



Effects of competition and herbivory on interactions between a hard coral and a brown alga

Jamaluddin Jompa^{a,b,c}, Laurence J. McCook^{a,*}

^a*Australian Institute of Marine Science and CRC: Reef Research, PMB 3, Townsville, M.C., Queensland 4810, Australia*

^b*Department of Marine Biology, James Cook University of North Queensland, Townsville, QLD 4811, Australia*

^c*Faculty of Marine Science and Fisheries, Hasanuddin University, Makassar 90245, Indonesia*

Received 8 November 2000; received in revised form 24 January 2002; accepted 8 February 2002

Abstract

Despite widespread acceptance of the negative effects of macroalgae on corals, very few studies have experimentally tested the competitive nature of the interaction, and most have ignored the potential effects of corals on algae. We report the effects of herbivory and competition on the growth of the branching scleractinian coral *Porites cylindrica* Dana and the creeping foliose brown alga *Lobophora variegata* (Lamouroux) Womersley, on an inshore fringing reef of the central Great Barrier Reef. *L. variegata* overgrows branches of *P. cylindrica* from the base up, forming a distinct boundary between the alga and the coral tissue. The experiment used exclusion cages to test for effects of herbivores, and removal of algae and coral tissue, at their interaction boundary, to test for inhibition of the competitors by each other. Comparisons of coral branches with the algae present or removed showed that the presence and overgrowth of the alga caused significant coral tissue mortality. Comparisons of branches with coral tissue unmanipulated or damaged showed that the coral inhibited the overgrowth by *L. variegata*, but that the algae were markedly superior competitors. Importantly, reduced herbivory resulted in faster algal growth and consequent overgrowth and mortality of coral tissue, demonstrating the critical importance of herbivory to the outcome of the competitive interaction. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Coral–algal competition; Coral reef; Herbivore exclusion; *Lobophora variegata*; Overgrowth; *Porites cylindrica*

* Corresponding author. Tel.: +61-7-47534362; fax: +61-7-4772-5852.

E-mail address: L.McCook@AIMS.Gov.Au (L.J. McCook).

1. Introduction

Understanding the effects of macroalgae on corals is becoming increasingly important as concerns mount about the influence of human development in promoting

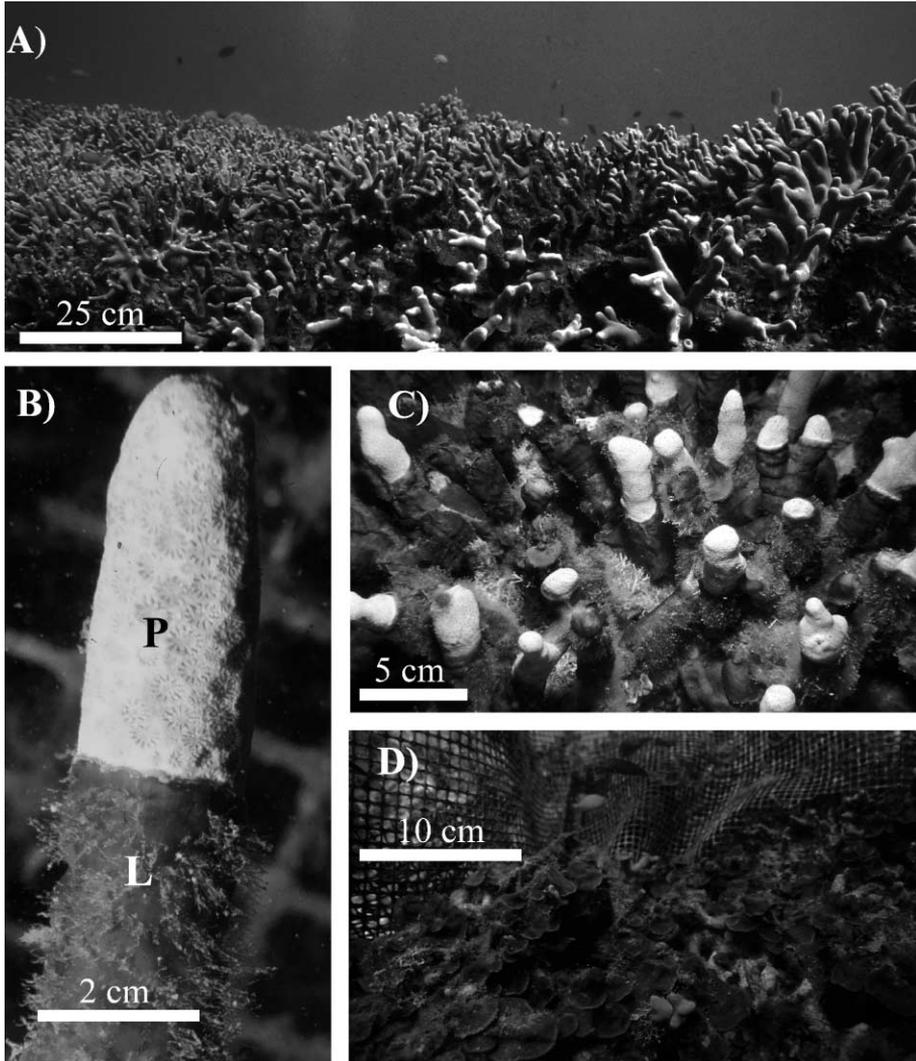


Fig. 1. (A) Colony of *P. cylindrica* on the reef slope of Cannon Bay, Great Palm Island, GBR. (B) Close-up of an individual *P. cylindrica* (P) branch with the brown alga *L. variegata* (L) growing around the base, as used in this experiment. (C) Colony showing *L. variegata* overgrowing the bases of most *P. cylindrica* branches. (D) After more than 1 year of herbivore exclusion (inside full cages), the alga almost completely overgrew all coral colonies, and the algal growth form commonly changed from creeping to foliose.

