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REPORT

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Competition between corals and algal turfs along a gradient of terrestrial influence in the nearshore central Great Barrier Reef

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Abstract Competition between benthic algae and corals is a key process in the community ecology of reefs, especially during reef degradation. However, there have been very few experimental tests for competition between corals and benthic algae, despite widespread assumptions that algae are generally superior competitors, especially in eutrophic conditions. This study tested for competition for space between the massive coral *Porites lobata* and algal filamentous turfs on three reefs along a cross-shelf gradient of terrestrial influence, by experimentally removing or damaging either corals or algae. The corals and algae were competing for space, but, significantly, the algae appeared to have little effect on coral growth. In contrast, corals significantly inhibited algal growth, suggesting *Porites* was the competitive superior. Importantly, coral growth was generally positive, even on the reef with the greatest terrestrial influence. Competitive outcomes did not support the argument that algae are more successful competitors in more eutrophic conditions.

Key words Coral–algal competition · *Porites* · Algal turfs · Epilithic algal communities · Algal overgrowth · Phase shifts · Nutrients · Terrestrial runoff · Coral reefs · Cross-shelf

Introduction

Competition between scleractinian corals and benthic algae is a critical process in determining the abundance of both groups on coral reefs, especially during reef degradation due to either overfishing or eutrophication. In either case, increased standing crop of benthic algae is considered to lead to competitive overgrowth of corals, resulting in a so-called phase-shift from abundant corals to algae (Done 1992; Lapointe 1997; Miller 1998; McCook 1999; McCook et al. 2000b). In particular, it is widely assumed that on eutrophic reefs, high nutrient availability leads to increased algal growth, in turn leading to increased competitive success against corals (e.g. Bell 1992; Lapointe 1997; Adey 1998), although such changes can only follow where herbivores are insufficient to consume the extra algal growth (Hughes et al. 1999; McCook 1999).

Although a wide range of observations suggest that coral–algal competition is widespread (Miller 1998; McCook et al. 2000b), proof of competition requires experimental demonstration that abundance of the competitors is inhibited by the presence or abundance of each other (Connell 1983; Underwood 1986). However, there have been surprisingly few unambiguous, experimental demonstrations that established corals and algae do compete (Hughes 1989; Coyer et al. 1993; Tanner 1995; Miller and Hay 1996; Miller and Hay 1998; reviewed by Miller 1998; McCook et al. 2000b). Most of these studies tested either larger, fleshy macroalgae or combinations of different algal functional groups (fleshy macroalgae and filamentous algae), although interactions with corals are likely to vary among algal forms (McCook et al. 2000b). Only one study has tested the effects of nutrients on coral–algal competition (Miller and Hay 1996), in a temperate system, not a tropical coral reef.

Much of the evidence commonly cited for coral–algal competition, and especially for nutrient effects on that competition, simply documents the appearance of abundant algae in areas previously occupied by corals. This does not demonstrate competitive exclusion of corals, since this pattern will generally result from algal colonisation of dead corals, whatever the cause of coral death (e.g. storm damage, bleaching, crown-of-thorns starfish). In such circumstances, algal abundance is the consequence, rather than the cause, of coral mortality (McCook et al. 2000b).

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Such distinctions in process are potentially significant, in terms of understanding and responding to potential human impacts such as eutrophication (McCook 1999). For example, on inshore reefs of the Great Barrier Reef, the presence of abundant algae in areas of high anthropogenic terrestrial runoff has been suggested to threaten coral populations on these reefs (Bell 1992), especially in areas where herbivore abundance is insufficient to control algal accumulation (McCook 1996, 1997). However, abundant corals persist on these reefs, even in areas with particularly high inputs of terrestrial sediments or nutrients, low herbivore abundance and high abundance of macroalgae (e.g. reef flat at Goold Island; Fig. 2 in McCook 1999, personal observations). Understanding the potential impacts of human land-use and runoff thus requires better understanding of the mechanisms of coral–algal competition, and of nutrient effects on that interaction.

The purpose of the present study was to test whether corals and algae were competing for space on these reefs, and whether the outcome of that competition is simply predicted by proximity to sources of terrestrial nutrients and sediments. The study focused on areas of direct contact between filamentous algal turfs and massive *Porites* corals, since observations suggested that larger macroalgae predominantly recruited among filamentous algal turfs, and that coral mortality was most commonly associated with overgrowth by the filamentous turfs (a separate, simultaneous study, to be reported elsewhere, tested the effects of large macroalgae on corals at the same sites).

