Differential competitive abilities between Caribbean coral species and a brown alga: a year of experiments and a long-term perspective

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ABSTRACT: The competitive replacement of corals by benthic algae is considered key to reef degradation. Such replacement could originate from direct competitive overgrowth of corals by algae or death of corals from other disturbances, followed by an increase in algal abundance. To assess the relative importance of these processes, this study experimentally tested the competitiveness of 6 Caribbean coral species against the brown alga *Lobophora variegata* on a fringing reef in Curaçao, Netherlands Antilles. This alga has a widespread distribution and is considered particularly aggressive towards corals due to its creeping growth form. We compared the growth of transplanted algae over living and dead coral, as well as coral tissue mortality in the presence and absence of transplanted algae over a 1 yr period. Competitive trends were also related to changes in species abundance from 1973 to 2002 on the same reef. The results indicated that only 1 species, *Agaricia agaricites*, was competitively inferior to *L. variegata* and suffered more tissue mortality when exposed to the algae. Surveys of naturally occurring interactions showed that less competitive species were generally more overgrown by *L. variegata*, further reinforcing our results. Importantly, *A. agaricites* experienced the greatest decline in percent cover from 1973 to 2002 among the studied species. A large proportion of this decline occurred following the die-off of *Diadema antillarum* in 1983, which generally marks the onset of increased algal abundance on Caribbean reefs. We concluded that Caribbean corals have different competitive abilities against algae, highlighting the complexity and species-specific nature of coral-algal interactions. Although our data supports that prior death of corals may be generally required for algae to become established, competition with algae could play a significant role in structuring coral communities by reducing the abundance of poor competitive species. We suggest that a species-by-species approach is needed to understand the factors influencing transitions from coral to algal dominance on Caribbean reefs.

KEY WORDS: Coral-algal competition · Algae · Coral · Competition · *Lobophora variegata* · Scleractinian · Caribbean

INTRODUCTION

Within the past 3 decades many Caribbean coral reefs have experienced 'phase shifts' in which benthic algae have replaced reef-building corals (Hughes 1994, Shulman & Robertson 1996, McClanahan & Muthiga 1998, McClanahan et al. 1999, Ostrander et al. 2000, Jackson et al. 2001, Edmunds 2002, Gardner et al. 2003). Such shifts are frequently attributed to 2 pro-cesses: (1) competitive overgrowth of corals by algae, or (2) coral mortality from external disturbances that precedes an increase in algal abundance (McCook et al. 2001). The former typically refers to the 'bottom-up' and 'top-down' views in which nutrient enrichment and/or declining herbivory increases the growth, cover and biomass of algae, leading to a shift in the competitive environment that enables algae to overgrow and kill corals (McCook 1999, Jompa & McCook 2002a).

The latter argues that algae need the death of corals to increase in abundance, with herbivory, nutrients and/or reproductive characteristics acting as interacting factors to drive the subsequent colonisation of algae (McClanahan & Muthiga 1998, McClanahan et al. 1999, 2001, Williams et al. 2001a,b, Diaz-Pulido & Mc-Cook 2002, 2003, 2004, 2005). Supporting this process is the importance of substratum availability in mediating algal abundance on Caribbean reefs (Williams et al. 2001a,b) and evidence that coral bleaching and disease have precipitated dramatic ecological shifts at several reef locations worldwide (Ostrander et al. 2000, Aronson & Pretch 2001, McClanahan et al. 2001, Diaz-Pulido & McCook 2002, Aronson et al. 2004).

While there is considerable debate over the relative importance of increased nutrients and reduced herbivory in controlling algal communities (Hughes et al. 1999, Lapointe 1999, 2004, Szmant 2002, McClanahan et al. 2004), both factors have been reported to enhance the growth and cover of algae, satisfying both views (e.g. Lapointe 1997, Miller et al. 1999, Stimson et al. 2001, Thacker et al. 2001, Jompa & McCook 2002a, McClanahan et al. 2002, 2003, 2005). In contrast, we have little information on the ability of algae to act as the initial cause of coral tissue mortality, a prerequisite for the former scenario. In particular, it is important to recognize that corals may have species-specific susceptibilities to algal overgrowth and hence that the relative importance of both processes in changes to algal dominated reefs may differ among species.

To date, there is little convincing evidence to suggest that algae can act as a direct cause of coral mortality. Most studies addressing the negative impact of algae on corals are either observational, describing the death of the coral tissue overgrown by algae, or correlative, showing opposite trends in coral and algal abundance over time (reviewed by McCook et al. 2001). Furthermore, although algae may affect coral growth, reproduction and recruitment (Sammarco 1982, Tanner 1995, Lirman 2001), they may have no or even positive effects on coral survival and mortality (Tanner 1995, Jompa & Mc-Cook 1998, McCook 2001, Jompa & Mc-Cook 2003a,b). Corals may actually inhibit algal growth and overgrow some algae (Bak et al. 1977, Ruyter van Steveninck et al. 1988, Meesters & Bak 1993).

Only recently have studies of coral-algal interactions used experimental manipulations of coral and algal competitors to investigate competition and associated mortality. At present, these studies suggest that the outcomes of coral-algal competition vary among functional groups of algae. For example, the creeping form of the brown alga *Lobophora variegata* has been reported to overgrow and kill corals (Jompa & McCook 2002a,b), whereas large, canopy-forming leathery macrophytes appear to have minor effects on coral sur-

vivorship (Jompa & McCook 1998, River & Edmunds 2001). McCook et al. (2001) proposed that much of the variability in coral-algal interactions may be related to the (physical, biological and chemical) properties of the algae and that these properties may be effectively summarised in terms of algal functional groups. However, even within a functional group, there may be differences in competitive potential among algal species. The filamentous red alga *Anotrichium tenue* has been shown to kill coral tissue by active overgrowth, while other mixed-species algal turfs did not cause any mortality of coral tissue (Jompa & McCook 2003a).

Very few of these studies have examined the potential role of corals in enhancing the complexity of coral-algal competition. Yet, there is evidence to suggest that different corals may also have different competitive abilities against algae. Scleractinian corals exhibit a wide variety of competitive mechanisms for acquiring or defending space (Lang & Chornesky 1990, Karlson 1999). These mechanisms result in complex dominance patterns among coral species (Lang 1973, Bak et al. 1982, Logan 1984, Chornesky 1989). Few of these mechanisms are known to occur against algae. However, corals have recently been shown to extrude mesenterial filaments over algae (Nugues et al. 2004). Interestingly, the effect of these filaments on the green alga *Halimeda opuntia* differed depending on coral species and was closely related to the physical properties of the filaments (i.e. length). Moreover, other studies suggest variable abilities of corals to inhibit algal growth (Ruyter van Steveninck et al. 1988), or have their growth affected by algae (Tanner 1995, Lirman 2001).

The purpose of our study was to examine the competitiveness of several Caribbean coral species against the brown alga *Lobophora variegata*. *Lobophora variegata* is a widespread and common alga on Caribbean reefs (van der Hoek et al. 1978, Hughes 1994, Ruyter van Steveninck & Breeman 1987, Diaz-Pulido & Diaz 1997) and worldwide (Jompa & McCook 2002a,b). It is often found overgrowing live tissue of scleractinian corals (Ruyter van Steveninck et al. 1988) and has been shown to cause coral mortality in the Indo-Pacific branching coral *Porites cylindrica* (Jompa & McCook 2002a,b). We first experimentally tested the ability of *L. variegata* to cause tissue mortality in 6 common species of Caribbean corals and the reciprocal effects of these species on algal growth. We then related our experimental results with (1) patterns of natural interactions between the studied coral species and *L. variegata*, and (2) temporal changes in their abundance from 1973 to 2002. This former comparison aimed to test the assumption that coral species with higher competitive abilities in our experiment should be less overgrown by the alga in the field. The latter represented

an attempt to assess whether these competitive abilities could influence coral community structure.