sedimentation, nutrient enhancement and overfishing, and consequent coral reef degradation. During these events, increased standing crop of benthic algae has been suggested to out-compete corals, leading to so-called ‘phase-shifts’ in which abundant corals are replaced by abundant benthic algae (Done, 1992; Lapointe, 1997; Miller, 1998; McCook, 1999). Despite the importance of coral–algal competition in understanding the process of phase-shifts, there have been relatively few direct, experimental studies of this interaction (i.e. Hughes, 1989; Coyer et al., 1993; Tanner, 1995; Miller and Hay, 1998; Jompa and McCook, 1998; McCook, 2001). Much of the available evidence for competition between corals and algae involves herbivore manipulations, correlative studies, and natural experiments, which do not explicitly demonstrate that competition with algae was inhibiting corals (or vice versa; McCook et al., 2001). Evidence for competition requires experimental manipulation of putative competitors to demonstrate that the abundance of one competitor is directly inhibited by the other competitor (Connell, 1983; Underwood, 1986; McArdle, 1996); in many cases, algal overgrowth appears to be the consequence of coral mortality from other causes (such as bleaching or storm damage; Diaz-Pulido and McCook, in press).

The outcomes of coral–algal interactions are likely to depend on the specific coral and algal taxa, and on other factors such as herbivory, habitat, water quality, disturbances, etc. (reviewed by Miller, 1998; McCook et al., 2001). Previous studies have reported variable outcomes, including macroalgal overgrowth of coral colonies (Chadwick, 1988; Hughes, 1989), inhibition of coral growth, survival and reproduction (Tanner, 1995) and even coral death (Potts, 1977; Sammarco, 1982; Lewis, 1986). However, corals are also capable of overgrowing the colonising algae (Bak et al., 1977; Meesters and Bak, 1993) and inhibiting algal growth (de Ruyter van Steveninck et al., 1988). Tanner (1995) found that most of the corals having contact with macroalgae were not overgrown by them.

In this study, we experimentally tested the effects of the brown alga, *Lobophora variegata* on the branching hard coral *Porites cylindrica* (Fig. 1), the reciprocal effects of the coral on growth of the algae, and simultaneously tested those effects under different levels of herbivory. Although a number of studies have suggested the importance of herbivory to coral–algal competition (e.g. Sammarco, 1982; Lewis, 1986; Hughes, 1994), only two have manipulated both herbivory and algal abundance (Miller and Hay, 1996, 1998), and only one previous study has directly examined effects of corals and algae on each other (McCook, 2001).

2. Materials and methods

2.1. Study site

This study was conducted on the reef slope (7–8 m depth) at Cannon Bay (18°41.1' S 146°35.2' E), Great Palm Island, Great Barrier Reef, Australia, close to the site used in McCook (2001). The site was dominated by colonies of *P. cylindrica* (~65% cover, based on four 20-m line-intercept transects). These colonies reach 2 m in height, suggesting they have been present at the site for a considerable time. 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 m^2) among the *P. cylindrica* colonies along the reef slope (Fig. 1). Other macroalgae were also commonly observed living on the base of coral branches, including *Amphiroa* spp., *Jania* sp., *Melanamansia* sp., *Dictyota* spp., *Hypnea pannosa*, and crustose coralline algae. While these macroalgae usually occupied only the base parts of the coral branches, *L. variegata* was often observed overgrowing and thus killing entire *P. cylindrica* branches, suggesting a more potent effect for this alga. The major herbivores observed at this site were roving herbivorous fishes, predominantly scarids, acanthurids and siganids, although territorial damselfishes were also present (personal observation; also Russ 1984). Sea urchins were rarely observed in this zone.

2.2. Experimental design

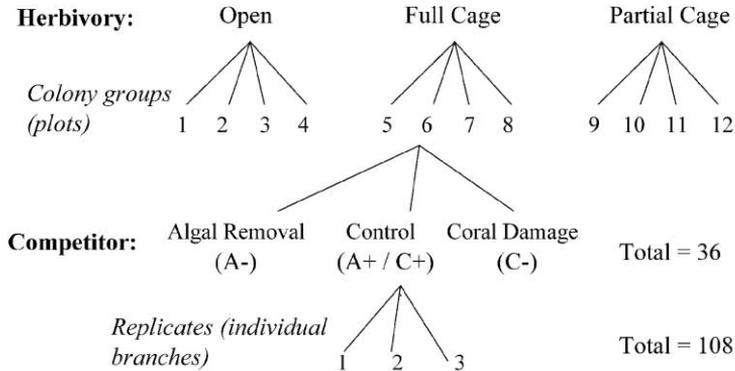
To test the hypotheses that the algal–coral interaction is competitive, and influenced by herbivory, we simultaneously manipulated competitors and herbivores in a multi-factorial design (Fig. 2A). Herbivore treatments consisted of four replicates each of full cages (herbivore exclusions), open plots (accessible to herbivores), and partial cages (partial controls for caging artefacts). Competitor treatment involved three replicates each of algal removal, untreated control, and coral damage treatments, providing separate tests for two effects: (i) the effect of *L. variegata* on *P. cylindrica*, by comparing coral tissue mortality and coral growth using algal removal and control (algae present) treatments; and (ii) the effect of *P. cylindrica* on *L. variegata* by comparing algal growth on coral damaged and control (coral present) treatments (Fig. 2B). We chose a nested factorial over a full factorial design (Fig. 2A) because the appropriate scale for herbivore manipulations was similar to the size of the *L. variegata* patches within the *P. cylindrica* colonies at the study site, whereas the competitor manipulations required a much smaller scale manipulation.

