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Algal growth and species composition under experimental control of herbivory, phosphorus and coral abundance in Glovers Reef, Belize

T.R. McClanahan [a,*], B.A. Cokos [b], E. Sala [c]

[a] *The Wildlife Conservation Society, P.O. Box 99470, Mombasa, Kenya*
[b] *CERC, Columbia University, NY, USA*
[c] *Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, La Jolla, CA 92093 0202, USA*

Abstract

The proliferation of algae on disturbed coral reefs has often been attributed to (1) a loss of large-bodied herbivorous fishes, (2) increases in sea water nutrient concentrations, particularly phosphorus, and (3) a loss of hard coral cover or a combination of these and other factors. We performed replicated small-scale caging experiments in the offshore lagoon of Glovers Reef atoll, Belize where three treatments had closed-top (no large-bodied herbivores) and one treatment had open-top cages (grazing by large-bodied herbivores). Closed-top treatments simulated a reduced-herbivory situation, excluding large fishes but including small herbivorous fishes such as damselfishes and small parrotfishes. Treatments in the closed-top cages included the addition of high phosphorus fertilizer, live branches of *Acropora cervicornis* and a third unmanipulated control treatment. Colonization, algal biomass and species composition on dead *A. palmata* "plates" were studied weekly for 50 days in each of the four treatments. Fertilization doubled the concentration of phosphorus from 0.35 to 0.77 μM. Closed-top cages, particularly the fertilizer and *A. cervicornis* additions, attracted more small-bodied parrotfish and damselfish than the open-top cages such that there was moderate levels of herbivory in closed-top cages. The open-top cages did, however, have a higher abundance of the chemically and morphologically defended erect algal species including *Caulerpa cupressoides*, *Laurencia obtusa*, *Dictyota menstrualis* and *Lobophora variegata*. The most herbivore-resistant calcareous green algae (i.e. *Halimeda*) were, however, uncommon in all treatments. Algal biomass increased and fluctuated simultaneously in all treatments over time, but algal biomass, as measured by wet, dry and decalcified weight, did not differ greatly between the treatments with only marginally higher biomass ($p < 0.06$) in the fertilized compared to open-top cages. Algal species composition was influenced by all treatments with a maximum between-treatment Bray–Curtis similarity of only 29%. The fertilized cages showed rapid colonization by a mixed turf community largely composed of the filamentous brown (*Hincksia mitchelliae*) and green (*Enteromorpha prolifera*) species. Algal cover in the fertilized cages leveled at 80% after 20 days compared to less than 50% in the other treatments. There was no evidence that *A. cervicornis* suppressed algal colonization compared to the unmanipulated controls. Instead, the herbivore susceptible *Padina sanctae-crucis* was the most abundant algae followed by *Jania capillacea* in this treatment in contrast to the more chemically defended *Dictyota menstrualis* that dominated the unmanipulated controls. We conclude that *A. cervicornis* was not suppressing algae as a group and its loss cannot account for the observed changes in algal abundance in most reefs except for creating space. In contrast, *A. cervicornis* appears to attract aggressive damselfish that may reduce herbivory by larger herbivores. Phosphorus enrichment can lead to rapid colonization of space by filamentous turf communities but not high biomass and dominance of erect frondose algae within 50 days. Moderate levels of herbivory by large-bodied herbivores promoted moderately herbivore-resistant erect brown and green algae that are commonly reported on disturbed reefs. Consequently, all the studied factors influenced algal communities but seldom as commonly predicted.

Keywords: Algal growth; Cage experiments; Herbivory; Nutrients; Phosphorus; Pollution

1. Introduction

Caribbean coral reefs have experienced a number of ecological disturbances over the past two decades that has resulted in domination of the substratum by turf and erect fleshy algae (Carpenter, 1990; Hughes, 1994;

* Corresponding author.
E-mail address: crcp@africaonline.co.ke (T.R. McClanahan).

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Shulman and Robertson, 1996; Lapointe et al., 1997; Szmant, 1997; McClanahan and Muthiga, 1998; McClanahan et al., 1999a, 1999b). The observed change is frequently associated with the death of corals through diseases, bleaching or other disturbances (Aronson and Precht, 1997; Ostrander et al., 2000; McClanahan et al., 2001a), competition with erect algae that has increased with reduced herbivory (Carpenter, 1990; Hughes, 1994; Lewis, 1986; McClanahan et al., 1996) or increased sea water nutrient concentrations (Smith et al., 1981; Littler et al., 1991; Lapointe, 1999). Changes appear to be persistent such that stony coral populations, particularly in the Caribbean, show little signs of recovery after disturbances and the establishment of erect algae (Connell, 1997; McClanahan et al., 2001b). The consequences of this change to algal dominated reefs include the reduction and recruitment of corals (Hughes, 1994; Tanner, 1995; Hughes and Tanner, 2000), reduced abundance of herbivorous fishes and their rates of herbivory (McClanahan et al., 1999b, 2000), and variable responses for predators of other invertebrates (such as amphipods and crabs) attached to erect algae (Wahl and Hay, 1995; Stachowicz and Hay, 1996; McClanahan et al., 1999b, 2001b).

