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The effects of top–down versus bottom–up control on benthic coral reef community structure

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Abstract While climate change and associated increases in sea surface temperature and ocean acidification, are among the most important global stressors to coral reefs, overfishing and nutrient pollution are among the most significant local threats. Here we examined the independent and interactive effects of reduced grazing pressure and nutrient enrichment using settlement tiles on a coral-dominated reef via long-term manipulative experimentation. We found that unique assemblages developed in each treatment combination confirming that both nutrients and herbivores are important drivers of reef community structure. When herbivores were removed, fleshy algae dominated, while crustose coralline algae (CCA) and coral were more abundant when herbivores were present. The effects of fertilization varied depending on herbivore treatment; without herbivores fleshy algae increased in abundance and with herbivores, CCA increased. Coral recruits only persisted in treatments exposed to grazers. Herbivore removal resulted in rapid changes in community structure while there was a lag in response to fertilization. Lastly, re-exposure of communities to natural herbivore populations caused reversals in benthic community trajectories but the effects of fertilization remained for at least 2 months. These results suggest that increasing herbivore populations on degraded reefs may be an effective strategy for restoring ecosystem structure and function and in reversing coral–algal phase-shifts but that this strategy may be most effective in the absence of other confounding disturbances such as nutrient pollution.

Keywords Algae · Nutrients · Herbivory · Phase-shifts · Restoration

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Introduction

Coral reefs around the globe have suffered significant declines over the last several decades where landscapes once dominated by reef-building corals have increasingly become dominated by fleshy turf and/or macroalgae (Hughes 1994; Ledlie et al. 2007; McCook 1999; Pandolfi et al. 2003). These phase-shifts or alternate stable states are believed to be the result of both global- and local-scale impacts. Globally, massive coral bleaching events associated with increases in sea surface temperature can result in coral mortality and subsequent algal overgrowth (Diaz-Pulido and McCook 2002). However, there is evidence that reefs can recover from such events in the absence of other forms of disturbance (Grottoli et al. 2006). Locally, coral loss can result from numerous anthropogenic activities. Most notably, increases in dissolved inorganic nutrients and/or reductions in the numbers of herbivores may allow
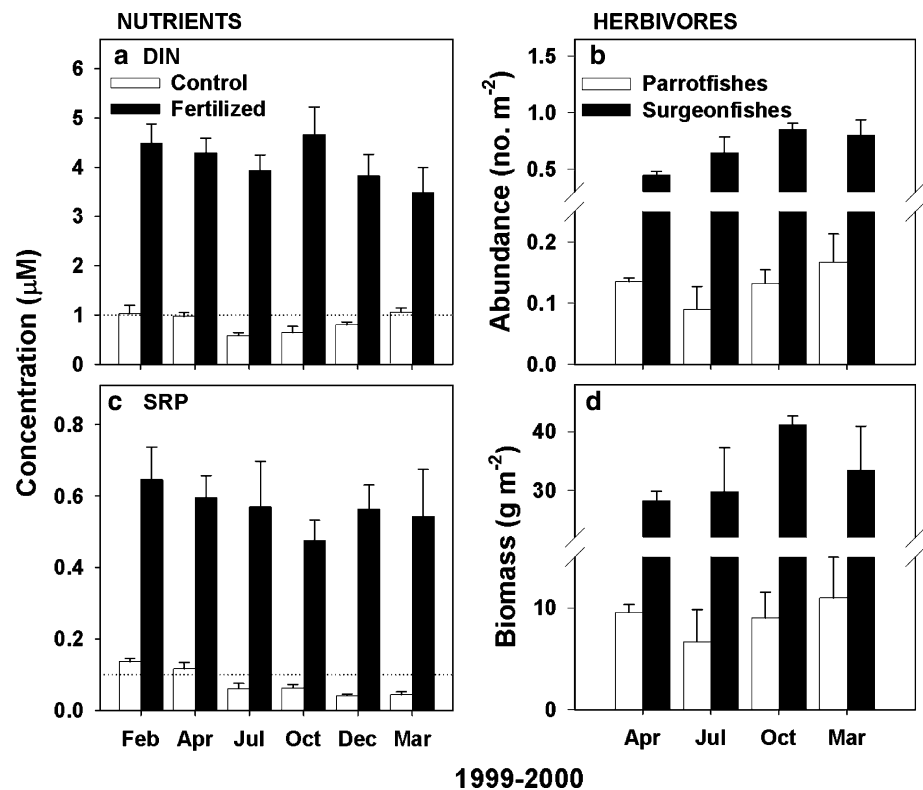
algae to outcompete and overgrow living coral (McCook et al. 2001). However, the relative importance of top–down versus bottom–up control in regulating benthic reef community structure has been the subject of debate (Hughes et al. 1999; Lapointe 1999). Single-factor laboratory and field manipulations have found that nutrient enrichment alone can increase algal growth rates and enhance various physiological parameters (e.g., photosynthetic rates and enzymatic activity; Lapointe 1997; Larned 1998; Littler et al. 1991) and reductions in herbivory often lead to increases in fleshy algal abundance and/or biomass (Carpenter 1986; Lewis 1986). But how these two factors interact in natural reef settings has been less clear.

