

EPIPHYTIC CYANOBACTERIA MAINTAIN SHIFTS TO MACROALGAL DOMINANCE ON CORAL REEFS FOLLOWING ENSO DISTURBANCE

PEGGY FONG,^{1,3} TYLER B. SMITH,^{2,4} AND MATTHEW J. WARTIAN¹

¹*Department of Ecology and Evolutionary Biology, University of California Los Angeles, 621 Young Drive South, Los Angeles, California 90095-1606 USA*

²*Division of Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149 USA*

Abstract. Macroalgal dominance of some tropical reef communities in the Eastern Pacific after coral mortality during the 1997–1998 El Niño Southern Oscillation (ENSO) was facilitated by protection from herbivory by epiphytic cyanobacteria. Our results do not support that reduction in number of herbivores was a necessary precursor to coral reef decline and shifts to algal reefs in this system. Rather, macroalgae dominated the community for several years after this pulse disturbance with no concurrent change in herbivore populations. While results of microcosm experiments identified the importance of nutrients, especially phosphorus, in stimulating macroalgal growth, nutrient supply alone could not sustain macroalgal dominance as nutrient-stimulated growth rates in our in situ experiments never exceeded consumption rates of unprotected thalli. In addition, thalli with nutrient-enriched tissue were preferentially consumed, possibly negating the positive effects of nutrients on growth. These tropical reefs may be ideal systems to conduct experimental tests distinguishing phase shifts from alternative stable states. Shifts were initiated by a large-scale disturbance with no evidence of a changing environment except, perhaps, dilution in herbivory pressure due to increased algal cover. Community establishment was most likely stochastic, and the community was likely maintained by strongly positive interaction between macroalgal hosts and cyanobacterial epiphytes that uncoupled consumer control of community structure.

Key words: *alternative stable states; coral reefs; facilitation; herbivory; macroalgal bloom; nutrients; phase shifts.*

INTRODUCTION

Investigating mechanisms causing and maintaining shifts among different states of ecological communities has been a central focus of research for many years (e.g., Estes and Palmisano 1974, Sutherland 1974). Current debate centers on whether these shifts are between alternative stable states or are phase shifts due to underlying differences in environmental conditions, and under what conditions shifts are stochastic or deterministic processes (e.g., Beisner et al. 2003, Bertness et al. 2004a, Petraitis and Dudgeon 2004a). Despite much debate, community shifts initiated by disturbance, frequently mediated by strong biotic interactions, and often sustained by accompanying changes in abiotic factors such as supply of nutrients or changes in physical habitat structure, have been documented in freshwater, terrestrial, and marine communities (reviewed in Schröder et al. 2005).

While most coral reef ecologists agree coral communities are undergoing worldwide declines with concurrent

shifts to algal domination, the underlying mechanisms causing and maintaining these shifts are hotly debated (e.g., Jackson et al. 2001, Aronson et al. 2003, Hughes et al. 2003, Pandolfi et al. 2003). Are they alternative stable states where two communities exist under the same set of environmental conditions, or phase shifts from one state to another caused by a threshold response to change in an environmental parameter? Most current evidence points to the latter for coral reefs (reviewed in Petraitis and Dudgeon 2004b), with some claiming that reduction in consumer populations via harvesting of herbivorous fishes is a necessary first step in this phase shift (e.g., Jackson et al. 2001). They reason that the force of herbivory is so strong in coral reef ecosystems with intact herbivore populations that herbivores virtually act as lawnmowers, limiting algal biomass accumulation and negating the impact of any other factor that may enhance algal productivity and growth, thus maintaining the competitive dominance of slower growing corals. Once herbivores are removed, faster-growing algae become competitively dominant and a phase-shift occurs. Others argue that reduced herbivory is not always needed to initiate a phase shift attributable to altered outcomes of competition. One alternative mechanism is for increased nutrient supplies to stimulate rapid growth and allow algae to escape control by herbivores, biomass to accumulate, a change in com-

Manuscript received 16 May 2005; revised 4 October 2005; accepted 22 November 2005. Corresponding Editor: P. D. Steinberg.

³ E-mail: pfong@biology.ucla.edu

⁴ Present address: Center for Marine and Environmental Studies, University of the Virgin Islands, 2 John Brewers Bay, St. Thomas, U.S. Virgin Islands 00802 USA.

petitive dominance from coral to algae, and ultimately a phase shift from coral to algae (Lapointe 1997).