The causes of this macroalgal overgrowth remain unresolved, controversial (Hughes et al., 1999; Lapointe, 1999; McCook, 1999; Miller et al., 1999; Koop et al., 2001) and may be interactive (Littler et al., 1991; Miller and Hay, 1996). The three most likely single factors contributing to the problem include: (1) reduced herbivory by sea urchins and large commercial fish, such as parrotfish and surgeonfish, (2) increased nutrient concentrations of phosphorus, and (3) loss of hard coral cover or an interaction of these three factors. We undertook a caging experiment to determine the importance of the above three single factors in influencing the secondary succession of algae growing on the surfaces of dead *Acropora palmata* skeletons (referred to as "plates"). Plates were exposed to the above three treatments and a control over a two-month period. We hypothesized that each of the above treatments would influence algal growth and species composition compared to caged and unmanipulated control plates.

2. Methods

2.1. Study sites

This study was undertaken in Glovers Reef, a large coral rimmed atoll, located approximately 45 km off the coast of mainland Belize. The atoll was gazetted as a marine reserve in 1993 and intermittent management has been in effect since 1995. All forms of resource extraction are prohibited in the small wilderness zone, while only subsistence fishing is permitted in the larger conservation zone. Nearly 850 patch reefs exist in this atoll's lagoon and most of them have become dominated by erect algae over the past 20 years, with the coral: algal ratio changing from 4 to 0.25 (McClanahan and Muthiga, 1998).

This study was conducted adjacent to a lagoonal patch reef in the conservation zone where fishing had been successfully excluded for 2–3 years prior to this study. The area was calm with no large waves, slow currents and a small tidal range. Grazing parrot and surgeonfishes were common in the study area (McClanahan et al., 2000, 2001b). The sea urchin *Echinometra viridis* is also common to these patch reefs but cryptic and seldom seen outside crevices and no *Diadema antillarum* were observed (McClanahan, 1999). Nutrient concentration studies have found highly variable nitrate levels but more stable values of 0.35–0.39 μM for SRP phosphates (P. Mumby, unpublished data).

2.2. Experimental design and methods

To determine the factors that control algal abundance we designed a caging experiment in which we measured algal abundance on dead coral plates (cut from dead *A. palmata* skeletons collected from the reef flat and cut with a stone blade of a hacksaw). Replicate plates were exposed to four treatments: (1) large-bodied finfish grazing (open-top cages), (2) fertilizer addition (closed-top cages with 1 kg Scott's high phosphorous slow-release fertilizer spread evenly beneath the plates at the start of the experiment and again after six weeks), (3) coral additions (closed-top with *A. cervicornis* branches added to the cages), and (4) reduced herbivory (here after referred to as "controls") without nutrients or corals added (closed-top cages). The high P Osmocote fertilizer was a 10:50:0 ratio with 10% nitrogen being ammonium and the 50% phosphorus being P_2O_5. Therefore, we added 500 g P_2O_5 and 100 g NH_4 to each fertilization treatment cage. Scott's fertilizer company reports the longevity of this fertilizer at 31 °C to be 45–60 days and we, therefore, reapplied after 42 days. Closed-top treatments were expected to simulate the Caribbean overfished condition where large herbivorous fishes have been removed and only small fishes such as damselfishes and small parrotfishes and surgeonfishes remain as grazers. Cages were constructed (60 cm length and 60 cm width and 30 cm height) with PVC frames and 3 cm meshed plastic caging material. Cages were tied to cement masonry blocks in 1–2 m of water to keep them solidly on the reef bottom. Cages were cleaned of algae and other settling organisms with wire brushes every other day from the start of the experiment to the end.

Water samples in the control and nutrient addition treatments were taken three times from within cages to determine the concentrations of inorganic phosphorus

with the lab spectrophotometer (Hach Company model DR/3000). The first set of samples was taken three weeks into the experiment and the second three weeks after that. The final sampling was done three days after the second kilogram of fertilizer had been added (and only three days after the second sampling had been completed as well). Two 25-ml water samples were taken from each cage. To test for P–PO_4 phosphorus concentrations, the ascorbic acid method was employed (low range 0–2.0 mg/l).

Frequent observations of herbivores and herbivory were made on all cages and counts of fish occupying the cages were made twice in the eight-week period. We compared the major groups of herbivorous fish in each of the treatments and cage types (ANOVA and SNK analyses).

Dead *A. palmata* with flat sides and having an approximate surface area of 1000 cm^2 were collected from the reef flat of Glovers Reef Atoll. Plates were scraped with wire brushes and a hacksaw blade to smooth bumps such that each "plate" started equally flat and smooth. After this treatment, crustose coralline algae still formed around 5% of the surface of these scoured plates. Eight *A. palmata* plates were then placed on the bottom and two were placed on the sides of the cages. Plates on the side of the cage had two holes drilled in them and were fastened to the cage with plastic ties. On several of the plates placed in the *Acropora* cage, *A. cervicornis* "nubbins" (3–7 cm in length) were attached using water proof epoxy putty and 5–10 replicate 40–60 cm living branches of this species were also placed on top of the dead *A. palmata* plates.

Algae were scrapped weekly from the coral plates with a razor plate from a 10×10 cm^2 area, placed in tin foil, weighted, dried, weighed, decalcified (0.4 M HCl) and weighed again to obtain wet, dry and decalcified weights. Scrapping was done to a new previously undisturbed plate every 7 days for 50 days. The samples were placed in the oven at 90–120 °C for 45–60 min to dry. In the seventh week, the two side plates from each of the cages were scraped and assessed similarly to the bottom plates. Algal weight was compared between the three treatments and control cages to determine the accumulation rates in each treatment and tested for significance with a two-way ANOVA with time and treatment being the two factors.

