

The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*)

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Abstract

Coral reef degradation often involves a phase shift from coral- to macroalgal-dominated reefs. Declining levels of herbivory or increasing supply of nutrients have both been suggested as a cause of increased algal abundance and consequent competitive overgrowth of corals. However, explicit demonstration of the processes involved and their relative strengths requires simultaneous tests of all three factors: competition, herbivory, and nutrient effects. We experimentally tested the factorial effects of nutrients and herbivory on the competitive interaction between a brown alga *Lobophora variegata* and a scleractinian coral *Porites cylindrica*. The results of the experiment show that coral tissue mortality was strongly enhanced by the presence of the competitor (*L. variegata*), and this effect was significantly greater when herbivores were excluded. In contrast, the coral growth (skeletal extension) of *P. cylindrica* was not significantly affected by any treatments. The addition of nutrients did not have a significant effect on corals overall, but had a small effect on algal growth and consequent coral tissue mortality when herbivores were excluded. The factorial combination of treatments in this experiment allows interpretation of the causal relationships between each factor, demonstrating that nutrient effects on algal growth only led to competitive effects on corals when herbivory was insufficient to consume excess algal growth and that both herbivore and nutrient effects on corals were dependent on the strength and outcome of the competitive interaction between corals and algae.

Coral reef degradation commonly involves a so-called phase-shift from reefs dominated by abundant corals to reefs dominated by abundant benthic algae (Done 1992; Hughes 1994; McCook 1999). There has been considerable, recent controversy over the relative importance of bottom-up (e.g., Lapointe 1997, 1999) and top-down (Hughes 1994; Hughes et al. 1999; Aronson and Precht 2000) factors in contributing to these changes, particularly in the context of declines in Caribbean reefs. According to the bottom-up model, excess nutrient supply results in an increased growth of benthic algae (e.g., Hanisak 1979; Lapointe 1997; Schaffelke and Klumpp 1998a,b; Schaffelke 1999), leading to overgrowth of corals and consequent reef degradation (Smith et al. 1981; Pastorok and Bilyard 1985; Bell 1992). The top-down model argues that algal biomass is predominantly controlled by her-

bivore consumption (e.g., Hay 1981, 1984; Lewis 1986; Hughes 1994; McCook 1996, 1997). In particular, there is evidence that on reefs with healthy populations of herbivores, herbivore consumption often closely matches changes in algal production so that increases in algal production or intrinsic growth do not generally result in increased accumulation of algal biomass (net growth; Hatcher and Larkum 1983; Carpenter 1986; Hatcher 1988; McCook 1999; Russ and McCook 1999).

Although the relative importance of nutrients and herbivory in controlling benthic algal abundance will depend on circumstances such as location, herbivore regimes, background nutrient supplies, disturbance regimes, etc. (e.g., Littler and Littler 1984; Miller 1998; McCook 1999; McCook et al. 2001b), it is important to recognize that both bottom-up and top-down perspectives assume that increased algal abundance will lead to decreased coral abundance by altering the competitive balance between algae and corals (Miller 1998; McCook 1999; McCook et al. 2001a). Thus, competition between corals and algae is a critical step in either model of reef degradation.

Despite the controversy, there have been few studies that simultaneously address more than one factor, especially experimentally (Hatcher and Larkum 1983; Miller and Hay 1996, 1998; Miller et al. 1999; Smith et al. 2001; Thacker et al. 2001), and in particular, very few that specifically demonstrate competition using unconfounded, multifactorial experimental tests (reviewed in McCook et al. 2001a). This makes it difficult to compare the relative importance of different factors. The scarcity of multifactorial studies is par-

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ticularly unfortunate given that the three processes appear to be interdependent a priori: accumulation of nutrient-induced algal growth depends on herbivore consumption rates, and the effects of both factors on coral abundance depend largely on coral–algal competition. Although there is limited evidence that benthic algae might competitively inhibit coral growth, survival, or reproduction and recruitment (Potts 1977; Sammarco 1982; Lewis 1986; Hughes 1994; Tanner 1995), there is very little experimental demonstration of changes in these competitive effects resulting from changes in nutrient or herbivore regimes (Miller and Hay 1996). Many previous studies have drawn conclusions about competitive effects based on designs that do not directly test the competitive nature of the interaction, often manipulating herbivory or other factors and assuming competitive effects (McCook et al. 2001a).