The corals examined included: (1) the encrusting or plate-like coral *Agaricia agaricites*, (2) the larger, exclusively plate-like coral *A. lamarcki*, (3) the mound-forming or plate-like coral *Mycetophyllia aliciae*, (4) the massive, mound-forming coral *Montastraea franski*, (5) the encrusting or plate-like coral *Meandrina meandrites*, and (6) the relatively small, encrusting coral *Porites astreoides*. Each of these species was commonly observed in close proximity to or in physical contact with *L. variegata*.

MATERIALS AND METHODS

Study sites. The experimental study and survey of natural interactions were conducted between 20 to 25 m depths on the reef slopes of the fringing reef at Carmabi Buoy 0, Piscaderay Bay, on the leeward south-west coast of Curaçao (Fig. 1). This site has an abundant population of *Lobophora variegata* at 20 m depth (~25% hard substrate cover, M. Nugues unpubl. data). This alga is present in high abundance year-round in Curaçao and does not experience seasonal dieback (Ruyter van Steveninck & Breeman 1987, M. Nugues pers. obs.). Other macroalgae were also present, including *Dictyota* spp., *Halimeda copiosa*, *Galaxaura* sp. and *Amphiroa* spp. However, *L. variegata* was the most common alga to overgrow corals, causing discoloration and the apparent death of underlying tissues (M. Nugues pers. obs.).

Data on long-term changes in reef coral communities were obtained from permanent quadrats placed at Carmabi Buoys 1 and 2 (Fig. 1). Both sites are located less than 500 m away from Carmabi Buoy 0. All 3 sites are connected by a continuous fringing reef and have similar topography and coral reef communities (for detailed descriptions of all sites see Bak 1977 and Van Duyl 1985).

Field experiment. We tested coral competitive ability against *Lobophora variegata* by implementing 3 competitor treatments: (1) recently dead coral in contact with transplanted algae (Treatment 1, Figs. 2A & 3A), (2) living coral in contact with transplanted algae (Treatment 2, Figs. 2B & 3B), and (3) living coral without algae (Treatment 3, Figs. 2C & 3C). This experimental design follows the one of Jompa & McCook (2002b) to test for competitive effects in coral-algal interactions and provided simultaneous tests for 2
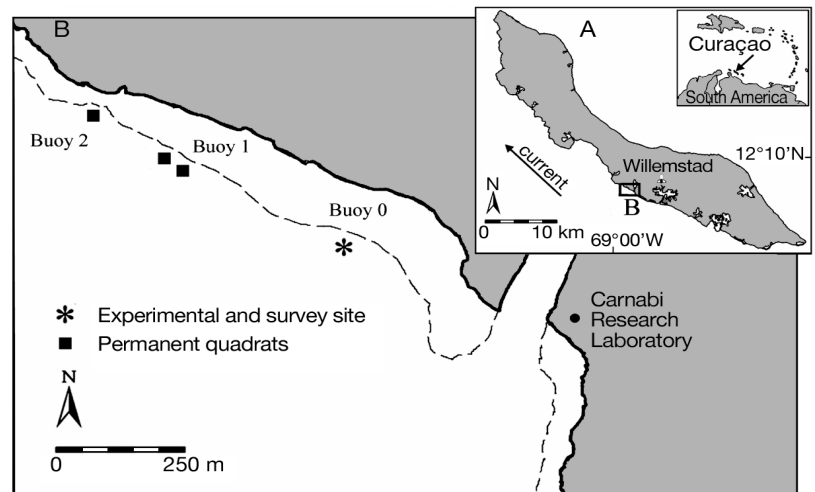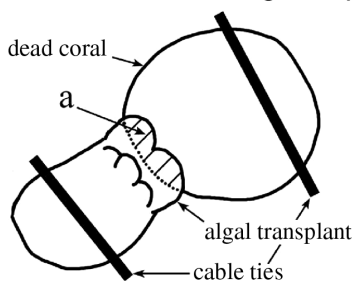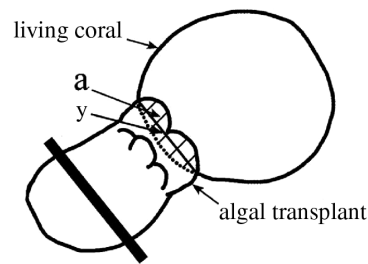

Fig. 1. Geographical location of study sites. (A) Curaçao. (B) Experimental and survey site (69° 58′26″ N, 12° 07′ 27″ W) and permanent quadrats. Hatched lines indicate 10 m depth reef contour
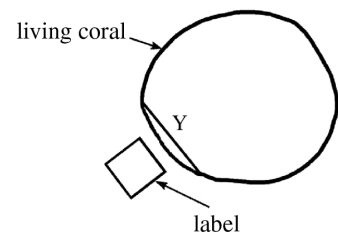

Fig. 2. Experimental treatments. (A) Treatment 1. (B) Treatment 2. (C) Treatment 3. Algal growth estimated by change in algal cover ('a' shown as a striped area) over initial (dead or living) coral surface area. Coral mortality defined as area of tissue mortality originating along colony perimeter overgrown by alga in initial photograph (Treatment 2) or along predetermined colony perimeter in front of each label (Treatment 3). To allow fair comparisons among treatments, predetermined perimeter was defined as perimeter delimited by straight line 'Y' in front of tag, where Y was average of all lengths of interaction (shown as 'y') estimated in Treatment 2

effects: (1) the effect of coral competition on *L. variegata* by comparing the growth of transplanted algae on dead and living coral (Treatments 1 vs. 2), and (2) the

effect of *L. variegata* on corals by comparing coral tissue mortality on living coral with and without transplanted algae (Treatments 2 vs. 3).

To obtain pieces of recently dead coral (Treatment 1), living corals were collected before the start of the experiment. Colonies were placed in freshwater for 48 h, cleaned of all soft tissue with a strong jet of freshwater and cut into several pieces (each ~250 cm² in surface area). In this way, sufficient replicates were obtained using 1 to 2 colonies per species. Each piece of dead coral was then attached onto randomly selected patches of dead coral rock using cable ties and plastic nails and tagged. Living coral colonies (Treatments 2 and 3) were randomly selected and tagged within the same experimental area. Colonies were chosen if they showed no sign of damage or stress (e.g. disease, bleaching, predation, mucous secretion) and were not overgrown by macroalgae or other invertebrates. They were randomly allocated to Treatments 2 or 3.

