results in open space (Hay 1981; Hixon and Brostoff 1996), (2) localized nutrient enrichment from animal excretion (Williams and Carpenter 1988), (3) alterations in benthic nitrogen fixation rates (Wilkinson and Sammarco 1983; Williams and Carpenter 1997), (4) changes in community structure from preferential removal and/or avoidance of distinct algal species (Borowitzka 1981; Sammarco 1983; Lewis 1986; Duffy and Hay 1990), (5) shifts in the pattern of succession by favoring distinct algal growth forms under different disturbance regimes (Hixon and Brostoff 1985; Scott and Russ 1987; Hixon and Brostoff 1996; McClanahan 1997), and (6) changes in net primary productivity and biomass (Hatcher and Larkum 1983; Carpenter 1986, 1990; Hughes et al. 1987). The degree of change that a herbivore or group of herbivores can impose on a system is determined by several factors, including the intensity of the disturbance (bite size), the frequency of the disturbance (number of bites), and the number and type of each grazer in the system.

Nutrient levels and herbivore intensity may also affect the density and canopy height of algal communities, both of which have been implicated as factors that may influence sediment trapping, accumulation and hydrodynamics in coral reef environments (Carpenter and Williams 1993; Steneck 1997; Airoldi and Virgilo 1998). Sedimentation, nutrient enrichment and the buildup of particulate matter on a reef may reduce light levels, decrease flow rates, increase boundary layer thickness and potentially lead to anoxia, thereby negatively impacting the metabolic efficiency of both coral (Kinsey and Davies 1979; Smith et al. 1981; Tomascik and Sander 1985, 1987; Rogers 1990; Stambler et al. 1991; Te 1992; Whittenberg and Hunte 1992; Green et al. 1997) and algal species (Carpenter 1986; Carpenter and Williams 1993). Many microinvertebrates are closely associated with these algal turfs (Brawley and Adey 1981; Hay et al. 1989) and can significantly alter algal biomass and community structure (Duffy and Hay 2000). Carpenter (1986) suggested that microherbivores are common only in areas inaccessible to other grazers such as wave-swept algal ridges, small crevices, and damselfish territories. The relationships between microinvertebrate abundance, algal functional form, biomass, and sediment abundance associated with benthic algal turfs have not been experimentally addressed in Hawaii, yet may be highly correlated and may provide insight into fine-scale processes associated with these communities.

The Relative Dominance Model (Littler and Littler 1984) suggests that the dominant photosynthetic space-occupying group (functional form) can be predicted as a function of long-term exposure to nutrients and herbivory, where herbivory alone is thought to be the more important controller of algal standing stocks on undisturbed reefs (McCook et al. 1997; Naim et al. 1997; Steneck 1997). Although this model has been supported via observations in field settings (Littler et al. 1991), there has been little experimental demonstration of benthic community responses to simultaneous changes in both nutrients and herbivory (Hatcher and Larkum 1983; Larkum and Koop 1997; Miller et al. 1999).

The role of eutrophication and herbivory in the formation of algal blooms throughout the tropics (see Smith et al. 1981; Hodgson 1994; Lapointe 1997, 1999; Hughes et al. 1999; McClanahan et al. 1999; McCook 1999; Miller et al. 1999) remains unclear in many cases. It is difficult to determine the causes of an ecological shift on a tropical reef after it has already occurred. Therefore, a manipulative ecosystem-level field experiment was conducted to investigate the kinetics of response and the simultaneous effects of multiple factors on benthic community structure and function on a Hawaiian reef.

Methods and materials

Study site

This study was conducted at Puako Reef (19°58.28′N, 155°50.70′W), on the leeward side of the island of Hawaii (Fig. 1). The study site was chosen because it represents a relatively young (approximately 0.33–0.45 million years) and apparently unimpacted fringing reef. The nearshore waters of the leeward coast of the island of Hawaii contain some of the richest coral reefs and associated fish and invertebrate faunas in the Hawaiian Islands (Parrish et al. 1982). Further, Puako is an enforced Fisheries Management Area (State of Hawaii, Department of Land and Natural Resources) where all invasive forms of net fishing are prohibited. The reef slope begins at a depth of 5 m following a drop off from the reef flat, and extends downward for approximately 200 m where it meets a sand flat at 30 m. The reef slope consists largely of unbroken thickets of *Porites compressa*, *P. lobata*, *Pocillopora meandrina* and *P. damicornis*; macroalgae are uncommon and crustose coralline and turf algae occupy cryptic crevices and coral skeleton substrates. This study was conducted within a 60 × 10-m^2 portion of the reef slope at approximately 12 m depth, following a depth contour parallel to shore. The coral cover in this area is consistently high (90% *Porites compressa*), with a rich and abundant herbivore community (Parrish et al. 1982) and moderate levels of water column nutrients (Table 1; see the following web site for nutrient data for Kaneohe Bay during the same period of time: http://www.hawaii.edu/cisnet/contents.htm).