The present study addressed this issue by simultaneously testing factorial combinations of the effects on corals of nutrients, herbivory, and competition with algae. This not only provides (1) a direct comparison of the relative magnitude of each effect but (2) does so for more than one level of the other factors, and most importantly, (3) the interaction terms in such a factorial experiment provide a direct test of the mechanisms by which the processes might interact. Thus, for example, the effects of nutrients and herbivores on corals are tested in the presence and absence of the algal competitor, indicating whether the effects of these factors depend on competition or influence the coral directly. We chose the naturally co-occurring brown alga *Lobophora variegata* (creeping or crustose morphology) and the branching scleractinian coral *Porites cylindrica* for this experiment because it provides an ideal experimental unit, allowing logistically simple manipulations of competitors, herbivores, and nutrients (Fig. 1; Jompa and McCook in press; see p. 249, 271 in Littler and Littler 2000). *L. variegata* is relatively common and widespread both on the Great Barrier Reef (GBR) and in the Caribbean, and is often abundant on degraded reefs (e.g., Diaz-Pulido and Diaz 1997 and references therein; Littler and Littler 2000).

Materials and methods

Experimental design and approach—We used a nested, fully factorial experimental design, with three factors: (1) competitor treatment, with two levels: *L. variegata* naturally present (unmanipulated) and *L. variegata* removal; (2) herbivory, with two levels: open plots exposed to natural levels of herbivory and caged plots with herbivores excluded; (3) nutrient treatments, with three levels: control or ambient water and medium- and high-pulsed nutrient additions. For each combination of treatments, we used four replicate plots (nested within the factorial treatment combinations) and two replicate coral–algal branches (experimental units) for each plot. Each plot consisted of a steel frame, to which the two branches were attached. The coral–algal branches were collected from reef slope colonies at Cannon Bay on Great Palm Island, and transplanted to the reef slope at the Orpheus Island Research Station for the experiment, which ran from February to May 2000.

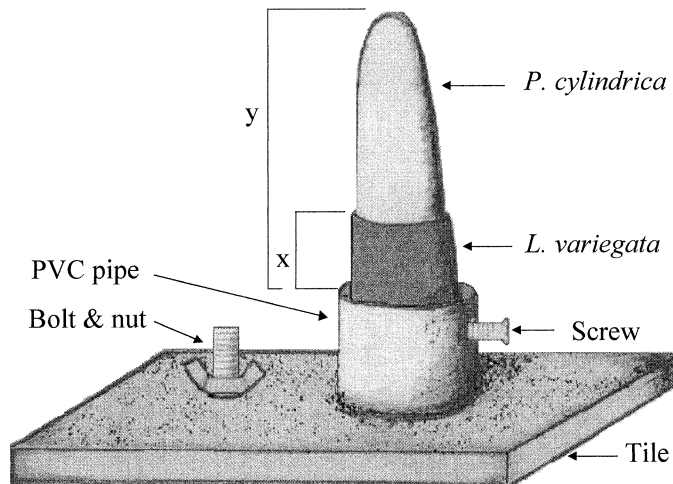


Fig. 1. Experimental units. Branches of *Porites cylindrica* with naturally occurring *Lobophora variegata* growing around the base of the branch were selected and transplanted to the study site. The *L. variegata* has a creeping morphology, growing closely adherent to and overlying dead coral skeleton, with only 1–2 mm overlap between the top edge of the *L. variegata* and the bottom margin of live coral tissue. Each coral–algal branch or unit was clamped by a stainless steel screw into a short length of PVC pipe, which was glued onto terra cotta tiles. The tile was attached to a steel frame with a bolt and wing nut, and the steel frames were anchored to the bottom. This method allowed specimens to be removed and reattached readily for the nutrient pulse treatments. Coral tissue mortality was estimated by the change in position of the border between live and dead coral tissue (x), relative to a reference mark (on the PVC pipe); that is, mortality here refers to upward retreat of the bottom of the live coral. Coral skeletal extension (y) was measured as the change in distance from coral tip to the reference marker; thus extension refers to upward growth.

Study sites—The specimens were collected from the reef slope (6–7 m deep) at Cannon Bay (18°41.1'S, 146°35.2'E), Great Palm Island, on the inshore central GBR, Australia, close to the site used by McCook (2001) and Jompa and McCook (in press). The site was dominated by colonies of *P. cylindrica* (~65% cover based on four 20-m line-intercept transects). These colonies appear to have been present at the site for a considerable time because they reached 2 m in height. The brown alga *L. variegata* was the most common of several macroalgae growing within the branches of *P. cylindrica*. The alga usually occupied and overgrew the basal parts of coral branches and formed distinct patches of variable size (~0.5 to 4 m²) among the *P. cylindrica* colonies along the reef slope.