As many coral reef algae are very seasonal, the experiments were run twice at different seasons. The first period was from May to November 1998 and the second period from November 1998 to May 1999. The experimental periods were limited to 6 months because after longer periods, some coral branches had been completely overgrown by *L. variegata*, especially within full cages. None of the response variables (Fig. 2B) could be measured subsequent to such overgrowth.

2.3. General approach and methods

Twelve similar plots were selected from patches of *L. variegata* within *P. cylindrica* colonies, based on shore-parallel transects along the reef slope, at approximately 7–8 m depth (below datum). Plot size, approximately $25 \times 25 \text{ cm}$, was chosen to include enough individual, similar coral branches with similar amounts of *L. variegata* growing on the base, to provide similar starting conditions for the competitive treatments. Plots were then randomly allocated to caging treatments. Within each plot (i.e. open, full cage or partial cage), nine individual coral branches were chosen with similar size and similar amounts of *L. variegata* growing on their bases (Fig. 1C) and randomly allocated to competitor

A). Experimental design:



B). Method

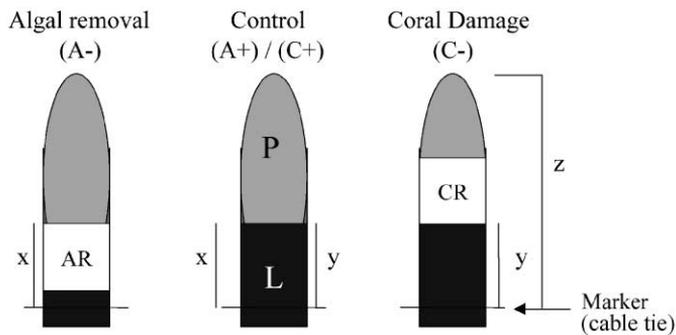


Fig. 2. (A) Experimental design. A nested factorial design involving two treatment factors (herbivore treatment and competitor treatments), with competitor treatments nested within colony plots. (B) Method. The effect of *L. variegata* on *P. cylindrica* was assessed by comparing coral mortality or skeletal extension in the presence of the alga (A+; control) with that in the absence of alga (A–). The effect of *P. cylindrica* on *L. variegata* was assessed by comparing algal growth in the presence of coral (C+) with that in its absence (C–). Coral tissue mortality was estimated by the change in position of the border between live and dead coral tissue (x), relative to a permanent reference marker (cable tie); i.e. mortality here refers to upward retreat of the bottom of the live coral. Coral skeletal extension was measured from coral tip to the reference marker (z); thus, extension refers to upward growth. Algal growth was estimated by change in position of the algal frond tip (y) relative to the reference point.

treatments (Fig. 2A). Each branch was labeled with a plastic tag attached to the base with a plastic cable tie.

2.3.1. Herbivore treatments

Herbivore exclusion cages were 75 cm by 75 cm × 75 cm (shaped to fit colony sizes in order to minimise coral damage), and were made of 12 mm plastic mesh

(Nylex, “Trical” high density polyethylene), similar to those used by McCook (1996, 1997). The cages were anchored with steel fence (star) pickets and plastic cable ties. The partial cages were similar to the full cages, but with two opposite sides open to allow grazing by herbivores. Open (uncaged) plots were marked with pickets. All cages were scrubbed every 1 to 2 months, as required, to remove fouling filamentous algae and sediments.

2.3.2. Competitor removal treatments

Algal removal treatment involved removing *L. variegata* from the base of the coral branches, to create a bare zone of approximately 20 mm between algal tissue and coral tissue (Fig. 2B “A –”). In the first period, algal removal was undertaken at 2- to 3-month intervals. Algal removal in the second experimental period was only done at the beginning of the experiment, potentially resulting in reduced effects. Coral damage treatment involved scraping coral tissue to approximately 2 mm depth for a height of 20 mm upward from the border with the algae, and was carried out every 2- to 3-month intervals to allow the *L. variegata* to grow without any effect from the corals. Removals were limited to about 20 mm to limit settlement of fouling organisms between the algal growth margins and live coral tissue.

2.3.3. Measurements and data analysis

Three response variables were measured (i) coral tissue mortality; (ii) coral skeletal extension; and (iii) algal growth (Fig. 2B). Coral tissue mortality refers to the loss of live coral tissue upward from the bottom of the branch (i.e. the border between live and dead coral tissue). Coral skeletal extension refers to the upward growth of the coral tip, and algal growth refers to the upward growth of the algal blade tip around the coral branch. All measurements were made relative to cable ties used as reference points, to the nearest 0.5 mm using calipers. Response variables used the difference between the initial and final measurements for each period.

Data analyses involved a three-factor ANOVA, with plots nested within herbivore treatment (Fig. 2), followed by post hoc Tukey’s HSD test, using Systat™ 8.0. Where the interaction between competitor and herbivore treatments was significant, analyses (ANOVA and Tukey’s HSD) were repeated within levels of each treatment factor. All data were tested for homogeneity of variance (Cochran’s test), outliers, and independence and normality of residuals (graphically). Based on these tests, data transformations were not necessary.