Relative cover of algae was measured weekly on five haphazardly selected plates per cage. Cover percentages were measured by dropping the point of a pencil down on each plate randomly 20 times and recording the functional group of algae underneath the pencil point. Algae were pooled into the following functional groups: turf algae, fleshy algae, encrusting red corallines, and calcareous green algae.

Five weeks after the beginning of the experiment algae were scraped from a 20×20 cm^2 area from a previously unsampled plate, sealed in plastic bags, and stored in a 4% formaldehyde solution. Algae were identified to the lowest possible taxon in the laboratory, following the nomenclature in Littler and Littler (2000). For each plate, the cover of each algal taxon (in cm^2) was determined using a reticulated field.

2.3. Statistical analyses

To test for differences in algal biomass and cover between treatments, two-way ANOVAs were performed on log-transformed data with time and treatment being the two independent variables. To test for differences in number and cover of algal taxa between treatments at five weeks after the beginning of the experiment, one-way ANOVAs were performed. To test for differences between individual treatments we used the SNK test for post-hoc comparison of means. To examine the variation in whole algal assemblages between experimental treatments we performed a detrended correspondence analysis (DCA) using algal cover data. This indirect gradient analysis removes the arch effect and allows reconstruction of the original gradient underlying the observed data (Hill and Gauch, 1980).

3. Results

Measured P was twice as concentrated in the fertilized cages and did not change over time (Table 1). While both damselfish and juvenile parrotfish grazed equally among the open-top cages, the territorial damselfish were most abundant in the closed cages, especially in the *A. cervicornis* and fertilizer addition cages (Table 2). By the final days of the experiment, each of the *A. cervicornis* cages was home to 2–4 dusky damselfish that rarely left (even when the cages were cleaned) and exhibited territorial behavior towards other fish species.

Algal biomass showed fluctuations, but significantly increased over time in all treatments (Fig. 1, Table 3). There were no significant differences in wet and dry biomass between treatments, and differences in decalcified

Table 1
Comparison of P–PO_4 concentrations ($x \pm$ sem) and ANOVA comparisons during three sampling periods in the fertilized and control cages

Mean	Fertilized		Control	
	Mean	SEM	Mean	SEM
Phosphorus				
mg/l	0.06	0.01	0.03	0.01
μM	0.77		0.35	
	F		*p*	
ANOVA	6.22		0.023	
ANOVA-time	1.76		NS	

Table 2
Fish abundance (individuals per cage, $x \pm$ sem) in each of the treatment and control cages as well as an ANOVA comparison of each treatment with the control cages[a]

Herbivores	Control	Open-top	Fertilizer	*Acropora*	ANOVA	
					F-statistic	*p*
Stegastes spp.	1.70 ± 67	0.75 ± 0.48	4.5 ± 0.65	3.5 ± 0.65	8.07	0.004
Scarus spp.	0.7 ± 0.67	0.5 ± 0.50	1.3 ± 0.63	0 ± 0	1.12	0.383

[a] LSD test also used to test for significant differences between treatment cages found that fertilized and *Acropora* treatments were not different, but they are both were different from the control.

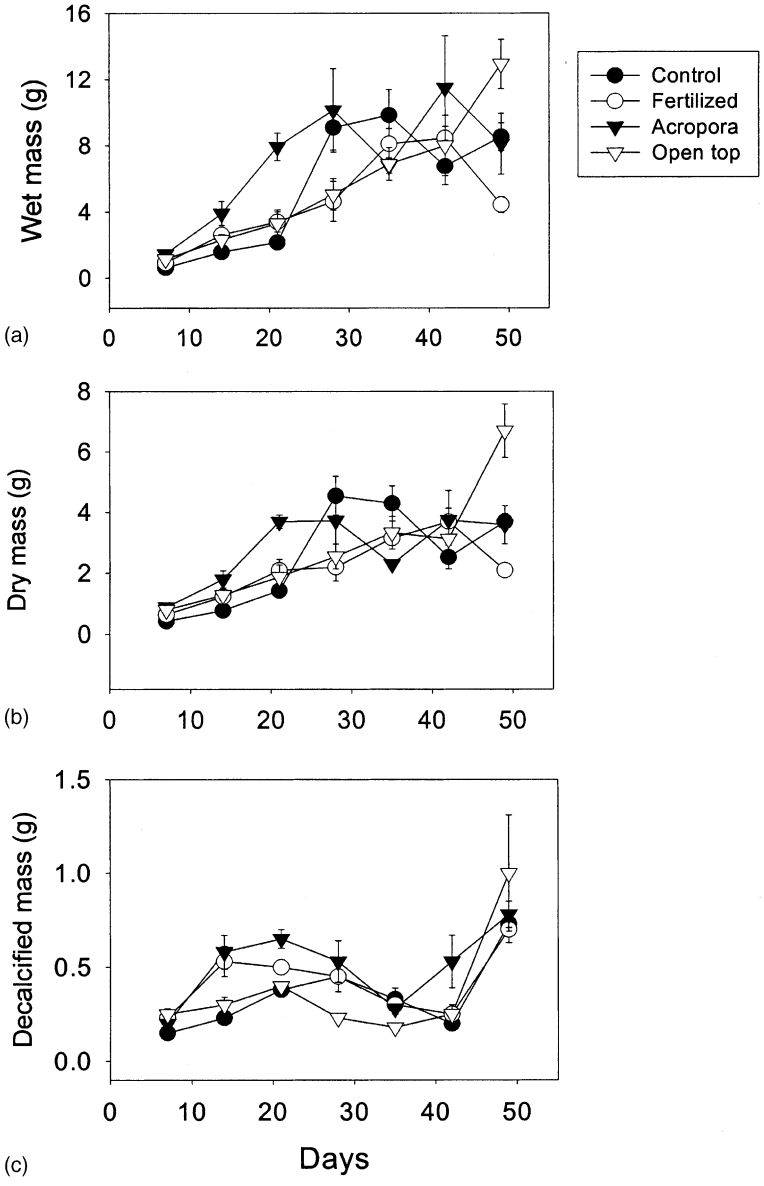

Fig. 1. Plots of (a) the wet weight, (b) dry weight and (c) decalcified weight of the algae as a function of the time since the initiation of the experiment in the three treatment and control cages. See Table 3 for statistical comparisons.