The experimental site was on the reef slope at Pioneer Bay, Orpheus Island, also in the Palm Island group (18°36.423'S, 146°29.359'E; close to the Research Station), at similar depth to the original habitat of the specimens (6 m). This site consists of mostly dead coral rubble of branching *Acropora* and *Millepora tenella* (apparently killed during the 1998 mass bleaching event). Both *P. cylindrica* and *L. variegata* occurred naturally in this area. The major herbivores observed at this site were roving herbivorous fishes, predominantly scarids, acanthurids, and siganids, although territorial damselfishes and sea urchins were also moderately

abundant. Overall, large herbivore abundances appear to be intermediate between those on offshore reefs and inshore reef flats (pers. obs.; see references in McCook 1996, 1997).

Specimen selection and preparation—Coral branches were selected to have relatively uniform size (~6 cm long and ~1.5 cm diameter) and to have similar amounts of *L. variegata* (~2.5 cm) growing in a creeping, adherent morphology on the basal part of the branch. Branches were cut off using a small handsaw, clamped to the attachment plates (Fig. 1), placed in large plastic bins (~65-liter “Nally” bins) underwater, brought to the research vessel, then transported under running seawater to the experimental site at Orpheus Island (~1 h travel). Specimens were maintained underwater and shaded at all times during both the transplantation process and the experimental procedures.

Experimental treatments—The competition treatment simply involved careful removal of all *L. variegata* from randomly selected branches, with half the branches left intact. The herbivore exclusion treatment involved large cages (40 × 40 × 25 cm) made of plastic mesh (Nylex, “Trical” high-density polyethylene), as used by McCook (1996, 1997) and Jompa and McCook (in press). The mesh size was 12 mm; thus, it only excludes larger herbivores. The mesh was attached to the steel frames, to which two coral–algal branches had been attached (i.e., plots). Open plots consisted of frames with no mesh. The number of specimens available was limited, so it was not feasible to include a partial cage treatment to test for caging artifacts and still use a fully factorial combination of all three factors (this would have required another 48 coral branches). Because previous experiments in this area (Russ and McCook 1999 and references therein), including several using the same mesh (McCook 1996, 1997) and even using the same coral and algal species (Jompa and McCook in press), have found minimal caging artifacts, we felt that the benefits of the factorial design outweighed the risks of caging artifacts.

Nutrient manipulations involved pulsed additions of nutrients for a 24-h period every 2–3 weeks for 3 months using reagent-grade ammonium chloride and sodium-dihydrogen phosphate (e.g., Schaffelke and Klumpp 1998b). Three levels of nutrients were applied: (1) controls, using ambient seawater at Orpheus Island (average concentrations 0.1 μM ammonium and 0.08 μM phosphate); (2) medium, an addition of 5 μM ammonium and 0.5 μM phosphate; and (3) high, an addition of 10 μM ammonium and 1 μM phosphate. These levels are within the range of naturally occurring short-term pulses in the area (e.g., Schaffelke and Klumpp 1998b). Nutrient pulses were given either on RV *Harry Messel* or at Orpheus Island Research Station using a separate 10-liter plastic bucket for each two branches. All specimens, including controls, were retrieved for the duration of the pulse treatment, and all were returned to the field immediately afterwards. The buckets were aerated to ensure adequate water movement and mixing, and the water was replaced every 3–4 h to maintain relatively constant nutrient levels. Shade cloth minimized stress to the corals. The effectiveness of the nutrient manipulations was tested by measuring tissue nutrient levels in *L. variegata*. Algal tissue was

removed from the base of *P. cylindrica* at the end of the experiment after applying the final 24-h nutrient pulse. Samples were dried at 60°C for 36 h and ground, and the concentration (% dry weight) of carbon and nitrogen were determined with a Perkin Elmer CHN Analyzer. Phosphorus was determined using ICP analysis.

Measurements and data analyses—Two response variables were measured: tissue mortality of *P. cylindrica* was calculated as the change in height of the border between live and dead coral tissue relative to a reference point (Fig. 1), and coral growth or linear extension of the branch was measured as the growth of the coral tip from the reference point (Fig. 1). All measurements were made using vernier calipers, to the nearest 0.5 mm. Note that in treatments with the alga present, the coral tissue mortality is equivalent to algal growth because the top edge of the alga corresponds to the bottom edge of the live coral.