Experimental design, study sites and methods

Experimental design, methods and statistical analyses

To test whether corals and algae were directly competing for space, the experiment compared the performance of each when its putative competitor had been experimentally removed or damaged, with its performance in control plots where the competitor was not manipulated, and at natural levels. If the interaction is competitive, then the success of one competitor should be improved by the removal of the other. The tests were repeated on three inshore fringing reefs that form a gradient of water quality conditions and terrestrial influence, to test whether the competitive success of the algae was enhanced under conditions of increased availability of nutrients and sediments. Water quality is used here as a shorthand term to refer collectively to the nutrient and sediment levels in the water.

The experimental design involved a two-factor ANOVA, with Competitor Treatments as one factor (three levels: Algal Removal, unmanipulated Controls and Coral Damage), and Reef as the second factor (three levels: Goold Island, Coolgaree Bay and Cannon Bay, both on Great Palm Island). Within each reef, four replicate 13 × 19 cm quadrats were randomly assigned to each treatment.

The method involved photographically monitoring the changes in position of boundaries between healthy, live tissue of *Porites lobata* and turf algae (Fig. 1), over a 7-month period, from October 1996 to May 1997. A shift in position of the boundary was taken as local success of the taxon that increased in area. Large colonies of massive *Porites* species, such as *P. lobata* and *P. lutea*, are common at the study reefs, and appear to be significant contributors to reef construction. Algal turf composition appeared fairly homogeneous among sites, and typical of algal turfs in the area (McCook et al., unpublished data), being dominated by species of *Sphacelaria*, *Hincksia* and *Jania*, as well as *Centroceras*, *Ceramium*, *Enteromorpha*, *Cladophora*, *Polysiphonia*, various Cyanophyta and small stages of Dictyotales and larger, corticated Rhodophyta. Quadrats were selected to include a direct boundary between the two groups, were marked with stainless-steel screws in three corners, and were then photographed using a Nikonos V camera with 35-mm lens and close-up filter and frame. Quadrats were then randomly allocated to treatments. Algal removal treatment involved wire brushing and scraping with a paint scraper to remove as much as possible of the algal turf in the plots, taking care to minimise damage to the coral tissue along the boundary. Coral damage involved wire brushing

