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Interactions between macroalgae and scleractinian corals in the context of reef degradation

Thesis submitted by

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27 MARCH 2001

Jamaluddin Jompa

Abstract

Competition between hard corals and macroalgae is important to the overall status of coral reefs, especially during reef degradation which often involves a "phase shift" from coral to algal dominated reefs. Declining levels of herbivory due to over-fishing (the "top-down" model), or increasing supply of nutrients (eutrophication, the "bottom-up" model) have both been suggested to cause increased algal abundance and consequent competitive overgrowth of corals. Despite the importance of coral-algal competition to either of these models, there is little direct evidence demonstrating competition with algae as the cause of coral declines, and in particular, very little evidence unambiguously demonstrating shifts in competitive balance due to either reduced herbivory or increased nutrient supply. This thesis aims to provide more experimental evidence on the processes, mechanisms and outcomes of the interactions between corals and algae for (i) a range of levels, from individual to community; (ii) a range of algal taxa and functional groups; and (iii) ranges of ecological factors such as water quality or nutrients and herbivory.

The first study compared the effects of a turfing, filamentous red alga, *Anotrichium tenue,* and general mixed, filamentous algal turfs, on massive *Porites* corals. Comparisons of plots with *A. tenue* present, *A. tenue* experimentally removed, and with mixed turfs only present, indicated that *A. tenue* was able to overgrow and kill healthy coral, whereas mixed algal turfs could not. These contrasting effects demonstrate the potential variability in coral-algal competitive effects and outcomes, even within a functional group.

I further explored this variability using three different algal species; the turfing, filamentous red alga *Corallophila huysmansii*, the non-turfing, large green filamentous alga *Chlorodesmis* spp., and the corticated red alga *Hypnea pannosa*. Experimental tests again indicate considerable variation in the effects on corals, with *C. huysmansii* causing considerable coral tissue mortality, whereas neither *Chlorodesmis* nor *H. pannosa* had major effects on the corals.

To explore how herbivory may affect coral-algal competitive outcomes, I examined the interaction between the creeping foliose brown alga, *Lobophora variegata*, and the branching coral, *Porites cylindrica*, under natural and experimentally reduced levels of herbivory. These experiments used exclusion cages to test for effects of herbivores, and removal of algae or coral tissue, at their interaction boundary, to test

for competitive inhibition of each competitor by the other. The results showed that overgrowth of the alga caused significant coral tissue mortality, but that the coral also inhibited algal growth. Nonetheless, the algae were markedly superior competitors. Importantly, reduced herbivory resulted in faster algal (net) growth and consequent overgrowth and mortality of coral tissue, demonstrating the critical importance of herbivory to the outcome of the competitive interaction.

This approach was extended to apply simultaneous, factorial tests of the effects of herbivores, nutrients and algal competitor on the coral. Coral tissue mortality was strongly enhanced by the presence of the algal competitor and this effect was significantly higher when herbivores were excluded. Addition of nutrients had no significant effect on corals overall, but had a small effect on algal growth and consequent coral tissue mortality when herbivores were excluded. The factorial design of this experiment not only provides the first direct comparisons of the strength of all 3 main effects, but also explores the interactions between those effects, and hence the processes involved. Importantly, whilst algal abundance and hence competitive impact were affected by herbivore consumption at all levels of nutrient supply, nutrient supply did not influence algal abundance except when consumption by herbivores was reduced.

Inshore reefs of the Great Barrier Reef commonly have extensive beds of large brown macroalgae (seaweeds) such as *Sargassum spp.,* that are widely assumed to have negative impacts on coral populations. To test this assumption, I compared coral performance in large (5 x 5 m) plots in which the macroalgal canopy was removed, with that in control plots with intact algal canopies. In one study, the macroalgae had a negative impact on corals, reducing their recruitment, growth and survival. However, a second study showed a surprising increase in coral bleaching in plots from which the *Sargassum* canopy had been experimentally removed. Combined bleaching and recovery results suggest that coral bleaching-related mortality was higher in the removal plots. Thus the protection from bleaching provided by the *Sargassum* canopy may benefit long-term coral populations, as well as competing with them.

Comparison of competitive outcomes involving different algal types and functional groups, and under different herbivory and nutrient levels suggests three general conclusions. Firstly, the outcomes of the interactions are variable depending on coral-algal taxa and/or group involved. Secondly, this variability is readily interpreted in terms of a limited number of mechanisms by which corals and algae can interact: direct overgrowth, shading, abrasion, chemical or allelopathic effects, pre-emption of space, and sloughing of epithelial or mucus layers. The potential importance of these mechanisms can in turn be interpreted in terms of a limited number of properties of the algal taxa involved. These properties, which include thallus size, structure, growth form, reproductive mechanisms, and allelochemical production, are largely, but not entirely, summarised by existing algal functional groups. Thirdly, the specific interactions between competition, herbivory and nutrient enhancement, in which nutrient effects depended on levels of herbivory, but not vice versa, suggest that "top-down" control appeared to over-ride "bottom-up" control of algal abundance and competitive impact. Given the central importance of coral-algal competition to the process of coral reef phase shifts, understanding the variability and complexity in that competition will have important implications for the prediction and consequences of such phase shifts.

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STATEMENT OF SOURCES

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

27 MARCH 2001

Jamaluddin Jompa

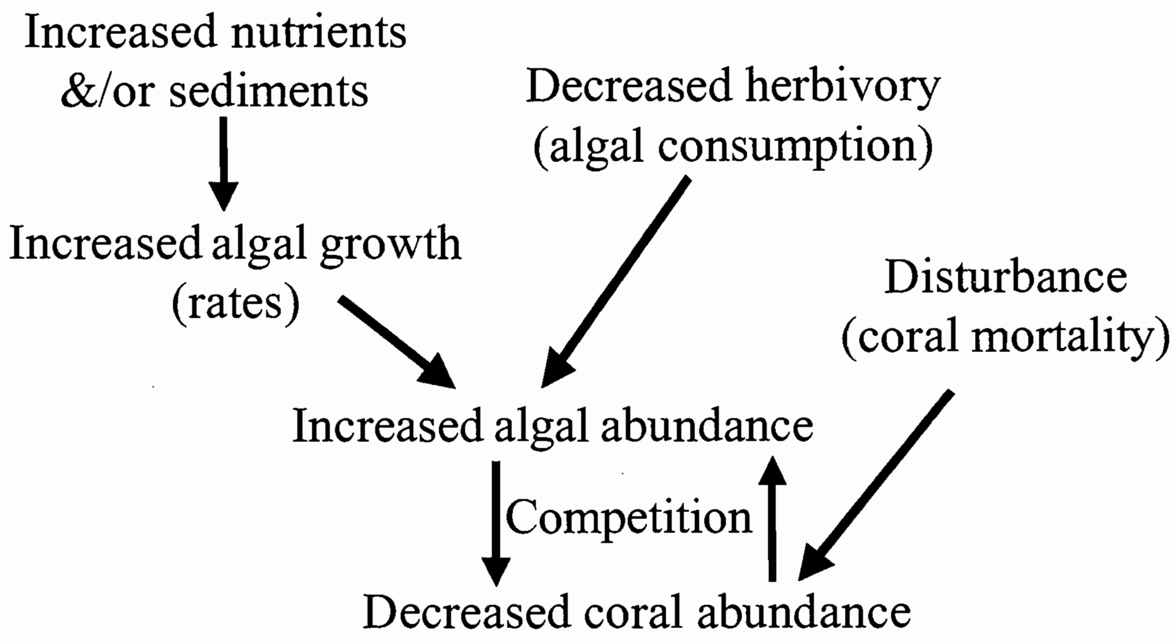
CHAPTER 1. General Introduction

1.1. Coral reef degradation, phase shifts, and the importance of coral-algal competition

Competition is an important process determining the structure and composition of benthic communities on coral reefs (Lang and Chornesky 1990; Karlson 1999). In particular, competition between hard corals and benthic algae is considered fundamental to the overall status of coral reefs, especially during reef degradation. Coral reef degradation commonly involves a so-called "phase-shift" from reefs dominated by abundant corals to reefs dominated by abundant benthic algae (Done 1992; Hughes 1994a; McCook 1999). There has been considerable, recent controversy over the relative importance of "bottom-up" (e.g. Lapointe 1997; 1999) and "top-down" (Hughes 1994a; Hughes et al. 1999; Aronson and Precht 2000) factors in contributing to these changes (Fig. 1.1), particularly on Caribbean reefs. According to the "bottom-up" model, excess nutrient supply results in an increased growth of benthic algae (e.g. Hanisak 1979; Lapointe 1997; Schaffelke and Klumpp 1997; 1998a; Schaffelke 1999), leading to overgrowth of corals, and consequent reef degradation (Smith et al. 1981; Pastorok and Bilyard 1985; Bell 1992; Naim 1993; Lapointe 1999). The "top-down" model argues that algal biomass is predominantly controlled by herbivore consumption (e.g. Hay 1981; 1984; Lewis 1985; 1986; Hughes 1994a; McCook 1996; 1997; Russ and McCook 1999) and that phase shifts are often the result of declines in herbivores, with consequent increases in algal abundance and competitiveness.