Data analyses involved a three-factor, nested analysis of variance (ANOVA) followed by post hoc Student–Newman–Keuls (SNK) tests. Where the interaction between treatments was significant, analyses (ANOVA and SNK tests) were repeated within levels of each treatment factor. In order to minimize the risks of overlooking relatively small nutrient effects (i.e., Type II errors), nutrient effects on coral tissue mortality (or, equivalently, on algal growth, see above) were specifically tested within the caged, alga-present treatment combination because it is in this treatment combination that any nutrient effects are most likely to be measurable. Treatment effect sizes (effect %_{aoc}) were estimated by the differences in mean response between treatments, expressed relative to the overall controls (i.e., with the alga present, in open plots, and with control ambient nutrient levels; effect %_{aoc} = 100 × [y₂ – y₁]/y_[algae+,open,control]); these effect sizes were calculated within groups where indicated by significant interactions. All data were tested for homogeneity of variance (Cochran’s test), outliers, and independence and normality of residuals (graphically). Based on these tests, no data transformation was needed for the analyses. Examination of data indicated that low *F*-ratios for some nutrient terms in the analyses appear to result from low numerator degrees of freedom and do not compromise or confound the interpretations.

Results

Coral tissue mortality—Coral tissue mortality data indicated a significant interaction between effects of the competitor, *L. variegata*, and herbivory, whereas the effects of nutrients and other interactions were not significant (Fig. 2, Table 1). Separate analyses carried out to explain the significant interaction indicated that (1) within the algal removal treatment, no consistent differences were detected in coral mortality between open and caged treatments (*P* = 0.910, effect %_{aoc} = 3.2%); (2) where the alga was present, coral tissue mortality was significantly higher in caged compared to open treatments (*P* < 0.001, effect %_{aoc} = 181%); (3) coral tissue mortality was always higher in the presence of alga compared to treatments where the alga had been removed for all levels of herbivory treatments (*P* < 0.001 in

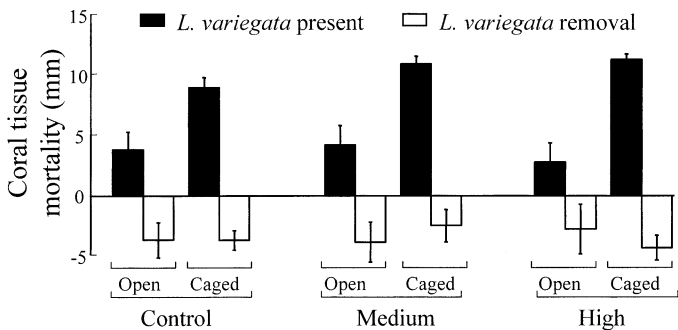


Fig. 2. Graph showing total mortality of coral tissue under different experimental treatments (Tables 1, 2). Control, medium, and high refer to nutrient treatments. Data are means of the total coral tissue mortality (mm \pm SEM) of eight replicates (averaged over four plots). Note that coral tissue mortality for *L. variegata* removal was almost always negative as a result of downward coral tissue regeneration after removal of the algal competitor.

all cases, effect %_{aoc} = -182% and -367% for open and caged treatments, respectively). Indeed, in the absence of the alga, coral tissue generally regrew downward over the bare skeleton. Thus, the effects of competition were generally relatively large, the effects of herbivore moderate, and the effects of nutrient treatments very small (effect %_{aoc} = 22% and 10% for medium and high treatments, respectively).

Although the effects of nutrients on coral tissue mortality were not significant in the overall analysis (Table 1), we also specifically tested for nutrient effects within the caged, alga-present treatment. This test, which amounts to a test of nutrient effects on algal growth, did indicate a small effect of nutrient treatments (Table 2). Post hoc SNK tests indicated that coral tissue mortality (in caged, algal removal treatments) was significantly higher in both medium- and high-nutrient treatments than at control levels ($P < 0.05$; effect %_{aoc} = 53% and 62%, respectively), whereas there was no significant difference between medium- and high-nutrient treatments.

Coral growth rate—The growth rates of coral tips (skeletal extension) were not significantly affected by any of the

treatments (Fig. 3, Table 3; effect %_{aoc} = 9, 7, and <3% for competition, herbivory, and nutrients, respectively). Furthermore, separate analyses within each level of all factors did not indicate any differences in coral growth among treatments ($P > 0.2$ in all cases).

Algal tissue nutrients—Algal tissue levels of both nitrogen and phosphorus were significantly enhanced in response to the nutrient pulse treatments (Fig. 4; $P < 0.001$ and 0.005 for N and P, respectively, whether expressed as a percentage of dry weight or as C:N and C:P ratios). SNK post hoc tests indicated that for percentage of dry weight, tissue nitrogen and phosphorus were significantly higher for high- ($P < 0.01$, $P < 0.05$, respectively) and medium-nutrient ($P < 0.01$ in all cases) treatments than in the control treatment but that medium- and high-nutrient treatments were not statistically different ($P > 0.05$ both for N and P). Although not statistically significant, it is interesting that tissue nitrogen showed an increasing trend at the higher level, whereas tissue phosphorus appeared to be saturated (Fig. 4).