A plethora of evidence supports the role of herbivores in limiting algal biomass on coral reefs; in contrast, the role of nutrients has been less well established (reviewed in Szmant 2002). Overall, results of laboratory and microcosm experiments demonstrate that reef algae are nutrient limited (e.g., Fong et al. 2003), while field experiments often have mixed results (e.g., Hatcher and Larkum 1983). Interpretation of these experiments is limited, in part, by the difficulty of relating results of laboratory or microcosm studies of the effects of nutrient addition to natural growth in high-energy, high-flow environments typical of reefs, and the related methodological challenge of effectively enriching *in situ* experiments in these same environments (reviewed in McCook 1999). In addition, a recent study suggests that, on the local scale, herbivores may selectively consume more opportunistic, fast-growing macroalgae that accumulate nutrient reserves in their tissues when enriched (Boyer et al. 2004), further confounding *in situ* enrichment experiments. There is similar evidence for selective consumption of enriched seagrass (McGlathery 1995). Thus, studies assessing the roles of both herbivores and nutrients in sustaining algal communities on coral reefs are important.

An alternative view from changes in top-down or bottom-up processes leading to phase shifts is that complex multiple stresses to coral communities may act alone or in concert to cause shifts to alternative community states on tropical reefs (Knowlton 1992, Aronson et al. 2003, 2004). For these shifts to be considered alternative stable states, theory requires that causative factors initiating changes must be pulse disturbances (Connell and Sousa 1983, Peterson 1984, Petraitis and Dudgeon 2004b; but see Beisner et al. 2003); coral reef examples include El Niño Southern Oscillation (ENSO)-related mortality (Glynn et al. 2001) and destructive fishing practices (Fox et al. 2005). Press forces that may act in concert with pulse disturbances to sustain algal dominance may include reduction in herbivory pressure and increases in nutrient supplies, resulting in the proliferation of opportunistic, fast-growing algae on newly opened space and/or dominance by algae that is physically or chemically defended from herbivory (reviewed in Knowlton 1992, Szmant 2002). Clearly, there is a need for studies that investigate the complex and potentially interacting ecological forces that maintain shifts to algal dominated tropical reefs after large-scale pulse disturbances.

Blooms of *Acanthophora spicifera* (Rhodophyta) covered by cyanobacterial epiphytes have been observed on several reefs in the Eastern Tropical Pacific since widespread coral mortality opened substrate for colonization during the 1997–1998 ENSO. These reefs were decimated by the 1982–1983 ENSO and suffered further coral mortality during the 1997–1998 event (Glynn et al. 2001). Bloom initiation coincided with La Niña conditions, with thermocline shoaling and mixing upwards

of nutrient-rich bottom water, but persisted for years past this environmental fluctuation. Herbivore populations have been monitored for over 25 years on Uva Island reef, with no overall trend of reduction in numbers (Glynn 1990, 2004). In this study, we quantified benthic dominance of the *A. spicifera*–cyanobacterial association on our two study reefs, and investigated several factors that may sustain their dominance after ENSO disturbance, including rates of herbivory, protection from herbivory by cyanobacterial epiphytes, and the potential for nutrient stimulation.

METHODS

Benthic cover of the *A. spicifera*–cyanobacterial association, total coral, and total algae on our study reefs in the Panamanian Gulf of Chiriquí was measured on Uva Island reef in 1999 and 2000 and on the Cavada Island reef in 2001 and 2002. The cyanobacterial epiphyte was putatively in the genus *Lyngbya*. Total algae was the sum of macroalgae, crustose corallines, and algal turfs. On Cavada reef, 1-m² quadrats were placed at regular intervals (5 m) along cross-reef-zone transects. On Uva reef, 1-m² quadrats were placed randomly along 30-m transects within reef zones in the southern portion of the reef. Percentage of cover was calculated by determining the cover category underlying 81 points within the 1-m² quadrat.

We assessed the importance of herbivory on biomass accumulation of *A. spicifera* by conducting two field experiments on our two study reefs. In February 2001 on Cavada reef, three areas (3–5 m apart) on the reef crest were haphazardly selected. Within areas, paired plots were assigned to either open or caged treatments. Within each plot, two thalli were marked with cable ties and height measured to the nearest millimeter. We did not remove epiphytes during this experiment. Cages were 20 × 20 cm (height × diameter) cylinders of high-density polyethylene with a mesh size of 1.4 cm (Memphis Net and Twine, Memphis, Tennessee, USA) attached to three rebar stakes driven into the substrate. The experiment lasted six days, when marked thalli were remeasured. Percent increase in height was averaged for the two thalli per plot, and the averages used in a paired *t* test to detect differences in means between caged and uncaged plots. A mark was lost from only one thallus, and in this case one change in height was used in the analysis. Another experiment was conducted on Uva Island reef in May 2000. *A. spicifera* thalli were collected from the bloom area, cleaned of macroepiphytes, placed in mesh bags, spun for 1 min in a salad spinner to remove excess water, and weighed. Samples of 5 g wet weight were cable tied together and attached to weighted ropes. Ropes with algae were anchored in seven different reef areas from the seaward reef base across the reef to the landward backreef; *n* = 7 replicates for each area. Herbivory rate was calculated as loss in grams over 24 hours. Data were analyzed with one-way ANOVA (with location as the factor) after being tested to be sure they

met ANOVA assumptions. Fisher's protected least significant difference (PLSD) tests were conducted after a significant ANOVA.