Although the relative importance of nutrients and herbivory, in controlling benthic algal abundance, will depend on circumstances such as location, herbivore

Figure 1.1. Diagram showing “bottom-up” versus “top-down” models of coral-algal "phase shifts". The bottom-up perspective emphasises the importance of nutrient supply to algal abundance. The top-down perspective emphasizes the importance of herbivory, as decreased algal consumption by herbivores also results in increased algal abundance. Importantly, both perspectives assume that increased algal abundance leads to decreased coral abundance through competition. Thus coral-algal competition is critical to the outcome of both models. Note also that external factors, such as disturbance, may cause similar shifts, with decreased coral abundance and increased in algal abundance. However, in such cases the causality is reversed: the increased algal abundance is the consequence and not the cause of coral mortality (Redrawn from McCook et al. 2000a).



regimes, background nutrient supplies, disturbance regimes, etc. (e.g. Littler and Littler 1984; Miller 1998; McCook 1999; 2001), it is important to recognize that both "bottom-up" and "top-down" perspectives assume that increased algal abundance will lead to decreased coral abundance, by altering the competitive balance between algae and corals (Miller 1998; McCook 1999; McCook et al. 2001). Thus competition between corals and algae is a critical step in both "bottom-up" and "top-down" models of reef degradation (Fig. 1.1).

1.2. Review of available evidence

Given the importance of competition between corals and benthic algae, it is worth reviewing what is known about the interaction. Benthic algae are generally considered to be widely competing with corals, apparently for space and/or light, and interactions between the two are frequently interpreted simply in terms of algal competitive superiority (e.g. Benayahu and Loya 1981; Pastorok and Bilyard 1985). However, there is relatively little direct evidence to demonstrate coral-algal interactions are competitive, or that competition is the direct cause of changes in relative abundance of corals and algae.

Based on the arguments of Connell (1983), Schoener (1983), Underwood (1986), and McArdle (1996), this section classifies studies according to the levels of evidence they provide that coral-algal interactions are in fact competitive: that is, evidence that the performance of either competitor is reduced by the presence of the other. This classification distinguishes between: i. experiments that directly manipulated abundance of either competitor (Appendix Table A.1); ii. experiments that manipulate herbivores, and thus are assumed to indirectly manipulate algal abundance (Appendix Table A.2); iii. "natural experiments" or comparisons and observations of correlations between algal and coral abundances (Appendix Table A.3); iv. direct observations of coral-algal interactions, at relatively small scales (Appendix Table A.4). (Individual papers may include data or evidence in more than one category). Studies are also classified within each table by location and region, methods and results, and by the algal taxa and functional group, and coral taxa and lifeform.

Proof of competition requires unequivocal evidence that the performance of the study organism is in some way inhibited by the presence of the putative competitor. That evidence can only be provided by (properly replicated and controlled) direct manipulation of the competitor, so that the only difference between treatments is the presence or abundance of the competitor, and any difference in response may be assumed due (directly or indirectly) to the competitor (Underwood 1986). All other approaches are *potentially* confounded by other factors. Although some examples are included to illustrate possible confounding factors, issues of causality and correlation are not argued in detail here (see e.g. previous refs, and Strong et al. 1984; Diamond 1986). In particular, without experimental evidence, the replacement or overgrowth of live coral by algae does not prove that the algae have outcompeted the corals: the coral may have been killed by some other, unrelated factor (e.g. bleaching, corallivory, storm damage, eutrophication, disease), potentially unknown to the researcher. The algae may have increased as a consequence of the coral loss, and may have been having little or no inhibitory effect on the corals (e.g. McCook 2001).

Recognition of the interpretive limitations of any study in terms of competitive causality does not amount to criticism of the study in its own right. Many of the studies reviewed were not intended to test the competitive nature of the interaction, or to demonstrate causality, but to document patterns or changes in community structure, or effects of herbivores. Such studies are intrinsically valuable, especially where they include long-term or large scale data, which are difficult to achieve with manipulative experiments.

The term "macroalgae" throughout this thesis refers to benthic algae visible with the naked eye, thus including small filamentous and blue-green algae and crustose coralline algae. The term "coral" is used for scleractinian or hard corals, and does not include octocorals (soft corals).

1.2.1. Direct experimental tests for competition

Only seven studies were found that directly tested competitive interactions between corals and algae (Appendix Table A.1), of which two were in temperate systems (Coyer et al. 1993; Miller and Hay 1996) rather than coral reefs. Most of the experiments tested effects of algae on corals, and only one tested effects of corals on algae (McCook 2001). Only two studies simultaneously tested competitive effects and herbivory, despite the importance of herbivory to algal abundance (Miller and Hay 1996; Miller and Hay 1998). Most studies demonstrated negative impacts of algae on corals, but these effects varied in intensity, and in one exceptional case, algae actually *protected* corals from bleaching (Jompa and McCook 1998, see also Chapter 3 for further analyses).

Also relevant are several studies (Appendix Table A.1) intended to examine coral recruitment or recovery from lesions, but which provide *de facto* tests of the effects of corals and algae on each other. The induction of coral metamorphosis by coralline algae (Heyward and Negri 1999) provides a second example of algae *enhancing* coral success. In the lesion studies, experimental damage to coral tissue (with control, undamaged areas) was followed initially by algal colonisation, but in general the corals regenerated, overgrowing and thereby outcompeting the algae. Algae did not colonise the control areas, and appeared to inhibit but rarely prevent coral recovery in damaged areas, indicating competitive superiority of the corals. Larger lesions persisted for longer periods, often leading to colonisation by more robust and competitively successful algal forms (Meesters and Bak 1993; Meesters et al. 1994; 1997).

Some differences in competitive potential may be discerned between algal groups, such as canopies of large, leathery algae that shade or whiplash corals, and smaller algae that directly contact or smother corals. However, these studies together still provide very limited coverage of different combinations of algal functional groups and coral lifeforms, and so provide a very limited basis for generalisations about coral-algal competition. Further, most manipulations were inevitably at relatively small scales (~0.1 to <10 m), although several did involve more than one reef or large scale transplantations.

1.2.2. Indirect experiments using herbivore manipulations

Indirect experimental evidence for competitive effects of algae on corals comes from experimental herbivore manipulations (Appendix Table A.2). Only 9 such studies were found to include data on coral abundance, and most indicated declines in corals, presumably in response to the general increase in algal abundance following herbivore exclusion. However, the effects on corals were often variable, or relatively minor. For example, two of the most cited papers in this context include Sammarco (1982), in which removal of *Diadema* alone led to *increased* coral abundance, and Lewis' (1986) classic herbivore exclusion experiment, in which the resulting decline in coral cover was only about 2% (coral abundance was initially relatively low). Unfortunately, most of these experiments were relatively small scale and short-term, and thus inevitably involved smaller, faster growing algal taxa (filamentous and corticated macrophytes).

Importantly, herbivore experiments (and natural experiments involving herbivore changes) are fundamentally tests for herbivore effects, not competition (and are intended as such by their authors). Although effects of algae on corals are generally the most or even the only reasonable interpretation, alternative explanations remain possible. For example, the herbivore exclusion procedure may produce artifacts detrimental to corals (e.g. shading, reduction in flow; not all experiments included procedural controls). Declines in corals could also result from the incidental exclusion of predators that would otherwise restrict corallivores (e.g. gastropods).

1.2.3. "Natural experiments" and correlative studies.

Considerably more evidence comes from the numerous comparisons of coral and algal abundance during "natural experiments" or along gradients, or simple inverse relationships between coral and algal abundance in space or time (Appendix Table A.3). Many of these comparisons have the advantage of wider generality than direct, planned experiments, due to larger spatial or temporal scales. However, as stated previously, causality is intrinsically more ambiguous in these cases, since the correlations observed may be coincidental or consequential, rather than causal.

For example, Crossland (1981) found lower coral growth in the presence of canopy forming algae and this has been widely cited as evidence for competitive inhibition by shading. However, separation of corals into shaded and unshaded was retrospective, since algae appeared in some plots and not others. Further, there was no evidence that the differences were caused specifically by shading, rather than, for example, abrasion by the algae, or by other unknown factors. Algal shading was assumed to be the cause of reduced coral growth, with the differences in algal growth unexplained. However there is no *a priori* evidence that causality might not be reversed (algal growth reduced as consequence of coral growth, in turn due to unknown factors), common (same factor/s cause increased algal growth and decreased coral growth), or even coincidental (unrelated factors cause coral and algal differences). Thus, other unmeasured differences between plots, such as variations in light, nutrient, sediment or herbivory regimes, may have contributed to the differences in both algal abundance and coral growth rates.

Similarly, in Potts (1977) demonstration of reduced coral growth inside damselfish territories, corals were not randomly allocated to treatments, but selected by the damselfish, presumably non-randomly (territory boundaries also changed during the study, so that some corals changed treatments). The damselfish may have selected less vigorous corals, or even have damaged the corals directly (Kaufman 1977). Further, aside from algal abundance, damselfish modify numerous aspects of their territories, including nutrient regime and algal composition (Russ 1987), which may modify coral growth rates. Thus, although valuable, these results should not be taken uncritically as evidence that the algae inhibited coral growth.

Importantly, even where abundant algae have replaced formerly abundant corals, the major cause of coral mortality may be external disturbances, rather than direct competition with the algae (e.g. freshwater kills in Kaneohe Bay: Smith et al. 1981; Kinsey 1988; hurricane at Discovery Bay: Hughes 1994a; Hunter and Evans 1995). Thus, although corals and algae may be competing for space, and competition may explain the algal bloom when corals are removed, the algae may not have directly outcompeted the corals.