Dead coral rocks covered with *Lobophora variegata* (e.g. dead plates of *Agaricia lamarckii*) were then transplanted next to the dead coral pieces (Treatment 1) and the living coral colonies assigned to Treatment 2 using cable ties and plastic nails (Fig. 2A,B). Transplants were positioned so that 2 to 3 algal blades overgrew a few cm² of coral tissue or skeleton, while not allowing any physical contact between the dead coral rock covered by the alga and the coral tissue or skeleton. The living coral colonies assigned to Treatment 3 had
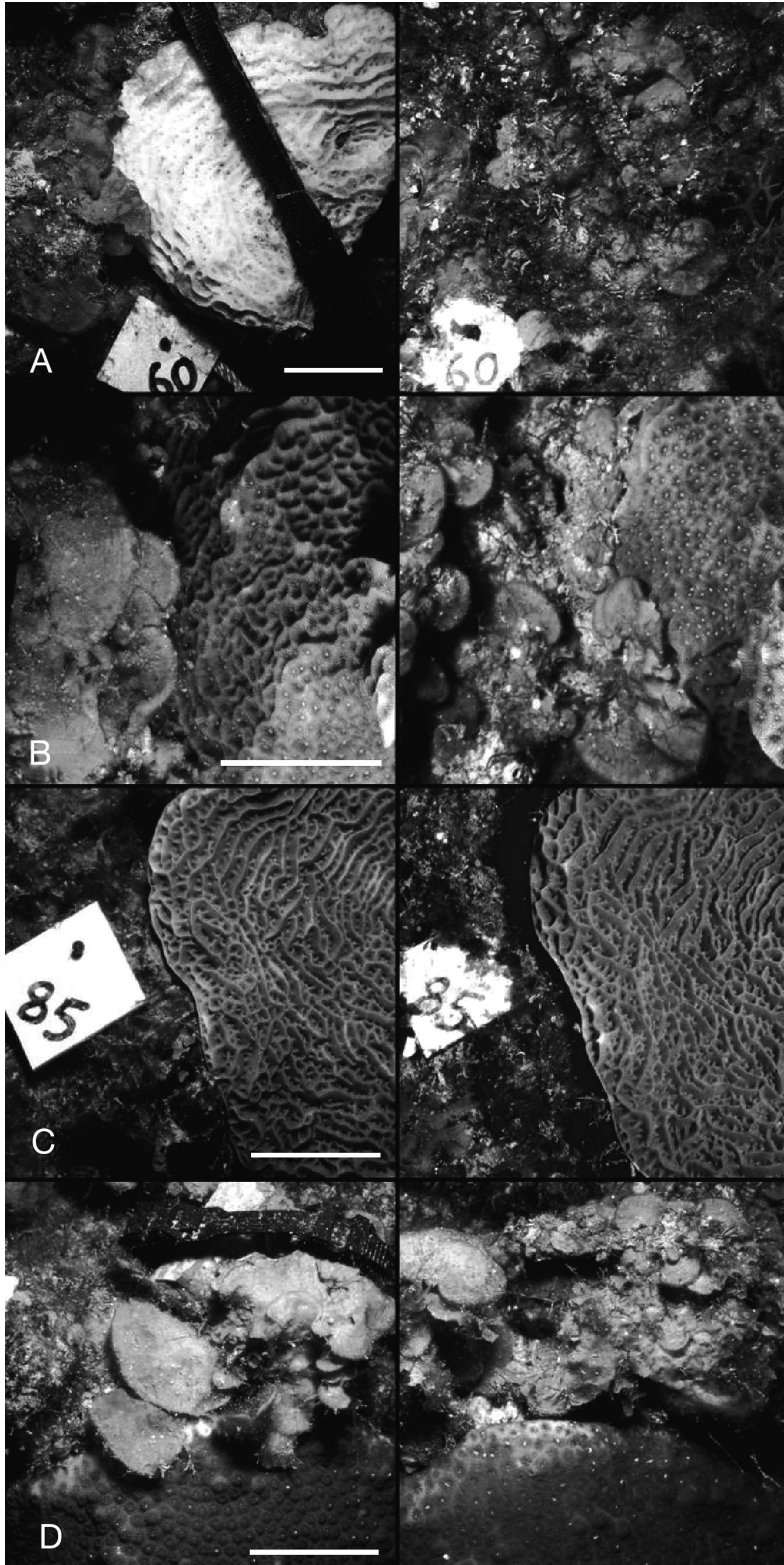

Fig. 3. Experimental treatments in initial (left) and final (right) months. (A) *Lobophora variegata* transplant next to piece of recently dead colony of *Agaricia agaricites* attached to substratum (Treatment 1; Fig. 2A). After 1 yr, the alga overgrew a large proportion of the dead colony. (B) *L. variegata* transplant next to living colony of *A. agaricites* (Treatment 2; Fig. 2B). After 1 yr, the alga overgrew part of the colony. (C) Living colony of *A. agaricites* and tag (Treatment 3; Fig. 2C). After 1 yr, no tissue mortality occurred along the colony margin. (D) *L. variegata* transplant next to living colony of *Montastraea franskii* (Treatment 2). After 1 yr, the alga completely retreated from the coral surface area. Scale bars = 5 cm

their plastic tag and nail inserted close to the coral margin to serve as manipulated control (Fig. 2C). All macroalgae, including naturally occurring *L. variegata*, were scraped off with a wire brush within a distance of 20 to 30 cm around each experimental interaction, taking care to minimize damage to the coral tissue or transplanted alga. For each coral species, 4 replicates were used for Treatment 1, and 9 to 11 replicates were used for Treatments 2 and 3.

The experiment was run over a 1 yr period (June 2002 to June 2003) to account for any seasonality in the alga. Replicates were photographed from a fixed distance and cleared of all externally interfering macroalgae at 2 to 3 mo intervals. To minimize parallax errors, digital photographs were taken by pointing the camera perpendicular to the tags, but repeated photographs were visually checked with the initial photograph after each dive and retaken within the next few days when necessary.

Measurements. Measurements were made on the first and final photographs. The growth of *Lobophora variegata* was calculated as the change in the surface area of *L. variegata* covering dead coral pieces or living colonies (i.e. change in 'a' in Fig. 2A,B). Negative values were assigned when the alga decreased in coverage over a colony. Coral mortality was measured as the area of coral tissue mortality associated with the transplant or tag. In Treatment 2, mortality was assessed along the colony perimeter overgrown by the alga in the initial photograph. Since *L. variegata* was absent in Treatment 3, we calculated the straight-line lengths of interactions between *L. variegata* and coral tissue in the initial photographs from Treatment 2 ('y' in Fig. 2B). We then used the mean length for each species ('Y' in Fig. 2C) to delimit the colony perimeter against which to assess mortality in Treatment 3. Mortality originating in the middle of the colony or outside our perimeter of measurement was not included. If coral tissue mortality was present underneath the algae, a second photograph was taken in which all *L. variegata* blades were removed to accurately measure mortality.

For all measurements, photographs were scanned and relevant boundaries traced using Adobe Photoshop 6.0 software. Initial and final tracings were overlaid and merged, and surface areas were measured using Scion image software.

Survey of natural interactions between *Lobophora variegata* and corals. Interactions between *Lobophora variegata* and the 6 coral species studied were surveyed at 20 to 25 m depth in March 2005 using 2 or 4 m wide belt transects varying in length from 10 to 25 m, depending on the colony densities. Transects were laid parallel to shore and separated by at least 3 m from each other. Sufficient transects were laid to obtain minimum samples of 50 colonies per species. For each colony, 3 variables were measured: (1) total colony perimeter; (2) length of colony perimeter overgrown by *L. variegata*; and (3) maximum reach over living tissue by the algae. The latter was defined as the maximum length of algal growth over living tissue perpendicular to the colony margin. Variables were measured to the nearest cm for the perimeter values or mm for the maximum reach using a flexible measuring tape. A colony was defined as an autonomous mass of skeleton with living tissue. As such, perimeters of separate patches of living tissue located on the same skeleton were summated. Similarly, if a colony was overgrown by *L. variegata* in several areas, all lengths of perimeter overgrown were combined.