Discussion

The most interesting aspect of the present study lies in the simultaneous, factorial tests for effects on the coral of an algal competitor, herbivory, and nutrient enhancement, thereby providing both direct comparisons of the magnitude of each effect and, critically, tests of the interactions and hence mechanistic relationships between those factors. The results demonstrated that coral tissue mortality was strongly affected by the presence of the competing macroalga and, to a lesser extent, by herbivory, as also found using in situ manipulations at Great Palm Island (Jompa and McCook in press). In contrast, any nutrient effect was relatively small and was found only when herbivory was experimentally excluded and algal competitors present. The effects of herbivores on corals were entirely dependent on the presence of the algal competitor, whereas competitive effects on coral mortality were less strongly dependent on herbivory.

The experimental demonstration that the coral tissue mortality at the interaction border was dependent on overgrowth

Table 1. Analysis of variance of the effects of nutrients, herbivory, and competitor (*L. variegata*) on tissue mortality of *P. cylindrica* (Fig. 2). Cochran's test indicates the homogeneity of variance (C critical value = 0.212). Data are not transformed.

Source	df	Mean square	F-ratio	P	Conclusion/SNK
Nutrient (N)	2	6	0.5	0.629	ns
Herbivory (H)	1	280	22.4	<0.001/0.910	*Open<caged/ns
Competitor (C)	1	2,678	214.1	<0.001*	*Removal<algae
N \times H	2	5	0.4	0.674	ns
N \times C	2	1	0.1	0.924	ns
H \times C	1	300	24.0	<0.001	*Significant
N \times H \times C	2	15	1.2	0.306	ns
Plot (N \times H \times C)	36	13	1	0.503	ns
Residual	48	13			

Cochran's C=0.158

* Details of herbivory and competition interaction and effects are explained fully in the text.

Table 2. Analysis of variance of nutrient effects within full-cage and algae-present treatments on tissue mortality of coral *P. cylindrica* (Fig. 2). Cochran's test indicates the homogeneity of variance (C critical value = 0.541). Data are not transformed.

Source	df	Mean square	F-ratio	P	Conclusion/SNK
Nutrient	2	13.300	6.224	0.020	high≅medium>control
Plot (Nutrient)	9	2.137	0.523	0.832	ns
Error (n=2)	12	4.084			
Cochran's C=0.225					

by the alga provides critical proof that the interaction is competitive: i.e., that coral tissue mortality is caused by algal overgrowth, rather than algal overgrowth responding to coral tissue mortality because of some unknown cause (McCook et al. 2001a). In situ reciprocal manipulations of corals and algae have shown that the coral also inhibits algal growth, although *L. variegata* is clearly the competitive dominant (Jompa and McCook in press). The strength of the competitive inhibition is demonstrated by the tissue growth or recovery (downward) over the bare skeleton, which consistently occurred in the absence of the algal competitor (Fig. 2). The strength of this competitive interaction is further demonstrated by the large effect sizes and by the strong competitive effects at all levels of the other treatment factors (herbivory and nutrients; Jompa and McCook in press).

L. variegata has also been observed overgrowing scleractinian corals at sites in the Caribbean (de Ruyter van Steveninck et al. 1988; Hughes 1994; Littler and Littler 2000) and appears to have relatively severe effects on corals compared to other macroalgae (such as filamentous turfs or upright macrophytes (e.g., Tanner 1995; Lirman 2001; McCook 2001)). These different effects are likely to result from differences in the mechanisms involved in coral–algal competitive interactions and from differences in algal growth strategies (reviewed by McCook et al. 2001a). Thus, the outcomes of this study are to some extent specific to the particular combination of coral and algal species (as well as the particular herbivore and nutrient regimes at the experimental site) and should not be generalized to other taxa or circumstances. However, it is worth noting that *L. variegata* is a very widespread and common species in both the Indo-Pacific and Caribbean. The species occurs from inshore reefs to oceanic reefs of the Great Barrier Reef (pers. obs.) and

has become relatively abundant during widespread reef decline in the Caribbean (Diaz-Pulido and Diaz 1997 and references therein; Littler and Littler 2000).