3. Results

3.1. The effects of herbivores and *L. variegata* on coral tissue mortality

Tissue mortality of *P. cylindrica* was significantly affected by both herbivore and competition (*L. variegata*) treatments in both periods (Fig. 3 and Table 1). In the first period, there was a significant interaction between these factors: the effects of competition with *L. variegata* were stronger when herbivores were excluded than when they were present

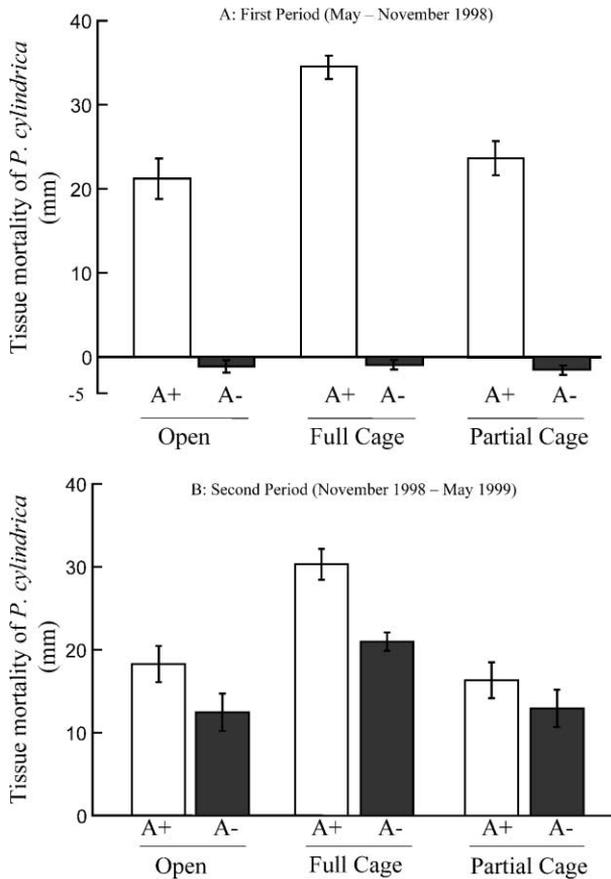


Fig. 3. Graphs showing total mortality of coral tissue under different experimental treatments (A+ = Algae [*L. variegata*] present, A- = Algal removal). Data are means of the total coral tissue mortality (mm \pm S.E.M.) of 12 replicates averaged over plots (see Fig. 2). Note that in the first period (regular algal removal), coral tissue mortality for A- was always negative as a result of downward coral tissue regeneration after algal removal.

(Fig. 3A), and herbivore treatments had no effect on coral tissue mortality where the algal competitor was removed. Where the algae were present, there was no significant difference between open plots and partial cages, but mortality was higher where herbivores were excluded. Coral tissue mortality was significantly higher in the presence of *L. variegata* in all plots, indicating an effect of algal competition even in open plots exposed to herbivores. Importantly, in the absence of *L. variegata*, coral tissue was actually able to regenerate downward, overgrowing dead skeleton (algal removal was performed repeatedly during this period), resulting in negative values for coral tissue mortality (Fig. 3A). The effects of competitor removal on coral tissue mortality in the first period were larger than those of herbivore exclusion (Fig. 3A).

In the second period, coral tissue mortality was also significantly affected by both factors, with significantly reduced mortality when the algal competitor was removed, and

Table 1

Analysis of variance of the effects on coral tissue mortality of herbivory and competition with *L. variegata*

Source	df	Mean-square	F-ratio	P	Conclusion
<i>First period (May–Nov. 1998)</i>					
Herbivory	2	365.95	6.99	0.015	
Competitor	1	15,842.00	333.14	0.000	
C*H	2	325.26	6.84	0.016	Significant ^a
Plot(H)	9	52.35	1.10	0.444	
C*Plot(H)	9	47.55	2.17	0.041	Significant
Residual (n=3)	48	21.95			
Cochran's C=0.18					
<i>Second period (Nov. 1998–May 1999)</i>					
Herbivory	2	1096.358	14.673	0.001	Cage>open ≈ partial
Competitor	1	1196.420	14.665	0.004	Algal removal>control
C*H	2	113.149	1.387	0.299	
Plot(H)	9	74.721	0.916	0.551	
C*Plot(H)	9	81.582	1.545	0.160	
Residual (n=3)	48	52.813			
Cochran's C=0.19					

Homogeneity of variance tests are shown as Cochran's *C*, the critical value for *C* here is 0.235; data are untransformed, and analysed independently for the first and second periods.

^a Analyses within levels of treatments indicate: no differences between herbivore treatments within algal removal (A –); cage>open ≈ partial within untreated control (A+); untreated control (A+)>algal removal (A –) within all levels of herbivory treatments.

when herbivores were present (Fig. 3B). However, in contrast to the first period, there was no significant interaction between herbivore and competitor treatments, and the effects of herbivore exclusion were larger than those of competitor removal. These differences between first and second periods are presumably due to the less frequent removal of *L. variegata* in the second period, which allowed regrowth of the alga, with consequent competitive effects on coral tissue mortality. Post hoc Tukey's HSD test on herbivory treatments revealed that coral tissue mortality was significantly higher with full cage treatments than in partial cages and open plots, whereas the latter two treatments were not statistically different.

After 12 months herbivore exclusion, *L. variegata* had completely overgrown and killed most corals in the fully caged plots (Fig. 1D). Such overgrowth was rare in uncaged plots.

3.2. The effects of herbivory and *L. variegata* on *P. cylindrica* growth

Coral skeletal extension was not significantly affected by any treatments in the first period (Fig. 4A, Table 2), whereas in the second period, *L. variegata* significantly reduced coral skeletal extension (Fig. 4B, Table 2). Fig. 4A suggests a similar but non-significant trend for reduced growth in the presence of *L. variegata* within fully caged and partially caged plots, but the reverse in open plots. There were no significant effects of herbivory during either period.