biomass between treatments were close to significant at $p = 0.05$. A post-hoc test of comparison of means found that differences in decalcified biomass between open-top and fertilized treatments were marginally significant at $p < 0.06$, and those between *Acropora* and fertilized treatments at $p < 0.08$.

The trajectory of algal cover over time for the different functional groups also exhibited significant fluc-

Table 3
Two-way ANOVA statistics for comparisons of (a) the wet, dry and decalcified weight, and (b) percent cover of the algae on the experimental plates

	Wet mass		Dry mass		Decalcified mass	
Biomass						
Effect	*F*	*p*	*F*	*p*	*F*	*p*
Time	16.04	<0.001	13.92	<0.001	11.97	<0.001
Treatment	1.42	0.27	1.00	0.39	2.70	0.05
Time × treatment	1.15	0.32	1.31	0.20	0.80	0.69
	Turf algae		Encrusting corallines		Calcareous green	
Cover						
Effect	*F*	*p*	*F*	*p*	*F*	*p*
Time	13.48	<0.001	2.07	0.11	0.42	0.74
Treatment	24.69	<0.001	5.61	<0.001	1.24	0.29
Time × treatment	0.41	0.98	0.85	0.63	0.75	0.75
	Fleshy algae		Total algae			
Effect	*F*	*p*	*F*	*p*		
Time	1.66	0.18	11.95	<0.001		
Treatment	3.45	0.004	16.99	<0.001		
Time × treatment	0.39	0.99	0.46	0.97		

tuations over time (Fig. 2, Table 3). The interaction between time and treatment was not significant, which indicates that all treatments showed similar relative fluctuations in algal cover over time. The cover of turf, fleshy, and total algae increased over time in all treatments, whereas calcareous green cover was very low and fluctuated without a definite pattern. Encrusting corallines generally decreased in all treatments, but remained the highest in the open-top cages.

Cover data suggest that there were significant differences in algal cover for all groups except for calcareous greens. The fertilized treatment had a turf algal cover 1.4, 1.5, and 2.2 times higher than found in the *Acropora*, control, and open-top treatments, respectively (SNK test, $p < 0.008$; Fig. 2, Table 3). The dominant turfs in the fertilized cages were *Hincksia mitchelliae* and *Entermorpha prolifera* (Table 5). The control treatment was dominated by *Dictyota menstrualis* and had an algal cover 1.4 times higher than the open-top treatment which was dominated by *Caulerpa cupressoides*, *Laurencia obtusa*, *D. menstrualis* and *Lobophora variegata*. The *Acropora* addition cages were dominated by *Padina sanctae-crucis* and *Jania capillacea* with lesser abundance of *D. menstrualis* and *Dichotrix penicillata*.

There were significant differences in decalcified biomass on the side of the cages between open-top and fertilized treatments (Fig. 1; Table 4, panel (a); SNK test; $p = 0.032$). Algal decalcified biomass at the end of the experiment was significantly different between plates at the bottom and at the side of open-top cages, that at the side being 2.5 times lower (Fig. 3; Table 4, panel (b); SNK test; $p = 0.027$).

The number of algal taxa five weeks after the beginning of succession did not show significant differences between treatments (ANOVA, $F = 0.27$, $p = 0.85$), nor did total algal cover ($F = 2.11$, $p = 0.15$) (Table 5). There were, however, large differences in the community structure of the algae in each treatment with the maximum Bray–Curtis similarity between treatments being only 29% for the comparison between *Acropora* and control treatments. The large differences were attributable to differences in the dominant species in each treatment as described above (Table 5). Detrended correspondence analysis plots show that the first axis, which explained 59% of the variance, separated the open from closed-top cages with the fertilized cage being the most distinct among the closed-top cages. The second axis, which explained only 16% of the variance, separated the control from the *Acropora* treatments (Fig. 4).

4. Discussion

Our experiment attempted to manipulate three important ecological factors in coral reefs, herbivory, phosphorous concentrations and coral cover. Each of these factors is predicted to control the abundance and species composition of benthic algae (Littler et al., 1991; Hughes et al., 1999; Lapointe, 1999; McCook, 1999). We found evidence that each factor did influence algae, but in different ways and mostly through differences in species composition. Below, we discuss the influence of the experimental method and each experimental factor.