Littler and Littler (1984) proposed the relative dominance model (RDM), a conceptual framework that predicts the dominant benthic photosynthetic functional group that would result from long-term exposure to differing levels of inorganic nutrients and herbivory (see Fig. 1 in Littler and Littler 1984). Despite the numerous factorial experiments that have simultaneously manipulated these top–down and bottom–up factors on coral reefs (Belliveau and Paul 2002; Burkepile and Hay 2009; Diaz-Pulido and McCook 2003; Hatcher and Larkum 1983; Jompa and McCook 2002; McClanahan et al. 2003; Miller et al. 1999; Smith et al. 2001; Sotka and Hay 2009; Thacker et al. 2001) few have actually examined changes in benthic species and/or functional group abundances and the results have been variable. Further, all of these factorial studies were: (1)

conducted on moderately to severely degraded, algal or cyanobacterial-dominated reefs with little to no living coral (0–16% cover); (2) conducted on relatively short time scales (12–200 days); and/or (3) performed under highly variable ambient conditions with differing or unquantified levels of herbivory and nutrient concentrations making cross-comparisons difficult. In a recent meta-analysis of some of these studies, herbivores were shown to have larger effects than nutrients on algal biomass (Burkepile and Hay 2006). However, in order to truly evaluate the RDM and to understand how overfishing of herbivores and nutrient pollution influence coral reef communities, studies need to be conducted over relevant time scales, on coral-dominated reefs with low nutrient concentrations and naturally high levels of herbivory. Results of such experiments are needed to inform management and conservation of coral reefs as the dominance of different functional groups will largely determine the function of the reef community as corals and crustose coralline algae (CCA) are reef builders and contribute to the structural complexity that many reef organisms depend upon while turf and macroalgae are faster growing, can facilitate bioerosion, and may inhibit coral growth and settlement (Birrell et al. 2008).

With the accelerated decline in reef health, it is also important to identify factors that may facilitate phase-shift reversals away from an algal-dominated state and towards a state that promotes coral recruitment and recovery (Bellwood et al. 2004; Pandolfi et al. 2005). The recent

increase in abundance of the herbivorous sea urchin, *Diadema antillarum,* on some shallow reefs in the Caribbean has resulted in reduced macroalgal cover and increased coral recruitment (Carpenter and Edmunds 2006). Experimental data from the Great Barrier Reef indicate that, after 3 years of herbivore exclusion, a benthic community dominated by *Sargassum* could be reversed (with cage removal) to dominance by coral and epilithic algae (Bellwood et al. 2006). However, it remains unclear how nutrient availability may interact with herbivores in the process of reef recovery or restoration. Will communities that have been exposed to significant nutrient enrichment and herbivore removal eventually revert back to a coral-dominated state once herbivores are returned?

The goals of this study were to determine the effects of top–down and bottom–up control on a coral-dominated reef using a long-term factorial field experiment on a reef slope on the island of Hawai'i with naturally abundant herbivores and low nutrient concentrations. We specifically tested how fertilization and herbivore removal independently and interactively affect benthic community composition. Following nearly a year and a half of exposure to experimental treatments, herbivore-exclusion cages were removed and communities were assessed to determine the effects of herbivore re-exposure on experimental communities with and without nutrient enrichment.

Materials and methods

Study site

This study was conducted on the reef slope at Puako Reef (19°58.28′N, 155°50.70′W) on the leeward side of the island of Hawai'i (Fig. S1). The nearshore waters of the leeward coast of Hawai'i contain some of the richest coral reefs and associated fish and invertebrate faunas in the Hawaiian Islands. Puako is an enforced Fisheries Management Area where net and aquarium fishing are prohibited. This study was conducted within a 600-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 ($\sim$70%, dominated by *Porites compressa* and *Porites lobata*), with an abundant herbivore community and fairly low levels of water column nutrients (Smith et al. 2001).

Experimental design

A randomized factorial block design with six replicates was used to test the effects of nutrient enrichment and herbivore exclusion on benthic reef community dynamics. Flat PVC (polyvinylchloride) tiles (50 cm^2) were used as

the experimental surfaces following experiments conducted by (Hixon and Brostoff 1985). PVC was chosen because it is chemically inert, can be easily manipulated to mimic the texture of natural substrates, supports biotic assemblages similar to the surrounding natural substrata (Hixon and Brostoff 1985) and provides for a controlled surface across treatments. Prior to beginning the experiment, all tiles were rough sanded until the surface resembled the texture of limestone. Twelve tiles were affixed to a plastic-coated galvanized metal rack (24 racks, 288 tiles) using small cable ties threaded through two ($\sim$1.3 mm) holes drilled into each tile and racks were affixed to the reef using large cable ties. Experimental blocks consisted of 10 × 10-m plots divided into four 5 × 5-m subplots. Each subplot contained two racks of tiles one for biomass estimates (see Smith et al. 2001) and the other to quantify community structure and each was randomly assigned to one of four treatments: control, nutrient enrichment, herbivore exclusion or both nutrient enrichment and herbivore exclusion (Fig. S1). Treatments were assigned to each block randomly and independently in January 1999. Monthly samples were collected beginning in February 1999 where one tile from each rack was randomly collected and placed in separate pre-labeled plastic bags prior to analysis.