Experimental design

A randomized factorial block design with six replicates (blocks) was used to test the effects of nutrient enrichment and herbivore exclusion and to control for inherent variations in algal assemblages on the reef at Puako (Fig. 2). Following experiments conducted by Hixon and Brostoff (1985, 1996) which demonstrated the adequacy and effects of artificial settling surfaces in conducting manipulative experiments, flat gray PVC (poly vinyl chloride) tiles 50 cm^2 in area were used as the experimental surface. This material was chosen primarily because it: (1) is non-destructive, (2) is chemically inert, (3) can be manipulated to mimic the texture of natural substrates and (4) it supports biotic assemblages similar to the surrounding substrates (Hixon and Brostoff 1985). Prior to beginning the experiment, all tiles were rough sanded until the surface resembled the texture of dry coral rock. Tiles were affixed to plastic-coated galvanized metal racks via cable ties for easy removal. Six tiles were affixed to each rack (24 racks). Racks were then attached to the reef using large cable ties. Tiles were left in situ from November 1998 to January 1999 to age and acquire a natural epilithic algal community.

Experimental blocks consisted of 10 × 10-m plots that were divided into four 5 × 5-m subplots. Each subplot contained a rack of tiles and was randomly assigned to one of four treatments:

Fig. 1 A Map of island of Hawaii, showing location of Puako Reef on leeward side of the Kona coast. **B** Aerial photograph showing fringing reef at Puako

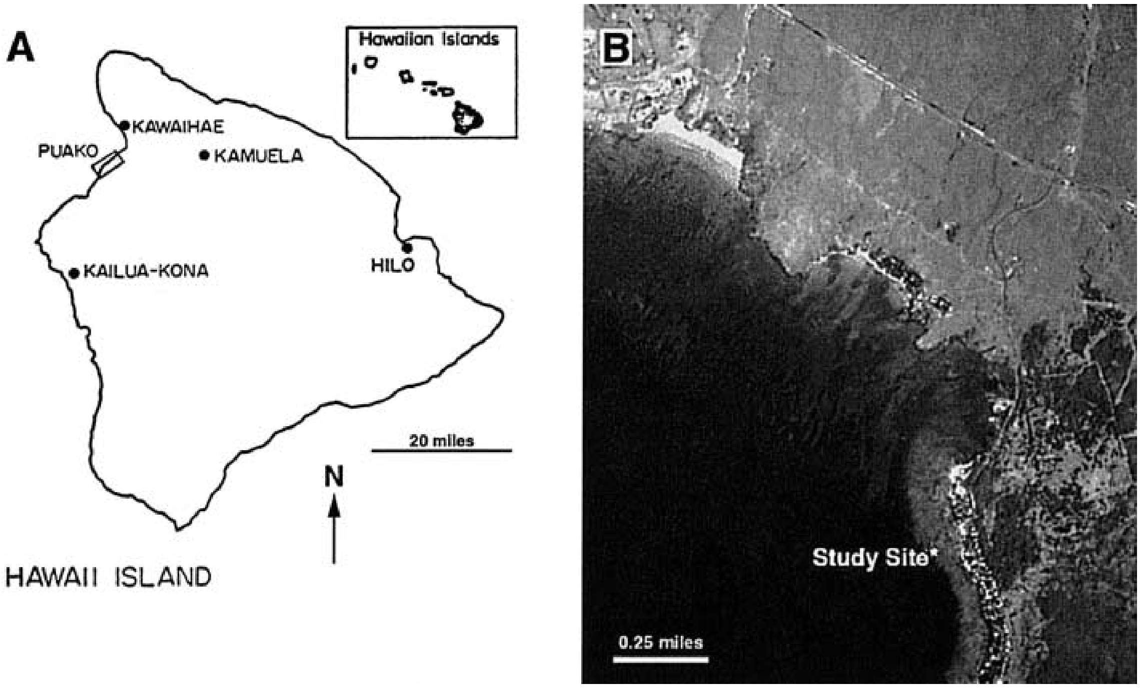

Table 1 Dissolved organic nitrogen and phosphorus concentrations (µM) in area adjacent to nutrient enrichment pots. Values are expressed as means ± SE in parentheses from samples collected on four separate dates during the experiment (January, February, March and May 1999). Distance is expressed in meters on a transect moving away from enrichment pots

Distance (m)	*n*	NH_4	NO_3	PO_4
0.00	4	148.80 (7.51)	94.35 (19.68)	22.38 (2.06)
0.25	4	5.42 (1.23)	1.88 (0.81)	1.26 (0.29)
0.50	4	1.76 (0.87)	0.95 (0.38)	0.61 (0.23)
1.00	4	1.04 (0.56)	0.68 (0.37)	0.34 (0.16)
Ambient	4	0.713 (0.22)	0.38 (0.11)	0.24 (0.07)

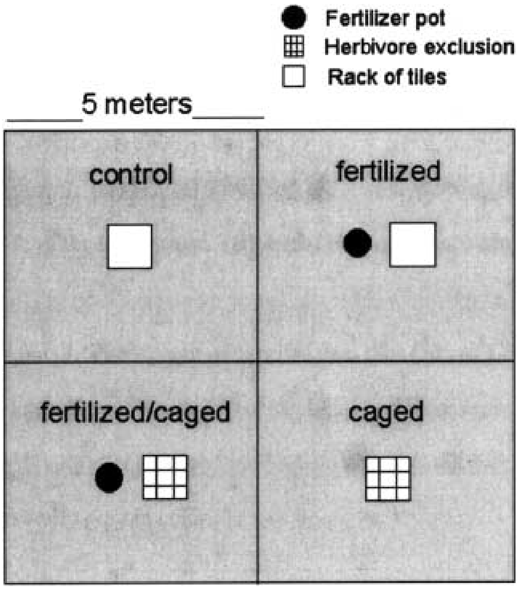

Fig. 2 Diagrammatic representation of experimental design, one of six blocks used in our experiment. All blocks were situated at a constant depth (12 m) and aligned back to back, parallel to shore

(1) control – no manipulation, (2) nutrient enrichment, (3) herbivore exclusion or (4) both nutrient enrichment and herbivore exclusion (Fig. 2). Treatments were assigned to each of the six blocks randomly and independently in January 1999. Each month beginning in February 1999, one tile from each treatment within each block was randomly collected by divers and placed in separate plastic bags prior to analysis.