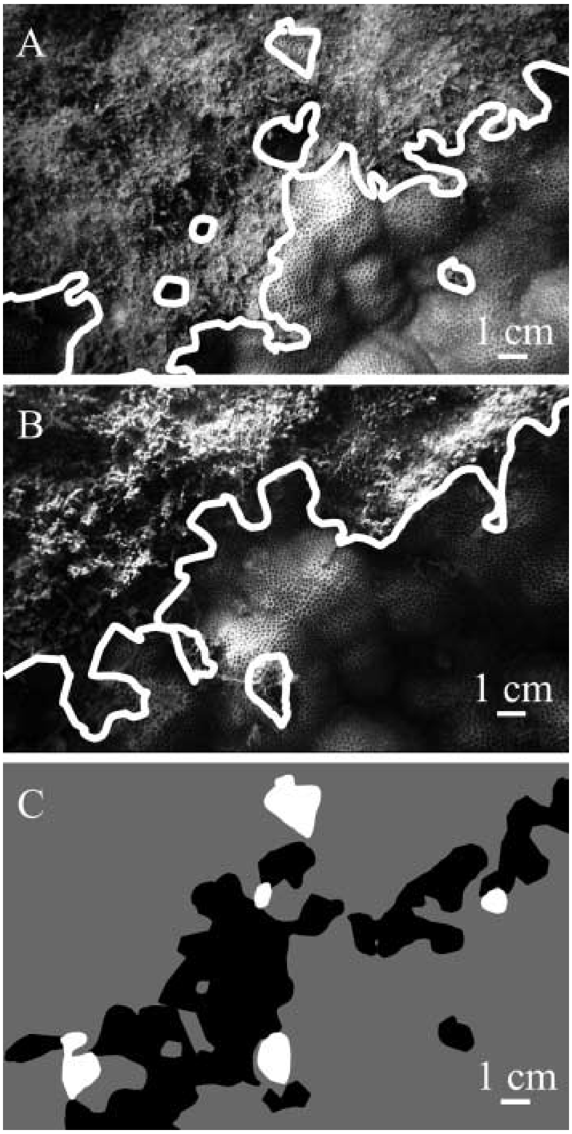


Fig. 1 Method for comparing initial and final boundaries between living *Porites lobata* tissue and filamentous turfs. **A** Plots (13 × 19 cm) were photographed prior to experimental treatments, and the boundary traced. **B** Plots were then rephotographed 7 months after experimental treatments, and the boundary again traced. **C** Comparisons of boundaries allowed determination of areas in which algal turf had overgrown coral (*white areas*), and areas in which corals had overgrown algal turf (*black shading*). The particular plot shown was from turf algal removal treatment at Goold Island, and had a net gain in area of coral of 13.9 cm^2

and scraping the coral to remove the top layer (≤ 5 mm) of tissue and mucus, but not completely removing the living coral tissue. Quadrats were then rephotographed 7 months later, using the three screws to position the camera in three dimensions, thereby minimising parallax differences between initial and final photographs.

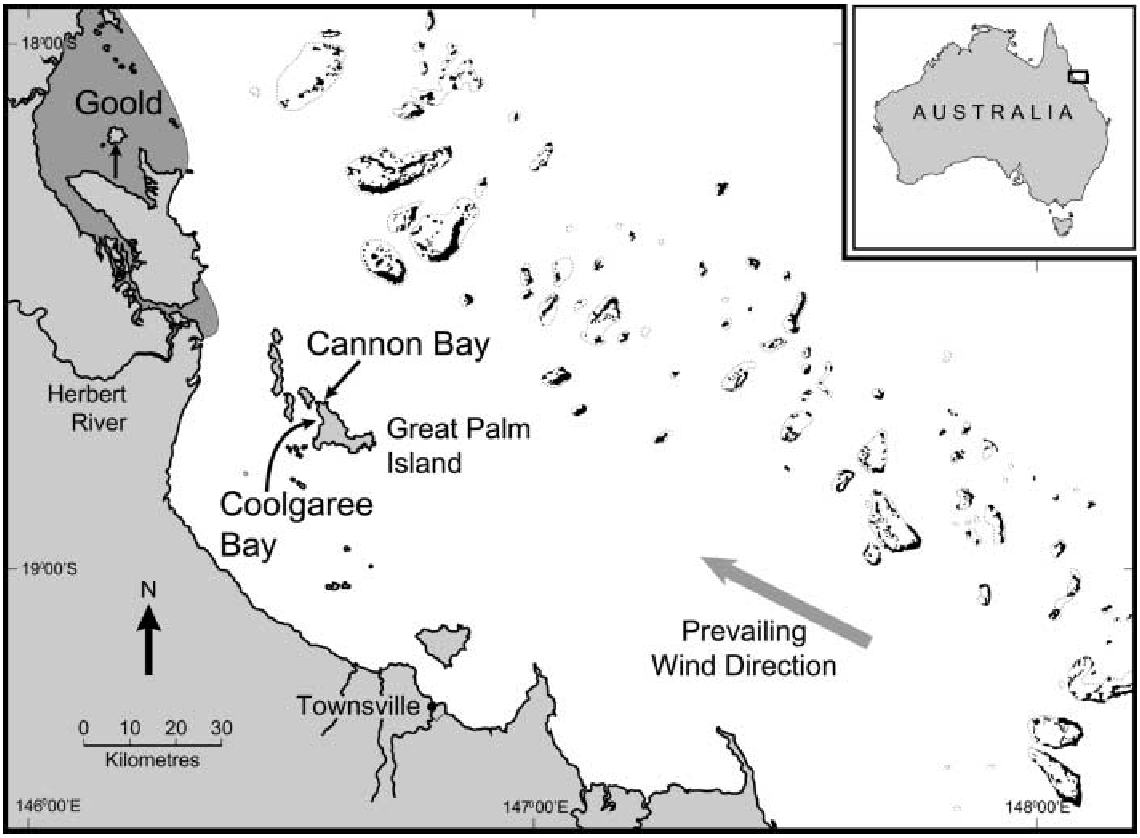
Slides of each quadrat were then projected onto plastic film, and the position of the boundary between corals and algal turfs traced, as well as marker screws, photograph frame and other features which allowed the accurate overlay of the two (initial and final) tracings. Initial and final tracings for each quadrat were then overlaid, and separate tracings made of areas that changed from coral to algal turf and vice versa. These pairs of tracings were then scanned and the areas measured using NIH Image 1.47 software. Subtracting the areas of coral to algal turf transition from the area of algal turf to coral transition gave a single, total area for each quadrat (positive numbers used to indicate an overall gain in area of coral at the expense of algae, negative numbers indicate an overall increase in area of algae). Data were analysed using a two-factor ANOVA and Student-Neuman Keuls (SNK) a posteriori comparisons of means, and percent of total sums of squares (%SST) used as estimates of the magnitude of effects. Data were tested for homogeneity of variance using Cochran's test.