Changes in coral communities between 1973 and 2002. Data on long-term changes in the cover of the 6 coral species studied were obtained from three 3×3 m permanent quadrats placed by R. Bak and colleagues in 1973 at a depth of 20 m close to our experimental site (Fig. 1). Detailed methodology can be found in Bak & Nieuwland (1995). In brief, R. Bak and colleagues established permanent quadrats along 3 transects running perpendicular to shore. Along each transect, one 3×3 m quadrat was laid at depths of 10, 20, 30 and 40 m. Whole quadrats were photographed every 2 to 6 yr from 1973 to 2002 using a Nikonos V underwater camera fitted with a 15 mm lens. Close-ups were also taken to facilitate species identification. The projected surface area of coral species was determined from photographs taken in 1973, 1983, 1992, 1997 and 2002 using a CalComp Drawing Board II and a digitizer program (EDC, Agricultural University Wageningen). Since only a maximum of 4 *Montastraea franski* colonies were present in the 3 quadrats at any one time, we also reported the percent cover for the whole genus (i.e. adding *M. annularis* and *M. faveolata*).

Statistical analyses. The initial length of interaction ('y' in Fig. 2B) and the initial area covered by the alga ('a'; Fig. 2A) were analysed using a 2-way ANOVA with species and competitor treatment (living vs. dead coral) as fixed factors to check that there were no significant differences among species or competitor treatment in the way that colonies were exposed to the algae at the beginning of the experiment. Differences in *Lobophora variegata* growth were tested using the same 2-way ANOVA. Since the interaction between the 2 factors was significant for this variable, separate 1-way ANOVAs within levels of each factor were carried out, followed by a post hoc Tukey's HSD test.

Coral tissue mortality data were not normally distributed and did not show homogenous variance even after transformation; thus, data were analysed using the Scheirer-Ray-Hare test, a non-parametric equivalent of a 2-way ANOVA (Dytham 1999), using species and competitor treatment (*Lobophora variegata* absent vs. *L. variegata* present) as independent variables. Analyses within levels of each factor were carried out using

Kruskal-Wallis or Mann-Whitney *U*-tests, followed by post-hoc comparisons using Mann-Whitney *U*-tests as appropriate. In order to compromise between a large overall Type I error (which would arise with an α of 0.05 for each separate test) and a large overall Type II error (which would arise with a strict application of Bonferroni correction, i.e. with an α of $0.05 \times 15^{-1} = 0.00333$), we used an α of 0.01 in each separate post-hoc test.

Data from the field survey were analysed for species effects on the percentage of overgrown colonies, the percentage of overgrown perimeter and the maximum reach of the alga. Note that the last 2 variables were averaged across overgrown colonies. Differences in the percentage of overgrown colonies were analysed using an heterogeneity *G* test, followed by a simultaneous test procedure (STP) to determine homogeneous groups (Sokal & Rohlf 1995). Species differences in the percentage of overgrown perimeter and maximum reach by the alga were tested using 1-way ANOVAs after appropriate transformations. Spearman rank-order correlation analyses (SPSS) were conducted to examine relationships between the experiment and field survey data.

Changes in the percentage cover from 1973 to 2002 were tested by repeated measure ANOVA with species as the between-factor variable and year as the within-factor variable following arcsine square root transformation. Separate tests were also carried out for each species and the genus *Montastraea*.

RESULTS

Preliminary tests

There were no significant differences among species or competitor treatment in either the initial length of coral-algal interaction or the initial surface area covered by alga (2-way ANOVA, p > 0.05 for main effects and interaction), thus all coral species and dead coral pieces were equally exposed to the algae at the start of the experiment.

Effect of coral competition on *Lobophora variegata* growth

Lobophora variegata growth was significantly reduced in the presence of living coral (Table 1, Figs. 3A,B & 4A). However, there was a significant interaction between coral species and competitor treat-

Table 1. *Lobophora variegata*. Results of 2-way ANOVA with growth as dependent variable, and coral species and competitor treatment (living vs. dead coral) as independent variables

Source	df	MS	*F*	p	Conclusions
Species	5	475.0	1.86	0.113	
Competitor	1	89192.0	348.51	0.000	
Species × Competitor	5	613.9	2.40	0.046	Significant[a]
Error	71	255.9			
Total	83				

[a]ANOVA tests within each level of treatment: no difference among species within dead coral; significant difference ($F_{5,58} = 5.99$, df = 5, p < 0.001) among species within living coral: *Agaricia agaricites* > all other species, with all other species not significantly different from each other; dead coral > living coral within all species
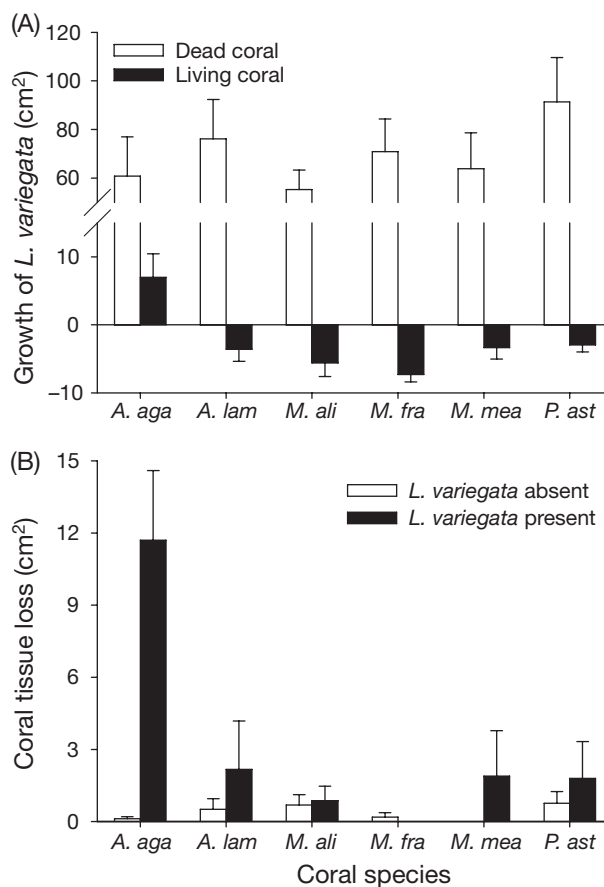

Fig. 4. Results of experimental study. (A) *Lobophora variegata* growth over dead and living coral tissue for each coral species. Data are mean (cm² ± SE) of 4 replicates for dead coral treatment and 9 to 11 replicates for living coral treatment. Growth can be negative as a result of a decrease in algal cover over initial coral surface area (Fig. 3D). (B) Coral tissue mortality in the absence and presence of *L. variegata* for each coral species. Data are mean (cm² ± SE) of 9 to 11 replicates for both treatments. Species abbreviations: *A. aga = Agaricia agaricites*, *A. lam = A. lamarcki*, *M. ali = Mycetophyllia aliciae*, *M. fra = Montastraea franski*, *M. mea = Meandrina meandrites*, *P. ast = Porites astreoides*

ment, indicating that the effect of coral competition on *L. variegata* growth differed among coral species. When the coral tissue was dead, there was no difference among coral species, but the growth of the alga was higher in *Agaricia agaricites* when the coral tissue was alive (Table 1). All species were able to significantly reduce the growth of the alga, but *A. agaricites* was the only species with which *L. variegata* growth was positive when the coral tissue was alive. In all other species, algal growth was negative. In some cases, the algae even completely retreated from the coral colony (Fig. 3D).