Experimental exclusion of large herbivores led to a significant increase in coral tissue mortality, although the magnitude of this effect was smaller than the competitor treatment, and critically, exclusion cages had no effects when the algal competitor was experimentally removed (Fig. 2; Jompa and McCook in press). This interaction, by demonstrating that the effects of exclusion cages were dependent on the overgrowth by the algal competitor, provides strong evidence that herbivores affected corals indirectly by removing their algal competitors. Although a number of herbivore exclusion experiments have previously suggested the importance of indirect effects of herbivory on corals via competition with macroalgae (Sammarco 1982; Lewis 1986; Stachowicz and Hay 1999; Lirman 2001), most have not directly demonstrated competition. Although two studies have previously demonstrated the competitive mechanism of the herbivore effect (Miller and Hay 1996, 1998), one of the studies found that herbivore control of algal competitors was partially offset by the direct effects of parrotfish grazing on the corals themselves (Miller and Hay 1998), in contrast to our results.

The importance of these herbivore effects in preventing algal overgrowth of the corals is emphasized by the size of the effects on coral tissue mortality (180% in plots with algae present). Thus, although *L. variegata* frequently overgrows the basal parts of *P. cylindrica* branches (see also Littler and Littler 2000), herbivory probably plays an important role in preventing the coral branches from being completely overgrown by the alga. In the field (Jompa and

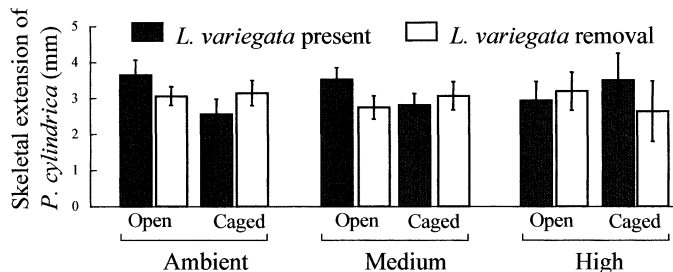


Fig. 3. Graph showing total coral skeletal extension under different experimental treatments (Table 3). Control, medium, and high refer to nutrient treatments. Data are means of total coral skeletal extension (mm ± SEM) of eight replicates.

Table 3. Analysis of variance of the effects of nutrients, herbivory, and competitor (*L. variegata*) on skeletal extension of *P. cylindrica* (Fig. 3). Other notes as Table 1.

Source	df	Mean square	F-ratio	P	Conclusion
Nutrient (N)	2	0.04	0.02	0.978	ns
Herbivory (H)	1	1.26	0.74	0.396	ns
Competitor (C)	1	0.83	0.48	0.491	ns
N × H	2	0.50	0.30	0.746	ns
N × C	2	0.22	0.13	0.881	ns
H × C	1	0.77	0.45	0.506	ns
N × H × C	2	3.20	1.88	0.168	ns
Plot (N × H × C)	36	1.71	1.11	0.369	ns
Residual	48	1.54			
Cochran's C=0.119					