Two experiments were conducted to assess the effects of epiphytic cyanobacteria on growth of and herbivory rates on *A. spicifera* in the bloom area of Uva Island reef. In March of 2003, we chose 20 plots (25×25 cm) within the visually homogeneous rubble area dominated by algae covered in epiphytes. Epiphytes were gently removed (brushing by hand) from thalli in 10 randomly chosen plots, and left intact on algae in the remaining 10 plots. Percentage of cover of algae was estimated using the point-intercept method (determining the percentage of points in a grid that overlaid the *A. spicifera*–cyanobacteria association) initially and after five days and the change in percentage of cover was calculated. Heights of 16 randomly selected thalli in each plot were measured and averages calculated. Initial averages were subtracted from final averages to calculate the change in height per plot after five days. *T* tests were used to compare the mean change in percentage of cover and height between cleaned and epiphytized thalli.

To compare the potential cost of epiphytism (e.g., reduced growth due to shading, nutrient competition) to benefits of epiphytism as protection from herbivory for *A. spicifera*, in March of 2004 we conducted a 2×2 factorial experiment varying protection from herbivory (with vs. without cages) and removal of epiphytes (cleaned vs. epiphytized). Treatments were randomly assigned to plots within the rubble area where the bloom occurred. Because the rubble benthos was topographically complex, open-bottomed cages were not considered adequate to protect thalli from herbivores. Thus, cages (constructed as above) were 15×10 cm (height \times diameter) complete cylinders with both tops and bottoms, while open plots consisted of bottoms only; all experimental units were held to the benthos with rebar stakes. Three to four rubble pieces with attached algae were placed in each cage or on each open plot base, and heights of four or five algal thalli were measured to the nearest millimeter. After five days, the change in height was calculated as described in the last paragraph. Data were analyzed with two-way ANOVA after being tested to be sure they met ANOVA assumptions. Comparison of algal growth of cleaned vs. epiphytized thalli within cages provided an estimate of the costs of being epiphytized without the confounding effect of herbivory. Comparison of algal net growth in cleaned vs. epiphytized open plots subject to herbivores estimated the benefits of protection provided by the epiphytes. Cage controls consisting of cages with no tops for the epiphytized treatment only demonstrated that cage effects were not significant (*t* test comparing epiphytized open to cage control, $df = 13$, *t* value = 0.738, $P = 0.4737$).

We explored the role of nutrients in sustaining algal growth and biomass accumulation using three experimental approaches. To determine if nitrogen (N) or phosphorus (P) limited growth of *A. spicifera* collected

from the Cavada Island reef in May 2000, we conducted a 2×2 factorial experiment with five replicates. Experimental treatments were ambient seawater with addition of $20 \mu\text{mol/L NO}_3$, $2 \mu\text{mol/L PO}_4$, $20 \mu\text{mol/L NO}_3 + 2 \mu\text{mol/L PO}_4$, and an ambient seawater control (abbreviated as +N, +P, +N+P, and C, respectively). Experimental units were plastic jars containing 500 mL of treatment seawater and 5 g wet weight of algae. Algal thalli were collected, cleaned of macroepiphytes, weighed as before, and trimmed to the correct size to include several apical growing tips. Jars were placed in a random array in an outdoor flow-through water table to maintain ambient temperature. Because experimental units were static and not flow-through, this experiment should be considered a "bioassay," or a simple attempt to determine if N or P is limiting, rather than an attempt to predict growth responses of algae in the field. Thus, growth rates can be compared within the experiment, but should not be extrapolated to natural systems. Jars were screened to reduce ambient light by approximately 30%. The experiment lasted three days, then algal biomass was again measured and percentage of change calculated. A two-way ANOVA tested for differences in means after data were tested to be sure they met ANOVA assumptions.

To determine if added nutrients would enhance growth of in situ algae on Uva Island reef in March 2002, we exposed algal thalli to ambient and enriched conditions across four reef zones. Algae were collected and weighed (as already described), placed in mesh bags (nylon window screening) to protect them from herbivores, and 10 replicates were anchored in each of four reefs zones (slope, base, crest, and flat). Five grams of slow-release fertilizer (Osmocote [Scots Miracle-Gro Company, Marysville, Ohio, USA], 15% N + 5% P) were placed in nylon stockings and attached to five of the replicates in each reef zone. Samples were anchored at least 2 m apart to reduce cross-contamination by nutrients. Preliminary data (P. Fong, *unpublished data*) demonstrated that our method of nutrient enrichment was undetectable (measured as storage in algal tissue) at >1 m distance. Growth after four days was calculated as above and subjected to a two-way mixed-model ANOVA (with the fixed factor of ambient vs. enriched and the random factor reef zone).