The nutrient enrichment treatment was accomplished by filling 20-cm-diameter unglazed clay flower pots (Chapman and Cragie 1978; Hatcher and Larkum 1983) with 1.4 kg of United Horticultural Supply turf fertilizer (11% NH_4, 10% NO_3, 7% P_2O_5). Pots were inverted and secured with epoxy to PVC holding plates. The drainage hole in each pot was stoppered with a rubber cork to provide slow diffusion of nutrients through the porous surfaces. Each month, all pots were retrieved by SCUBA divers, emptied, scrubbed and refilled. Tile racks were placed within 0.5 m of the pots. In order to quantify enrichment levels, water samples were collected for analysis on transects away from the pots on four sampling dates (January, February, March and May 1999) immediately following enrichment (Table 1). Water samples were collected via SCUBA using sterile 50-cc syringes at 0, 0.25, 0.50 and 1 m distances away from the pots. Ambient water samples were also collected at the same depth (10 m) but outside of the experimental area. Upon returning to the surface, the samples were transferred to acid-washed 100-ml polypropylene bottles, stored on ice and frozen. Samples were analyzed for nitrate, ammonium and phosphate concentrations using a Technicon Autoanalyzer II at Analytical Services, University of Hawai'i (Walsh 1989).

Herbivore exclusion cages were constructed out of 1-inch-diameter galvanized wire mesh (35 × 35 × 35 cm). These cages were secured directly over the top of the tile racks to exclude adult, intermediate (urchins) and macroherbivores (acanthurids and scarids), but not juveniles or microherbivores. Cages were cleaned of fouling cyanophytes approximately every 2 weeks by divers and were completely replaced once during the study when rusting became apparent. At the time of replacement, however, the cages were still intact but beginning to lose integrity. Cage controls were not used because of extensive data from Hawaiian reefs showing a lack of significant caging effects in similar experiments (Hixon and Brostoff 1985; Stimson et al. 1996). Further, to quantify any cage effects on flow, water motion velocities were calculated using clod cards placed on the inside and outside of cages (Jokiel and Morrissey 1993).

Following each collection, tiles were kept in seawater and refrigerated until analyzed for biomass, sediment and abundance of mobile invertebrates at the University of Hawaii, Botany Department. Upon analysis, each tile was rinsed with seawater to remove sediment and invertebrates. Sessile invertebrates such as serpulid worms, tunicates and bryzoans were removed from tiles prior to conducting biomass estimates. Tiles were rinsed with fresh water to remove salt. Algal material was then scraped from the tiles and fresh weights were immediately obtained. This material was then oven dried at 60 °C until a constant dry weight was attained. Algal samples were then decalcified using 5% HCl for 24–48 h (depending on thickness of calcium carbonate), rinsed with fresh water, filtered and then dried again at 60 °C to estimate total algal biomass, fleshy algal biomass and calcified weight (weight remaining after decalcification subtracted from total biomass).

The amount of sediment and the number of mobile microinvertebrates were quantified for each experimental treatment to determine whether there were significant differences in the abundance of these variables between treatments and to explore possible relationships between algal biomass, functional form, sediment trapping and microinvertebrate abundance. The abundance of microinvertebrates on tiles was determined for broad taxonomic categories (crustaceans, polychaetes and gastropods). The sediment collected from tiles was filtered and rinsed with fresh water through GF/C glass microfibre filters, then dried to a constant weight at 60 °C.

Data analysis

There was a positive association between the means and variances for all of the nutrient data. Therefore a log transformation was utilized prior to analysis to adequately satisfy the ANOVA assumption of homoscedasticity. A one-way analysis of variance (ANOVA) was performed on these data to determine if significant enrichment occurred with distance from the fertilizer source. Tukey's posthoc pairwise comparisons were used to determine if nutrient concentrations were greater at the experimental tiles (0.25 m) than ambient levels. A two-sample t-test was applied to the clod card data to determine if the herbivore exclusion cages had a significant effect on flow.

Four-factor analyses of variance for nutrient enrichment, herbivore exclusion, time (all fixed factors), and block (random factor) were carried out on the biomass data for each of the algal functional groups (total, fleshy and calcified), sediment and total invertebrates. A positive association between the means and variances for all of the biomass data dictated a log transformation of data prior to analysis to adequately satisfy the ANOVA assumption of homoscedasticity. The three-way interaction as well as all two-way interactions between fixed variables were included in the models; however, interactions involving the random variable (block) were not included. A conservative test for compound asymmetry was also performed on the time variable for each ANOVA because of the inherent similarity among samples that were close together in time versus those that were far apart. Tukey's posthoc multiple comparisons were used to determine how the means of the treatments differed. All analyses were conducted using Minitab version 12.1. Photographs were taken of every tile to visually record treatment effects over time (Fig. 3).