Effect of *Lobophora variegata* on coral tissue mortality

The presence of *Lobophora variegata* had a significant effect on coral mortality, but this effect varied among coral species (Table 2 & Fig. 4B). Mann-Whitney *U*-tests for each individual species indicated that only 1 species of the 6 studied (*Agaricia agaricites*) experienced more tissue mortality when exposed to the alga. Mortality did not differ among species when the algae were absent, but when the algae were present there was a significant difference among species. Mortality was higher in *A. agaricites* than all other species except *A. lamarcki* (Table 3).

Natural interactions between *Lobophora variegata* and corals

The percentage of overgrown colonies varied significantly among species (heterogeneity *G*-test, G_H = 73.05, df = 5, p < 0.001). Values ranged between 14% for *Mycetophyllia aliciae* and 73% for *Agaricia agaricites* (Fig. 5A). STP tests showed that 3 species groups {*A. agaricites*}, {*A. lamarcki, Porites astreoides*}

Table 3. Coral tissue mortality. Results of post-hoc multiple comparisons (pairwise comparisons and mean ranks; Mann-Whitney *U*-test) of tissue mortality experienced by different coral species when exposed to *Lobophora variegata*. Kruskal-Wallis test showed significant differences among species (χ^2 = 20.90, df = 5, p = 0.001). Species abbreviations as in Fig. 4. * = p < 0.01, ns = not significant (p > 0.01)

	Mfra	Mmea	Past	Mali	Alam	Aaga
Mfra	20.50					
Mmea	ns	24.25				
Past	ns	ns	28.60			
Mali	ns	ns	ns	28.89		
Alam	ns	ns	ns	ns	29.50	
Aaga	*	*	*	*	ns	46.45

and {*M. aliciae, Montastraea franski, Meandrina meandrites*} formed homogenous sets. The percentage of overgrown perimeter per overgrown colony ranged from 0.7% for *M. franski* to 5.7% for *P. astreoides* (Fig. 5B). Differences among species were also significant (1-way ANOVA on arcsine square root transformed data: $F_{5,121}$ = 8.2, p < 0.001). Post hoc Tukey's HSD test showed 3 homogenous groups: {*A. agaricites, M. meandrites, P. astreoides*}, {*A. lamarcki, M. aliciae, M. meandrites*} and {*A. lamarcki, M. aliciae, M. franski*}. The extent of overgrowth varied more than 4-fold among species, and ranged from 0.14 cm for *M. franski* to 0.66 cm for *A. lamarcki* (Fig. 5C). This significantly differed among coral species (1-way ANOVA on log-transformed data: $F_{5,121}$ = 11.3, p < 0.001). Post hoc Tukey's HSD test revealed that {*A. agaricites, A. lamarcki, P. astreoides*}, {*M. aliciae, P. astreoides*} and {*M. aliciae, M. franski, M. meandrites*} were homogenous groups.

All the above parameters showed significant, or marginally significant, correlations with the growth of *Lobophora variegata* onto living coral and coral tissue mortality when the algae were present (Table 4).

Changes in coral communities between 1973 and 2002

Coral cover within the permanent quadrats declined or remained steady depending on species (Fig. 6). This was supported by a significant interaction between year and species (Table 5). *Agaricia agaricites* and *Meandrina meandrites* were the most abundant species in 1973 with 6.6 and 5.5% cover, respectively. Both species significantly declined in cover from 1973 to 2002, experiencing 88 and 68% losses,

Table 2. Coral tissue mortality. Results of Scheirer-Ray-Hare test with tissue mortality as dependent variable, and coral species and competitor treatment (*Lobophora variegata* absent vs. *L. variegata* present) as independent variables

Source	SS	SS/MS$_{total}$	df	p	Conclusions
Species	10530.3	16.84	5	0.000	
Treatment	1394.1	2.23	1	0.140	
Species × Treatment	8510.4	13.61	5	0.020	Significant[a]

[a]Kruskal-Wallis or Mann-Whitney tests within each level of treatment: no difference among species within *L. variegata* absent; significant difference (Kruskal-Wallis test: χ^2 = 20.90, df = 5, p = 0.001) among species within *L. variegata* present (see Table 3 for post-hoc comparisons); *L. variegata* present > *L. variegata* absent for *Agaricia agaricites* only (Mann-Whitney test: *U* = 13.0, df = 5, p = 0.001)
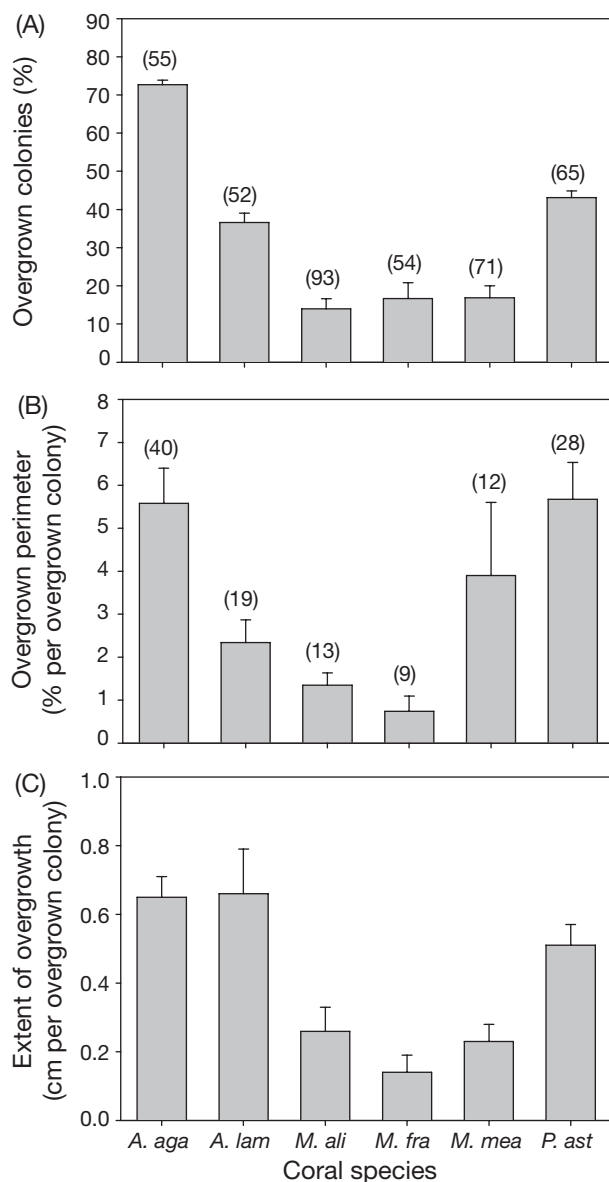
Fig. 5. Natural interactions between *Lobophora variegata* and 6 coral species at experimental site. Values are mean (±1SE) for each coral species. (A) Percentage of overgrown colonies; n = total number of colonies; SE = $\sqrt{[p \times (1 - p)n^{-1}]}$; p = proportion of algal retreat, n = number of colonies (Sokal & Rohlf 1995). (B) Percentage of colony perimeter overgrown by alga; n = number of overgrown colonies. (C) Maximum reach over living coral tissue by the alga; n values as in (B). Species abbreviations as in Fig. 4

respectively. *Agaricia agaricites* showed a strong decline between 1983 and 1991, followed by a smaller but steady decrease in cover from 1991 to 2002. *Meandrina meandrites* experienced a major loss between 1973 and 1983. After 1991, its cover remained relatively steady. In contrast, all other species, including the genus *Montastraea*, showed no significant variation in coverage.