Study sites, terrestrial influence and water quality

The study sites were on the reef slope of three fringing reefs on nearshore continental islands of the central Great Barrier Reef (Fig. 2), and were chosen to represent a cross-shelf gradient in exposure to terrestrial influences. This gradient arises from the differences in cross-shelf position, combined with differences in exposure to runoff from the Herbert River, the nearest large river in the area. The fringing reef at Goold Island (18°10.9′S, 146°10.2′E) is approximately 16 km from the mainland, and is surrounded by shallow (~6 m), very turbid water with fine, terrigenous muddy bottom sediments. As flood plumes in this region generally move northward up the coast, Goold Island lies directly in the path of flood plumes from the Herbert River, exposing the reef to considerable terrigenous sediment and nutrient inputs (Fig. 2; Brodie and Furnas 1996; Klumpp et al. 1999; G. Brunskill, AIMS, personal communication). Winds in this region are predominantly from the southeast, so the reef at Goold Island is also frequently exposed to very high levels of suspended material from the shallow fetch from Hinchinbrook Island, with its extensive mangroves. Such pulsed disturbances can have strong effects on turf algal growth (Brodie and Furnas 1996; Russ and McCook 2000). Great Palm Island is further offshore (approximately 30 km), is rarely exposed to river runoff, and is surrounded by deeper waters, and more carbonate sediments (Wolanski and van Senden 1983; Brodie and Furnas 1996; Klumpp et al. 1999). The study site at Coolgaree Bay (18°41.6′S, 146°34.4′E) is on the sheltered, inshore side of Palm Island and is close to the site used by McCook (1997). Cannon Bay (18°41.1′S, 146°35.1′E) is exposed to the more offshore waters of the reef-free channel, driven by the southeasterly winds. These environmental differences are reflected in the composition of reef biota, with Palm Island being intermediate between Goold Island and mid-shelf reefs. In particular, the reef slope at Goold Island has relatively abundant *Sargassum*, whereas the reef slopes on the Palm Island reefs have very little large macroalgae (McCook 1996, 1997).

These cross-shelf differences, in terrestrial influence and proximity to sources of terrestrial nutrients and sediments, may also result in some differences in dissolved nutrient levels. Quantitative water quality comparisons are available from data collected specifically for the present study (dissolved inorganic and total

Fig. 2 Map of central GBR showing study reefs on inshore continental islands. Goold Island is much closer to the mainland coast, is situated in a large, shallow muddy bay with abundant terrigenous sediments, and is influenced by floodwaters from Herbert River. In contrast, Great Palm Island is rarely affected by flood plumes, and has less terrigenous sediments. *Darker shading* indicates typical location of flood plume from Herbert River (redrawn from Brodie and Furnas 1996)



nitrogen and phosphorus, chlorophyll a, suspended particulate matter, turbidity and salinity; October 1998), as well as from another study at Goold Island and Cannon Bay (McCook, unpublished data; dissolved inorganic nitrogen and phosphate for April 1998) and from Klumpp et al. (1999) for Goold Island and Coolgaree Bay (total water column nitrogen and phosphorus, suspended solids for February and April 1992, January, March and May 1993 and February 1994). All water samples for the present study were taken approximately midway between substrate and surface (i.e. approx. 1.5–3 m, depending on tide). Dissolved nutrient concentrations were measured on six replicate samples of filtered (0.45 μm Sartorius Minisart) water, frozen immediately after collection, and later analysed using a Skalar segmented flow autoanalyzer (Ryle et al. 1981). Total dissolved nutrients were measured similarly following 8 h UV photo-oxidation. Chlorophyll a fluorescence was measured on six replicate 250-ml samples filtered onto precombusted Whatman GF/F glass-fibre filters. Suspended particulate matter was measured on three replicate 1 l samples filtered onto pre-weighed Nucleopore polycarbonate filters (0.4 μm), dried at 60 °C. Salinity was measured on duplicate samples of unfiltered water, and turbidity was measured using Secchi depth (single measurement at each reef). Water quality data (except Secchi depth) were analysed using a one-way ANOVA and SNK tests (at $P = 0.05$) following Cochran's test for homogeneity of variance.