Results

Efficiency of nutrient enrichment

Nutrient concentrations decreased exponentially with distance from the enrichment pots (Table 1). One-way ANOVAs were examined for each of the three nutrients with distance as the factor. At 0.25 m from the enrichment pots, ammonium, nitrate and phosphate concentrations were all significantly higher than ambient levels ($P = 0.014$, 0.050 and 0.023, respectively). The water samples were taken immediately following refertilization, and therefore represent the highest concentrations to which the community and tiles were exposed. However, there was always fertilizer remaining in the pots at the time we collected them for refertilization, suggesting that some level of fertilizer was still diffusing out after a month. At 1 m from the fertilizer pots, enrichment of ammonium, nitrate and phosphate was not detectable in comparison to background levels ($P = 0.99$, 0.94 and 0.99, respectively). Because each treatment within a block was separated from the next by at least 5 m, subplots adjacent to fertilized treatments should not have been impacted by nutrient enrichment.

Herbivore exclusion

Mean flow in our study area and the area inside the exclusion cages was 3.99 ± 0.72 and 3.47 ± 0.52 cm/s,

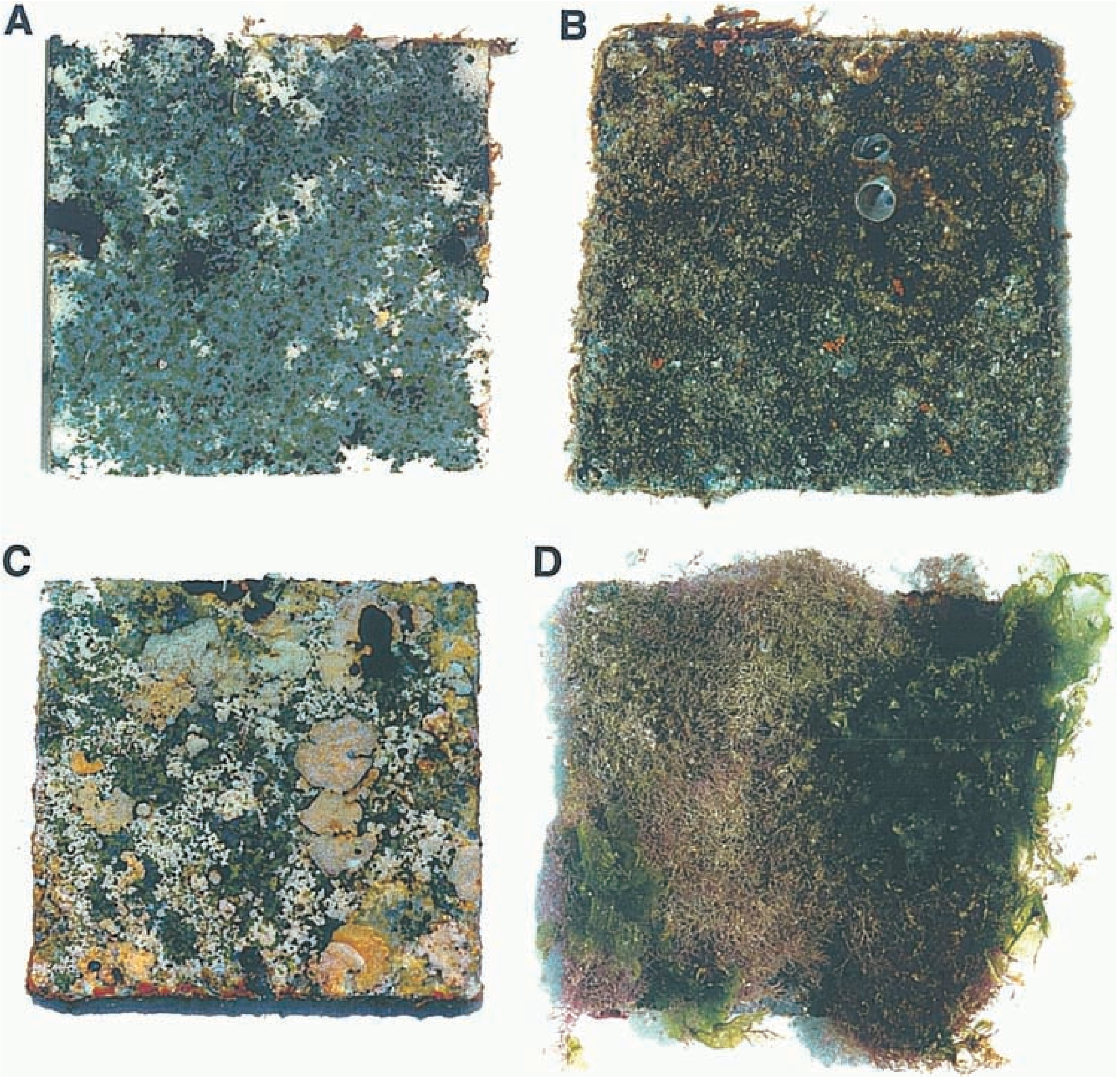

Fig. 3 Experimental tiles (50 cm^2) following 6 months' exposure to treatment conditions. **A** Control, **B** herbivore exclusion, **C** nutrient enrichment and **D** both herbivore exclusion and nutrient enrichment. All tiles are constructed out of PVC and are naturally gray in color

respectively ($n=8$ for both samples). There was no significant difference in water motion between the area inside the herbivore exclusion cages and outside (T = 1.66, $P=0.12$) as measured by the clod card technique.