To investigate whether herbivores consumed more enriched algae, in May 2000 we performed the above experiment with three variations. First, after collecting the algae we cultured half for three days with slow-release fertilizer in batch culture. The other half were kept in ambient seawater. Initial tissue N was greater in enriched ($2.60\% \pm 0.04\%$ [mean \pm SE]) than in ambient ($2.40\% \pm 0.04\%$) algae (*t* test, $df = 8$, $P = 0.006$), but differences in P ($0.14\% \pm 0.004\%$ enriched vs. $0.13\% \pm 0.003\%$ ambient) were not significant. Second, algae were exposed to herbivores as they were anchored without being enclosed in mesh bags. Finally, instead of testing effects across reef zones, we chose four locations within the reef slope, where herbivory rates measured

TABLE 1. Benthic cover of the *Acanthophora spicifera*–cyanobacterial association, total coral, and total algae on study reefs.

Reef, year, and zone	Cover (%)		
	<i>A. spicifera</i> – cyanobacteria	Total coral	Total algae
Cavada Island 2001			
All zones	59.5 ± 4.0	19.8 ± 3.5	74.6 ± 3.7
Cavada Island 2002			
All zones	66.1 ± 5.8	3.9 ± 1.7	nd
Uva Island 1999			
Base	22.2 ± 9.9	14.8 ± 5.4	65.2 ± 7.4
Slope	0.8 ± 0.5	26.5 ± 4.6	57.3 ± 6.4
Flat	1.3 ± 0.7	14.3 ± 4.6	77.54 ± 8.1
Uva Island 2000			
Base	77.2 ± 6.8	9.3 ± 5.1	89.8 ± 4.9
Slope	0.3 ± 0.3	4.0 ± 3.6	74.0 ± 5.5
Flat	0.0 ± 0.0	9.9 ± 3.2	84.6 ± 3.8

Notes: Total algae is the sum of macroalgae, crustose corallines, and algal turfs. Data are means ± se; nd = no data collected. All sample sizes are $n = 10$ quadrats, except for Cavada Island 2002 (all zones), $n = 19$ quadrats.

previously were highest. Herbivory rates over 24 h were calculated as loss from initial biomass and subjected to a two-way mixed-model ANOVA with the fixed factor of ambient vs. enriched and the random factor of location.

RESULTS

The *Acanthophora spicifera*–cyanobacterial association observed first in the southern portion of the reef base of Uva Island reef in 1999 dominated benthic cover in this area by 2000 (Table 1) and persisted for at least six years. On Cavada Island reef, the *A. spicifera* association dominated all reef zones in both years measured, covering ~60% of the benthos. In general, *A. spicifera* co-occurred with an “understory” of algal turfs and crustose coralline algae; only rarely were other upright macroalgae found within blooms. Throughout the six years we observed *A. spicifera* domination of a whole reef (Cavada) or a reef zone (Uva), thalli were always coated with filaments of cyanobacteria.

The *A. spicifera* association sustained net biomass accumulation in both uncaged and caged treatments on the Cavada reef crest (Fig. 1A). However, algal thalli increased in height faster when protected from herbivores (paired t test; $df = 2$, $t = 5.730$, $P = 0.0291$), demonstrating the importance of herbivory in limiting algal standing-stock during blooms. Thalli grew nearly twice as high when large herbivores were excluded, but still increased in height by over 40% in six days with herbivores. On Uva Island reef, herbivory rates varied across the reef (Fig. 1B, one-way ANOVA, $F_{6,42} = 5.367$, $P = 0.0003$), with highest rates on the slope and lowest on the reef base where the algal bloom occurred. Rates varied from 18% to 73% removal of the initial 5-g sample across all reef zones, demonstrating spatial variability in the importance of herbivory on Uva Island reef.

A. spicifera maintained net biomass accumulation in the presence of herbivores only when it was covered with cyanobacterial epiphytes on Uva Island reef (Fig. 2A and B). When comparing algae in cleaned vs. epiphytized plots in 2003, epiphytized algae increased both cover by ~5% (t test; $df = 18$, $t = -2.859$, $P = 0.0104$) and thallus height by ~2.5 cm (t test; $df = 18$, $t = -7.603$, $P < 0.0001$) over five days. When epiphytes were removed, cover was reduced by almost 10% and thalli did not grow taller.

The effect of epiphytes on biomass accumulation of *A. spicifera* thalli, measured as change in height, differed between caging treatments, resulting in interaction (Table 2A, Fig. 2C). Within cages, epiphytes reduced thallus growth by ~50%. This estimated the cost in growth to the algae of bearing epiphytes. In contrast, only thalli that were epiphytized maintained positive biomass accumulation in open plots exposed to herbivores. This comparison between cleaned and epiphytized thalli exposed to herbivores estimated the benefit of protection from herbivores provided by the cyanobacteria. As biomass accumulation was similar between caged/cleaned and open/epiphytized plots, these results suggest that epiphytism was as efficacious in reducing herbivory as were our cages.