Water quality data for the three study reefs are compared in Fig. 3. In general, Goold Island values were significantly higher (or lower for salinity and Secchi depth), compared to those on the Palm Island reefs. Concentrations of ammonium, combined nitrate and nitrite, total inorganic nitrogen, total dissolved nitrogen and inorganic phosphorus were all significantly higher at Goold than at the other two reefs. The same patterns were apparent for chlorophyll a, suspended solids and salinity. Only total dissolved phosphorus concentrations showed no significant differences among reefs. Differences between Coolgaree Bay and Cannon Bay were smaller and less consistent, with only two differences statistically significant and those not consistent in direction (suspended solids and combined nitrate and nitrite). Dissolved nutrients at Goold Island were close to the threshold concentrations for eutrophic coral reefs proposed by Bell (1992), Bell and Elmetri (1995) and Lapointe (1997). These patterns are supported by the earlier data. Dissolved inorganic nitrogen and phosphate data from April 1998 were higher on Goold Island, although nitrogen differences were not significant at that date (means and SEM for nitrogen: 1.36 ± 0.14 and 1.25 ± 0.17 μM for Goold and Cannon Bay respectively; for phosphate: 0.119 ± 0.005 and 0.059 ± 0.007 μM for Goold and Cannon Bay respectively; $P < 0.0001$). Similarly, Klumpp et al. (1999) found total nitrogen concentrations of 11.2 and 8.65 μM and total phosphorus concentrations of 0.46 and