Particular caution is required in interpreting causality in studies based on correlations in cover of algae and corals (Appendix Table A.3). Despite the general assumption that the inverse correlations are caused by competition (e.g. Benayahu and Loya 1981), the patterns may simply reflect coincident differences in other factors influencing their distributions, or causality may even be reversed. For example, offshore to inshore reversals in coral and algal abundance could be due to coral intolerance of inshore turbidity and algal susceptibility to the abundant herbivores on offshore reefs (coincident causality; e.g. McCook 1996; 1997). The same pattern could also arise because corals are killed by inshore sediment loads, allowing algae to persist (Umar et al. 1998).

Several of the other studies listed (Appendix Table A.3) warrant particular mention. The relatively long time span of temporal comparisons by Shulman and Robertson (1996; 7 years), Connell et al. (1997; 30 years), Rogers et al. (1997; 7 years) and the long time span and broad coverage of some of the *Diadema* die-off studies (e.g. Hughes et al. 1987; Hughes 1989; Steneck 1994; 9 years; 1994a; 1996; 17 years; Edmunds and Carpenter 2001; 20 years), makes them particularly valuable, especially since most include considerable background data and evidence for the competitive nature of the changes documented. Historical synthesis of coral and algal abundances and terrestrial runoff in Kaneohe Bay suggest that changes in reef composition involve complex and uncertain interactions between freshwater kills, eutrophication, sedimentation and coral-algal competition (Banner 1974 include little hard data on coral or algal abundances; in contrast Smith et al. 1981; Hunter and Evans 1995; 20 years).

1.2.4. Direct observations of apparent competition.

Finally, another source of evidence for coral-algal competition comes from numerous direct observations of small-scale interactions (Appendix Table A.4), many supported by photographs, in which corals appear to be overgrown by algae. Although suggestive, such observations do not necessarily prove that the algae are killing the coral. Any area of coral tissue killed by other causes (e.g. corallivorous fish or invertebrate feeding, temporary sediment burial, bleaching) will generally be rapidly colonised by algae, whereas adjacent healthy coral tissue may continue to vigorously defend itself from algal recruitment or vegetative overgrowth. Thus, unless experimental evidence is also available, close matches between coral tissue damage and algal overgrowth may not indicate algal competitive success, but rather the successful competitive exclusion of algal growth from areas of healthy coral tissue (de Ruyter van Steveninck et al. 1988; McCook 2001).

Several of the listed observations illustrate the variability of coral-algal interactions. Littler and Littler (1997b) provide contrasting photographs of coral recruits apparently overgrowing filamentous turf algae, but also of filamentous turfs apparently killing adult corals. Littler and Littler (1997a) appear to demonstrate algae overgrowing and killing healthy coral tissue by means of allelochemicals, a process otherwise undocumented (but see also de Nys et al. 1991for soft corals and Chapters 2 & 3 of this thesis). De Ruyter van Steveninck, et al. (1988) documented inhibition of algal growth rates by proximity to corals, the only detailed demonstration of coral effects on algae. Finally Coyer et al. (1993) and Lirman (2001) noted polyp retraction in response to algal brushing, providing otherwise scarce evidence for the mechanisms of competition.

1.2.5. Summary of published evidence

Overall, there is little evidence that unambiguously demonstrates competition between corals and reef algae, and very little demonstrating competitive overgrowth of corals by algae. Only seven of the 57 papers reviewed provided direct experimental tests for competition. Much of the available evidence is indirect, anecdotal or correlative, and provides little understanding of the processes by which algae may replace corals. Interpretations of algal competitive superiority are frequently justified by citing one of a limited number of specific studies (in particular Potts 1977; Birkeland 1977; Crossland 1981; Smith et al. 1981; Sammarco 1982; Lewis 1986), many of which were not designed to test competition. Interactions between corals and algae appear variable in both mechanism and process, yet there has been relatively little attempt to explore or understand that variability. Therefore more experimental evidence is needed to better understand the variability, mechanisms, outcomes and importance of coral-algal competitive interactions.

1.3. Thesis Outline

This thesis aims to provide more conclusive evidence on coral-algal interactions for (i) a range of levels, from individual to community; (ii) a range of algal functional groups; and (iii) ranges of other ecological factors, including in particular, water quality or nutrients, and herbivory. The approach at the individual level examines in detail competition between several specific coral and algal taxa (Chapters 2, 3, 4 and 5). Chapter 2 describes the lethal effect of the turfing, filamentous red alga *Anotrichium tenue* on the massive corals *Porites* spp, contrasting this to the negligible effects of general mixed algal turfs. Chapter 3 provides more examples of coral-algal competition, involving *Corallophila huysmansii*, another turfing, filamentous red alga that had lethal effects on corals; the non-turfing, large filamentous green alga *Chlorodesmis spp.*, and a red corticated alga *Hypnea pannosa*. The last two taxa generally had only minor effects on corals.

To explore how herbivory may affect coral-algal competitive outcomes, Chapter 4 examines the effect of the creeping form of a widespread, brown alga, *Lobophora variegata*, on a branching coral, *Porites cylindrica*, under natural and reduced levels of herbivory. This naturally co-occuring combination of alga and coral provide an ideal experimental unit, allowing logistically simple manipulations of potential competitors. I also used this alga-coral pair in Chapter 5 to test the effects of both nutrients and herbivory on the coral-algal competitive interaction. I tested, for the first time, the effects of all three factors, herbivory, nutrients, and competition, simultaneously in a fully factorial design. This is particularly important in the context of recent controversy over the 'top-down' vs 'bottom-up' models of reef degradation, because both models implicitly assume algal competitive superiority over corals (Section 1.1). The experiments in Chapters 4 and 5 required slightly different approaches. Chapter 4 uses *in situ* colonies in their original habitat, more complete controls for caging artifacts, and, importantly, tests for the effects of corals on algae, as well as vice versa. Chapter 5 also incorporated factorial manipulation of herbivory and competition, but this experiment required the use of transplanted coral branches to facilitate the nutrient treatments, which made it impractical to sacrifice sufficient corals for the extra treatments used in Chapter 4. Thus the two experiments are complementary in approach, particularly to the herbivory-competition interaction.

Chapter 6 examines the effects of a macroalga on corals on inshore reefs at the community level. These inshore reefs are often dominated by canopies of large, leathery macrophytes such as *Sargassum* spp., and have relatively low levels of herbivory and high levels of terrestrial nutrients and sediments (McCook 1996; 1997; 2001). This chapter reports an unusual coral-algal interaction in which the canopy forming macroalgae appeared to reduce the effect of bleaching on corals. This study included two reefs along a gradient of terrestrial influence, allowing comparison of the outcome of coral-algal interactions between the two reefs.

In terms of the range of approaches, the range of individual to community levels is addressed by comparing competitive outcomes between individual corals and algae in specific taxa (Chapters 2, 3, 4, & 5) with the impacts on overall coral assemblages of community level removal of algal canopies (Chapter 6). The range of algal functional groups examined include small, turfing filamentous algae (Chapters 2 & 3), a large, non-turfing filamentous alga (Chapter 3), a creeping corticated foliose alga (Chapters 4 & 5), a corticated macrophyte (Chapter 3), and large, canopy-forming, leathery macrophyte algae (Chapters 6). The role of herbivory on the competition is addressed by caging experiments to manipulate the access of the large herbivores (Chapters 4 & 5). Finally, the impact of nutrients or water quality are addressed both as a direct experimental manipulation of inorganic nutrients (Chapter 5) and also as a natural gradient in proximity to terrestrial inputs of nutrients and sediments (Chapters 2 & 6). Chapter 7 provides overall discussion and interpretation of the separate studies.

Appendix A contains summary tables classifying the available literature on coral –algal competition, referred to in section 1.2 above. Finally, several manuscripts based on the work in this thesis have been submitted to scientific journals for publication, of which one has been published, two accepted, and one is in review. The abstracts of these papers are provided in Appendix B.

CHAPTER 2. Contrasting effects of filamentous turf algae on corals: Massive *Porites* are unaffected by mixed species turfs, but are killed by the red alga *Anotrichium tenue*

2.1. Introduction

Interactions between corals and algae appear variable in both mechanism and process, yet there has been relatively little attempt to explore or understand that variability. It appears that much of this variability can be understood in terms of the limited number of competitive mechanisms by which benthic algae can affect corals (McCook et al. 2001). Algal functional groups (Littler 1980; Littler and Littler 1984; Steneck and Dethier 1994) are able to provide an effective summary of the competitive potential of different algae, because these groups are based on the ecological properties and structure of the algae. Hence the groups may indicate the potential mechanisms by which the algae can compete or interact with corals. For example, filamentous algal turfs and canopy-forming leathery macrophytes have very different potential to inhibit corals. Canopy-forming macrophytes may effectively shade large areas of substrate, but having relatively small holdfasts, will not directly overgrow or smother significant areas of live coral tissue (McCook et al. 2001).

However, even within a functional group, there may be considerable differences in competitive potential, particularly for competitive mechanisms reflected by accepted functional group classifications. For example, filamentous algae have been reported both to overgrow and kill corals (Potts 1977; Littler and Littler 1997a), and to be overgrown and displaced by corals (McCook (2001), particularly during recovery from lesions (Bak et al. 1977; Meesters et al. 1994; van Woesik 1998). Early in 1999 I observed an unusually high number of massive *Porites* colonies being partly overgrown by a single species of turfing, filamentous red alga (*Anotrichium tenue)* on the fringing reefs of the Palm Islands, Great Barrier Reef (GBR). This phenomenon provided an opportunity to compare the competitive effects of this species with that of the general, mixed-species filamentous turfs, thus allowing a comparison within an algal functional group.