Table 4. Correlation matrix (Spearman rank correlation) between *Lobophora variegata* growth next to living corals and coral mortality when *L. variegata* was present in the transplantation experiment (Fig. 4A,B) and the parameters estimated from the field survey (Fig. 5A–C). Correlations based on mean values for each species (n = 6 species). Significance levels: [+] = p < 0.l, [*] = p < 0.05, [**] = p < 0.01

	L. variegata growth	Coral mortality
Overgrown colonies	0.886[*]	0.771[+]
Overgrown perimeter	0.943[**]	0.829[*]
Extent of overgrowth	0.783[+]	0.899[*]

DISCUSSION

The results of this study are important for several reasons. Firstly, they demonstrated that coral species have different competitive abilities against the brown alga *Lobophora variegata*. Coral species exhibited different mortality rates when exposed to the alga and different abilities to inhibit its growth. *Agaricia agaricites* was the only species for which algal growth was positive and that was overall competitively inferior to the alga. As stated earlier, much emphasis has been placed on the role that algae play in the variability of coral-algal interactions (McCook 2001, McCook et al. 2001, River & Edmunds 2001, Jompa & McCook 2002a,b, 2003a,b). Our study is the first manipulative experiment to focus on Caribbean coral species competitiveness. Our results provided strong evidence that corals increase the complexity of coral-algal interactions by exhibiting species-specific competitive abilities against algae.

Secondly, contrary to the bottom-up and top-down views of coral reef degradation in which algae act as the initial cause of coral tissue mortality, algae appeared to cause mortality in a very limited number of coral species. *Lobophora variegata* is considered as a relatively potent competitor against corals due to its creeping growth form and opaque, thick foliose thallus (Jompa & McCook 2002a,b). It can come into contact with most coral species (M. Nugues pers. obs.). Yet, our study showed that all corals were able to significantly inhibit the growth of the alga, and only 1 species of the six studied (*Agaricia agaricites*) experienced greater tissue mortality when exposed to *L. variegata* over a 1 yr period.

Finally, while algae may cause coral mortality in a limited number of coral species, this study supported that competition with algae could play a significant role in structuring reef coral communities. Although *Agaricia agaricites* was the only species affected by *Lobophora variegata* in our experiment, this coral exhibited the highest decline in cover (88%) from 1973 to 2002. This decline has been steady since the die-off
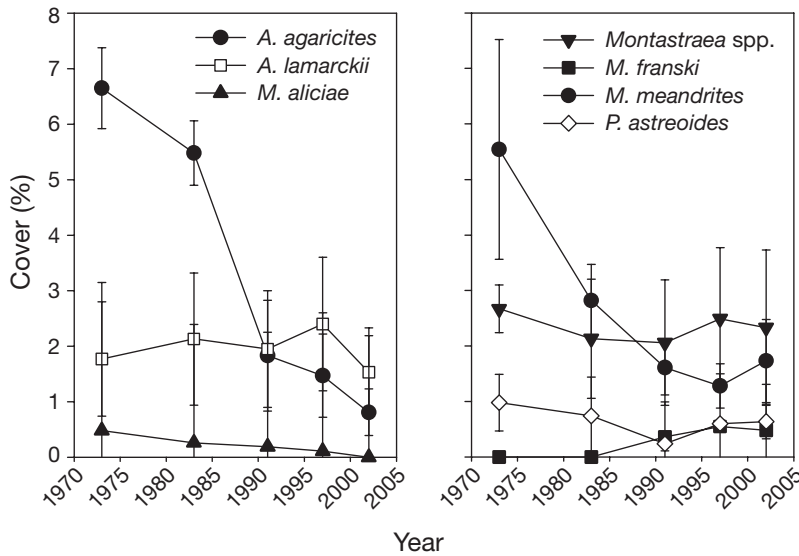
Fig. 6. Percent cover of 6 coral species and the genus *Montastraea* from 1973 to 2002 at 20 m depth, close to our experimental site. Data are mean (% total projected reef area ± SE) of 3 permanent quadrats. Coral species: *Agaricia agaricites*, *A. lamarcki*, *Mycetophyllia aliciae*, *Montastraea franski*, *Meandrina meandrites*, *Porites astreoides*

Table 5. Repeated measures ANOVA of percent coral cover with species as between factor variables and year (1973, 1983, 1991, 1997 vs. 2002) as within-factor variables. Data were arcsine square root transformed prior to analysis

Source	SS	df	MS	*F*	p	Conclusions
Test of between-subjects effects:						
Species	27.80	5	5.57	4.92	0.011	
Error	13.60	12	1.13			
Test of within-subjects effects:						
Year	3.29	4	0.82	6.58	0.000	
Year × Species	8.62	20	0.43	3.44	0.000	Significant[a]
Error	6.01	48	0.13			

[a]Repeated measures ANOVA tests for each species indicate significant difference among years for *Agaricia agaricites* ($F_{4,8}$ = 12.26, p = 0.002) and *Meandrina meandrites* ($F_{4,8}$ = 13.95, p = 0.001)

of *Diadema antillarum* in 1983 that generally marks the onset of increased algal abundance on Caribbean reefs (Ruyter van Steveninck & Bak 1986, Ruyter van Steveninck & Breeman 1987, Hughes 1994). *Meandrina meandrites* also experienced a significant decrease in abundance, but part of this decrease occurred prior to the die-off of *D. antillarum*, and this decrease seems to have leveled off since 1991 despite the continuous presence of algae (R. Bak pers. obs.).

The vulnerability of *Agaricia agaricites* during periods of increased algal abundance is further supported by 2 earlier studies that looked at changes in reef coral communities following the die-off of *Diadema antil-*

larum. In the same study area but using a different census method, Ruyter van Steveninck & Bak (1986) found that *A. agaricites* declined more severely than all other species combined between October 1983 and May 1984. In Jamaica, Hughes (1989) reported a 97% loss in cover for *A. agaricites* over a 4 yr period following the die-off of *Diadema antillarum*, while other taxa declined but less sharply.

It is important to recognise that these experimental results have several limitations. Firstly, they are specific to the particular grazing intensity and nutrient regime experienced at our site, and thus not all aspects can be generalised to other locations. The role of herbivory and nutrients in mediating coral-algal interactions has been suggested by several studies (Potts 1977, Sammarco 1980, 1982, Lewis 1986, Hughes 1994, Miller & Hay 1996, 1998, Lapointe 1997, Lirman 2001, McClanahan et al. 2002, 2003, 2005, Diaz-Pulido & McCook 2003, 2005). Jompa & McCook (2002a) experimentally tested the effects of nutrients and herbivory on the competition between *Lobophora variegata* and the coral *Porites cylindrica.* They demonstrated that a decrease in herbivory can result in increased algal growth rates and coral tissue mortality from algal overgrowth; nutrients only increased algal growth and coral mortality in conditions of reduced herbivory. It is clear that, in our study, a decline in herbivory and/or increase in nutrients could lead to an increase in the competitive advantage of *L. variegata* over corals and, consequently, increased coral mortality from algal overgrowth.