Nutrient enrichment

Nutrient enrichment was accomplished by filling 20-cm-diameter unglazed clay pots (Hatcher and Larkum 1983) with 1.4 kg of United Horticultural Supply turf fertilizer (11% NH$_4$, 10% NO$_3$, 7% P$_2$O$_5$). Pots were inverted and secured with epoxy to PVC holding plates. The drainage hole in each pot was closed with a rubber stopper to provide slow diffusion of nutrients through the porous surfaces. Each month, pots were retrieved by divers, emptied, cleaned and refilled with fertilizer. Pots were placed 0.25 m from the experimental racks and all fertilized plots were at least 5 m from unfertilized plots. Nutrient concentrations were determined for both ambient and enriched plots throughout the experiment. Water samples were collected the day after enrichment from just above the settlement tiles (0.25 m from the pots) for enriched plots and outside of the experimental area (25 m away) for ambient samples every 2 months. Twice during the study (April and October) samples were collected 0.25 m from the pots immediately before fertilizer replacement to determine if enrichment was still evident after 30 days of deployment. Water samples were collected using sterile 50-ml syringes, filtered using a GF/C filter, rinsed in triplicate and stored in acid-washed 100-ml polypropylene bottles. Samples were stored on ice until returned to shore at which point they were frozen until analyzed for nitrate,

ammonium and phosphate concentrations using a Technicon autoanalyzer II at the University of Hawai'i.

Herbivore exclusion

Herbivore-exclusion cages ($35 \times 35 \times 35$ cm) were constructed from galvanized hardware cloth (2.5 cm diameter). Cages were secured over the top of the tile racks using cable ties to exclude medium to large sized grazing sea urchins and fishes. Cages were cleaned every 2 weeks by divers and were replaced half way through the study. Cage controls were not used but neither light nor flow regimes were found to differ in and outside of cages (Smith et al. 2001). Fish and macroinvertebrates were surveyed 4 times throughout the experiment to quantify the abundance and biomass of herbivores (surgeonfish, parrotfish and sea urchins) using standard belt transects (25×4 m, $n = 4$ transects per survey).

Re-exposure to natural herbivore populations

After 420 days of experimental manipulation, herbivore-exclusion cages were removed to determine if and how exposure to herbivores would alter benthic community structure following long-term caging and nutrient treatments. All experimental tiles were left in situ, exposed to grazers for approximately 8 weeks while fertilization continued. The experiment was terminated and all tiles were removed in May 2000.

Response variables

Following collection in the field, all tiles were stored in individual pre-labeled bags in 4% buffered formalin in seawater prior to analysis. Samples were transported to the University of Hawai'i and were analyzed for community composition. All samples were rinsed with seawater to remove sediment and mobile invertebrates. A plastic frame with a 4×4-cm monofilament grid was constructed to fit over the top of the tiles to distinguish 16 cells on each tile. Each cell was examined and the abundance of all visible species was recorded using a stereomicroscope. For further taxonomic confirmation, individual algal samples were collected under a dissecting microscope and permanent slides were made and examined using a compound microscope. All organisms that recruited to the tiles were categorized into the following functional groups: turf algae (all uni- and multiseriate filamentous species generally <2 cm in height and cyanobacteria), macroalgae (upright and encrusting species), crustose coralline algae (CCA) (encrusting Corallinales), and sessile invertebrates (including scleractinian corals).

Data analysis

For abundance of individual functional groups, four-way mixed model ANOVAs were used with nutrients, herbivores and time treated as fixed effects, while block was treated as a random effect. Functional group percent cover data were arcsin square root transformed to satisfy the assumptions of homogeneity of variances and normality of residuals. A conservative test for compound asymmetry was used for "time" to address the auto-correlated nature of time series data (although not true repeated measures).

To determine if community structure (at the species and functional group levels) varied across treatments, a multivariate randomization procedure was used in PRIMER-e v6. Bray-Curtis similarity measures were calculated for all communities across treatments, times and blocks. These distance matrices were then analyzed using PERMANOVA which analyzes distance measures in a linear model with categorical variables to test for significance of factors using 9,999 permutations. Pairwise tests among factors were analyzed to determine if and when treatment effects caused significant differences in community structure. Non-metric multidimensional scaling (nMDS) ordination was used to visualize similarities in community structure across treatments and over time. The nMDS procedure displays samples in two-dimensional space by preserving the ranked similarities among all samples; thus, the closer together two points are the more similar they are in composition. In order to view how communities changed in relation to treatments over time, successional trajectories were plotted using the multivariate centroid for each time by treatment combination using principal coordinates analysis (Anderson and Willis 2003).

ANOVAs were used to test whether the return of herbivores affected benthic functional group abundance after 420 days of herbivore exclusion. PERMANOVA was used to determine if and how communities changed after cages were removed and specific pairwise comparisons tested whether herbivore effectiveness varied according to nutrient treatment.