4.1. Caging effects

Strict control of each of these factors was difficult to achieve. Fully caged treatments intended not to exclude

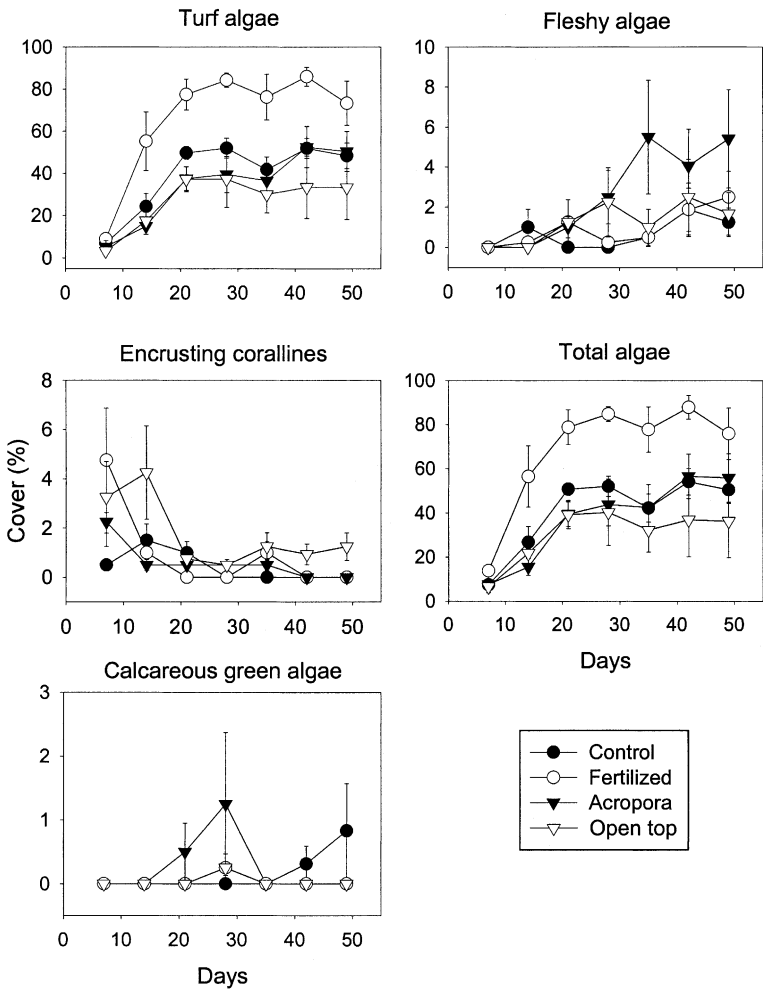

Fig. 2. Plots of the percent cover of the plates as a function of time since the initiation of the experiment in the three treatment and control cages. See Table 3 for statistical comparisons.

Table 4
ANOVA statistics for comparisons of decalcified weight: panel (a) between treatments at the side of cages, and panel (b) between position (side or top of cages) and treatment

Panel (a)		
Effect	*F*	*p*
Treatment	2.47	0.049
Panel (b)		
Effect	*F*	*p*
Position	7.25	0.01
Treatment	0.72	0.55
P × T	2.12	0.11

all herbivorous fishes but to simulate the loss of large-bodied herbivorous fishes by fishing. Thus closed-top cages were expected to have small fishes such as damselfishes and small parrotfishes, whereas open-top cages were to be grazed by larger parrotfishes and surgeonfishes as well and hence have the highest levels of herbivory. Our counts of small parrotfish and damselfish suggest that these small-bodied herbivores were statistically more abundant in the closed than open-top cages. Nevertheless, open-top cages were successful in eliminating herbivory by the larger herbivores such as adult parrotfish, surgeonfish, chubs and sea urchins. These larger herbivores are expected to be a major portion of total herbivory (Carpenter, 1986; McClanahan et al., 1994) and their biomass has been reduced in these reefs through fishing (McClanahan et al., 2001b) and, in the case of sea urchins, diseases (Lessios et al., 1984). Nonetheless, determining absolute levels of herbivory for each treatment is difficult because of our measured caging effect. This may be one factor that contributed to the minor differences in algal biomass but more pronounced differences in species composition between treatments.

4.2. Herbivory effects

We can conclude that herbivory differed qualitatively, closed-top cages having greater herbivory by small fish than open-top cages which had more herbivory by large

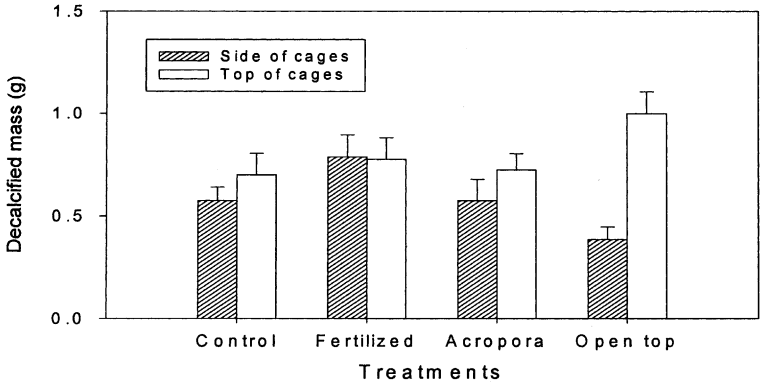

Fig. 3. Comparison of the algal abundance at the end of the experiment for plates on the bottom and side of the cages. Bars are standard errors of the mean.