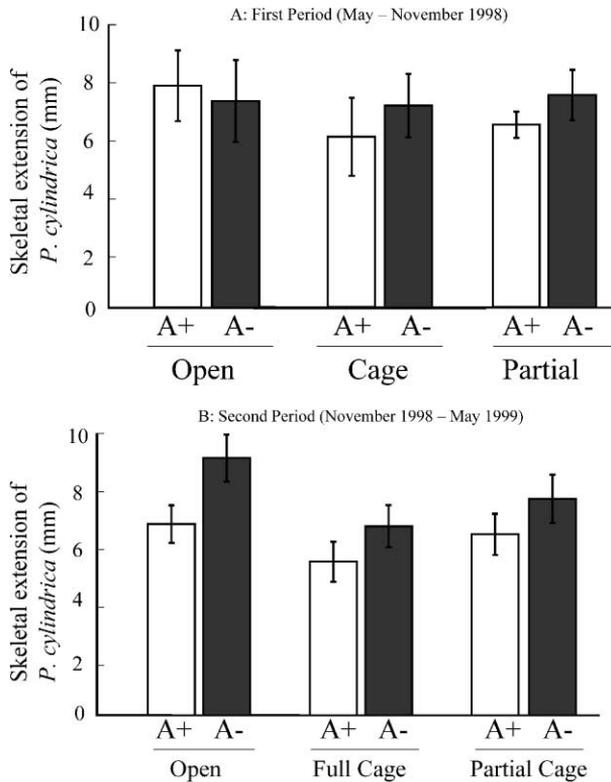


Fig. 4. Graphs showing total coral skeletal extension under different experimental treatments (A += Algae present, A – = Algal removal). Data are means of total coral skeletal extension (mm \pm S.E.M.) of 12 replicates.

3.3. The effects of herbivory and competition with *P. cylindrica* on *L. variegata* growth

L. variegata growth was significantly reduced by herbivory and competition with *P. cylindrica* during both study periods (Table 3 and Fig. 5). Post hoc Tukey's HSD test for both periods showed that *L. variegata* growth was significantly higher in the full cage treatment (herbivore exclusions) compared to partial cages and open plots, while the latter two treatments were not significantly different. Importantly, *L. variegata* growth was significantly greater when coral tissue was removed or killed compared to those at the control treatment, indicating that the corals inhibited algal growth. The effects of competition treatments (0–25% reduction in algal growth) were smaller than those of herbivore exclusion (approximately 50% reduction in algal growth). Although the interaction between the two factors was not significant (Table 3), ANOVAs within herbivore treatments suggested that differences in algal growth between coral competitor treatments were only significant within full cage treatments ($P < 0.05$) for the first and second periods, compared to $P > 0.4$ and $P > 0.9$ for open plots and $P > 0.3$ and $P > 0.2$ for

Table 2

Analysis of variance of the effects on coral skeletal extension of herbivory and competition with *L. variegata*

Source	df	Mean-square	F-ratio	P	Conclusion
<i>First period (May–Nov. 1998)</i>					
Herbivory	2	3.608	0.498	0.624	No significant treatment effects
Competitor	1	3.337	0.474	0.508	
C*H	2	3.233	0.459	0.646	
Plot(H)	9	7.249	1.030	0.483	
C*Plot(H)	9	7.036	0.760	0.653	
Residual (n=3)	48	9.253			
Cochran's C=0.104					
<i>Second period (Nov. 1998–May 1999)</i>					
Herbivory	2	22.531	2.259	0.160	Algal removal>control
Competitor	1	50.000	10.128	0.011	
C*H	2	2.531	0.513	0.615	
Plot(H)	9	9.975	2.020	0.155	
C*Plot(H)	9	4.937	0.767	0.647	
Residual (n=3)	48	6.441			
Cochran's C=0.08					

Note as for Table 1.

partial cages). This suggests that inhibition of algal growth by corals may have been stronger in the absence of herbivores (Fig. 5).

The complete algal overgrowth observed after 12 months herbivore exclusion (Fig. 1D) also resulted in a change in algal growth form, from the creeping morphology of algae

Table 3

Analysis of variance of the effects on *L. variegata* growth of herbivory and competition with *P. cylindrica*

Source	df	Mean-square	F-ratio	P	Conclusion
<i>First period (May–Nov. 1998)</i>					
Herbivory	2	2686.774	12.576	0.002	Cage>open ≈ partial
Competitor	1	938.889	10.454	0.010	Coral removal>control
C*H	2	215.524	2.400	0.146	
Plot(H)	9	213.646	2.379	0.106	
C*Plot(H)	9	89.813	1.741	0.105	
Residual (n=3)	48	51.580			
Cochran's C=0.13					
<i>Second period (Nov. 1998–May 1999)</i>					
Herbivory	2	2926.097	40.562	0.000	Cage>open ≈ partial
Competitor	1	475.347	5.702	0.041	Coral removal>control
C*H	2	138.347	1.660	0.243	
Plot(H)	9	72.139	0.865	0.584	
C*Plot(H)	9	83.366	1.081	0.349	
Residual (n=3)	48	77.125			
Cochran's C=0.16					

Note as for Table 1.