Results

Effectiveness of experimental treatments

Nutrient treatments resulted in significant enrichment of both dissolved inorganic nitrogen (0.85 µM $\pm$ 0.57 vs. 4.11 µM $\pm$ 0.17 for control and enriched plots, respectively) and phosphorus (0.077 µM $\pm$ 0.009 vs. 0.57 µM $\pm$ 0.035 for control and enriched plots, respectively; Fig. 1a, c). After 30 days of nutrient enrichment both DIN and SRP declined in concentration but remained elevated in

Fig. 2 Abundance (mean percent cover, ±1 SE) of benthic functional groups including **a** turf algae, **b** invertebrates, **c** macroalgae, **d** open space, **e** crustose coralline algae (*CCA*), and **f** scleractinian coral in control (*white circles*), fertilized (*black circles*), herbivore-excluded (caged, *white triangles*) and fertilized and caged (*black triangles*) treatments during monthly surveys from February 1999 up to and including May 2000. Cages were removed from treatments in March 2000, indicated by the *vertical line* and *shaded area*
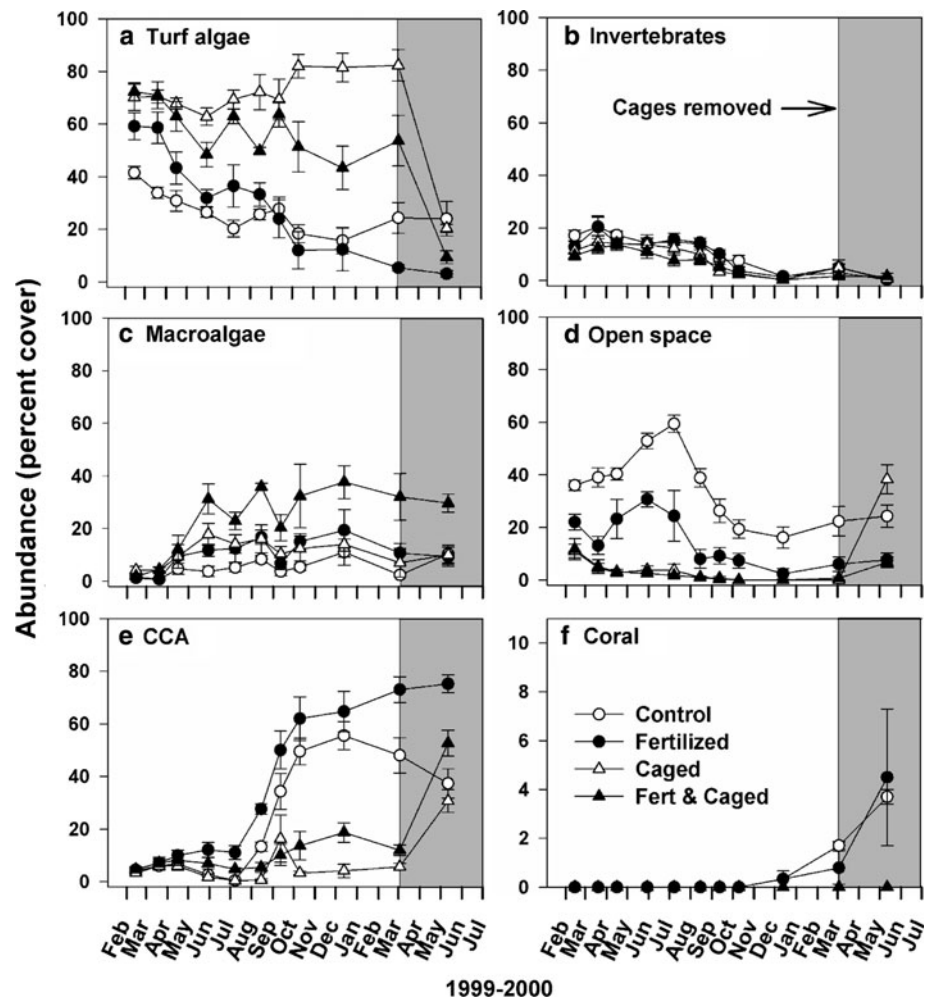
comparison to unfertilized control plots (Fig. S2). Caging treatments prevented large mobile herbivores from accessing experimental tiles. Results of repeated surveys over the experimental area identified that the fish community at Puako reef was dominated by herbivores, primarily browsers and excavating grazers (Table S1; Fig S3). The most abundant species were the surgeonfishes *Ctenochaetus strigosus* and *Zebrasoma flavescens* and the parrotfish *Chlorurus sordidus*. Total abundance and biomass of herbivorous fishes at Puako was relatively high (Fig. 1b, d) in comparison to other heavily fished reefs in the Pacific but below values reported from protected reefs in the north-western Hawaiian Islands (Friedlander and DeMartini 2002; Jennings and Polunin 1997). The sea urchins *Tripneustes gratilla* and *Heterocentrotus mamillatus* were also common.

Effects of nutrient enrichment and herbivore removal on benthic communities

A total of 118 species of benthic algae and invertebrates were identified (macroalgae 24, turf algae 82, cyanobacteria three, CCA three, sessile invertebrates six including

two species of coral) on the experimental tiles (Table S2). Four-way ANOVAs of percent cover data showed different responses among the functional groups (Table S3). Macroalgae were most common on surfaces that were fertilized and from which herbivores were excluded; turf algae were most abundant on surfaces from which herbivores were excluded. CCA and benthic invertebrates were most common on surfaces exposed to grazers. Uncolonized space was most common on control surfaces (Fig. 2).