fishes. Sea urchins were not observed in or near the cages and did not influence the study. Microherbivores such as amphipods were not studied, and were not expected to vary greatly between treatments or to substantially contribute to total herbivory (Carpenter, 1986). Nonetheless, the open-top cages were the most distinct among the treatments in terms of cover, having the lowest total algal cover, the highest encrusting red coralline algal cover, the lowest decalcified algal mass on the side of cages, and having a high abundance of chemically defended moderately herbivore-resistant erect algal genera, such as *Caulerpa*, *Laurencia*, *Dictyota* and *Lobophora* (Littler et al., 1983; Hay, 1984; Hay et al., 1987, 1988; Lewis, 1986; Duffy and Hay, 1994). The species *C. cupressoides* found in our open-top cages is one of the most herbivore-resistant species of *Caulerpa* (Lewis, 1986). Calcareous greens are reported to be more herbivore resistant than the above genera (Littler et al., 1983; Hay, 1984; Lewis, 1986), but we found very few of these species in our experimental plates. A longer study may be required to examine the response of calcareous green and the larger and slower colonizing brown algae (i.e. *Sargassum* and *Turbinaria*) to these treatments (McClanahan, 1997). A whole patch reef algal reduction experiment in these same patch reefs found that algal biomass returned in two months, the length of this caging study, but taxonomic composition of the algal canopy took nearly one year to return to the pre-reduction levels (McClanahan et al., 2001b). Maintaining cages and regular sampling over one year is difficult and was, therefore, not attempted in this study.

Herbivory in the open-top cages, while probably the highest among the treatments, was not as high as the maximum levels of herbivory found on many coral reefs. The sites were within a lagoonal area protected from fishing for about three years and this management has enhanced populations of some herbivorous fish (McClanahan et al., 2001b). Nonetheless, standard *Thalassia* herbivory assays in these patch reefs report daily bite frequencies of around 30% (McClanahan and Muthiga, 1998; McClanahan et al., 2001b). This is considerably lower than the 75% bite frequencies reported for other unfished back and lagoonal reef sites using similar methods (Hay, 1984; McClanahan et al., 1994). The difference may be due to the short time since the exclusion of fishing or some other ecological characteristics of the patch reef habitat. For example, reef lagoons often have lower levels of herbivory than outer reef slope habitats (Hay, 1984). Consequently, herbivory in the open-top treatment was probably only moderate when viewed on the larger scale of herbivory in different habitats and management and this may explain the high abundance of algal species with moderate defenses against herbivores. These species might be replaced by more herbivore-resistant species, such as calcareous green algae, or faster growing algae, such as many turf species, if herbivory was higher in this treatment. It would, therefore, appear that moderate levels of herbivory are responsible for the high abundance of moderately defended erect algae (Miller and Hay, 1996) found in this experiment and dominating the patch reefs in this location (McClanahan and Muthiga, 1998).

4.3. Fertilization effects

Among the three closed-top cage treatments, the fertilization treatment was the most distinct with the control and live *A. cervicornis* treatments being most similar. Fertilization in this experiment doubled the concentrations of phosphorus and the green alga *E. prolifera* was very common in this treatment. Nitrate–nitrogen concentrations are often quite variable and seasonal in tropical environments compared to phosphorus (McClanahan, 1988; Bell, 1992), and spatially have a standard deviation 3–4 times larger than phosphorus (Kleypas et al., 1999), and coral reefs often produce rather than consume nitrate–nitrogen (Pilson and Betzer, 1973; Wilkinson et al., 1984). Phosphorus is likely to be among the most limiting and influential nutrient in this carbonate environment (Littler et al., 1991; Bell, 1992) and

Table 5
Species composition and cover (cm^2, $x \pm$ sem) of algal taxa on coral plates under the different experimental treatments, seven weeks after the beginning of the experiment. +<0.03 cm^2. Bray–Curtis similarity of the four treatments given at the bottom