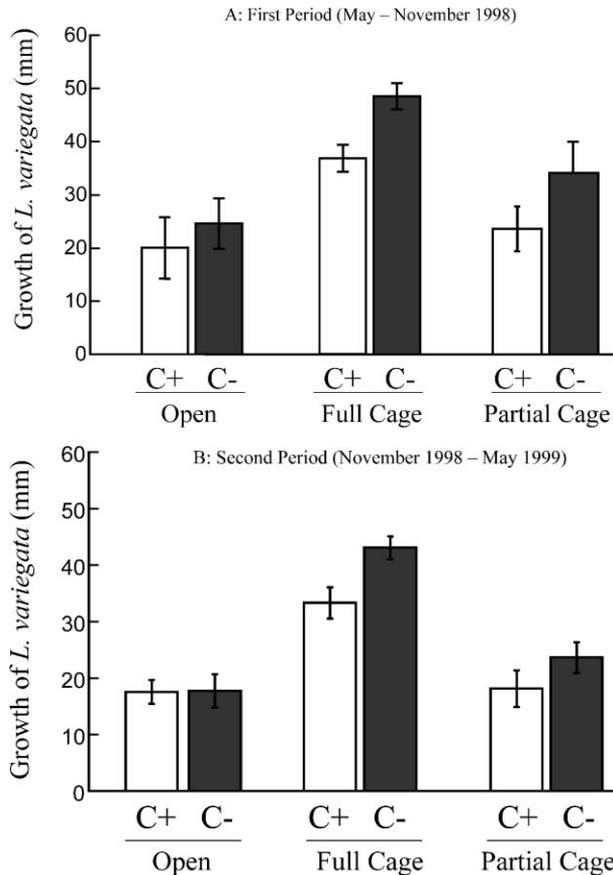


Fig. 5. Graphs showing total *L. variegata* growth under different experimental treatments (C+ = Coral present (control), C- = Coral damage). Data are means of total algal growth (mm \pm S.E.M.) of 12 replicates.

attached to the coral branches, to foliose, horizontal fronds. This foliose form was rare in plots exposed to herbivores.

4. Discussion

The results of this study are significant in particular because they provide direct causal evidence for a specific example of the widely accepted view of coral–algal competition as mediated by herbivory, and because they demonstrate reciprocal inhibition by both competitors of each other (McCook et al., 2001). The creeping form of the brown alga *L. variegata* caused tissue mortality of *P. cylindrica*, apparently by adherently overgrowing from the basal part of the coral branches upward, consequently smothering and killing the underlying coral tissue (“overgrowth” mechanism in McCook et al., 2001). Removal of *L. variegata* demonstrated that coral tissue mortality was caused by the alga,

rather than reflecting algal overgrowth of coral tissue already dead or stressed by other factors. The viability of the coral in the absence of the algae was emphasized by the ability of the corals to expand downward over the bare skeleton previously covered by the alga (before removal; Fig. 3A), during the first experimental period.

The presence of *L. variegata* also reduced coral skeletal extension (upward growth) of the branches, although only during the second period, and these effects were much smaller than those on tissue mortality (Table 2). The relatively minor impact on coral growth probably reflects the separation between the site of coral growth, at the branch tips, and the site of overgrowth, at the base of the coral branches where the coral tissue contacted the algae. This separation suggests that the competitive effect on coral growth results from the stress or metabolic costs of defending the lower tissue. The difference between experimental periods in effects on coral growth appears primarily accounted for by a difference in growth in open plots (Fig. 4), but the cause of that difference remains uncertain.

Although *L. variegata* was able to overgrow and kill live tissue of *P. cylindrica*, the coral was also able to inhibit the growth of the algae, although to a lesser degree. Algal growth was slower where the algal growth margin was in direct contact with live coral tissue/polyp (coral–algal interface) than where the coral tissue was experimentally removed/damaged (Table 3 and Fig. 5), indicating that the competitive inhibition by these two species was mutual. However, the inhibition of *L. variegata* by *P. cylindrica* was substantially less (<25%) than that of the algae on the corals (>100% for repeated removals), and the interaction between the two species uniformly resulted in algal overgrowth of corals (indicated by positive algal growth and coral tissue mortality: Figs. 3 and 5). Thus, *L. variegata* was competitively superior to *P. cylindrica* in this study, for both experimental periods and for all herbivore treatments.

The inhibition of *L. variegata* by corals was also observed by de Ruyster van Steveninck et al. (1988), where all coral species studied reduced growth rates of *L. variegata* when the alga was a close distance (< 1 cm) from the periphery of coral colonies. They suggested two possible mechanisms for this inhibition: mechanical damage by mesenterial filaments or sweeper tentacles (“stinging, etc.” in McCook et al., 2001), indicated by damaged margins of algal blades; and chemical (allelopathic) defence. We could not distinguish between these two possible mechanisms in our study: we did not observe any distinctive difference in the condition of algal growth margins between competitor treatments within full cages. Some damage to algal blades was observed in the open and partial cages, but this was most likely due to be grazers. Algal growth inhibition by allelochemicals has been shown for sea anemones (Bak and Borsboom, 1984) and alcyonacean soft corals (Coll et al., 1987).