Microcosm bioassays using algae from the Cavada Island bloom demonstrated primary limitation by P (Fig. 3A, Table 2B). Addition of N and P together appeared to increase growth more than addition of P alone; however, the interaction between N and P was not significant, suggesting that, if present, secondary N limitation was weak. Exposure to N and P in situ increased algal growth

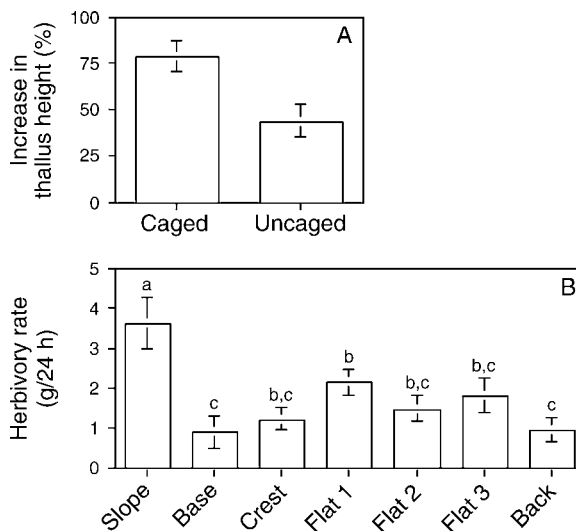


FIG. 1. In situ experiments quantified the effects of herbivory on two reefs where *Acanthophora spicifera* dominated community structure: (A) Cavada Island in March 2001, caged (herbivores excluded) vs. uncaged growth as increase in thallus height over six days; (B) spatial patterns in herbivory across Uva Island reef in May 2000. Bars with shared letters are not significantly different by Fisher's protected least significant difference (PLSD) tests. Error bars represent ±se.

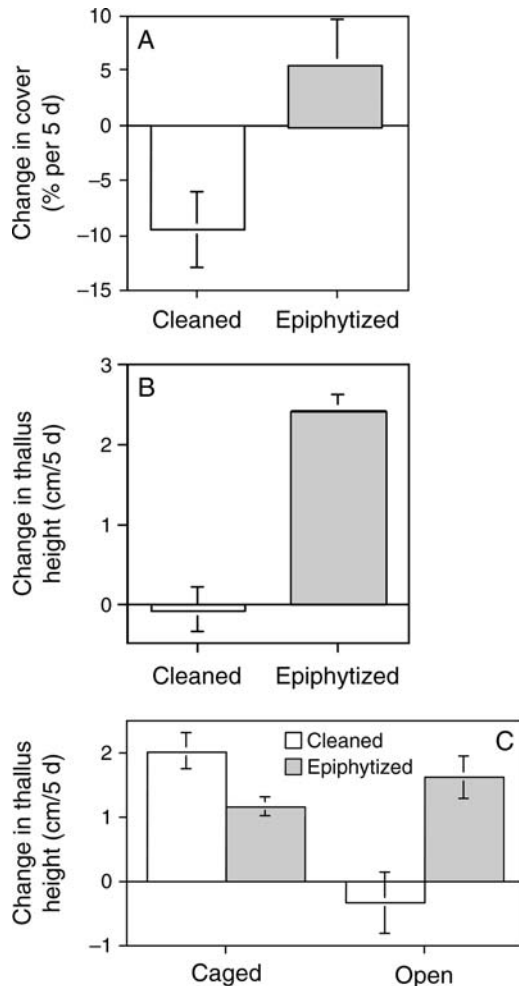


FIG. 2. In situ experiments demonstrated protection from herbivory by cyanobacterial epiphytes: (A) change in percentage of cover; (B) change in thallus height of cleaned plots and plots with epiphytes on Uva Island reef in March 2003; (C) change in thallus height for an experiment varying epiphyte and herbivore presence in March 2004 on Uva Island reef. Error bars represent \pm SE.

across all reef zones tested (Fig. 3B, Table 2C). In some zones, growth more than doubled in the presence of slow-release fertilizer, approaching 30% over four days (maximum, 7.5% per day). Herbivores selectively grazed algal tissue enriched in nutrients (Fig. 3C, Table 2D) across all locations on the reef slope. Herbivory was up to four times greater on enriched algae. Although herbivory rates appeared spatially variable, differences among locations were not significant.