Taxa	Treatment			
	Control	Fertilized	*Acropora*	Open-top
Dictyota menstrualis	5.93 ± 3.09	1.81 ± 1.73	3.63 ± 1.89	1.08 ± 0.92
Jania capillacea	0.93 ± 0.79	2.81 ± 1.98	9.28 ± 9.24	0.05 ± 0.03
Dichotrix penicillata	0.69 ± 0.61	0.90 ± 0.47	2.66 ± 2.14	0.14 ± 0.05
Lobophora variegata	0.48 ± 0.48	0.73 ± 0.44	0.13 ± 0.13	1.00 ± 0.34
Digenea simplex	0.33 ± 0.33	0.19 ± 0.19	+	+
Padina sp.	0.19 ± 0.19	0.04 ± 0.04	0.06 ± 0.06	0.18 ± 0.10
Encrusting *Corallinaceae*	0.19 ± 0.12	+	+	+
Lophosiphonia cristata	0.18 ± 0.12	0.08 ± 0.08	0.31 ± 0.31	0.05 ± 0.05
Wurdemannia miniata	0.13 ± 0.06	2.14 ± 0.89	0.04 ± 0.04	0.05 ± 0.03
Chondria dasyphylla	0.13 ± 0.08	0.58 ± 0.21	0.16 ± 0.10	+
Centroceras clavulatum	0.06 ± 0.04	0.13 ± 0.06	0.03 ± 0.03	+
Neomeris annulata	0.03 ± 0.03	0.08 ± 0.03	0.08 ± 0.08	+
Hincksia mitchelliae	0.03 ± 0.03	18.00 ± 13.2	0.38 ± 0.83	0.03 ± 0.03
Bryopsis pennata	0.03 ± 0.03	0.63 ± 0.63	+	+
Sphacelaria tribuloides	0.03 ± 0.03	0.45 ± 0.26	0.23 ± 0.16	0.13 ± 0.09
Halimeda sp.	0.03 ± 0.03	0.19 ± 0.19	+	+
Acetabularia polyphysoides	0.03 ± 0.03	+	0.03 ± 0.03	+
Dichotrix sp.	0.03 ± 0.03	+	+	+
Herposiphonia tenella	0.03 ± 0.03	+	+	+
Enteromorpha prolifera	+	14.75 ± 11.9	+	+
Cladophora laetevirens	+	0.88 ± 0.52	+	+
Enteromorpha flexuosa	+	0.38 ± 0.38	+	+
Padina gymnospora	+	0.30 ± 0.18	0.40 ± 0.40	+
Amphiroa fragilissima	+	0.29 ± 0.24	+	+
Valonia macrophysa	+	0.08 ± 0.08	+	+
Spyridia filamentosa	+	0.06 ± 0.06	+	+
Phyllodictyon anastomosans	+	0.05 ± 0.05	+	0.06 ± 0.06
Lyngbya confervoides	+	0.04 ± 0.04	+	+
Ceramium flaccidum	+	+	+	+
Chondria sp.	+	+	0.03 ± 0.03	+
Cladophora sp.	+	+	+	+
Botryocladia sp.	+	+	+	+
Bryopsis sp.	+	+	+	+
Caulerpa cupressoides var. *mamillosa*	+	+	+	2.25 ± 2.25
Ceramium cruciatum	+	+	+	+
Chaetomorpha aerea	+	+	+	+
Champia parvula	+	+	+	+
Chondria floridana	+	+	0.10 ± 0.10	+
Dasya rigidula	+	+	+	+
Dictyosphaeria cavernosa	+	+	+	0.03 ± 0.03
Dictyota cervicornis	+	+	0.85 ± 0.85	+
Dictyota sp.	+	+	+	0.08 ± 0.08
Ectocarpus elachistaeformis	+	+	0.06 ± 0.06	+
Enteromorpha chaetomorphoides	+	+	0.03 ± 0.03	+
Herposiphonia secunda	+	+	+	+
Laurencia obtusa	+	+	+	2.13 ± 2.13
Laurencia sp.	+	+	+	+
Lyngbya polychroa	+	+	0.03 ± 0.03	+
Lyngbya sp.	+	+	+	+
Neomeris sp.	+	+	+	+
Padina sanctae-crucis	+	+	13.50 ± 13.50	+
Pneophyllum fragile	+	+	+	+
Polysiphonia sp.	+	+	+	+
Rhizoclonium riparium	+	+	+	+
Stylonema alsidii	+	+	+	+
Total algal cover, cm^2	9.40 ± 4.42	45.53 ± 16.3	31.99 ± 13.21	7.23 ± 3.93
Number of algal species	14.00 ± 3.58	15.75 ± 2.01	14.25 ± 2.25	12.75 ± 1.11
Bray–Curtis similarity coefficients				
Control	1.00			
Fertilized	0.17	1.00		
Acropora	0.29	0.18	1.00	
Open-top	0.25	0.19	0.09	1.00

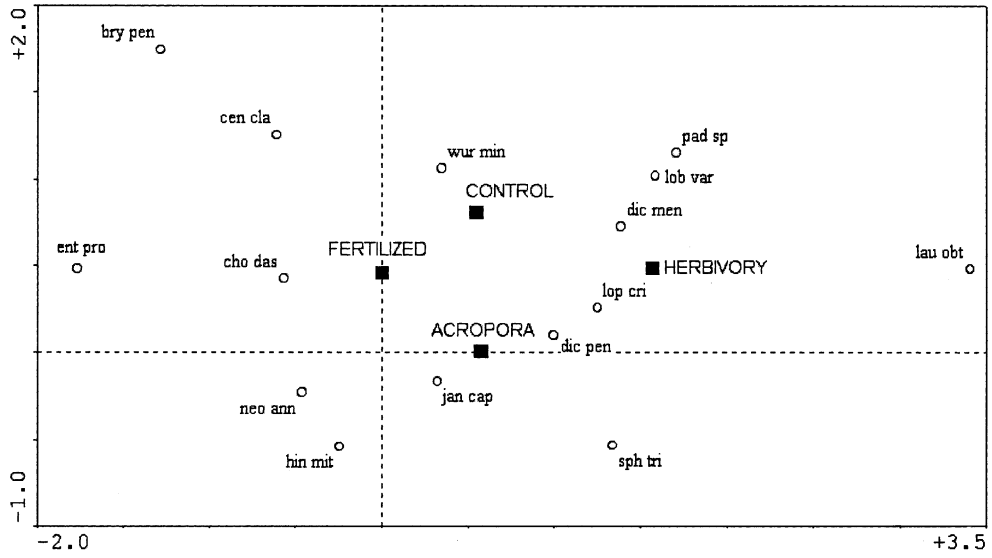

Fig. 4. Detrended correspondence analysis of the algal species cover data. The first canonical axis explain 59.3% of the variance, and the second 16.4%. Species codes: bry pen: *Bryopsis pennata*, cen cla: *Centroceras clavulatum*, cho das: *Chondria dasyphylla*, dic pen: *Dichotrix penicillata*, dic men: *Dictyota menstrualis*, ent pro: *Enteromorpha prolifera*, hin mit: *Hincksia mitchelliae*, jan cap: *Jania capillacea*, lau obt: *Laurencia obtusa*, lob var: *Lobophora variegata*, lop cri: *Lophosiphonia cristata*, neo ann: *Neomeris annulata*, pad sp: *Padina* sp., sph tri: *Sphacelaria tribuloides*, wur min: *Wurdemannia miniata*.

its enrichment appeared to influence the rate of colonization, maximum cover and species composition in the fertilization treatment. Although algal biomass was only marginally higher than other treatments, fertilized cages had a rapid expansion of cover and cover leveled at about twice that of the other treatments. The algal cover was composed largely of two species, the brown *H. mitchelliae*, and the green *E. prolifera* with more minor contributions of *J. capillacea* and *D. menstrualis*. Encrusting coralline red algae started at around 5% of the plate cover in this treatment but were eliminated from the canopy within 20 days. They may have, however, persisted under the canopy of colonizing turf and erect algae.