Reduction of herbivore pressure resulted in both increased algal growth (net growth), and increased coral tissue mortality. The relative effects of competition and caging treatments on growth of *L. variegata* in this experiment (Fig. 5) suggest that herbivory was inhibiting net algal growth more strongly than competition with the corals. Herbivory also had larger effects on algal growth (approximately 50% reduction: Fig. 5) than on coral tissue mortality (approximately 40% reduction: Fig. 3), and, significantly, herbivory had no effect on coral tissue mortality when the algae had been removed. Together, this provides strong evidence that the effects of herbivores on corals were indirect, and mediated by the algal competitors, as widely assumed. Numerous previous studies on coral reefs have indicated that herbivore exclusion caused increased algal biomass and

consequently reduced coral growth and/or survival (Sammarco, 1980, 1982; Connell, 1983; Lewis, 1986; Hughes, 1989; Done, 1992; Miller and Hay, 1996, 1998; Stachowicz and Hay, 1999), but few have provided such specific, direct evidence for the exact mechanism. In this example, top-down control of algal competitors by herbivores appears critical to the ability of the corals to persist in these plots (Aronson and Precht, 1999; Hughes et al., 1999; McCook, 1999; Lapointe 1997).

It appears that the caging treatments provided effective herbivore exclusions, with minimal caging artifacts. Partial cage treatments were consistently not significantly different to open plots, and significantly different to full cages (where any differences existed), and all caging treatment effects were consistent with reduced herbivory, suggesting that the cage structure itself had minor effects other than excluding herbivores. Although cages may have artifacts due to shading of either algae or corals, any such effect was minor in this study, since algal growth was higher in full cages and similar (or non-significantly higher) in partial cages, compared to open plots (Fig. 5 and Table 3), and caging effects on coral skeletal extension were not significant (Table 2 and Fig. 4). Similarly, the patterns of coral skeletal extension among caging treatments (Table 2 and Fig. 4) are not consistent with a confounding effect of excluding coral predators, in contrast to the results of Miller and Hay (1998).

Although algal growth was strongly reduced by herbivory and to a lesser extent by competition, the results show that algal growth was generally greater than coral skeletal extension in this study. In open plots, exposed to natural levels of herbivory, upward overgrowth of *L. variegata* on *P. cylindrica* was about 20 mm during both 6-month periods, whereas coral growth was only around 10 mm upward in the same plots. Thus, the study plots appear to be undergoing a net loss of coral tissue. This suggests either that a general overgrowth of *P. cylindrica* by *L. variegata* is taking place in this area, or that *P. cylindrica* is able to persist despite this overgrowth. In particular, it seems likely that rates of herbivory may increase as the algae approach the top of the coral branches, as the algae become more accessible to larger herbivorous fishes. Thus, the structure of the coral colonies may provide a refuge for this alga from herbivory.

Comparison of the competitive interactions in this study with other published studies support the suggestion (McCook et al., 2001) that *L. variegata* may be a relatively potent coral competitor, perhaps because this creeping growth form maximizes damage to underlying coral tissue (Table 6 in McCook et al., 2001). In contrast, Tanner (1995) and Miller and Hay (1998) found a variety of primarily upright macroalgae which had relatively minor effects on coral mortality, several studies have found filamentous turfs to be poor competitors with corals (e.g. Meesters and Bak, 1993; van Woelk, 1998; McCook, 2001), and there is evidence that canopy-forming *Sargassum* beds may have little or no competitive effects on understory corals (Jompa and McCook, 1998; McCook, 1999).

The results of this study provide only one specific example of the range of potential coral–algae–herbivore interactions, rather than representing a general pattern. However, *L. variegata* may be a particularly important species, as it is relatively widespread and common although not abundant on healthy coral reefs, and is often abundant on degraded reefs, especially in the Caribbean (e.g. Hughes, 1994; Refs. in Diaz-Pulido and Diaz, 1997). On the GBR, *L. variegata* is found from inshore fringing reefs, where it occurs as a relatively large, upright and leafy form, to offshore reefs and the Coral Sea reefs, where it

often occurs as a small, cryptic, creeping form in refuges from herbivores (unpublished data). This combination of distribution and plastic growth form suggests a potentially significant role in overgrowth of coral populations, in contrast to algae such as *Sargassum*, which, although very abundant on inshore reefs, is extremely rare on offshore reefs (McCook et al., 1997), and has limited dispersal capability (McCook, 1997).

In conclusion, these results provide a clear, specific example of a benthic alga which is competitively superior to a scleractinian coral, but which is at least partially limited by herbivory. *L. variegata* could overgrow and kill live tissue of *P. cylindrica*, despite competitive inhibition of the alga by the coral. The extent of algal overgrowth and consequent coral tissue mortality was strongly limited by herbivory, but even at ambient levels of herbivory, *L. variegata* was still competitively superior to *P. cylindrica*. Experimental exclusion of herbivores resulted in extensive overgrowth and mortality to corals, and near-complete dominance by the alga. These results have clear implications in terms of the importance of herbivore abundances for sustainable coral populations on these near-shore reefs.

Acknowledgements

We thank G. Diaz-Pulido, R. Cumming, C. Arango, A. Walli, D. Egli, G. Arango, A. Chin, F. Olivier, C. Bastidas, K. Finstad, for their considerable help with the field work, G. Diaz-Pulido, H. Choat, T. Done, J. Tanner and T. Hughes for the discussion, and the reviewers for improving the manuscript. We acknowledge AIMS for providing a research vessel and the crew of the R.V. *Harry Messel* for their support in the field. This work was supported by the CRC-Reef, Department of Marine Biology, JCU and an AusAID fellowship for J.J. This is AIMS Contribution No. 1086. [AU]