Significant positive fertilization effects were found for all functional groups except for turf algae for which negative effects were detected. Significant but variable caging effects were found for all functional groups; turf and macroalgae were enhanced by herbivore removal while CCA, invertebrates and uncolonized space were enhanced in the presence of herbivores. Many caging × time and fertilization × time interactions were also significant indicating that some functional groups responded differently to the treatments over time. While initially variable, most functional groups began to stabilize after about 12 months (Fig. 2). Functional groups that are known to grow more slowly and are often dependent on specific

settlement cues [i.e., CCA for corals (Harrington et al. 2004)] showed the most pronounced delays in recruitment and abundance.

Multivariate analysis of benthic community composition (for both species and functional groups) revealed that nutrient enrichment and herbivore exclusion both had significant effects on community structure (Table S4). Significant interactions between the two factors and subsequent pairwise comparisons indicated that each treatment combination resulted in unique experimental communities. The random block factor was significant for the species-level analysis but not for the functional-group analysis, showing that unique species assemblages were present at small spatial scales (e.g., within 100 m^2), but assemblages were similar among blocks at the coarser functional group level.

Community composition within treatments also changed over time as indicated by the time × treatment interactions (Table S4) and detailed comparisons of these interactions (Table S5) show that community structure changed rapidly (in less than 1 month for both analyses) in response to caging treatments but the community-wide response to nutrient enrichment occurred more slowly (3–4 months). These differences were largely due to the rapid settlement and domination of early colonizing filamentous turf algae in the caging treatments. Uncaged treatments were initially dominated by a more mixed assemblage of invertebrates and turf algae with areas of uncolonized space, but were later dominated by slower growing organisms such as CCA and scleractinian corals (Fig. 3). Initially, communities in the fertilized and unfertilized treatments were similar and were colonized by filamentous turf algae but eventually CCA (on uncaged surfaces) and macroalgae (on caged surfaces) increased in abundance with fertilization while uncolonized space and turf algae (on uncaged surfaces) dominated unfertilized treatments. At the end of over a year of experimental manipulation community structure in each treatment was unique (Fig. 3). As shown in the nMDS plot of the treatment by time centroids, experimental communities in all four treatment combinations diverged and had unique successional trajectories over time (Fig. 4).

Re-exposure to natural herbivore populations:

Increased grazing pressure associated with the removal of exclusion cages led to significant changes in benthic community composition as indicated by the lack of caging effects (no residual effects of caging present) for many of the different functional groups (Table S6). Cage removal led to decreases in turf algal abundance and benthic (non-coral) invertebrates, and increases in CCA and uncolonized space (Fig. 2). Significant caging effects were detected for CCA and nearly significant effects for macroalgae,
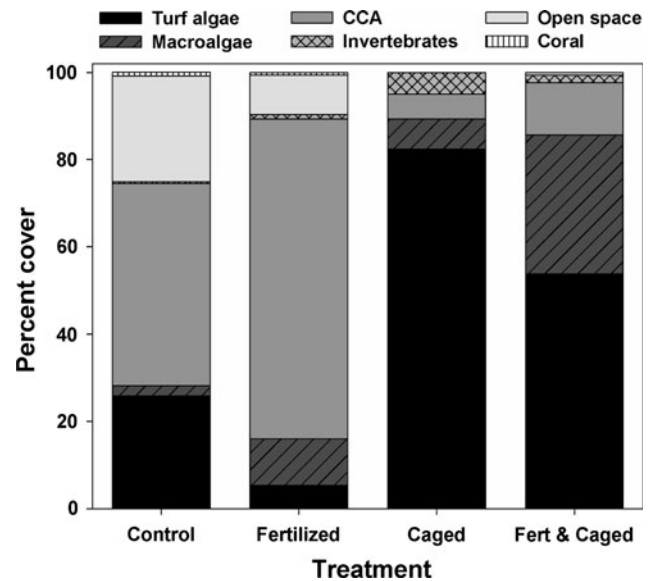
Fig. 3 Community structure in the four experimental treatments (control, fertilized, caged, fertilized and caged) in March 2000 at the end of 13 months of manipulation. Data shown are the mean values for each functional group which are defined in the text (see Fig. 2 for SE)
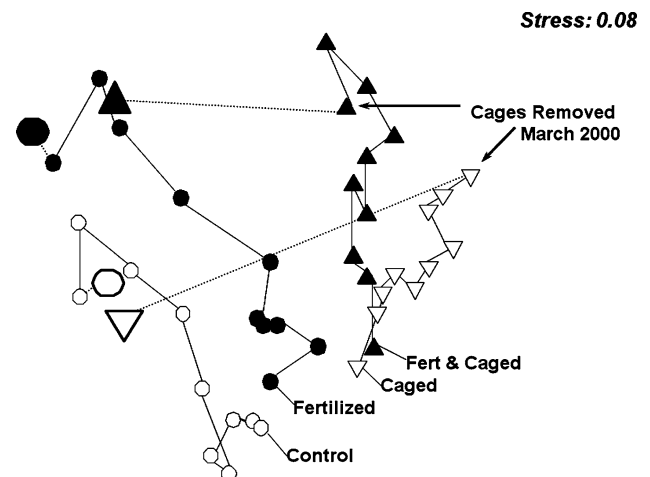
Fig. 4 Successional trajectories showing how the similarity of communities changed over time in the four treatments (control, fertilized, caged, fertilized and caged). Each point represents the multivariate centroid calculated from principle coordinates analysis for each treatment by time combination. These centroids were then ordinated using non-metric multidimensional scaling to visualize how community similarity changed over time across the different treatments. Points that are closer together in ordination space are more similar in terms of community functional group abundance. *Stress* is a measure of how well the multivariate community data are displayed in two dimensional space; values less than 0.2 are considered a good fit. Sampling began in February 1999 (the treatment labels indicate the first data point for each treatment) and ended in May 2000 (indicated by the *enlarged data points*). Cages were removed from caged treatments in March 2000