DISCUSSION

Algal dominance of some tropical reef communities of the Eastern Pacific that was initiated by ENSO disturbance of coral was facilitated by the protection from herbivory afforded by epiphytic cyanobacteria. Numerous studies have established that many tropical macroalgae are expert in chemical warfare, accumulating

secondary compounds that deter herbivory (reviewed in Hay 1996). However, *A. spicifera* has long been considered highly palatable (Lewis 1986), and our results support that undefended algal thalli are rapidly consumed. In contrast, filamentous cyanobacteria in the genus *Lyngbya* have a wide diversity and abundance of chemical defenses that effectively deter consumption by herbivorous fishes and invertebrates (Nagle and Paul 1998, 1999). Other positive interactions where physically or chemically defended organisms have provided protection to palatable organisms by proximity or crypsis have been documented (reviewed in Hay 1996). However, to our knowledge, ours is the first documentation that this form of facilitation was responsible for maintaining a change in community structure up to the scale of an entire reef. Since cyanobacterial blooms on tropical reefs appear to be increasingly common (Nagle and Paul 1999), further research into community effects is needed.

Our results do not support the contention that reduction in numbers of herbivores was a necessary precursor to coral reef decline and shifts to algal dominance. Rather, at least on some reefs of the Eastern Pacific, macroalgae dominated benthic communities for several years after the pulse disturbances of ENSO-related coral mortality, even in the presence of abundant herbivores. The conclusion that reductions in herbivory were not necessary rests on two assumptions. The first is that the 25-yr monitoring data showing no decrease in abundance of herbivorous fishes (Glynn 1990, 2004) represents "natural" herbivore abundance. Certainly it is possible that historical (>25 yr ago) numbers of

TABLE 2. Results of statistical tests for two-way ANOVAs.

Source	df	F	P
A) Effects of herbivory and epiphytes on algal growth			
Caged vs. uncaged	1	8.648	0.0058
Epiphytized vs. cleaned	1	2.782	0.1043
Interaction	1	19.139	0.0001
Residual	32		
B) Effect of nutrients on algal growth			
N addition	1	1.626	0.2205
P addition	1	14.634	0.0015
Interaction	1	4.163	0.0582
Residual	16		
C) Effects of nutrients and reef zone on algal growth			
Reef zone	3	1.409	0.2581
Nutrient treatment	1	17.517	0.0002
Interaction	3	0.246	0.8634
Residual	32		
D) Effects of nutrients and location on reef slope on algal growth			
Location	3	2.55	0.0727
Nutrients	1	18.450	0.0002
Interaction	3	0.354	0.7868
Residual	32		

Notes: Panels (C) and (D) are mixed models with reef zone and location, respectively, being random factors. Levels of factors are described in *Methods*.

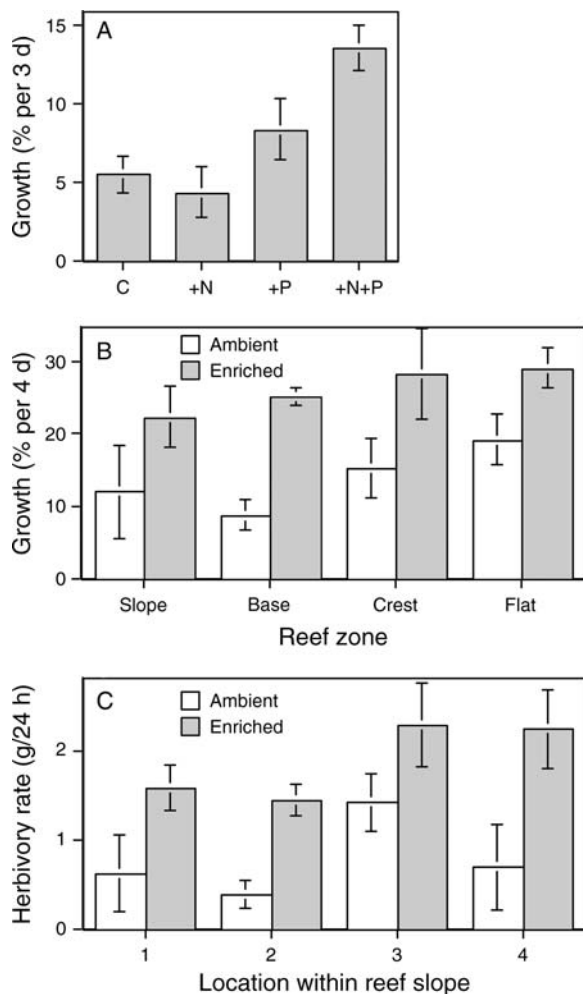


FIG. 3. Experiments investigating the role of nutrients. (A) A microcosm "bioassay" experiment tested for nitrogen vs. phosphorus limitation in May 2000 with algae from Cavada Island; treatments are +N, nitrogen enrichment; +P, phosphorus enrichment; +N+P, nitrogen and phosphorus enrichment; and C, ambient seawater (control). (B) An in situ experiment tested the effects of enriched vs. ambient nutrient supplies on the growth of algae in different zones on Uva reef in March 2002. (C) An in situ experiment quantified herbivory on enriched and ambient algal tissue outplanted to Uva reef in May 2000. Error bars represent \pm SE.