2.2. Approach, study sites and methods

This study aims to describe the extent and the process of *A. tenue* overgrowth, and its effects on corals, using a combination of several approaches. These include: (1) a detailed description of the colonization process at a small scale; (2) an experimental test to determine the extent to which *A. tenue*, or mixed algal turfs, were the direct cause of coral tissue mortality; and (3) broader-scale observations, intended to establish the extent to which the patterns described in the more detailed work were site or species specific. These observations include i. a comparison of the time course of overgrowth at two reefs, and ii. a survey of the occurrence of *A. tenue* overgrowth at a cross-continental shelf scale, and of the specificity of the infection to particular coral taxa.

2.2.1. Study sites

Most of the detailed monitoring work (section 1), and the experiment study (section 2) were conducted on the reef slopes of the fringing reef at Cannon Bay, Great Palm Island (Fig. 2.1; 18°41.1' S 146°35.2'E), at 3-5 m depth. This site is located approximately 30 km from the coast and has approximately 20% cover of massive *Porites* spp. The intensity of *A. tenue* infection at this site (section-3.i) was compared to a site at Pioneer Bay, Orpheus Is. (18°36.4' S 146°29.4'E) at approximately the same depth (3-5 m). The latter site is situated about 20 km from the coast and was also dominated also by massive *Porites* spp. The frequency of *A. tenue* overgrowth (section-

3.ii) was surveyed at seven reefs across the continental shelf in the central section of the Great Barrier Reef (GBR), Australia (Fig. 2.1). Surveyed reefs range from those very close to the mainland, and strongly influenced by terrestrial runoff (Goold and Pandora, approximately 12 km offshore), through inshore (Orpheus and Great Palm) and mid-shelf reefs (Rib and Trunk, approximately 60 km from the coast) to the outer-shelf (Myrmidon, approximately 110 km from the coast), where terrestrial influence is minimal (for more detail descriptions of the study reefs, see Done 1982; Russ and McCook 1999; McCook 2001)

2.2.2. Methods

2.2.2.1. *A. tenue* colonisation of live coral tissue: small –scale patterns

Description of *A. tenue* colonization patterns involved monitoring changes in occupation patterns of healthy, damaged and dead coral tissue, *A. tenue* overgrowth, and general, mixed species algal turfs (Fig. 2.2A). *A. tenue* overgrowth of massive *Porites spp.* usually occurred at the lower edge of the live coral tissue, forming distinct bands or zones. Descriptions are based on photographic monitoring of fixed plots and qualitative observations of wider areas. Algal turfs were sampled within the distinctive "zones"(as shown in Fig. 2.2A) for microscopic identification.

2.2.2.2. Effects of *A. tenue* and mixed algal turfs on corals: Experimental test

The second approach involved two elements 1) an experimental test to determine the extent to which *A. tenue* actually caused coral tissue damage or death, rather than simply overgrowing coral tissue damaged by some other unknown cause, and 2) comparison of the effects of overgrowth by *A. tenue* and general mixed-species algal turfs. The experimental design compared coral mortality in three treatments: i. plots in which *A. tenue* was naturally present; ii. plots in which the alga had been

Fig. 2.1. Map of the central GBR showing study sites from the very inshore (Goold Island), to the mid-shelf and outer-shelf reefs (Rib, Trunk, and Myrmidon). In comparison to the mid- and outer-shelf reefs, the inshore reefs are influenced by relatively high inputs of terrestrial sediments and nutrients. Goold Island in particular is strongly influenced by sedimentation and flood plumes from the Herbert River (indicated by darker shading).

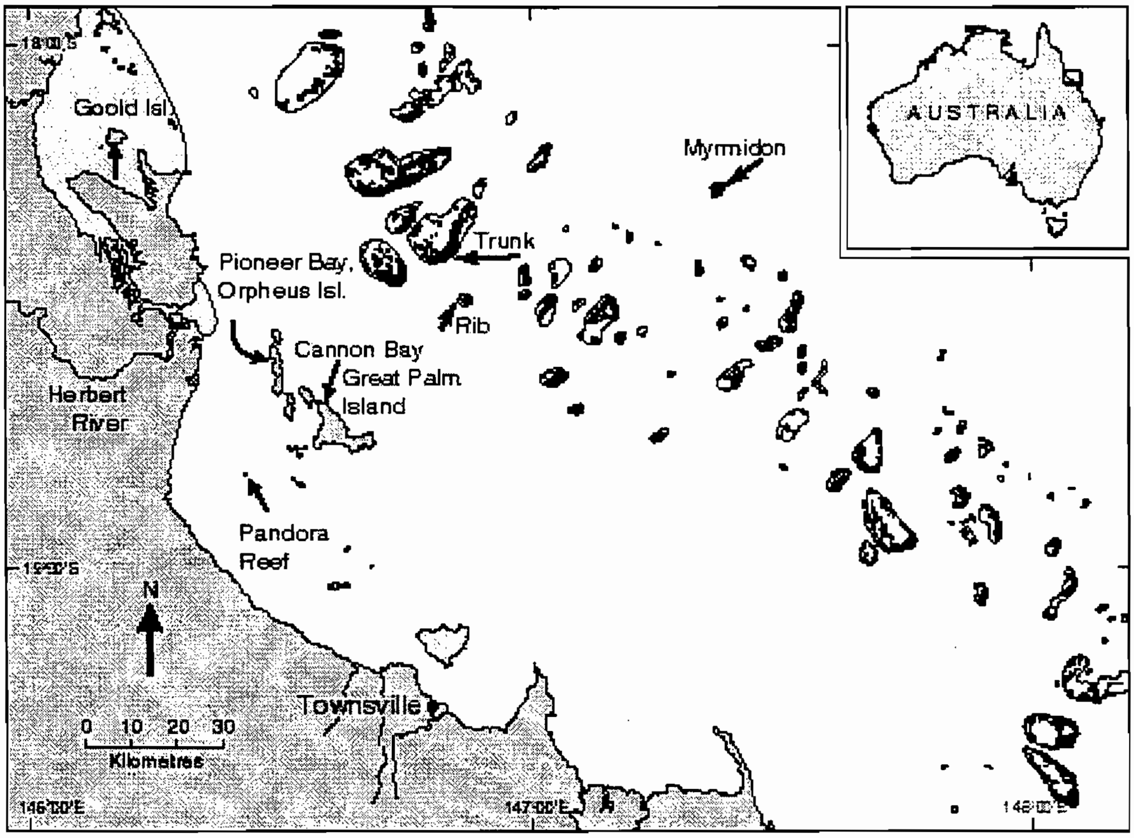
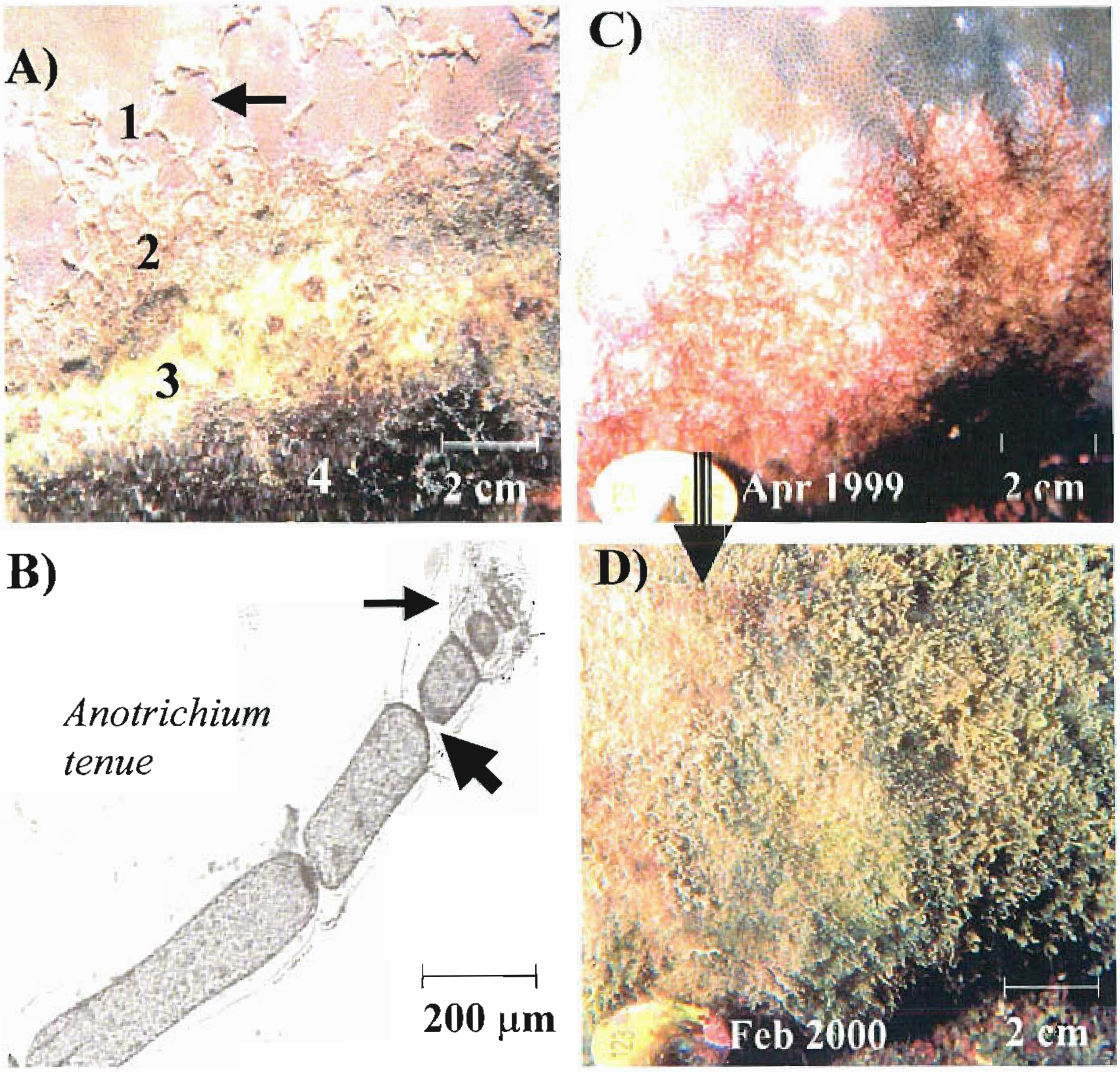