indicating that herbivores did not significantly reduce, and in fact, enhanced the abundance of these groups on previously caged tiles. Multivariate analyses indicated that community structure remained unique despite cage removal (Table S7); however, these differences were entirely due to the interaction term where, after exposure to herbivores, communities in the caged-only treatments became more similar to control communities while assemblages in the caged and fertilized treatments became more similar to fertilized communities (Fig. 4; Table S7). Thus, exposure to herbivores significantly altered community structure but did not completely remove the effects of fertilization (Fig. 4) in the 2 months following cage removal.

Discussion

In the face of global change and associated impacts such as warming and acidification it has become increasingly important to identify the role of, and interaction between, local stressors in altering benthic coral reef community structure. While several other studies have examined the role of nutrients and herbivores on reefs, most have measured specific species responses (Diaz-Pulido and McCook 2003; Jompa and McCook 2002), changes in algal biomass, chlorophyll and/or nutrient content (Belliveau and Paul 2002; Hatcher and Larkum 1983; McClanahan et al. 2003; Miller et al. 1999; Smith et al. 2001; Thacker et al. 2001), and those that have measured changes in species assemblages (Burkepile and Hay 2009; McClanahan et al. 2003; Miller et al. 1999; Sotka and Hay 2009; Thacker et al. 2001) have done so in degraded or algal-dominated habitats. While these studies are valuable for understanding how algal communities may respond to herbivore removal and nutrient enrichment they do not provide any information about how these factors affect the competitive relationships between corals and different functional groups of algae. The ability to predict the response of coral reef communities to both global and local stressors requires that we understand how these factors alter community structure away from the desired coral-dominated state.

Our results show that after over a year of manipulation completely unique benthic assemblages had developed in each of the treatment combinations, identifying that top–down and bottom–up factors independently and interactively influence the structure and hence, the function of benthic reef communities. Specifically we found that under control conditions (with herbivores, without fertilization) CCA and uncolonized space dominated; in fertilized plots (with herbivores) CCA also dominated but they were more abundant than in control plots and macroalgae were also present; in herbivore-exclusion plots (without fertilization)

filamentous turf algae dominated; and finally, in plots with both herbivore exclusion and nutrient enrichment communities consisted of more mixed assemblages with fleshy turf and macroalgae as the dominant components (Fig. 3). Further, we found that reef building corals only colonized tiles exposed to herbivory highlighting the importance of grazers in facilitating coral recruitment. Grazers not only promoted coral and CCA abundance but also severely limited the abundance of turf and macroalgae (combined cover <30%). We also found that macroalgae showed a positive response to fertilization in both open and caged plots (larger effects inside cages) suggesting that nutrient enrichment can influence benthic macroalgal abundance even when herbivores are present. Based on these findings, our study partially supports the RDM (Littler and Littler 1984); however, more time would be needed to adequately test this model as it can take upwards of 50 years for corals to become dominant on new lava substrata in the Hawaiian Islands (Grigg and Maragos 1974). Finally, we found that increased herbivory can facilitate rapid reversals in benthic successional trajectories away from fleshy algal dominance, but herbivores alone were not able to completely ameliorate the effects of nutrient enrichment (Figs. 2, 4) in the 2 months that the herbivores had access to the previously caged communities. It is, however, possible that if given a longer duration the natural herbivore community could have reversed community successional trajectories even in the presence of nutrient enrichment.

While other studies have examined the simultaneous effects of top–down and bottom–up control on benthic reef communities with the majority showing large effects of herbivores little to no effects of nutrient enrichment (summarized by Burkepile and Hay 2006), our results suggest that these studies may not have been conducted on ecologically relevant time scales. Here we show that both fertilization and herbivore exclusion can alter benthic community structure but they do so at different temporal scales. Reduced herbivory led to rapid changes in benthic communities (1 month), but the effects of nutrient enrichment were not realized until 3–4 months. Therefore, the lack of strong nutrient-enrichment effects noted in other studies may simply reflect the short duration of these experiments. A recent nutrient-enrichment study conducted across a natural gradient in herbivore abundance over 24 months found similar benthic algal responses to those reported here (Littler et al. 2006) highlighting the need to conduct experiments on temporal scales that are consistent with the growth rates and successional sequence of the species or functional groups of interest. To date, this study is the only factorial nutrient-enrichment/herbivore-removal study that has been conducted for long enough and under the appropriate conditions to facilitate coral larval settlement and growth, albeit on artificial settlement tiles.