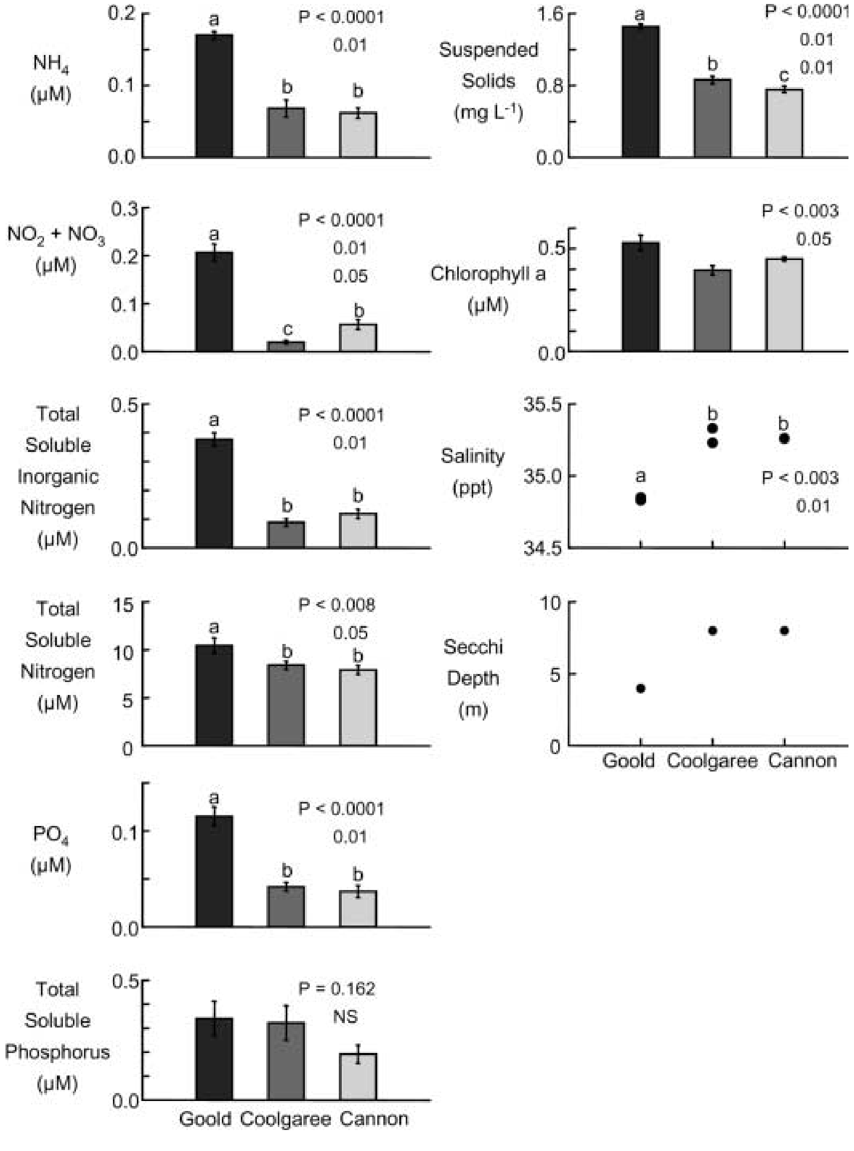


Fig. 3 Levels of nutrients, suspended solids, salinity and turbidity at the three study sites. Data are means (±SEM); *letters* above each bar indicate statistically different groups using SNK test; uppermost *P* values are for ANOVA, other *numbers* indicate *P* values for SNK where significant; further details are given in the text. Data indicate higher levels of terrestrial influence at Goold Island than Great Palm Island reefs, but provide little resolution of differences between Coolgaree Bay and Cannon Bay. Bell (1992), Bell and Elmetri (1995) and Lapointe (1997) have suggested a "nutrient threshold" of ~1 μm dissolved inorganic nitrogen, and 0. 1–0.2 μm dissolved inorganic phosphorus, beyond which coral reefs may be considered eutrophic. Goold Island is close to eutrophic by this criterion, although the idea of a single threshold concentration has limitations (Szmant 1997; Hughes et al. 1999; McCook 1999)

0.33 μM for Goold and Palm Islands respectively, averaged over all six sampling dates, and found suspended solids, particulate nitrogen and particulate phosphorus to all be significantly higher at Goold Island than at Palm Island (over all sampling dates). Finally, turbidity measurements (Secchi depth) from March 1996, July 1997, April 1998 and August 2000 all found turbidity to be higher at Goold Island, as in Fig. 3, although values varied considerably between dates. Thus, the patterns in the quantitative data were consistent with the qualitative descriptions of terrestrial influences. Undue emphasis should not be placed on particular nutrient levels, since such data can vary considerably within relatively small spatial and temporal scales, because supply rates are more critical than concentrations, and because salinity or turbidity stress, or interactions between stresses, may be as important as any specific nutrient fraction (Atkinson 1988; Larned and Atkinson 1997; Szmant 1997; McCook 1999).

It should be emphasised that comparisons among reefs amount to a natural experiment, and that reefs differ in numerous aspects besides the availability of nutrients, etc. Any differences detected between reefs can be considered in terms of *possible* roles of differences in terrestrial runoff or nutrient supply, but those roles are intrinsically confounded by other differences. Thus, this study can neither prove nor disprove a causal role of terrestrial runoff or nutrients (Strong et al. 1984). The purpose is to test whether the competitive outcomes are consistent with possible effects of terrestrial runoff, rather than to test nutrient effects directly.

Results

The results of the experiment were clear cut (Fig. 4, Table 1). There was no significant interaction between competitor treatments and reef, indicating that competitive interactions were consistent among reefs, and differences between reefs were consistent among treatments. Algal removal had no significant effect on the growth of the corals, whereas coral damage caused a large and significant increase in area of algal turf. Thus the presence of the coral was significantly inhibiting the growth of the algae, whereas the algae were not significantly affecting coral growth. Competitor treatments accounted for 34% of total variation (%SST).

There were highly significant differences between reefs, accounting for 20% of total variation, but these were not consistent with the idea of decreased coral competitiveness on the more nearshore reef. Corals on Goold Island, with higher nutrient concentrations, significantly outperformed those on the two reefs on Great Palm Island across all three treatments. This was the opposite of the pattern expected based on nutrient availability and terrestrial influence.