Fig.2.2. Detail of the overgrowth by the filamentous red alga, *A. tenue*, on a massive *Porites* coral. A) Algal overgrowth forms distinctive 'zones': (1) healthy coral tissue; (2) live coral colonized by *A. tenue*; (3) recently dead coral (bleached); (4) mixed algal turfs. Observations of the time course, and experimental work, showed that the process involved active encroachment of *A. tenue* onto live coral tissue, causing coral death. Coral tissue initially overgrown by *A. tenue* died and was subsequently colonised by blue green algae, and then by mixed algal turfs. Arrow shows single algal filaments trapping substantial quantities of sediment, apparently enhancing damage to underlying coral tissue. B) Photomicrograph showing the distinctive characteristics of an apical branch of *A. tenue* with transverse segmentation jointed with pit-connections (lower, thicker arrow) and trichoblasts around the apical cells (upper, thinner arrow). *A. tenue* is usually pale pink or brown in colour, the thallus is sparsely branched, most of the axes may be loosely prostrate (with erect axes of ~ 0.5 – 1 cm high) and attached by rhizoids into corallites. C) Photograph taken from an *A. tenue* treatment plot at the initial sampling (April 99) showing the alga growing on live coral of massive *Porites* causing pale and bleached coral tissue. The alga was encroaching toward healthy coral tissue. D) Photograph taken from the same plot (as C) at the final sampling (February 00) showing that all coral tissue in the plot had been overgrown by mixed algal turfs.



experimentally removed; and iii. plots in which mixed algal turfs were naturally present and *A. tenue* was not. Thus any difference in coral mortality between the first two treatments can be assumed due to *A. tenue* overgrowth, and the third treatment provides a comparison with the more widespread, general mixed species filamentous algal turfs, indicating the extent to which any effect is specific to *A. tenue.*

Each treatment included 10 replicate, small (10 x 10 cm^2) plots, located on massive *Porites* colonies, chosen to include approximately 50 % healthy coral tissue, and marked with nails and tags. There were 20 plots selected to include *A. tenue* (e.g. Fig. 2.2C), from which 10 were allocated randomly to the *A. tenue* removal treatment and the rest left intact as controls (*A. tenue* present). Ten plots also were placed on the border between healthy coral tissue and mixed turf algae overgrowing dead coral skeleton. Plots were generally on the lower side of the coral. *A. tenue* removal treatment involved carefully removing the alga from the plots, by hand or with a fine-pointed hobby knife, to minimize damage to underlying coral tissue. *A. tenue* did not generally recolonize the coral tissue following initial removal, so that subsequent algal removal was not necessary.

Plots were monitored photographically and mapped by hand, over a period of 10 months from April 1999 to February 2000. As *A. tenue* overgrowth generally formed four distinct zones (Fig. 2.2A), I estimated the area of (1) healthy coral tissue; (2) *A. tenue* growing on live coral tissue; (3) recently dead coral skeleton; and (4) mixed algal turfs. Areas were estimated from slides projected onto a 100 cm^2 grid representing the 10 x 10 cm plots, with reference to the field-drawn maps where necessary. Data analysis was based on the change in percent cover of dead coral within each plot, relative to cover at the initial date. Dead coral included recently dead coral skeleton and established mixed algal turfs (zones 3 and 4 in Fig. 2.2A). Data analyses used repeated measures analysis; as the interaction between treatment and time was significant, separate analyses were performed for each treatment, followed by post hoc Bonferroni tests (Underwood 1998). Data were tested for homogeneity of variance (Cochran's test), independence and normality of residuals (graphically).

2.2.2.3. Distribution and species specificity: Larger-scale patterns

To place the detailed and experimental work in a broader context, I examined three aspects of the *A. tenue* overgrowth: the time course of overgrowth, the occurrence and frequency of overgrowth across the continental shelf, and the specificity of the processes to massive *Porites*. The time course of overgrowth and extent of coral mortality was compared over ten months at two reefs (Cannon Bay, Palm Island and Pioneer Bay, Orpheus Island) separated by about 15 km. Ten plots with *A. tenue* present were established at Pioneer Bay, for comparison to the similar plots established at Cannon Bay. A t-test was used to compare the percent coral mortality between the two sites after 10 months.

Frequency of *A. tenue* overgrowth of live coral tissue was surveyed on seven reefs across the continental shelf in the central section of the GBR (Fig. 2.1). Surveys involved 3 to 6 dives of approximately one hour around reef crests and slopes at all sites, recording frequency of occurrences, and coral taxa overgrown. Although the phenomenon has a quite distinctive appearance and is distinguishable easily in the field (e.g. Fig. 2.2A & 2.2C), I collected samples of the alga for microscopic confirmation of the species identification.

2.3. Results

2.3.1.1. *A. tenue* colonisation of live coral tissue: small –scale patterns

Observations and photo-monitoring showed that most live coral tissue overgrown by *A. tenue* eventually died. The time course of colonization followed a fairly uniform pattern. *A. tenue* colonized live coral tissue, generally at the boundary with dead coral skeleton and mixed algal turfs (Fig. 2.2A: zone 2). The colonized coral tissue bleached and then died. *A. tenue* filaments disappeared from the dead coral tissue, apparently colonizing adjacent, live coral tissue (Fig. 2.2A: zone 3). The dead coral tissue was colonized subsequently by blue-green algae and one to two months later by mixed-species, filamentous algal turfs (Fig. 2.2A: zone 4). Microscopic examination of algal specimens indicated that the recently dead area (zone 3) generally was dominated by thin blue-green algae, including *Schizothrix*, *Calothrix,* Oscillatoriales and Coccogonales. Composition of the mixed algal turfs became similar to those on the mixed algal turf treatment plots, and generally were dominated by species of *Polysiphonia, Cladophora, Centroceras, Sphacelaria, Hincksia, Ostreobium, Herposiphonia*, with very little, if any, *A. tenue*.

The coral tissue overgrown by *A. tenue* was generally bright pink in colour, apparently a symptom of stress caused by the presence of the alga. I often observed substantial amounts of sediments and mucus adhering to individual filaments of *A. tenue* (Fig. 2.2A: arrow). Removing this sediment sometimes revealed pale, bleached or dead coral tissue underneath. It appears that this trapped material may increase or accelerate the extent of coral tissue damage.

2.3.1.2. Effects of *A. tenue* and mixed algal turfs on corals: Experimental test

Coral tissue mortality was markedly and significantly higher in the plots with *A. tenue* present than either plots in which *A. tenue* had been experimentally removed, or plots with general, mixed species algal turfs present (Fig. 2.3). Repeated measures analysis indicated a significant interaction between time and treatment (Table 2.1). Separate analyses within treatments revealed that coral mortality significantly increased through time only when *A. tenue* was present, whereas mortality in the other two treatments (*A. tenue* removal and mixed algal turfs) did not change significantly during the same time period.

Analysis of between-treatment differences at the final sample date (Fig. 2.3) indicates that coral mortality in the plots with *A. tenue* present was significantly higher ($P = 0.008$) than in plots with the *A. tenue* experimentally removed, demonstrating that the *A. tenue* was in fact the direct cause of much of the coral tissue mortality. Coral tissue mortality in plots with mixed algal turfs present was negligible, and significantly less ($P < 0.001$) than in those with *A. tenue* present (Fig. 2.3). Thus, relative to the general, mixed-species algal turfs, *A. tenue* was exceptionally effective at overgrowing the corals. Indeed, the mixed algal turfs were relatively harmless to the corals. The slight increase in coral mortality in the *A. tenue* removal treatment at the end of the experiment was apparently caused by new *A. tenue* colonization in two plots.

2.3.1.3. Distribution and species specificity: Larger-scale patterns:

The overall time course of *A. tenue* overgrowth was very similar for Cannon Bay and Pioneer Bay (Fig. 2.4). Coral tissue mortality at the end of the study was also similar for the two sites ($P = 0.7$). *A. tenue* showed a general, gradual decline at both sites over the ten month period of the study.

Fig. 2.3. Graph showing the time course of coral tissue mortality for each treatment at each observation at Cannon Bay, Great Palm Island. Data are changes in percent cover of dead coral tissue, relative to the initial date (means ± S.E. of 10 replicates). Coral tissue mortality was significantly higher in plots with *A. tenue* present than in the other treatments.