herbivores were higher. However, in most places where herbivore populations have declined historically, the rate of the decline has accelerated during the recent, recorded past (Pandolfi et al. 2005). This pattern did not occur in the area of the Eastern Tropical Pacific with benthic community shifts (Glynn 1990, 2004), although decreases in abundance and size of herbivores have been recorded in more populated areas of the region (Smith 2005). The second assumption is that the number of herbivores is a good estimate of herbivory rate in this system. While this may be true for many coral reefs, large disturbances such as ENSO open large portions of the substrate to algal colonization that may increase resource availability and

functionally decrease herbivory pressure even with constant numbers of herbivores (Williams et al. 2001); this would be a phase shift in response to changing conditions. However, unless herbivore populations are regulated by factors other than food resources, one would expect compensatory increases in population size to eliminate the algal bloom over time, and no such compensatory increases occurred. While it was clear that herbivory was an important force on the study reefs as unepiphytized macroalgal biomass was diminished or canopy heights reduced by herbivory across all reef zones, herbivory did not eliminate algal dominance in these reef systems over the six years of study.

We believe it was unlikely that a change in nutrient supply alone such as occurs during La Niña conditions could sustain macroalgal dominance in this system. Clearly nutrient supply was important to primary productivity. Our bioassay experiments showed that macroalgae from the bloom that dominated all zones of Cavada Island reef was primarily limited by P and may be secondarily limited by N. Furthermore, elevated nutrient supply to algae transplanted across all reef zones on Uva Island reef increased growth. These results suggested that La Niña conditions may have facilitated the initiation of the macroalgal blooms. However, nutrient-stimulated growth rates (maximum of 7% per day) never exceeded consumption rates of unprotected thalli of *A. spicifera* (minimum of 18% per day). In addition, thalli with nutrient enriched tissue were preferentially consumed, presumably negating the positive effects of nutrients on growth of opportunistic, fast-growing species that can store nutrients.

Our results suggested that this tropical reef system may be an ideal area to test experimentally whether this large-scale community shift was a phase shift as is commonly thought to occur on other reef systems, or represents alternative stable states. To be a phase shift, there must be an underlying change in an environmental parameter, such as herbivory pressure, that triggered a threshold response in the community. It is possible that widespread coral mortality changed herbivory pressure without changing herbivore numbers by diluting the force of herbivory over a larger grazing area; thus, to test for a phase shift it will be necessary to study the relationship between herbivore numbers, areal grazing rates, and benthic community structure in this system. To be alternate stable states, the shift must meet several criteria (reviewed Petraitis and Dudgeon 2004b), including that each state is self-sustaining over many generations. While our observations certainly exceeded many generations of the macroalga, they did not cover a single coral generation; therefore the jury will remain out on stability for many years to come. However, several of the criteria for shifts between alternate stable states were met. First, the shift was in response to a large-scale pulse disturbance, the 1997–1998 ENSO that caused widespread coral mortality (Glynn et al. 2001). Second, this shift was most probably initiated by stochastic rather than deterministic

events as establishment of the algal community must have been initiated through co-occurrence of a sufficient supply of larval or asexual recruits of both the macroalgal host and the cyanobacterial epiphyte. These were most likely stochastic processes as they occurred across many reef zones at least on Cavada Island reef, suggesting occurrence across many environmental gradients. Third, once established, algal dominance was maintained by strong positive associations within the algal community that reduced herbivory. Bertness et al. (2004b) suggested that stochastic events may be more important in areas where strong determinism associated with consumer control is relaxed. In our systems, we found that the positive interaction between macroalga and cyanobacterial epiphytes uncoupled consumer control of community structure. Thus, large-scale and long-term experiments investigating alternate stable states should be a focus of future study in this tropical reef community.

ACKNOWLEDGMENTS

Funding from this study was provided by the Biological Oceanography Program, U.S. NSF grant OCE-0002317 to P. W. Glynn and P. Fong and a Smithsonian Tropical Research Institute Short-Term Predoctoral fellowship to T. B. Smith. We thank Peter Glynn for his advice and encouragement on all aspects of this research; he is a mentor and cherished friend to us all. R. Cohen, C. Hueerkamp, A. Romanski, D. Manzillo, and the captain and crew of the R.V. Urraca all provided enthusiastic help in the field.