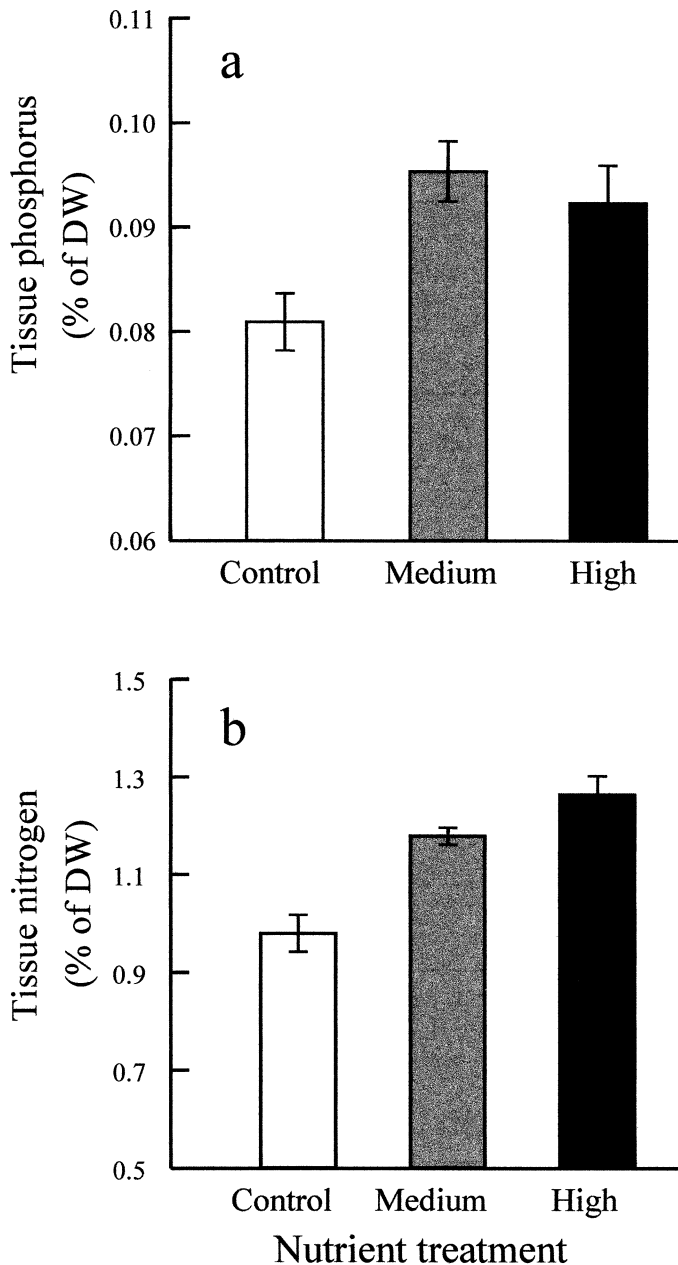


Fig. 4. Graphs showing algal tissue nutrient levels at the end of the experiment expressed as percentage of dry weight of phosphorus (a) and nitrogen (b) for *L. variegata* tissue under different nutrient treatments. Data are means (\pm SEM) of eight replicates.

McCook in press), it appears that larger, roving herbivorous fishes can remove algae overgrowing the upper parts of *P. cylindrica* branches but are excluded from the basal parts by the tightly packed branching structure of the colonies. Herbivore mediation of algal competition appears critical to the persistence and survival of these corals (Jompa and McCook in press).

Although overall nutrient effects on coral tissue mortality were not significant and were very small compared to the effects of the competitor (*L. variegata*) and herbivory (Fig. 2, Table 1), addition of nutrients did significantly increase

coral tissue mortality within full cages when *L. variegata* was present (Table 2). Furthermore, algal tissue nutrient levels were significantly enhanced in nutrient addition treatments (Fig. 4). These results are important because, together, they demonstrate that the nutrient treatments in this experiment were effective, not only in increasing nutrient supply to the plants (tissue nutrient data) but also in doing so sufficiently to enhance algal growth (Table 2). Furthermore, the relatively small difference between medium- and high-nutrient treatments suggests that pulse concentrations were sufficient to be near to saturating growth responses (at this pulse frequency), again suggesting that the relatively small effect of the nutrient treatments does not represent ineffective treatments but genuinely represents a relatively weak effect compared to the much larger effects of competition and herbivory. It appears that *L. variegata* growth was not strongly limited by nutrient supply.

Interestingly, the lack of nutrient enhancement of coral tissue mortality in the absence of *L. variegata* shows that the effect was not a direct effect on the physiology of the corals (cf. Stambler et al. 1991; Hoegh-Guldberg et al. 1997; Ferrier-Pages et al. 2000) but an indirect effect of enhanced growth of the algal competitor (Miller and Hay 1996). Although this conclusion supports the accepted mechanism of the bottom-up view of nutrient effects on corals (in the absence of herbivores), it emphasizes the importance of the competitive interaction to that effect. Because the strength of coral-algal competitive interactions could vary considerably (Miller 1998; McCook et al. 2001a), the strength of the bottom-up effects on corals (where expressed) will presumably also vary.

However, the expression of nutrient effects on algal competitiveness was strongly dependent on exclusion of herbivores. Presumably herbivore removal of algal biomass masked any nutrient-related differences in intrinsic algal growth rates or production, leaving no differences in *net* algal growth to accumulate as increased algal biomass and, hence, increased algal competitiveness. Algal competitiveness depends directly on biomass, not production, and algal biomass can only accumulate if tissue production exceeds tissue losses, including losses to herbivores; that is, *net* growth only occurs if *intrinsic* growth exceeds losses (Hatcher and Larkum 1983; McCook 1999). Assuming nutrients enhanced *intrinsic* algal growth similarly, whether herbivores were present or not, then apparently algal consumption also increased, resulting in no increase in algal biomass and competitiveness (i.e., no *net* algal growth; open plots with *L. variegata* present in Fig. 2). Thus, the results of this study support the argument that algal biomass or abundance (and hence competitiveness) on coral reefs is often regulated by consumption rates, rather than production/growth rates, and consumption rates often respond to absorb any changes in production (Hatcher and Larkum 1983; Carpenter 1986; Steneck 1988; McCook 1999; Russ and McCook 1999). For example, after an apparent, large-scale nutrient pulse, Russ and McCook (1999) reported a fivefold increase in production of epilithic algal communities, but this increase was closely matched by increased algal consumption, resulting in no changes to algal standing crop. Because nutrient enhancement affects algal growth, it can

only affect algal competitiveness when that increased growth exceeds the consumption capacity of herbivores.