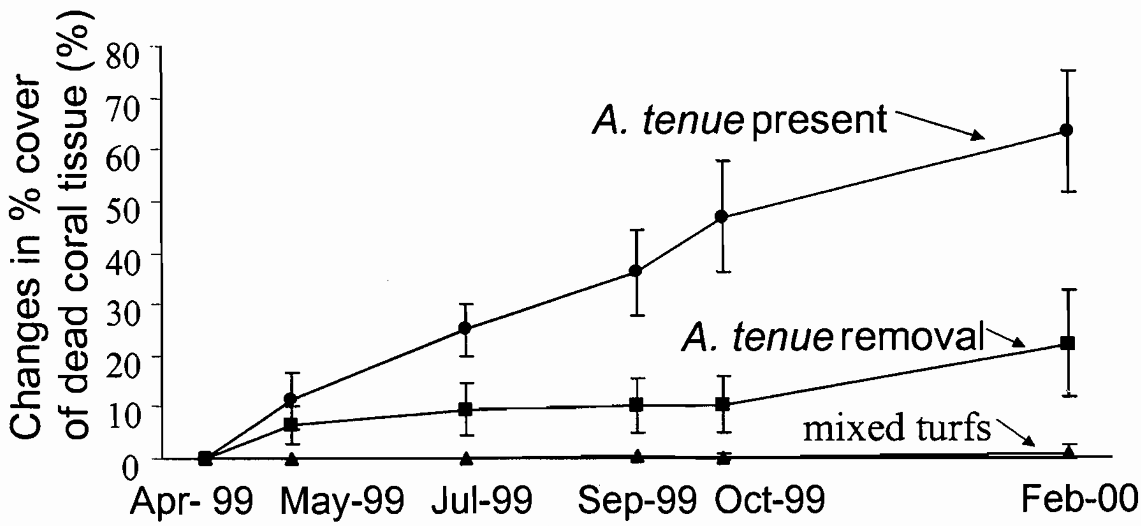
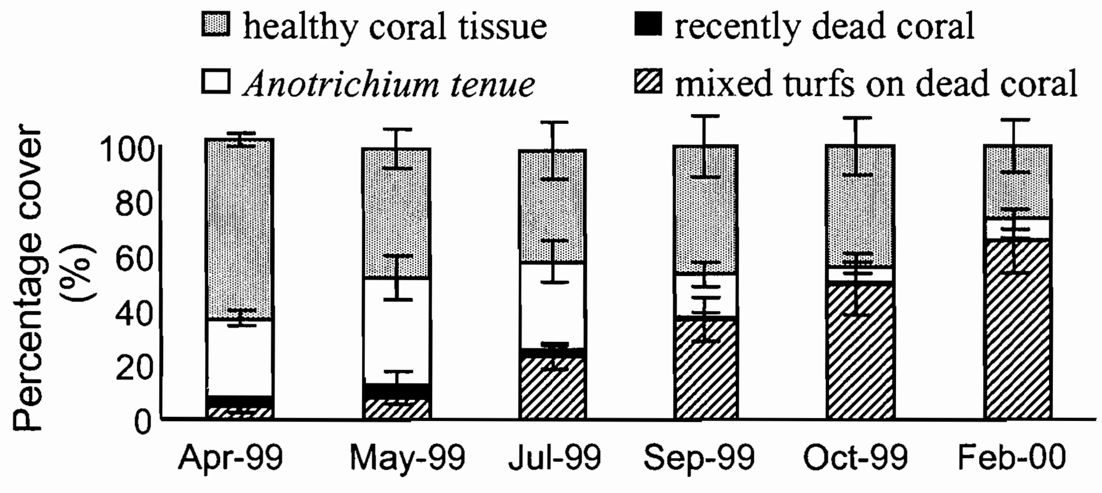


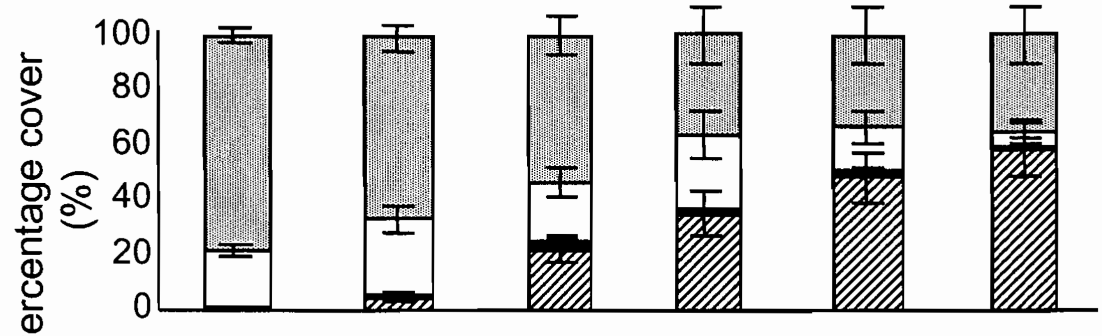
Table 2.1. Repeated measure analyses on the effect of treatment and time on the percentage of coral tissue mortality, for the experimental comparison of the contrasting invasiveness of *A. tenue* compared to mixed algal turfs on massive *Porites*.

Source	d.f.	Mean-Square	F-ratio	P
Treatment	2	19621.7	166.5	< 0.001
Times	4	2237.2	16.8	< 0.001
Treatment * Times	8	1060.8	18.9	< 0.001
Plot(Treatment)	27	1978.0	9.0	< 0.001
Time * Plot(Treatment)	108	117.8		

Fig. 2.4. Graphs showing the percent cover for each observation and categories (shown on Fig. 2A); healthy coral tissue, *A. tenue* overgrowth, recently dead coral, and already mixed algal turfs, at Cannon Bay and Pioneer Bay. Data are means of the percent cover for each category (± S.E.) of 10 replicates.



A. Canon Bay, Gt. Palm Island



B. Pioneer Bay, Orpheus Island

Surveys of reef crests and slopes indicated that 60% of the massive *Porites* colonies at Cannon Bay, and 40% of those at Pioneer Bay had patches of *A. tenue* overgrowth, with patches varying between 50-200 cm in length and up to 5 cm in width. In contrast, the phenomenon was relatively scarce at Pandora Reef (~ 5 % of colonies surveyed) and was not found at the very inshore reef (Goold) nor at the mid-shelf (Rib and Trunk) and outer-shelf reefs (Myrmidon). The majority of corals observed with *A. tenue* overgrowing live tissue were massive *Porites (*predominantly *Porites lobata, lutea* and *australiensis*), although it was also observed, much less frequently, overgrowing live, foliose *Turbinaria spp.,* encrusting to foliose *Montipora spp.* and branching *Porites annae*. No other coral species were observed with *A. tenue* overgrowth, including the branching *Porites cylindrica*, a widespread and abundant species in this area. Overgrowth appeared generally to develop at the border between the live coral and mixed algal turfs, although approximately 5 % of patches occurred completely within live coral tissue, suggesting the alga was able to attach to live tissue, either by settlement or by vegetative fragmentation. Massive *Porites* colonies of up to 50 cm diameter were observed to have been completely killed, apparently by *A. tenue* overgrowth.

2.4. Discussion

The combined small-scale observations and experimental results provide strong evidence that overgrowth by *A. tenue* is the direct cause of coral tissue death, rather than simply a symptom or consequence of previous tissue damage or coral stress. Given the scarcity of experimental evidence for coral-algal competition (Chapter 1), this study is therefore significant simply as an example of competitive overgrowth of live coral by a benthic alga.

However, this overgrowth also stands in strong contrast to the results for the general, mixed-species algal turfs, which were not able to overgrow the live coral tissue in any of the plots. Thus these turfs were very poor competitors with the corals, as previously found in this area by McCook (2001). The interpretation, that the competitive ability of *A. tenue* is exceptional among the filamentous turfing algae, is strengthened by the observations, first that the general turfs are a mixture of a large number of species, none of which overgrew live coral tissue, and second that the *A. tenue* patches have much lower biomass (per unit area) than the mixed turfs, yet are still much more effective competitors. Mixed turf colonisation generally followed coral tissue death caused by the *A. tenue*, so that *A. tenue* appears to act as a colonising species, in effect creating new substrate but subsequently being replaced by more typical turfs.

Thus it seems that the ability of *A. tenue* to overgrow and kill live coral tissue is exceptional, and that in general on these reefs, filamentous algal turfs are not able to overgrow live coral tissue, but are relatively poor competitors, having little effect on corals, at least on relatively large, mature corals (McCook et al. 2001). Only three previous published studies have reported lethal effects of algal turfs on corals. Potts (1977) suggested that mixed turf algae caused coral mortality as a result of the metabolic costs to the corals of removing sediments trapped by the turf algal mats. Littler and Littler (1997a) found that a non-filamentous, but turf forming macroalga *Dasyopsis spinuligera* overgrew corals in the Caribbean. They suggested that the likely mechanism involved was allelochemical or a secondary-substance produced by the alga causing coral death. Genin et al (1995) observed that a non-turfing filamentous, macroalga *Enteromorpha*, which bloomed in response to deep vertical mixing in the Gulf of Eilat, apparently caused extensive coral death. Notwithstanding the exceptional environmental conditions that might also have contributed to coral stress or death, the authors suggested that coral mortality was mainly due to overgrowth by thick algal mats which effectively shaded the corals and blocked water flow, resulting in anaerobic conditions with high levels of H_2S. In contrast, most studies have reported minor effects of algal turfs on corals or even suggest that corals were competitively superior to the algal turfs (e.g. Fishelson 1973; Bak and Steward-van Es 1980; Meesters et al. 1994; Genin et al 1995; van Woesik 1998; McCook 2001).