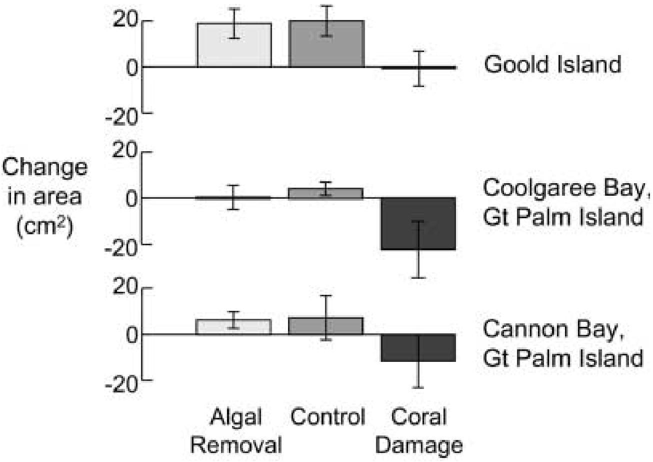


Fig. 4 Change in area of corals and algae, for each treatment and reef (Table 1). Data are means (±SEM) of four replicates; *positive values* indicate corals gained area at expense of algae, *negative values* indicate algae gained area at expense of corals

It is also significant that average coral growth was positive at all three reefs (except where experimentally damaged). That is, corals appear to have generally been overgrowing and outcompeting the algal turfs, especially at Goold Island where terrestrial influence was apparently highest.

Discussion

The results of this study are significant for several reasons. Firstly, they demonstrate that the massive coral *Porites lobata* generally was in competition for space with filamentous algal turfs, at the study sites. As stated earlier, there have been very few experimental demonstrations of coral–algal competition (Miller 1998; McCook et al. 2000b) and the present study is the first manipulative experiment to focus on filamentous algal turfs, a group that is often in direct contact with corals. Secondly, contrary to widespread assumptions, the algae do not appear to be the superior competitor in this case: the turfs were having negligible impacts on the corals, whereas the corals were significantly inhibiting algal turf growth. Indeed, the corals were competitively successful in gaining space, even (especially) in the relatively eutrophic conditions at Goold Island. Finally, and most importantly in the context of

Table 1 Analysis of variance of change in area of corals (Fig. 4). *%SST* Percentage of total sums of squares accounted for by each factor, an estimate of magnitude of effect of each factor; *Alg. Rem.* is the Algal Removal treatment; *Cor. Dam.* is Coral Damage treatment. Critical value of Cochran's C statistic here is 0.403. Differences between Control and Algal Removal treatments, and between Goold Island and Cannon Bay reefs were significant at $P = 0.01$ in Student-Neuman Keuls (*SNK*) tests

Source	d.f.	Mean-square	F-ratio	*P*	%SST	SNK
Treatment	2	2870.242	10.332	0.000	34	Control∼Alg. Rem. > Cor. Dam.
Reef	2	1692.481	6.093	0.007	20	Goold > Cannon∼Coolgaree
Treatment × Reef	4	35.010	0.126	0.972	1	
Error ($n = 4$)	27	277.792			45	
Cochran's C	0.28					

reef degradation, coral competitive success was highest at the site with highest apparent influence of terrestrial runoff of sediments and nutrients.

It is important to recognise the limitations intrinsic to interpretation of between-reef differences in terms of impacts of terrestrial runoff. It is clear that the differences in competitive outcome between reefs are not consistent with a major inhibitory effect of terrestrial influences on the interaction tested here. However, these results cannot disprove such an effect. Numerous confounding factors could account for the differences between reefs, and it is quite possible that real effects of nutrients were overshadowed by other, unidentified effects. No obvious differences between sites (e.g. light, depth, flow rates, etc.) that could easily account for the patterns seen were noted, however. Thus it seems likely that, overall, if nutrient supply or terrestrial runoff is inhibiting coral success on these reefs, the inhibition is relatively minor in comparison to other, unrecognised but stronger influences that support coral growth.

The potential outcomes of the competitive interaction may also be limited by the life-history characters of the competitors. *Porites lobata* grows mainly outwards, rather than laterally, so that it has limited potential to invade space cleared of algae. However, the positive growth shown in the results suggests this was not a serious limitation to the experimental design.