Effects of treatments on algal biomass

There was virtually no change in biomass over time on the control tiles. All experimentally manipulated tiles began to increase in biomass following the first month of exposure to treatments; this pattern continued over time (Fig. 4). Both reduced herbivory and nutrient enrichment had significant effects on algal biomass for each of the categories examined (Table 2). Differences among sampling times and blocks were also significant. The significant block term can primarily be attributed to one block that responded with much higher biomass for all treatments (especially fertilization) than any of the other blocks. This observation is most likely tied to the presence of the territorial damselfish *Stegastes fasciolatus* within this block. Virtually all of the interaction terms, excluding the three-way interaction, were significant, suggesting that mean biomass accumulation varied between the treatments and over time. The interaction between caging and nutrient enrichment was highly significant. The general pattern showed that tiles exposed to both caging and nutrient enrichment treatments simultaneously had greater amounts of calcified, fleshy and total dry weight than all other tiles (Fig. 4, Table 3). The dry weight biomass on the control tiles remained consistently low over time.

At the end of the 6-month sampling interval, tiles exposed to nutrient enrichment alone were dominated by crustose coralline algae, whereas tiles in herbivore exclusion cages were colonized by filamentous turfs and sessile invertebrates (Fig. 3). The control tiles had typically very low cover with some small patches of bryozoa, crustose coralline algae and cyanobacteria. Tiles exposed to both treatments simultaneously frequently had crustose coralline algae underlying macroalgae, large colonies of cyanobacteria, and dense assemblages of turf algae. All tiles in the nutrient enrichment treatments had greater total and calcified weight than the caged treatments alone arising from the abundance of crustose coralline algae on these tiles (Fig. 4). Tiles in the herbivore exclusion treatments had greater fleshy algal biomass than the other tiles.

Total dry weight biomass on control tiles was significantly different compared to that on all treatment tiles (Tukey's pairwise comparisons: $P<0.001$ for all three tests; Table 3). Dry weights on tiles in the combined nutrient-enriched and caged treatment were significantly different compared to those tiles in either enriched or caged treatments alone (Tukey's pairwise comparisons: $P=0.0196$ and <0.001, respectively). Total biomass from the caged and the enriched tiles was not significantly different (Tukey's pairwise comparisons: $P=0.2894$).

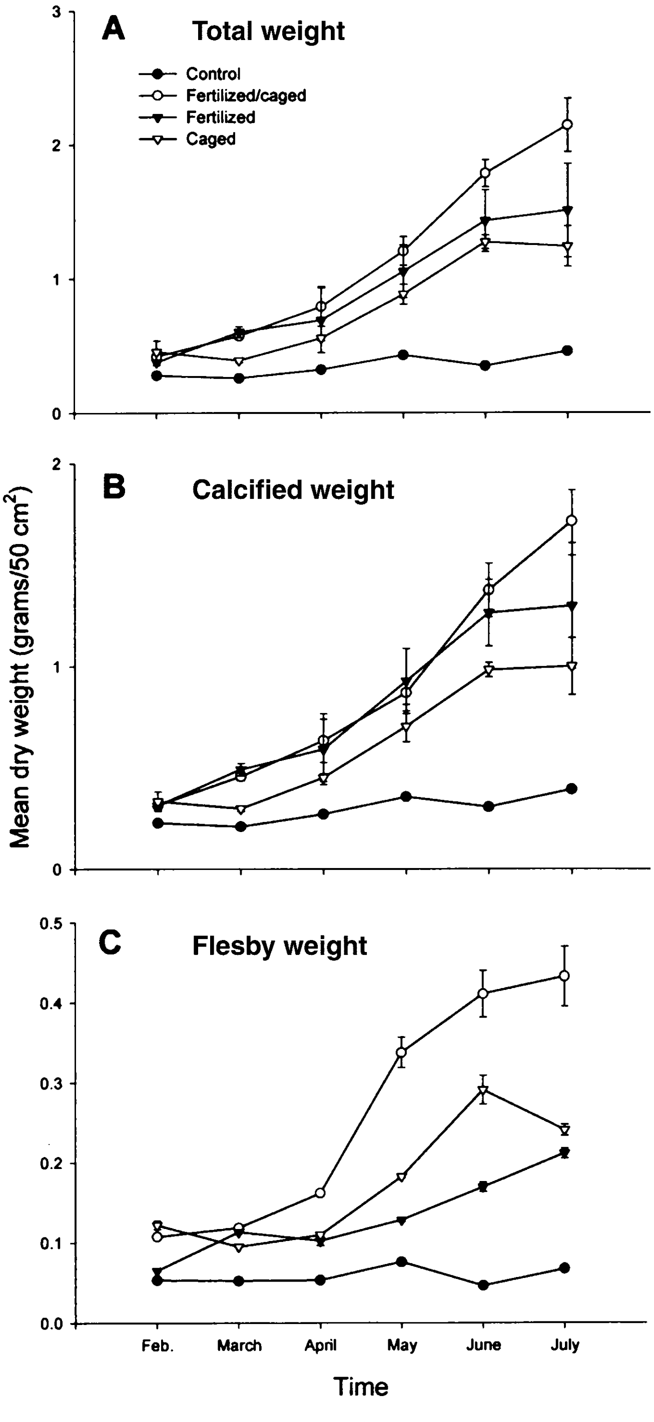

Fig. 4 Mean algal biomass (g/50 cm^2) on experimental tiles under factorial nutrient enrichment and herbivore exclusion treatments over a 6-month sampling interval. **A** Total dry weight (including CaCO$_3$), **B** calcified dry weight and **C** fleshy dry weight; $n=6$ for all samples; *bars* are ±SE of means; legend for **B** and **C** is same as that for **A**