It is useful to consider the mechanisms which might allow *A. tenue* to exert such exceptional effects on the corals. Two factors seem relevant, the ability to colonize live coral tissue, despite defensive mechanisms by the corals (such as stinging, mucus secretion, etc. Lang and Chornesky 1990), and the ability to kill underlying coral tissue. Although I do not have direct evidence, so that other explainations remain possible, it is likely that both these abilities are due to allelochemical substances released by the alga, as the patterns of tissue death are not consistent with any of the other competitive mechanisms possible for algae on corals (Table 7.1). Although numerous other filamentous algae from the same family as *A. tenue* (the Ceramiaceae), with similar growth habits (i.e. creeping and branching, erect axes, with rhizoids; Price and Scott 1992) were abundant among the mixed turf algae at the study sites, only *A. tenue* was observed overgrowing massive *Porites* corals. My observations also suggest that the extent of coral tissue damage was increased significantly by the tendency of individual *A. tenue* filaments to trap coral mucus and/or sediments and detritus (e.g. Fig 2.2A: arrow). By interfering with the cleaning mechanisms of the coral, the alga may be causing tissue stress to areas much larger than the otherwise relatively small algal filaments.

It is intriguing that whatever the mechanisms involved, they appear effective for few coral taxa, since *A. tenue* overgrowth was relatively specific. This specificity is not obviously related to either growth form or taxonomic affinities. Although most common on massive *Porites*, and recorded on the branching *P. annae*, I never recorded *A. tenue* on the branching *Porites cylindrica*, which is widespread, and particularly abundant at Cannon Bay and Pioneer Bay. In contrast, I frequently observed another filamentous Ceramiaceae, *Corallophila huysmansii*, overgrowing *P. cylindrica* on these reefs, but did not find it on massive *Porites* (see Chapter 3). *P. cylindrica* has similar sized corallites (~1.5mm) to the massive *Porites* species studied here. Similarly, my observations of *A. tenue* on foliose, encrusting and branching corals are not consistent with a specificity to a particular life-form.observations of *A. tenue* on foliose, encrusting and branching corals are not consistent with a specificity to a particular life-form. It is also likely that the effectiveness of *A.tenue* as a competitor would vary not only with the coral taxa, but also with other factors, such as microhabitat, light regime, etc.

The combined results of the broader surveys and the comparison of overgrowth between sites suggest that the phenomenon is not widespread, but that the effects are not site-specific: where *A. tenue* overgrowth occurs it is likely to have similar effects to those documented here. Although *A. tenue* was more abundant on live corals at Cannon Bay than at Pioneer Bay, the pattern of coral overgrowth was similar at both sites. A survey of algal turf settlement on inshore reefs in this area indicated that *A. tenue* is not common in algal turfs, and was more common on Great Palm Island (unpubl. data) than on other islands in the Palm group, or on Goold Island. The species has also been reported from Malaysia (Masuda et al. 1999) and South Africa (Norris and Aken 1985), and so is presumably widespread. Thus, although the results do not suggest that this alga poses a significant threat, as a pathogen, to coral populations at larger spatial scales, the possibility can not be entirely dismissed. In particular, *A. tenue* overgrowth was not recorded on either the reef most influenced by terrestrial runoff, nor the reefs most removed from such influences, suggesting that the phenomenon is unlikely to be a symptom or consequence of anthropogenic changes in terrestrial runoff.

In summary, the results of this study demonstrate a marked contrast in competitive effects on corals between a single species of turfing, filamentous red alga, *A. tenue*, and a broad range of species with similar growth forms and even taxonomic affinities. The species present in the general algal turfs at these sites were not able to colonise or significantly affect live tissue of massive *Porites* colonies. In contrast, *A. tenue* was able to colonize live coral tissue, causing tissue death and serving as a colonizing species for general algal turfs. It appears that this competitive ability may be due to allelochemical or similar properties, but is only effective against a relatively few coral taxa. The results illustrate the extent of variability in the processes and outcomes of coral-algal interactions, even within an algal functional group, algal family, coral life-forms and coral genera.

CHAPTER 3. Variable effects on corals of competitive interactions with three species of macroalgae with different properties and growth forms.

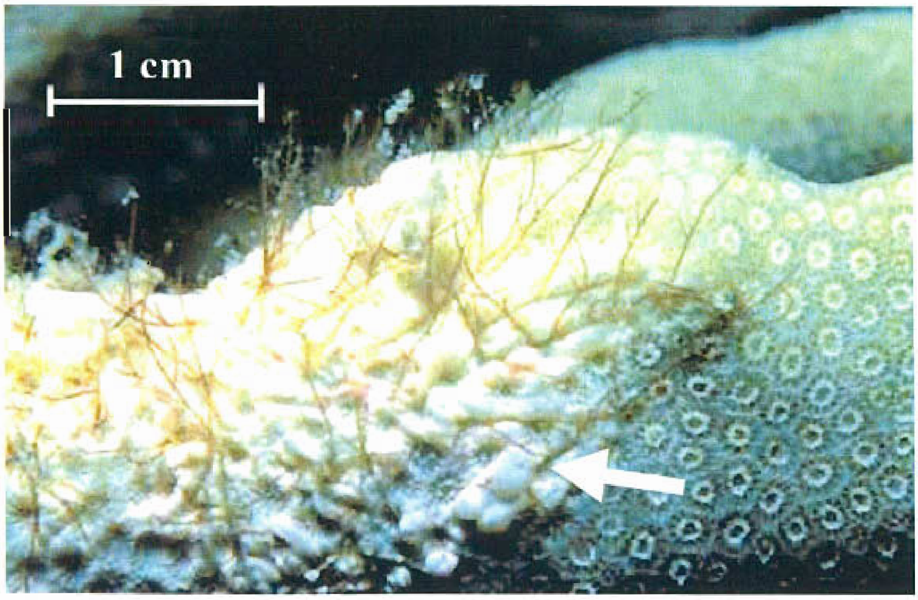
3.1. Introduction

As outlined in Chapter 1, different types of algae may have variable effects on corals, and much of this variation may be related to properties of the algae, including physical (e.g. size, structure, growth form), biological (e.g. sexual or vegetative mechanisms) and even chemical characteristics (allelopathic or secondary metabolites). Many of these properties may be effectively summarized in terms of the algal functional groups (Littler 1980; Littler and Littler 1984; Steneck and Dethier 1994; discussion in McCook et al. 2001).

This chapter contrasts the effects of three different types of macroalgae on corals. The algae examined include a small turfing, filamentous red alga, *Corallophila huysmansii*, the larger, filamentous but non-turfing, green algae, *Chlorodesmis* spp., and a corticated red alga, *Hypnea pannosa*. Each of these algae were commonly observed living on or in direct contact with live corals and therefore potentially have negative impacts on the coral tissue.

These specific alga-coral interaction pairs were chosen because they appeared to represent a range of effects and processes. The previous chapter suggests that most filamentous, turfing algal species are unable to overgrow live coral tissue, with the distinct exception of *A. tenue* and *C. huysmansii* apparently overgrows live tissue of the branching coral *P. cylindrica* (Fig. 3.1), with considerable associated damage to the coral tissue. As with *A. tenue*, I decided to investigate the extent to which the alga was able to invade live coral and the extent to which the alga was causing the coral tissue damage, relative to general algal turfs.

Figure 3.1. Photograph showing tissue death of the branching coral, *Porites cylindrica*, following overgrowth by filaments of the red alga, *Corallophila huysmansii*. The severity of the tissue response to such sparse and fine filaments suggest that the mechanism may involve allelochemical effects; arrow shows swollen coral tissue around algal filaments.



Chlorodesmis spp, commonly known as 'turtle-weed', is a bright green, upright (i.e non-turfing), filamentous alga which is widespread and conspicuous on Indo-Pacific reefs, growing as thick tufts or patches, often surrounded by live coral tissue (Fig. 3.2). Although common, the alga is rarely if ever abundant or extensive, with patches rarely growing larger than 20-30 cm in diameter. Despite being highly conspicuous, *Chlorodesmis* patches appear able to persist even in areas with relatively high levels of herbivory, apparently because the filaments contain high levels of the secondary metabolite (Chlorodesmium) with herbivore deterrent properties (Ducker 1976; Paul et al. 1990; Craig et al. 1997). Given this herbivore resistance, it was of interest to explore why the alga does not overgrow larger areas of coral, and achieve more extensive patches.

Hypnea pannosa is one of a number of fleshy algae commonly observed growing within the branches of *Porites cylindrica* colonies (Fig. 3.3), but with distinctly different structure and growth form to those of *C. huysmansii* (above) and of *Lobophora variegata* (Chapters 4 and 5), both of which grow on the same coral species. Although a corticated alga (Littler 1980; Steneck and Dethier 1994), *H. pannosa* grows as a reticulate mass, and is relatively brittle, porous and translucent, in contrast to the delicate turfing habit of the filamentous *C. huysmansii* and the robust, creeping and adherent foliose morphology of the brown foliose alga, *L. variegata* (e.g. in Chapters 4 and 5). The species has been observed in this growth habit on branching corals over wide latitudinal and cross-shelf ranges on the GBR, and on S. E. Asian reefs (McCook unpubl. data). Indeed a number of algal taxa are commonly found growing within branching coral colonies as clumps or mats, including *H. pannosa*, *L. variegata*, *Melanamansia glomerulata* (Ceramiales, Rhodophyta) and various species of *Laurencia* (Ceramiales, Rhodophyta). The *H. pannosa*- *P. cylindrica* interaction therefore provided

Fig. 3.2. *Chlorodesmis fastigiata* growing amidst live coral, on Rib Reef, midshelf central GBR. Despite being highly conspicuous, *Chlorodesmis* tufts apparently deter herbivores by means of secondary metabolites, but nonetheless remain as small patches and do not grow into extensive beds. A) Photograph taken on the *Chlorodesmis* plot (February 1999). B) Photograph taken from the same plot (as A) 2 months later (April 1999) showing the algal seasonal dieback, but reappeared again on the same plot in the following observation (see result)