Comparison of the present results with previous experimental and observational studies supports the conclusions that competitive outcomes between corals and algae vary considerably, probably vary among algal functional groups, are not consistently in favour of the algae and that filamentous algae can rarely colonise healthy coral tissue. The only study to have directly tested nutrient effects on coral–algal competition (Miller and Hay 1996) found differing effects for brown and red seaweeds, again indicating that the processes are variable, in this case between algal groups. A number of natural (non-manipulative) experiments have suggested that algal turfs have variable effects on corals (e.g. Bak et al. 1977; Littler and Littler 1997; more complete review in McCook et al. 2000b). For example, damselfish territories, generally dominated by filamentous turf assemblages, have variable effects on corals, inhibiting growth of established corals in one study (Potts 1977) and substantially enhancing coral recruitment in another (Gleason 1996). Several studies of massive coral recovery from lesions have also generally shown that these corals are able to overgrow filamentous turf algae (Meesters and Bak 1993; Meesters et al. 1994, 1997; van Woesik 1998). Algal turfs may generally be less successful competitors with corals than larger fleshy algae, such as *Lobophora*, *Dictyota* or *Halimeda* (e.g. Hughes 1989; Miller and Hay 1996, 1998; Lirman 2000), perhaps because of the different potential mechanisms for the algae to compete with the corals (McCook et al. 2000b). Of the seven specific competitive mechanisms discussed by McCook et al. (2000a, Tables 5 and 6), the experimental methods used here provide little direct evidence about which is involved in the *P. lobata*–turf interaction. Nevertheless, the growth forms of the competitors provide some indications, since, as a massive coral with very small polyps, *Porites lobata* is probably limited to direct overgrowth of the turfs. The need for coral injury before algal overgrowth emphasises the ability of healthy *Porites lobata* to prevent algal colonisation or overgrowth, probably by means of mucus secretion (G. Diaz-Pulido and McCook, unpublished observations).

The conclusions that corals were the competitive superior, and that algal overgrowth required prior coral injury, are consistent with the suggestion that algal overgrowth is often not caused by competitive exclusion by algae of established corals (McCook et al. 1997). Many acute disturbances, such as storm damage, bleaching or crown-of-thorns outbreaks, will result in large areas of dead coral which are rapidly colonised and overgrown by algae, since the algae grow and colonise much faster than corals. After such disturbances, coral mortality will be the cause of algal abundance, rather than vice versa, whether their interactions are competitive or not. In fact there are potentially three different competitive dynamics operating in this scenario: (1) in the "equilibrium" pre-disturbance conditions, algae may (or may not) be competitively inferior to established corals; (2) immediately post-disturbance, algae are released from competitive inhibition by corals by the disturbance, and rapid colonisation of new substrate by algae makes them short-term superior competitors to recruiting or recovering corals; (3) post-disturbance, in the long term, algae may (or may not) competitively pre-empt space and prevent or limit coral recruitment (or recovery; McCook et al. 2000b). The critical point is that algae may replace corals and subsequently competitively exclude coral *recruitment* and recovery, without necessarily being competitively superior to *established* corals.

These distinctions are potentially significant in the context of management of reef decline, since they support suggestions that the impacts of terrestrial runoff may be more complex than simple enhancement of algal competitiveness with established corals (McCook 1999; McCook et al. 2000a). The present results indicate that turf algal growth was not sufficient to outcompete established *Porites lobata* corals on inshore reefs of the central GBR, and was not higher on the most inshore of the reef. Previous work also found that, in the absence of corals, growth rates of algal turfs were not higher on inshore reefs than offshore, even after a pulse of terrestrial runoff (Russ and McCook 2000). Similarly, the abundance of *Sargassum* on inshore reefs is apparently not a direct consequence of the higher nutrient availability (McCook 1996), and enhanced terrestrial inputs may actually directly inhibit these macroalgae (Umar et al. 1998). Therefore, the limited available evidence does not support the assumption that the current levels of terrestrial inputs to these reefs will lead simply and directly to widespread algal overgrowth of otherwise healthy, established corals. Focus on a single, overly simple process for impacts of anthropogenically enhanced terrestrial runoff may risk overlooking other impacts (Szmant 1997; Aronson and Precht 1999; Hughes et al. 1999; McCook 1999; McCook et al. 2000a) which are more complex and difficult to detect, but critical to sustainability of coral populations.

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