Clearly more data are needed to understand how naturally coral-dominated benthic communities respond to these top–down and bottom–up manipulations.

Most grazer-exclusion studies have found that herbivores primarily control fleshy algal biomass and cover (Burkepile and Hay 2009; Carpenter 1986; Diaz-Pulido and McCook 2003; Hatcher and Larkum 1983; Hughes 1994; Hughes et al. 2007b; Littler et al. 2006; McClanahan et al. 2003; Miller et al. 1999; Smith et al. 2001; Sotka and Hay 2009; Thacker et al. 2001) with the degree of control varying across herbivore guilds (Carpenter 1986) and algal species assemblages (Lewis 1986; Mantyka and Bellwood 2007; McClanahan et al. 2003). The specific composition of the herbivore community will also affect benthic community structure as feeding mode (scraping, excavating and browsing) and preferred food resources (algal species and functional group) vary greatly among species. Even within a guild, particular herbivore species can differentially affect benthic community composition (Bellwood and Choat 1990; Bellwood et al. 2006; Burkepile and Hay 2008; Carpenter 1986; Hoey and Bellwood 2007). A recent study by Burkepile and Hay (2008) found that maintaining herbivore species richness may be critical for preserving coral reefs, because complementary feeding by different herbivores produces positive, but indirect, effects on corals. Other studies have suggested that herbivore species richness may be critical for the resilience of reefs by conferring greater functional redundancy of each feeding type (Nystrom 2006 but see Bellwood et al. 2003). Many eastern Pacific and Caribbean reefs are thus thought to be functionally compromised (Bellwood et al. 2004) as they have low herbivore species richness (Bellwood et al. 2005) and lack siganids and batfishes that have been shown to have large impacts on the benthos in the Indo-Pacific (Bellwood et al. 2006; Mantyka and Bellwood 2007).

Herbivore removal has consistently been shown to promote opportunistic filamentous algae which, in some cases, are eventually outcompeted or replaced by various species of macroalgae (Carpenter 1986; Miller et al. 1999; Thacker et al. 2001). Other studies have shown that reduced herbivory can increase the number and growth of macroalgal propagules (Diaz-Pulido and McCook 2003). Communities dominated by fleshy algae trap sediments (Smith et al. 2001), abrade, shade and smother corals (Box and Mumby 2007; McCook et al. 2001), can serve as vectors of specific diseases (Nugues et al. 2004), and may cause more general forms of coral mortality by releasing compounds that enhance microbial activity and cause hypoxia on coral surfaces (Smith et al. 2006). Thus, herbivores are highly important for promoting the abundance of reef-building organisms and in maintaining a calcifying, reef-accreting environment.

Nutrient-enrichment studies have resulted in much more variable benthic responses likely due to a number of factors including different spatial scales, variable ambient nutrient concentrations, low levels of fertilization, different flow regimes or flux and inadequate time scales. Typically, when herbivores are present, the effects of nutrient enrichment tend to be less pronounced or even undetectable (Burkepile and Hay 2006; Miller et al. 1999; Thacker et al. 2001) because herbivores often consume any excess production caused by fertilization, but our study shows that, if given enough time, differences in community composition can arise. With nutrient enrichment, slow-growing CCA and encrusting fleshy macroalgae eventually increased in abundance relative to unfertilized communities. These increases in CCA in the fertilized-only treatment may be the result of higher consumption rates of fleshy algae and thus reduced competition between fleshy algae and CCA on these tiles as some studies have shown that herbivores may preferentially consume nutrient-enriched algae (Boyer et al. 2004; Burkepile and Hay 2009). When herbivores are removed or reduced, nutrient enrichment may become more important and cause synergistic effects as seen here and in a recent meta-analysis (Burkepile and Hay 2006). Without herbivores, nutrient enrichment has been shown to cause increases in algal physiological parameters (photosynthetic and enzymatic rates) and growth rates (Lapointe 1997; Larned 1998; Littler et al. 1991) and community dominance often shifts from turf algae to one or a few weedy species such as *Ulva* or *Cladophora* (Lapointe 1997; Smith et al. 2005). Thus the effects of nutrients on benthic reef communities are clearly important and the degree of importance seems to be driven by the abundance of herbivores.

While experimental studies are needed to determine cause and effect in natural communities it is difficult to control for all possible confounding effects and completely avoid experimental artifacts. Many studies on coral reefs have used artificial settlement tiles as experimental units because they are easy to manipulate in comparison to the natural benthos. In our study we used tiles constructed out of PVC, a chemically inert artificial surface that allows for easy control and manipulation. PVC has been found to promote the abundance of CCA on short time scales in other studies (Adey and Vassar 1975) but we found strong differences in benthic communities among our treatments suggesting that the settlement surfaces were not driving these differences. Nonetheless, our study did use non-natural substrata and may be constrained by: (1) unnatural trajectories due to the lack of surface porosity and endolithic organisms, (2) differences in grazing activity from herbivores as planar surfaces make algae more susceptible to grazing by *Scarus* spp. than *Chlorurus* spp., and (3) limited spatial scales. Despite these limitations, artificial

tiles do control for any variability that may exist in natural substrata and have been commonly used in hundreds of ecological studies.