Previous experiments testing factorial combinations of nutrients and herbivory for effects on fleshy algae have varied in terms of nutrient effects but have all emphasized the importance of herbivory (Hatcher and Larkum 1983; Miller and Hay 1996; Miller et al. 1999; Smith et al. 2001; Thacker et al. 2001). For example, Hatcher and Larkum (1983) found that nutrients limited algal growth, whereas grazers limited standing crop (abundance), although in some zones, grazers did not clearly predict standing crop. In contrast, Miller et al. (1999) found a strong effect of herbivory with negligible effect of nutrients (with no interaction) on macroalgal abundance. The expression of nutrient effects in the presence of herbivores will clearly depend on the intensity of local herbivory, and the palatability of algal species (Stimson et al. 2001; Thacker et al. 2001). In a series of studies on temperate reefs, Miller and Hay (1996) found that different groups of algae varied in their susceptibility to grazing, their nutrient limitation, and their competitive effects on corals but that enhanced nutrients only enhanced algal growth in the absence of herbivores.

These conclusions have several significant implications. First, studies that demonstrate nutrient enhancement of algal growth cannot be presumed to imply competitive consequences for corals without establishing the context in terms of herbivory regimes and competitive circumstances. Second, the risks of nutrient enrichment promoting algal overgrowth of corals will be most significant under low herbivory regimes, such as areas or zones with high fishing pressure or where herbivores are naturally scarce or ineffective. Furthermore, the consequences of that enrichment will depend on the competitive mechanisms and effectiveness of the resident algae (discussed in McCook 1999).

In contrast to the effects on coral tissue mortality at the interaction border, none of the treatments significantly affected the growth of coral branch tips (Fig. 3, Table 3). Overall growth rates of *P. cylindrica* in this study were similar to those measured in the original habitat. Although measurements using in situ branches found variable effects of herbivory and competition on growth at branch tips, these effects were consistently much smaller than those at the coral–algae boundary (Jompa and McCook in press). The minimal competitive effects of the algae on coral branch growth is presumably due to the physical separation between the algae and the coral tips because the upper border of the algal blades during this study period remained more than 2 cm from coral tips throughout the experiment. This separation would therefore also explain the lack of any indirect effects through the algal competitor of herbivory or nutrients on coral growth. However, no direct effect of nutrients on coral growth was apparent either, despite previous evidence that nutrient enhancement can cause reductions in coral growth (e.g., Stambler et al. 1991; Hoegh-Guldberg et al. 1997; Ferrier-Pages et al. 2000). This result should be interpreted cautiously because the length of this experiment (3 months) might be insufficient for nutrient effects on coral growth to become apparent (Hoegh-Guldberg et al. 1997). If such effects did occur, they could strongly influence coral competitive abilities, especially in synergy with increased algal

growth. The absence of any consistent effects of the caging treatment on coral growth supports the suggestion that caging artifacts were minimal. Finally, the minimal effects of the treatments on growth at the branch tips means that the effects on coral tissue mortality at the interaction border are approximately equivalent to the overall effect of the treatments on the net growth of the coral.

The results of this study demonstrate the relative strengths of algal competition, herbivory, and nutrient supply in affecting the survival of a coral and the mechanisms of those effects. Overgrowth by an algal competitor had a strong effect on the coral at all levels of the other factors. Herbivory also had a strong effect, but only indirectly by limiting growth of the algal competitor. The effects of nutrient enhancement in this experiment were small and were expressed only in the absence of herbivores. Overall, the results support the mechanistic view that competition between the coral and the algae is regulated by herbivore control of algal abundance and that nutrient enhancement will only influence algal abundance and hence competitiveness when herbivores are scarce, either naturally or as a result of human impacts. Although small-scale experiments such as this cannot be scaled up directly to community-level changes such as phase shifts and cannot be assumed to be general to other taxa, the present study does demonstrate the value of understanding and testing the mechanisms and processes involved and the relationships between them. This mechanistic approach can provide a broader basis for the interpretation and management of phase shifts, including not only bottom-up and top-down explanations, but also the important roles of processes and interactions such as competition.

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