LITERATURE CITED

- Aronson, R. B., J. F. Bruno, W. F. Precht, P. W. Glynn, C. D. Harvell, L. Kaufman, C. S. Rogers, E. A. Shinn, and J. F. Valentine. 2003. Causes of coral reef degradation. *Science* **302**:1502–1504.
- Aronson, R. B., I. G. Macintyre, C. M. Wapnick, and M. W. O'Neill. 2004. Phase shifts, alternative states, and the unprecedented convergence of two reef systems. *Ecology* **85**:1876–1891.
- Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. *Frontiers in Ecology and Environmental Science* **1**:376–382.
- Bertness, M. D., G. C. Trussell, P. J. Ewanchuk, and B. R. Silliman. 2004a. Do alternate stable community states exist in the Gulf of Maine rocky intertidal zone? Reply. *Ecology* **85**:1165–1167.
- Bertness, M. D., G. C. Trussell, P. J. Ewanchuk, B. R. Silliman, and C. M. Crain. 2004b. Consumer-controlled community states on Gulf of Maine rocky shores. *Ecology* **85**:1321–1331.
- Boyer, K. E., P. Fong, A. R. Armitage, and R. A. Cohen. 2004. Elevated nutrient content of macroalgae increases rates of herbivory in coral, seagrass, and mangrove habitats. *Coral Reefs* **23**:530–538.
- Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. *American Naturalist* **121**:789–824.
- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. *Science* **185**:1058–1060.
- Fong, P., K. E. Boyer, K. Kamer, and K. A. Boyle. 2003. Influence of initial tissue nutrient status of tropical marine algae on response to nitrogen and phosphorus additions. *Marine Ecology Progress Series* **262**:111–123.
- Fox, H. E., P. J. Mous, J. S. Pet, A. H. Muljadi, and R. L. Caldwell. 2005. Experimental assessment of coral reef rehabilitation following blast fishing. *Conservation Biology* **19**:98–107.
- Glynn, P. W. 1990. Coral mortality and disturbances to coral reefs in the tropical eastern Pacific. Pages 55–126 in P. W. Glynn, editor. *Global ecological consequences of the 1982–83 El Niño–Southern Oscillation*. Elsevier, Amsterdam, The Netherlands.
- Glynn, P. W. 2004. High complexity food webs in low-diversity eastern Pacific reef-coral communities. *Ecosystems* **7**:358–367.
- Glynn, P. W., J. L. Maté, A. C. Baker, and M. O. Calderón. 2001. Coral bleaching and mortality in Panamá and Ecuador during the 1997–98 El Niño–Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982–83 event. *Bulletin of Marine Science* **69**:79–109.
- Hatcher, B. G., and A. W. D. Larkum. 1983. An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. *Journal of Experimental Marine Biology and Ecology* **69**:61–84.
- Hay, M. E. 1996. Marine chemical ecology: what's known and what's next? *Journal of Experimental Marine Biology and Ecology* **200**:103–134.
- Hughes, T. P., et al. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* **301**:929–933.
- Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**:629–638.
- Knowlton, N. 1992. Threshold and multiple stable states in coral reef community dynamics. *American Zoologist* **32**:674–682.
- Lapointe, B. 1997. Nutrient thresholds for eutrophication and macroalgal overgrowth of coral reefs in Jamaica and southeast Florida. *Limnology and Oceanography* **42**:1119–1131.
- Lewis, S. M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs* **56**:183–200.
- McCook, L. J. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* **18**:357–367.
- McGlathery, K. J. 1995. Nutrient and grazing influences on a subtropical seagrass community. *Marine Ecology Progress Series* **122**:239–252.
- Nagle, D. G., and V. J. Paul. 1998. Chemical defense of a marine cyanobacterial bloom. *Journal of Phycology* **34**:43.
- Nagle, D. G., and V. J. Paul. 1999. Production of secondary metabolites by filamentous tropical marine cyanobacteria: ecological functions of the compounds. *Journal of Phycology* **35**:1412–1421.
- Pandolfi, J. M., et al. 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* **301**:955–958.
- Pandolfi, J. M., J. B. C. Jackson, N. Baron, R. H. Bradbury, H. M. Guzman, T. P. Hughes, C. V. Kappel, F. Micheli, J. C. Odgen, H. P. Possingham, and E. Sala. 2005. Are U. S. coral reefs on the slippery slope to slime? *Science* **307**:1725–1726.
- Peterson, C. H. 1984. Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? *American Naturalist* **124**:127–133.
- Petraitis, P. S., and S. R. Dudgeon. 2004a. Do alternate stable community states exist in the Gulf of Maine rocky intertidal zone? Comment. *Ecology* **85**:1160–1165.
- Petraitis, P. S., and S. R. Dudgeon. 2004b. Detection of alternative stable states in marine communities. *Journal of Experimental Marine Biology and Ecology* **300**:343–371.
- Schröder, A., L. Persson, and A. M. De Roos. 2005. Direct experimental evidence for alternative stable states: a review. *Oikos* **110**:3–19.
- Smith, T. B. 2005. The dynamics of coral reef algae in an upwelling system. Dissertation. University of Miami, Miami, Florida, USA.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. *American Naturalist* **108**:859–873.
- Szmant, A. M. 2002. Nutrient enrichment on coral reefs: is it a major cause of coral reef decline? *Estuaries* **25**:743–766.
- Williams, I. D., N. V. C. Polunin, and V. J. Hendrick. 2001. Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series* **222**:187–196.