Secondly, our experimental approach necessitated the selection of healthy-looking colonies and regular clearing of all externally interfering algae. Both actions could have minimised the influence of other factors that affect coral-algal competition. For instance, the coral *Porites astreoides* has been suggested as being highly susceptible to algal overgrowth (Sammarco 1980, 1982). At our survey site, this species had a relatively high percentage of overgrown colonies. Its percentage of overgrown perimeter and maximum reach by the alga were statistically no different to those of *Agaricia agaricites* (Fig. 5). Yet, unlike *A. agaricites*, this species did not experience a significant increase

in tissue mortality from the alga in our experiment (Fig. 4). It is possible that additional factors affect this species in natural conditions and indirectly facilitate algal overgrowth. Sammarco (1980) suggested that lesions resulting from urchin predation could increase invasion by algae and other competitors in *P. astreoides*. However, *P. astreoides* is also more effective in regenerating lesions and overgrowing invasive algae than *A. agaricites* at this depth on the reef (Bak & Steward van Es 1980).

The reason why *Agaricia agaricites* is a poor competitor against *Lobophora variegata* is unknown, but probably depends upon mechanisms of interaction. Previous studies on interactions between *L. variegata* and corals proposed 3 possible mechanisms: (1) mechanical damage by mesenterial filaments or sweeper tentacles, (2) allelopathy, and (3) the involvement of grazers defending coral margins (Ruyter van Steveninck et al. 1988, Jompa & McCook 2002b). Nugues et al. (2004) found that corals can use mesenterial filaments against *L. variegata* when placed in direct contact with the alga. *L. variegata* blades in contact with corals have visibly damaged growth margins compared to blades growing away from corals (Ruyter van Steveninck et al. 1988, M. Nugues pers. obs.). However, it is unknown whether mesenterial filaments are effective in preventing *L. variegata* overgrowth and whether this could explain differences in competitive abilities among coral species. Lang (1973) established a hierarchy among coral species based on their ability to digest their competitors by extruding mesenterial filaments. Interestingly, *A. agaricites* ranked low in this hierarchy, but so did *A. lamarcki* and *Porites astreoides*. In short-term experimental interactions between corals and the alga *Halimeda opuntia* where mesenterial filaments were also observed, *Montastraea annularis* caused extensive discoloration in the alga, but *A. agaricites*, *P. astreoides* and *Meandrina meandrites* all had little or no impact (Nugues et al. 2004).

There was a good correlation between our experimental results and the pattern of natural interactions between *Lobophora variegata* and corals, which supported the findings of our experiment. Coral species having a high competitive ability, i.e. low levels of coral mortality in the presence of the alga (e.g. *Montastraea franksi* and *Mycetophyllia aliciae*, Fig. 4B), had generally low percentages of colony or perimeter overgrown by the alga in the field (Fig. 5A,B). Vice versa, *Agaricia agaricites*, which was competitively inferior to the alga and experienced a high level of mortality, was extensively overgrown by the alga — i.e. more than 70% of the colonies were overgrown. Surveys of coral-algal interactions are only a snapshot view of these interactions and do not give information on their long-term outcomes. This correlation could

merely reflect the fact that poor coral competitors generally have a growth form that renders them more susceptible to algal overgrowth (Hughes 1989). However, our study suggested that naturally occurring interactions may be a good indicator of species-specific differences in competitive ability.

In an attempt to improve conceptual understanding of coral-algal competition, McCook et al. (2001) proposed algal functional groups and coral life forms as factors to predict the variability of these interactions. Algal functional groups proved to work relatively well (Jompa & McCook 2003b); however, an exception is already evident within the filamentous algal group. This group appears to be a poor competitor against corals (McCook 2001), but recently the filamentous red alga *Anotrichium tenue* has been shown to kill coral tissue by active overgrowth (Jompa & McCook 2003a). Coral life forms probably influence the initial chance of encounter with specific algae. For example, the branching structure of *Madracis mirabilis* provides a suitable habitat for the green alga *Halimeda opuntia*; therefore, both parties are frequently interacting (M. Nugues pers. obs.). Encrusting low relief corals are likely to be more exposed to filamentous or creeping algae such as *Lobophora variegata* (Birkeland 1977, Bak & Engel 1979, Hughes 1989). However, once algae are interacting with corals, coral life forms could have limited influence. In our experiment, *Agaricia agaricites* share similarities in growth form with *A. lamarcki* and *Meandrina meandrites*, but it was the only species to be overgrown and killed by *L. variegata*. As suggested by McCook et al. (2001), a species-by-species approach may be the way forward to predict coral-algal competition on the less diverse Caribbean reefs.

Clearly, we are still far from understanding the complexity of coral-algal interactions. Our study added to this complexity by demonstrating that Caribbean corals have different competitive abilities against *Lobophora variegata*. Only 1 coral species was competitively inferior to the alga, supporting a limited role for algal overgrowth as an initial cause of coral mortality. However, this species was also the one that experienced the strongest and most continuous decline since the die-off of *Diadema antillarum* in 1983 on our study reef. Our results suggest that a species-specific approach is needed to understand the processes influencing the widespread replacement of corals by algae on Caribbean reefs.

LITERATURE CITED

Aronson RB, Precht WF (2001) White-band disease and the changing face of Caribbean coral reefs. Hydrobiologia 460:25–38

Aronson RB, Macintyre IG, Wapnick CM, O'Neill MW (2004) Phase shifts, alternative states, and the unprecedented convergence of 2 reef systems. Ecology 85:1876–1891

Bak RPM (1977) Coral reefs and their zonation in the Netherlands Antilles. AAPG Stud Geol Am Assoc Pet Geol 4:3–16

Bak RPM, Engel S (1979) Distribution, abundance and survival of juvenile hermaptypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Mar Biol 54:341–351

Bak RPM, Steward-Van Es Y (1980) Regeneration of superficial damage in the scleractinian corals *Agaricia agaricites* f. *purpurae* and *Porites astreoides*. Bull Mar Sci 30:883–887

Bak RPM, Nieuwland G (1995) Long-term change in coral communities along depth gradients over leeward reefs in the Netherlands Antilles. Bull Mar Sci 56:609–619

Bak RPM, Brouns JJWM, Heys FML (1977) Regeneration and aspects of spatial competition in scleractinian corals *Agaricia agaricites* and *Montastrea annularis.* Proc 3rd Int Coral Reef Symp 1:143–148

Bak RPM, Termaat RM, Dekker R (1982) Complexity of coral interactions: influence of time, location of interaction and epifauna. Mar Biol 69:215–222

Birkeland C (1977) The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proc 3rd Int Coral Reef Symp 1:15–21

Chornesky EA (1989) Repeated reversals during spatial competition between corals. Ecology 70:843–855

Diaz-Pulido G, Diaz JM (1997) Algal assemblages in lagoonal reefs of Caribbean oceanic atolls. Proc 8th Int Coral Reef Symp 1:827–832

Diaz-Pulido G, McCook LJ (2002) The fate of bleached corals: patterns and dynamics of algal recruitment. Mar Ecol Prog Ser 232:115–128

Diaz-Pulido G, McCook LJ (2003) Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. Ecology 84:2026–2033

Diaz-Pulido G, McCook LJ (2004) Effects of live coral, epilithic algal communities and substrate type on algal recruitment. Coral Reefs 23:225–233

Diaz-Pulido G, McCook LJ (2005) Effects of nutrient enhancement on the fecundity of a coral reef macroalgae. J Exp Mar Biol Ecol 317:13–24

Dytham C (1999) Choosing and using statistics: a biologist guide. Blackwell Scienctific Publications, Oxford

Edmunds PJ (2002) Long-term dynamics of coral reefs in St. John, US Virgin Islands. Coral Reefs 21:357–367

Gardner TA, Côtò IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide decline in Caribbean corals. Science 301:958–960

Hughes TP (1989) Community structure and diversity of coral reefs: the role of history. Ecology 70:275–279