References

- Aronson, R.B., Precht, W.F., 1999. Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. *Coral Reefs* 45, 251–255.
- Bak, R.P.M., Borsboom, J.L.A., 1984. Allelopathic interaction between a reef coelenterate and benthic algae. *Oecologia* 63, 194–198.
- Bak, R.P.M., Brouns, J.J.W.M., Heys, F.M.L., 1977. Regeneration and aspects of spatial competition in the scleractinian corals *Agaricia agaricites* and *Montastrea annularis*. *Proc. 3rd Int. Coral Reef Symp.* Miami, 143–148.
- Chadwick, N.E., 1988. Competition and locomotion in a free-living fungiid coral. *J. Exp. Mar. Biol. Ecol.* 123, 189–200.
- Coll, J.C., Price, I.R., Konig, G.M., Bowden, B.F., 1987. Algal overgrowth of alcyonacean soft corals. *Mar. Biol.* 96, 129–135.
- Connell, J.H., 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* 122, 661–696.
- Coyer, J.A., Ambrose, R.F., Engle, J.M., Carroll, J.C., 1993. Interactions between corals and algae on a temperate zone rocky reef: mediation by sea urchins. *J. Exp. Mar. Biol. Ecol.* 167, 21–37.
- de Ruyter van Steveninck, E.D., Van Mulekom, L.L., Breeman, A.M., 1988. Growth inhibition of *Lobophora variegata* (Lamouroux) Womersley by scleractinian corals. *J. Exp. Mar. Biol. Ecol.* 115, 169–178.
- Diaz-Pulido, G., Diaz, J.M., 1997. Algal assemblages in lagoonal reefs of Caribbean oceanic atolls. *Proc. 8th Int. Coral Reef Symp.* Panama 1, 827–832.

- Diaz-Pulido, G., McCook, L.J., in press. The fate of bleached corals: patterns and dynamics of algal recruitment. *Mar. Ecol.: Prog. Ser.*
- Done, T.J., 1992. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologica* 247, 121–132 (The ecology of mangrove and related ecosystems).
- Hughes, T.P., 1989. Community structure and diversity of coral reefs: the role of history. *Ecology* 70, 275–279.
- Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551.
- Hughes, T.P., Szmant, A.M., Steneck, R.S., Carpenter, R., Miller, S., 1999. Algal blooms on coral reefs: what are the causes? *Limnol. Oceanogr.* 44, 1583–1586.
- Jompa, J., McCook, L.J., 1998. Seaweeds save the reefs?!: *Sargassum* canopy decreases coral bleaching on inshore reefs. *Reef Res.* 8, 5.
- Lapointe, B.E., 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnol. Oceanogr.* 42, 1119–1131.
- Lewis, S.M., 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol. Monogr.* 56, 183–200.
- McArdle, B.H., 1996. Levels of evidence in studies of competition, predation, and disease. *N. Z. J. Ecol.* 20, 7–15.
- McCook, L.J., 1996. Effects of herbivores and water quality on the distribution of *Sargassum* on the central Great Barrier Reef: cross-shelf transplants. *Mar. Ecol.: Prog. Ser.* 139, 179–192.
- McCook, L.J., 1997. Effects of herbivory on zonation of *Sargassum* spp. within fringing reefs of the central Great Barrier Reef. *Mar. Biol.* 129, 713–722.
- 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.
- McCook, L.J., 2001. Competition between coral and algal turfs along a gradient of terrestrial runoff in the nearshore central Great Barrier Reef. *Coral Reefs* 19, 419–425.
- McCook, L.J., Price, I.R., Klumpp, D.W., 1997. Macroalgae on the GBR: causes or consequences, indicators or models of reef degradation? *Proc. 8th Int. Coral Reef Symp.* 2, 1851–1856.
- McCook, L.J., Jompa, J., Diaz-Pulido, G., 2001. Competition between corals and algae on coral reefs: a review of available evidence and mechanisms. *Coral Reefs* 19, 400–417.
- Meesters, E.H., Bak, R.P.M., 1993. Effects of coral bleaching on tissue regeneration potential and colony survival. *Mar. Ecol.: Prog. Ser.* 96, 189–198.
- Miller, M.W., 1998. Coral/seaweed competition and the control of reef community structure within and between latitudes. *Oceanogr. Mar. Biol. Annu. Rev.* 36, 65–96.
- Miller, M.W., Hay, M.E., 1996. Coral–seaweed–grazer–nutrient interactions on temperate reefs. *Ecol. Monogr.* 66, 323–344.
- Miller, M.W., Hay, M.E., 1998. Effects of fish predation and seaweed competition on the survival and growth of corals. *Oecologia* 113, 231–238.
- Potts, D.C., 1977. Suppression of coral population by filamentous algae within damselfish territories. *J. Exp. Mar. Biol. Ecol.* 28, 207–216.
- Russ, G.R., 1984. Distribution and abundance of herbivorous fishes in the central Great Barrier Reef: I. Levels of variability across the entire continental shelf. *Mar. Ecol.: Prog. Ser.* 20, 23–34.
- Sammarco, P.W., 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. *J. Exp. Mar. Biol. Ecol.* 45, 245–272.
- Sammarco, P.W., 1982. Echinoid grazing as a structuring force in coral communities: whole reef manipulations. *J. Exp. Mar. Biol. Ecol.* 61, 31–55.
- Stachowicz, J.J., Hay, M.E., 1999. Mutualism and coral persistence: the role of herbivore resistance to algal chemical defense. *Ecology* 80, 2085–2101.
- Tanner, J.E., 1995. Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. *J. Exp. Mar. Biol. Ecol.* 190, 151–168.
- Underwood, A.J., 1986. The analysis of competition by field experiments. In: Kikkawa, J., Anderson, D.J. (Eds.), *Community Ecology: Pattern and Process*. Blackwell, Melbourne, Australia, pp. 240–268.
- van Woesik, R., 1998. Lesion healing on massive *Porites* spp. corals. *Mar. Ecol.: Prog. Ser.* 164, 213–220.