Sediment and mobile invertebrates

Despite some variation in the first 2 months of the experiment, caged tiles typically exhibited higher levels of sediment than nutrient-enriched or control tiles

Table 2 Results of four-way factorial analyses of variance for log transformed algal dry weights. All factors excluding the blocking variable were treated as fixed effects. Total algal biomass includes both fleshy and calcified components. C Caged; *N* nutrient enrichment; *T* time

Factor	Total algal biomass		Calcified weight		Fleshy biomass	
	F	*P*	*F*	*P*	*F*	*P*
Cage	120.50	< 0.001	75.18	< 0.001	54.96	< 0.001
Nutrients	118.14	< 0.001	98.69	< 0.001	95.42	< 0.001
Time	66.91	< 0.001	61.59	< 0.001	33.80	< 0.001
Block	13.89	< 0.001	12.80	< 0.001	9.39	< 0.001
C × N	30.12	< 0.001	28.25	< 0.001	12.94	< 0.001
N × T	6.15	< 0.001	5.40	< 0.001	4.88	< 0.001
C × T	2.07	0.074	1.90	0.1000	5.85	< 0.001
C × N × T	1.34	0.252	1.30	0.2670	1.52	0.1880

Table 3 Mean ($n=6$) of algal functional group biomass (dry weight in g tissue/50 cm^2) and standard error of the mean (in *parentheses*) from experimental tiles in each treatment at end of 6-month sampling interval. *Both* Herbivore exclusion and nutrient enrichment; *Caged* herbivore exclusion

Treatment	Total biomass	Fleshy biomass	Calcified weight
Control	0.45845 (0.0215)	0.06750 (0.0034)	0.39095 (0.0191)
Both	2.14720 (0.1200)	0.43283 (0.0303)	1.71437 (0.0969)
Nutrient enriched	1.50882 (0.1040)	0.21192 (0.0125)	1.29690 (0.0921)
Caged	1.24050 (0.0709)	0.24100 (0.0167)	0.99950 (0.0593)

(Fig. 5A). The factorial analysis of variance for sediment dry weight (Table 4) showed that all main factors were significant, including the interaction between nutrient enrichment and caging. Sediment collected from control tiles was significantly less than that collected from any of the experimental tiles (Tukey's multiple comparisons: $P<0.001$ for all three tests). Tiles in the caged-only treatments had significantly higher sediment than in any of the other experimental tiles (Tukey's multiple comparisons: $P<0.001$ for fertilized, $P=0.009$ for both fertilized and caged). Tiles in the caged and fertilized treatment had more sediment than fertilized-only-treatment tiles (Tukey's multiple comparisons: $P=0.050$).

Mobile microinvertebrates were quantified on all experimental tiles to account for possible mesograzer effects and to explore possible relationships between algal biomass, functional group and invertebrate abundance. All invertebrates examined were most abundant on the caged tiles, followed by caged and nutrient enriched, nutrient enriched alone, and controls (Table 5). The number of microinvertebrates on all tiles, including controls, appeared to increase over time (Fig. 5B). The results of the factorial analysis of variance (Table 4) again showed that all of the main factors were significant including the interaction between nutrient enrichment and caging. Caged tiles and caged and nutrient-enriched tiles supported a significantly higher number of mobile microinvertebrates than both control and nutrient-enriched only tiles (Tukey's multiple comparisons: $P<0.001$ for both tests). Control tiles had a consistently lower number of mobile invertebrates than any of the experimental tiles (Tukey's multiple comparisons: $P<0.001$ for all three tests).

The total number of mobile invertebrates collected from tiles was positively correlated with total algal dry weight ($r=0.675$, $n=144$, $P<0.001$). The total number

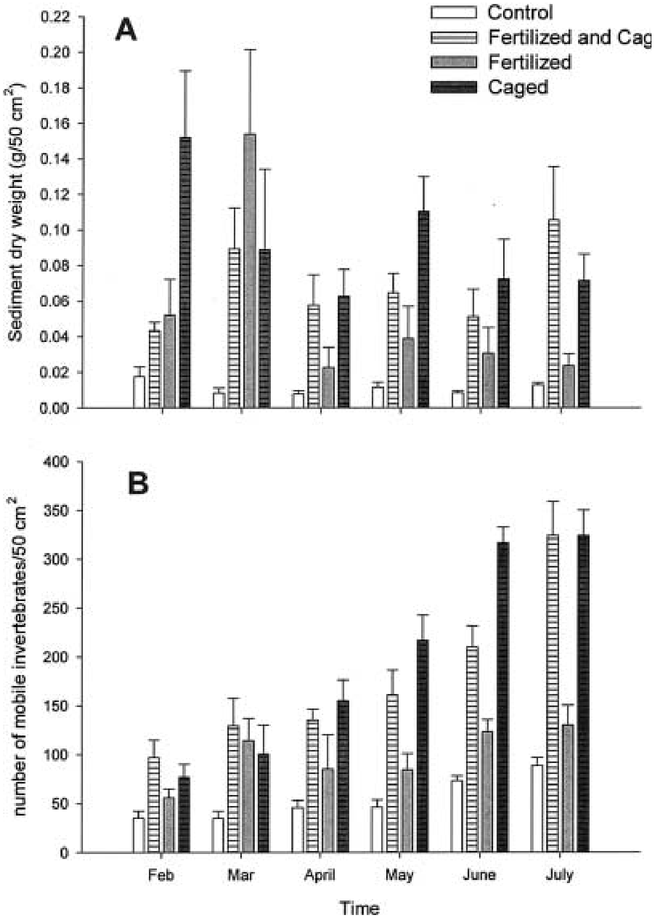

Fig. 5 Mean values of **A** sediment dry weight accumulated on tiles (g/50 cm^2) and **B** number of mobile invertebrates (number/50 cm^2) over the 6-month sampling interval from each experimental condition; $n=6$ for all samples; *bars* are ±SE of means; legend for **B** is same as that for **A**