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265: 1547–1551

Hughes TP, Szmant AM, Steneck RS, Carpenter RC, Miller S (1999) Algal blooms on coral reefs: what are the causes? Limnol Oceanogr 44:1583–1586

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA and 15 others (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638

Jompa J, McCook LJ (1998) Seaweeds save the reef?!: *Sargassum* canopy decreases coral bleaching on inshore reefs. Reef Res 8:5

Jompa J, McCook LJ (2002a) The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*). Limnol Oceanogr 47:527–534

Jompa J, McCook LJ (2002b) Effects of competition and herbivory on interactions between a hard coral and a brown alga. J Exp Mar Biol Ecol 271:25–39

Jompa J, McCook LJ (2003a) Contrasting effects of turf algae on corals: massive *Porites* spp. are unaffected by mixed-species turfs, but are killed by the red alga *Anotrichium tenue*. Mar Ecol Prog Ser 258:79–86

Jompa J, McCook LJ (2003b) Coral-algal competition: macroalgae with different properties have different effects on corals. Mar Ecol Prog Ser 258:87–95

Karlson RH (1999) Dynamics of coral communities. Kluwer Academic, Dordrecht

Lang JC (1973) Interspecific aggression by scleractinian corals. II. Why the race is not only to the swift. Bull Mar Sci 23:260–279

Lang JC, Chornesky EA (1990) Competition between scleractinian reef corals—a review of mechanisms and effects. In: Dubinsky Z (ed) Ecosystems of the world, Vol 25. Coral Reefs. Elsevier, Amsterdam, p 209–252

Lapointe BE (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnol Oceanogr 42:1119–1131

Lapointe BE (1999) Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs (reply to the comment by Hughes et al.). Limnol Oceanogr 44: 1586–1592

Lapointe BE (2004) Phosphorus-rich waters at Glovers Reef, Belize? Mar Pollut Bull 48:193–195

Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. Ecol Monogr 56: 183–200

Lirman D (2001) Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs 19: 392–399

Logan A (1984) Interspecific aggression in hermatypic corals from Bermuda. Coral Reefs 3:131–138

McClanahan TR, Muthiga NA (1998) An ecological shift in a remote coral atoll of Belize over 25 years. Environ Conserv 25:122–130

McClanahan TR, Aronson RB, Pretch WF, Muthiga NA (1999) Fleshy algae dominate remote coral reefs of Belize. Coral Reefs 18:61–62

McClanahan TR, Muthiga NA, Mangi S (2001) Coral and algal response to the 1998 bleaching and mortality: interactions with reef management and herbivores on Kenyan reefs. Coral reefs 19:380–391

McClanahan TR, Cokos BA, Sala E (2002) Algal growth and species composition under experimental control of herbivory, phosphorus and coral abundance in Glovers Reef, Belize. Mar Pollut Bull 44:441–451

McClanahan TR, Sala E, Stickels PA, Cokos BA, Baker AC, Starger CJ, Jones IV SH (2003) Interactions between nutrients and herbivory in controlling algal communities and coral condition an Glover's Reef, Belize. Mar Ecol Prog Ser 261:135–147

McClanahan TR, Sala E, Mumby PJ, Jones S (2004) Phosphorus and nitrogen enrichment do not enhance brown frondose 'macroalgae'. Mar Pollut Bull 48:196–199

McClanahan TR, Steneck RS, Pietri D, Cokos B, Jones S (2005) Interactions between inorganic nutrients and organic matter in controlling coral reef communities in Glovers Reef Belize. Mar Pollut Bull 50:566–575

McCook LJ (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 LJ (2001) Competition between corals and algal turfs along a gradient of terrestrial influence in the nearshore central Great Barrier Reef. Coral Reefs 19:419–425

McCook LJ, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19:400–417

Meesters EH, Bak RPM (1993) Effects of coral bleaching on tissue regeneration potential and colony survival. Mar Ecol Prog Ser 96:189–198

Miller MW, Hay ME (1996) Coral-seaweed-grazer-nutrient interactions on temperate reefs. Ecol Monogr 663:323–344

Miller MW, Hay ME (1998) Effects of fish predation and seaweed competition on the survival and growth of corals. Oecologia 113:231–238

Miller MW, Hay ME, Miller SL, Malone D, Sotka EE, Szmant AM (1999) Effects of nutrients versus herbivores on reef algae: a new method for manipulating nutrients on coral reefs. Limnol Oceanogr 44:1847–1861

Nugues MM, Delvoye L, Bak RPM (2004) Coral defence against macroalgae: differential effects of mesenterial filaments on the green alga *Halimeda opuntia*. Mar Ecol Prog Ser 278:103–114

Ostrander GK, Armstrong KM, Knobbe ET, Gerace D, Scully EP (2000) Rapid transition in the structure of a coral reef community: the effects of coral bleaching and physical disturbance. Proc Nat Acad Sci USA 97:5297–5302

Potts DC (1977) Suppression of coral populations by filamentous algae within damselfish territories. J Exp Mar Biol Ecol 28:207–216

River GF, Edmunds PJ (2001) Mechanisms of interaction between macroalgae and scleractinians on a coral reef in Jamaica. J Exp Mar Biol Ecol 261:159–172

Ruyter van Steveninck ED de, Bak RPM (1986) Changes in abundance of coral-reef bottom components related to mass mortality of the sea urchin *Diadema antillarum*.

Mar Ecol Prog Ser 34:87–94

Ruyter van Steveninck ED de, Breeman AM (1987) Deep water vegetations of *Lobophora variegata* (Phaeophyceae) in the coral reef of Curaçao: population dynamics in relation to mass mortality of the sea urchin *Diadema antillarum*. Mar Ecol Prog Ser 36:81–90

Ruyter van Steveninck ED de, van Mulekom LL, Breeman AM (1988) Growth inhibition of *Lobophora variegata* (Lamouroux) Womersley by scleractinian corals. J Exp Mar Biol Ecol 115:169–178

Sammarco PW (1980) *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. J Exp Mar Biol Ecol 45:245–272

Sammarco PW (1982) Echinoid grazing as a structuring force in coral communities: whole reef manipulations. J Exp Mar Biol Ecol 61:31–55

Shulman MJ, Robertson DR (1996) Changes in the coral reef of San Blas, Caribbean Panama: 1983 to 1990. Coral Reefs 15:231–236

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, New York

Stimson J, Larned ST, Conklin E (2001) Effects of herbivory, nutrient levels, and introduced algae on the distribution and abundance of the invasive macroalgae *Dictyosphaeria cavernosa* in Kanoehe Bay, Hawaii. Coral Reefs 19:343–357

Szmant AM (2002) Nutrient enrichment on coral reefs: is it a major cause of coral reef decline? Estuaries 25:743–766

Tanner JE (1995) Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. J Exp Mar Biol Ecol 190:151–168

Thacker RW, Ginsburg DW, Paul VJ (2001) Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. Coral Reefs 19:318–329

Van den Hoek C, Breeman AM, Bak RPM, Van Buurt G (1978) The distribution of algae, corals and gorgonians in relation to depth, light attenuation, water movement and grazing pressure in the fringing coral reef of Curaçao, Netherlands Antilles. Aqua Bot 5:1–46

Van Duyl FC (1985) Atlas of the living reefs of Curaçao and Bonaire, Netherlands Antilles. Publ Found Sci Res Caribb Reg 117:1–13

Williams ID, Polunin NVC (2001a) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs 19:358–366

Williams ID, Polunin NVC, Hendrick VJ (2001b) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. Mar Ecol Prog Ser 222:187–196