The response to fertilization reported here differs from the minor response reported from the ENCORE fertilization experiment undertaken in the lagoon of One Tree Island, Great Barrier Reef, Australia (Koop et al., 2001). This difference can not be attributed to different levels of fertilization as the ENCORE experiment increased P–PO_4 from a background of 0.26 μM to above 2.0 μM whereas in our experiment we only doubled P–PO_4 from a background of 0.35 μM. The most likely explanation, therefore, is that the ENCORE experiment did not cage out herbivores as we did and the herbivory was able to compensate for any changes in the algal community that might be attributed to increased algal growth. The ENCORE experiments did not, however, report increased algal growth from fertilization and even control reefs had among the highest reported algal production rates at around 10 g C/m^2/day. They did find higher nutrient uptake by filamentous compared to crustose algae but this did not result in increased biomass. The ENCORE experiment did not focus greatly on the algal species composition of their treatments and this combined with the expected higher herbivory rates in the ENCORE study may explain the reported differences.

The ENCORE and this study both started with P–PO_4 concentrations of between 0.26 and 0.35 μM which some coral reef scientists believe is above a P–PO_4 threshold for eutrophication (0.1 μM) where erect algae can dominate the substratum (Bell, 1992; Lapointe, 1997). By this threshold hypothesis all treatments were to become dominated by erect algae irrespective of the fertilization and herbivory treatments. If nutrients were not limited then there would not be increased algal growth in the ENCORE experiment. This was, however, not the case for our study and the most P–PO_4 rich treatment was dominated by small filamentous rather than erect algae at least up to the 50 days. Algal reduction studies in these same reefs suggest that 50 days is sufficient time for erect algal biomass to recover if the conditions are appropriate (McClanahan et al., 2001b). It may be that P–PO_4 facilitated a bloom of turf algae that was maintained by damselfish over this time period. Damselfish in the *Acropora* cages did not, however, promote turf but rather erect and branching coralline algae. Consequently, the effect of damselfish would need to be complex and interactive with nutrients and corals to explain the patterns on both nutrients and damselfish presence.

Kleypas et al. (1999) summarizing information on ~1000 coral reefs found an average P–PO_4 concentrations of 0.13 μM, a standard deviation of 0.08 and a maximum of 0.54 μM. This would suggest that over half of the coral reefs of the world are above the proposed

threshold and yet these reefs are seldom described as dominated by erect algae. The Glovers sites would, however, be near the upper limits of $P–PO_4$, despite their remote offshore location. Our findings do not, however, support the threshold hypothesis for dominance by erect algae and suggest, rather, that herbivory by both small and large herbivores is an important factor in controlling algal species composition and functional groups.

4.4. Coral effects

The similarity between the *A. cervicornis* additions and the controls suggest that *A. cervicornis* or associated small-bodied herbivores were not greatly suppressing algal colonization. In fact, the *A. cervicornis* addition had a large abundance of the highly herbivore-susceptible *Padina* (Hay, 1984; Lewis, 1986; McClanahan, 1999) which suggests that the combination of territorial damselfish and the exclusion of large-bodied herbivores enhanced the survival of this genus. *J. capillacea* was also quite abundant in this treatment and further investigation will be required to determine the effects of *A. cervicornis* or associated herbivores on this species. It is common to observe these two algal species on the patch reefs of Glovers often associated with territorial damselfish and, perhaps, their defense against large-bodied herbivores plays an important role in promoting these species. Control cages housed about half the abundance of damselfish as the *A. cervicornis* addition cages but no *Padina* and less *Jania*. Small-bodied parrotfish were more important grazers in control than *A. cervicornis* addition cages, probably due to less aggression by damselfish and this may have promoted greater dominance by *D. menstrualis*. Regardless, the findings suggest that *A. cervicornis* and associated herbivores do not directly suppress erect algal abundance. The loss of coral cover may promote increased algae cover through increased space for colonization (Ostrander et al., 2000; McClanahan et al., 2001a; Williams et al., 2001), but this study did not find any evidence for suppression of algae by *A. cervicornis* and associates, particularly damselfish.

The experiment was not designed to test the relative dominance paradigm (RDP) (Littler et al., 1991) but there were a number of notable differences between the predictions of this model and our findings. For example, the RDP predicts high coralline algae under high nutrients and grazing, turf algal dominance under low grazing and low nutrients and frondose macroalgae under high nutrients and low grazing. Our findings are considerably different from these predictions. High grazing in this study, although moderate on the larger scale of coral reefs, promoted frondose macroalgae and high nutrients promoted turf algae and inhibited crustose corallines. These differences may be due to the absolute scale of nutrients and herbivory as discussed above where our study sites started at both a high nutrient and low herbivory level such that no truly high herbivory and low-nutrient conditions occurred. Clearly, to better understand the factors contributing to the ecological state and degradation of coral reefs more experimental studies are needed across the full scale and possible interactions of herbivory and nutrient concentrations.

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