Table 4 Results of four-way factorial analysis of variance for log transformed sediment weight and number of mobile invertebrates collected from settlement tiles in each of four treatments over a 6-month sampling interval. Block variable was treated as a random factor; all other variables were treated as fixed factors. *C* Caged; *N* nutrient enrichment; *T* time

Factor	Sediment weight		Total mobile invertebrates	
	F	*P*	*F*	*P*
Cage	207.11	< 0.001	266.34	< 0.001
Nutrients	4.87	0.029	14.27	< 0.001
Time	2.97	0.015	36.42	< 0.001
Block	10.87	< 0.001	6.03	< 0.001
C × N	34.83	< 0.001	29.25	< 0.001
N × T	1.62	0.160	1.44	0.217
C × T	0.44	0.820	1.36	0.246
C × N × T	1.56	0.178	1.29	0.272

Table 5 Mean ($n = 6$) ± SE (in *parentheses*) of sediment dry weight (g/50 cm^2) and total number of mobile invertebrates, crustaceans, polychaetes and gastropods (number/50 cm^2) collected from experimental tiles in each treatment at end of 6-month sampling interval. *Both* Herbivore exclusion and nutrient enrichment; *Nutrient* nutrient enrichment; *Cage* herbivore exclusion

Treatment	Sediment	Total invertebrates	Crustaceans	Polychaetes	Gastropods
Control	0.011 (0.001)	54.5 (4.4)	37.7 (3.2)	7.4 (1.1)	9.4 (1.1)
Both	0.069 (0.008)	178.5 (15.8)	132.7 (11.2)	25.0 (3.4)	20.8 (3.4)
Nutrient	0.042 (0.010)	96.7 (9.7)	70.5 (7.2)	13.9 (2.4)	12.4 (1.0)
Cage	0.100 (0.012)	203.8 (18.0)	153.1 (14.1)	29.2 (2.7)	21.5 (2.7)

of polychaetes and gastropods was more correlated with calcified weight than with fleshy biomass ($r = 0.516$, 0.496 for calcified weights versus 0.482 and 0.416 for fleshy weight respectively, $n = 144$, $P < 0.001$ for both tests), whereas the total number of crustaceans was highly correlated with fleshy algal biomass ($r = 0.648$, $n = 144$, $P < 0.001$). The total number of microinvertebrates was also positively associated with time ($r = 0.518$, $n = 144$, $P < 0.001$) and sediment dry weight ($r = 0.502$, $n = 144$, $P < 0.001$). Multiple regression was not performed on the data because of multicolinearity between many of the variables.

The overall mean and standard errors for each treatment at the end of the experiment are shown in Table 5. Relationships between sediment dry weight and biomass of different algal functional groups showed that sediment dry weight was positively correlated with both fleshy algal biomass ($r = 0.208$, $n = 144$, $P = 0.014$) and calcified weight ($r = 0.171$, $n = 144$, $P = 0.044$).

Discussion

The relative abundance of fleshy versus calcified algal biomass on experimental tiles in this study generally supports the Relative Dominance Model proposed by Littler and Littler (1984). In addition, this study documents a marked response by the algal community over a short time period to differences in both herbivory and nutrient levels. Clearly, benthic algal communities in Hawaii can shift rather rapidly in response to either of these factors. While the response of algal communities to herbivory has been demonstrated previously, this study is novel in showing a significant nutrient response. Although we used broad categories (fleshy versus calcareous) for algal biomass estimates, the data provide valuable insight into the mechanisms that may influence benthic community dynamics. More data are needed, however, on the fine scale processes and interactions between coral, algae, herbivores and the topographic components of a given reef in order to understand the broad scope of mechanisms involved in phase shifts in tropical locales.

Steneck (1997) found that coralline abundance and herbivory were positively correlated, thereby illustrating “disturbance tolerance” by these algae. However, in this study, with herbivory held constant, coralline abundance was much lower on control tiles than nutrient-enriched tiles, suggesting that the nutrient enrichment treatment did influence coralline abundance. All settlement tiles exposed to nutrient enrichment had significantly higher levels of calcified dry weight than those not exposed to enrichment. This suggests two processes: (1) crustose coralline algae may be nutrient limited at this site and/or that (2) herbivory was sufficiently high to prevent the establishment of fleshy turf or macroalgae on these tiles. Nutrient enrichment accelerated coralline algal growth to a level that exceeded grazing pressure; herbivores did not consume these coralline algal species because of other abundant food sources. Perhaps the increased nutrients facilitated coralline algal recruitment. Another possibility may be that nutrient enrichment treatment accelerated growth and turnover rates of fleshy algae but that herbivores consumed the propagules before they were able to fully establish.