Authors of a recent global synthesis have suggested that coral to macroalgal phase shifts are not as common as scientists tend to believe, and because of the lack of macroalgal dominance on reefs around the world, they conclude that coral reefs must be more resilient than previously thought (Bruno et al. 2009). Based on the data reported here and numerous other studies summarized by Birrell et al. (2008) we believe that fleshy turf algae may be as or more detrimental to corals than larger macroalgae. Our data show that corals and CCA are much less abundant, or not present at all under conditions that promote turf algal dominance. Vermeij and Sandin (2008) recently showed that coral larvae are less likely to survive if they are adjacent to turf algae and Barott et al. (2009) have documented that coral surfaces in direct contact with turf algae are often hypoxic, suggesting that coral mortality may be occurring at these interaction zones. Therefore, we suggest that coral–algal phase shifts should be thought of as shifts away from calcifying, reef-accreting communities dominated by corals and CCA to communities dominated by faster growing fleshy turf and macroalgae. The lack of dominance by macroalgae is not an ideal indicator of reef resilience as this metric does not provide any information about how the communities are actually structured. Perhaps a better way to gain insight into the resilience of a particular reef is to examine the abundance of corals, CCA and coral recruits as these organisms (or life stages) are all necessary components of the ability of a reef to recover from a disturbance event.

The large continuum that exists in nature among nutrient-enriched communities with and without herbivores seems to provide evidence against a "universal" nutrient concentration that will cause fleshy algal blooms as proposed by Lapointe (1999). The Nutrient threshold hypothesis suggests that, regardless of herbivore abundance, algal blooms will occur at 1.0 μM DIN and 0.1 μM SRP. However, herbivores are known to respond to increases in primary production by increasing consumption rates (Worm and Lotze 2006) and preferentially feeding on nutrient-enriched algae (Boyer et al. 2004); given enough time, herbivore populations may also respond by increasing in number. Further, many reefs exist in naturally high-nutrient environments (Leichter et al. 2003) and in the absence of human disturbance, remain dominated by corals. Hypothetically, if such nutrient thresholds did exist for reef communities, similar thresholds should exist for the level of herbivory. For example, a given number (or biomass) of herbivores should be able to consume a predictable amount of algal production. Some important questions that remain are: how many herbivores are enough to

maintain a community dominated by reef-building calcifiers? How do nutrients alter these dynamics? Are there specific herbivory to productivity ratios that are needed to maintain a coral-dominated state?

As phase-shifts from coral to algal dominance on tropical reefs increase around the globe, questions related to the potential for reef restoration have emerged. It has been suggested that increasing herbivore populations may help to reverse these community trajectories to a state that would promote higher coral and CCA abundance (Hughes et al. 2007a; Mumby et al. 2007a). A recent study in Australia showed that reef communities that had become dominated by macroalgae after 3 years of experimental herbivore exclusion underwent rapid reversal to dominance by coral and epilithic algae following cage removal (Bellwood et al. 2006). Previously abundant *Sargassum* populations were essentially extirpated by a "sleeping functional group" of fishes, namely the batfish *Platax pinnatus*, which had previously been regarded as an invertivore. This sort of trophic and dietary flexibility in coral reef organisms is important and may explain why true multi-level trophic cascades have rarely been documented in these systems. Our study corroborates and adds to the results of Bellwood et al. (2006) by providing an experimental nutrient-enrichment component to test whether an increase in herbivores could compensate for any nutrient-enrichment effects. We found that herbivores were able to reverse community trajectories in 2 months in the absence of fertilization but not entirely in the nutrient-enriched communities. Further, we found that community structure remained unique in treatments that had been fertilized, largely due to the abundance of apparently unpalatable macroalgae (e.g., *Lobophora*, *Peyssonnelia*, *Codium*) and CCA that were not consumed. These results suggest that restoring herbivore populations on reefs that have been overfished may help to reverse phase-shifts but if other impacts such as nutrient pollution exist, herbivore replenishment may not be the only key to recovery.

Results of this and several other studies have identified similarities and differences in how coral reef communities respond to nutrient enrichment and the removal of grazers, experimental simulations of anthropogenic impacts on reefs. However, scaling the results of these small-scale experiments up to the reef community or landscape level is difficult and should be treated with caution. We still lack a basic understanding of how species assemblages change across gradients in these variables. Specifically, how do the effects of herbivores vary across different population densities, size classes or according to guild composition (browsers, scrapers, excavators; urchins vs. fishes)? How does algal productivity and reef community structure vary across a range of nutrient concentrations? Lastly and most importantly, how do nutrients, herbivores and benthic

communities dynamically interact? Some of these questions have been explored conceptually and using simulation models (Mumby et al. 2007b) but more quantitative field data are needed. In the face of global change and accelerating reef loss we need to gain a better understanding of the factors that are necessary to both prevent and reverse community wide phase-shifts. How many herbivores are enough and what are appropriate target concentrations for nutrients given naturally variable rates in herbivory? By identifying the dynamic relationships between nutrients, herbivores and coral reef community structure we may be able to develop more effective management and restoration strategies to promote and preserve the reef-building capacity of these systems.

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