Observations of coralline algal growth in this study (≈1 mm/month) were higher than those reported elsewhere (Littler and Littler 1984) and appear to have been accelerated due to nutrient enrichment. High levels of nutrients on reefs (namely phosphorus) have been shown to decrease coral calcification rates and, thus, overall growth rates (Kinsey and Davies 1979; Smith 1984;

Tomascik and Sander 1985; Green et al. 1997). If this process is further compounded with an increase in coralline algal growth rates, competitive interactions may favor algal rather than coral dominance.

Tiles in herbivore exclusion treatments had consistently higher levels of fleshy algal biomass than controls, suggesting that the rapid growth rates of fleshy turf algae, perhaps because of their upright fleshy morphologies and high surface to volume ratios, prevented coralline algae from settling. Macroalgae were never observed on controls or tiles exposed to caging or nutrient enrichment alone. Initially, all caged tiles were colonized by small filamentous turf algae. However, tiles in the caged and nutrient-enriched treatment began showing a shift toward macroalgal dominance after approximately 4 months. The appearance of the frondose chlorophyte *Ulva fasciata* (Fig. 3D) on these tiles was one of the most dramatic observations, as this species of *Ulva* is not found naturally near the experimental site (J. Smith, personal observations), yet *Ulva* spp. are known to inhabit areas of high nutrient concentrations and low herbivory in other areas (Lapointe and Tenore 1981). Some species of macroalgae are found on subtidal reefs in Hawaii, but usually escape herbivory through either chemical defense, physical defense or by occupying cryptic habitats. This research suggests that macroalgal growth and subsequent success on exposed surfaces may be the result of relatively short-term exposure to both top-down and bottom-up factors. Other studies have shown that macroalgae can and will establish on surfaces removed from herbivory without the presence of increased nutrients (Hay 1981; Carpenter 1986; Lewis 1986). The apparent lack of macroalgae on tiles exposed to only herbivore exclusion in our study may be the result of intense grazing of young macroalgal propagules by microherbivores and juvenile fishes. More research needs to be conducted to clarify the effects of this diminutive but diverse group of herbivores on benthic community structure in the tropical Pacific.

The presence of both fleshy macroalgae and coralline algae on tiles simultaneously exposed to caging and nutrient enrichment (Fig. 3) suggests that these two algal forms can coexist on both short- and long-term scales under the appropriate physical and biological parameters (Steneck 1997). Despite documentation of coralline abundance in areas characterized by abundant herbivorous echinoderms and fishes, control tiles in this study were virtually bare when compared to fertilized tiles. Thus, the lack of dominance by coralline algae on control tiles seems to arise from nutrient limitation rather than herbivore pressure. However, the persistence and subsequent abundance of corallines on nutrient-enriched tiles is most likely the result of continual removal of fleshy algal propagules by herbivores (Wanders 1977) and accelerated growth rates via fertilization. This observation is consistent with the existence of coralline algal ridges that are dominant on highly exposed reef crests throughout the tropics which are constantly exposed to high flux rates (nutrient delivery) and herbivory (Littler and Littler 1984).

Sediment collected from experimental tiles showed interesting relationships with algal functional group biomass. Sediment was more abundant in the presence of fleshy algae than coralline algae. The canopy height of algal turfs has been shown to influence microscale flow rates and may have an impact on sediment trapping, and could therefore prevent transport of sediments off of a reef (Carpenter and Williams 1993). This process may be critical if the trapped particulate matter contains high levels of nutrients. Sedimentation has also been shown to adversely affect coral reproduction (Rogers 1990). The interrelationships between algal biomass, sediment accumulation and nutrient content could have significant implications to reef health and recovery following large physical disturbances. The synergistic effects of these factors need to be examined more thoroughly.

The abundance of mobile microinvertebrates in this study is much higher than previously reported (Carpenter 1986; Hixon and Brostoff 1996). This may be the results of scale of sampling, as virtually all of the invertebrates observed here were less than 2 mm in size and were enumerated microscopically. Nevertheless, the abundance of these organisms was positively correlated with both fleshy and calcified algal dry weights. Crustaceans were more commonly found on caged tiles where fleshy algae dominated, whereas gastropods and polychaetes were more common in the presence of calcified algae. Because of the profusion of microinvertebrates recorded in this study, algal biomass recorded for the caged treatments may actually be underestimates of true treatment effects if the tiles had been completely removed from herbivory (assuming that some of these invertebrates were grazers). However, the number of microinvertebrates continued to increase with algal biomass over time suggesting that the invertebrate effects were not large enough to significantly depress algal standing crop to control levels. The overall treatment effects observed here were consistently large regardless of microinvertebrate abundance.

Algal blooms on tropical reefs have been attributed to either eutrophication (Lapointe 1997, 1999) or a reduction in herbivory via overfishing or disease (Hughes and Connell 1999). It is often difficult to pinpoint the exact cause of any major phase shift on a reef due to the complex nature of these ecosystems and the lack of adequate and consistent long-term data. The past history and combined effects of multiple stressors on tropical reefs must be examined in order to understand the underlying factors that influence community structure (Hatcher 1997; Hughes and Connell 1999; Miller et al. 1999). In order to assess the magnitude that various stressors may have on reef ecosystems, we need to continue conducting manipulative field experiments that address these factors in conjunction and alone. This research demonstrates that both bottom-up and top-down factors alone can influence algal standing crop and community composition. When both biotic and abiotic factors are examined simultaneously, however, the effect can be much larger than that of either factor alone.

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