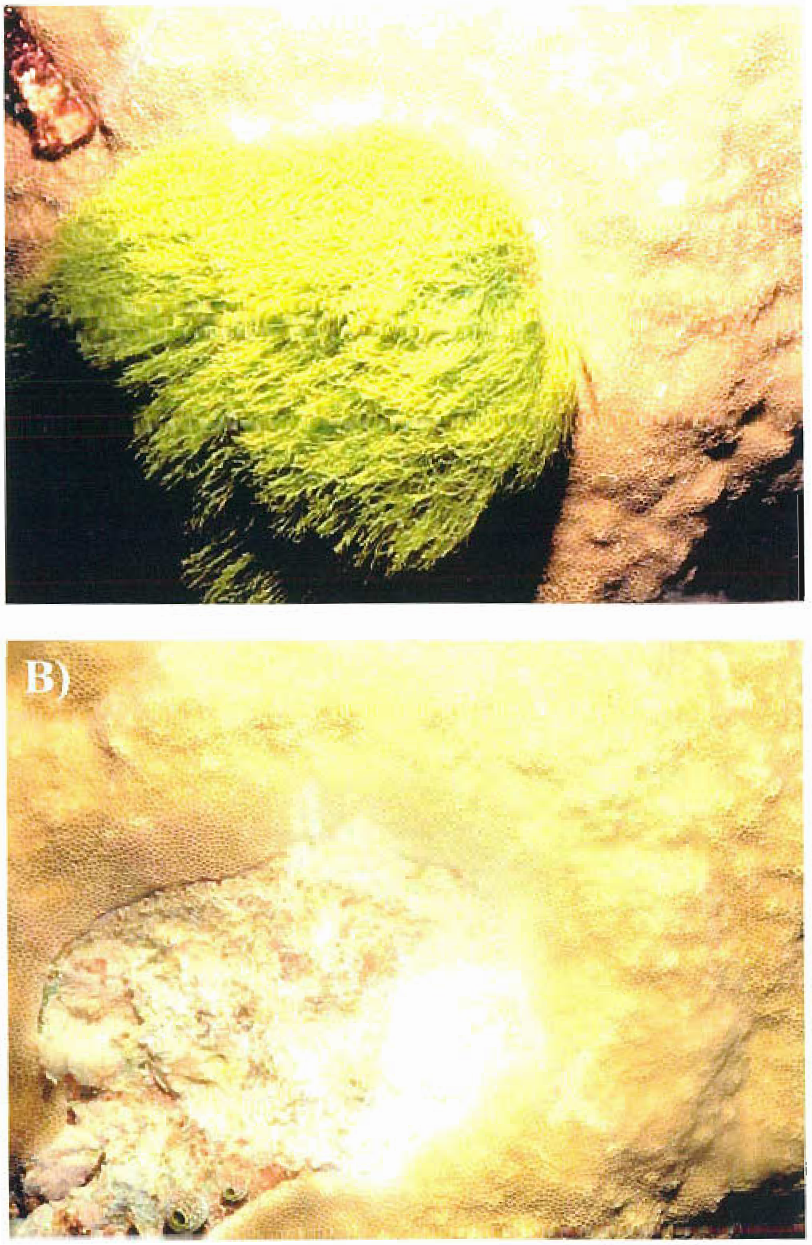
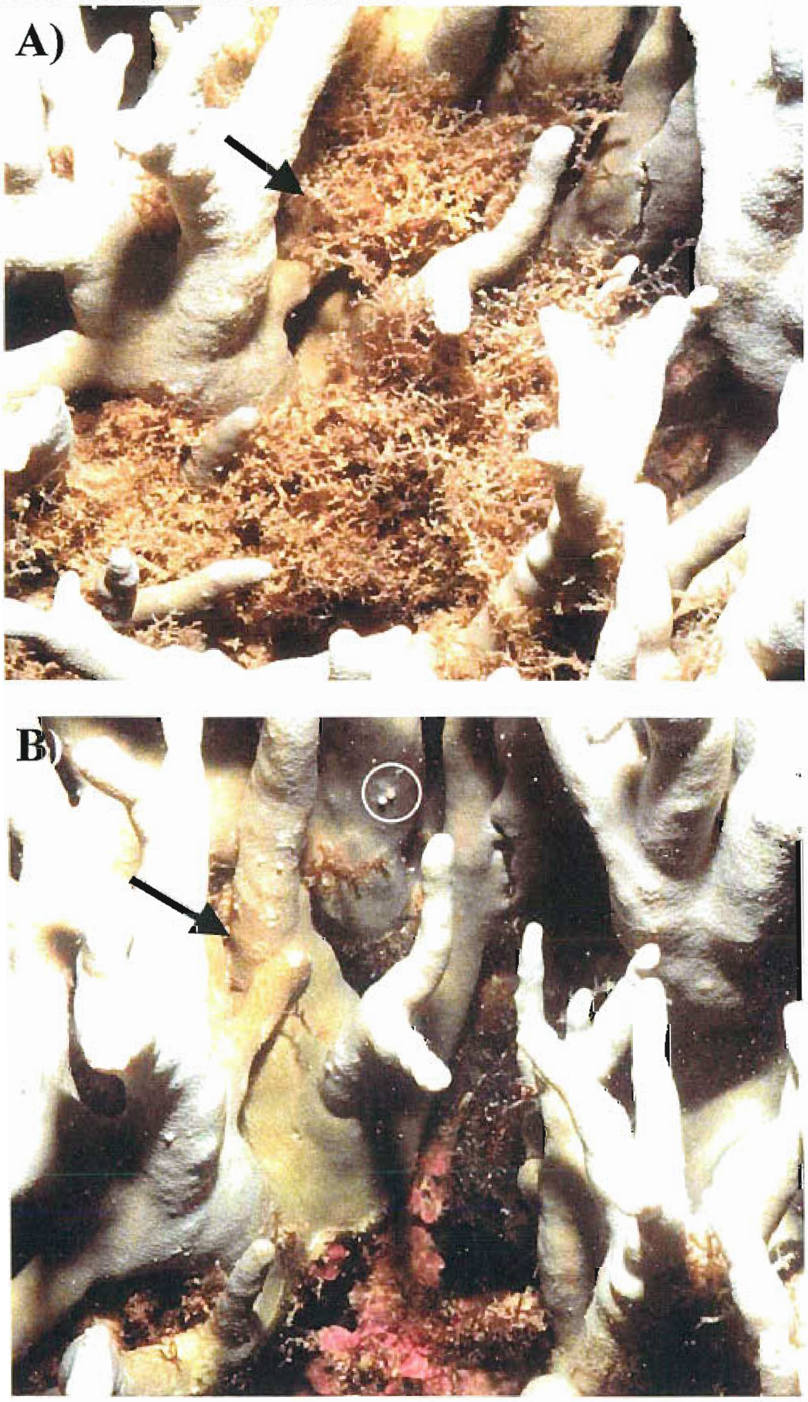


Figure 3.3. The red corticated alga, *Hypnea pannosa*, commonly observed growing within the branches of *P. cylindrica.* The structure of the coral branches probably provides a refuge for this alga from herbivory (Chapter 4). However, the coral tissue seemed relatively unaffected by the presence of this alga. A) Photograph showing *H. pannosa* grew within the coral branches. B) Photograph taken a few months later at the same place after manually removing the alga. Arrows show examples of coral tissue in relatively healthy condition, although darker in colour (B). Minor tissue lesions (e.g. circle in B) were also sometimes observed.



both useful contrasts to other interactions in this thesis, and an example of an algal-coral interaction with wide geographic relevance.

3.2. Methods

3.2.1. Study species and sites

The first study, on the interaction between *C. huysmansii* and *P. cylindrica*, was conducted on the reef slope (7-8 m depth) at Cannon Bay (18°41.0' S 146°35.2'E), Great Palm Island, Great Barrier Reef (GBR), Australia, close to the site used in Chapter 2. The site was dominated by colonies of *P. cylindrica* (~ 65% cover, based on four 20 m line-intercept transects), of which many have fleshy macroalgae, especially *L. variegata*, growing as mats around the bases of branches. During a survey of the site, a number of colonies were found to have the filamentous turfing species *C. huysmansii* growing on live tissue of *P. cylindrica*, usually as relatively small patches, but occasionally completely overwhelming and killing patches of *P. cylindrica* up to 1 m.

The effect of *H. pannosa*, on the same coral species, *P. cylindrica*, was investigated on the reef crest (3-5 m) at Little Pioneer Bay (18°36.0' S 146°29.3'E), Orpheus Island, GBR. *P. cylindrica* was also abundant at this site, but, in contrast to Cannon Bay, the dominant macroalga growing within the coral branches at this site was *H. pannosa*.

The interaction between *Chlorodesmis* spp and corals was monitored at a reef flat site (1-2 m; 18°28.5' S 146°52.7'E) and a reef slope site (8-10 m; 18°28.4' S 146°52.8'E) on Rib Reef, in the central GBR (Fig. 2.1). The algae occupied small dead patches amidst live tissue of massive *Porites spp.* (predominantly *P. lobata*) and *Favites spp.* and encrusting *Montipora spp.*, and *Chlorodesmis* filaments were in direct contact with surrounding coral tissue. Although the *Chlorodesmis* patches studied were

Chlorodesmis fastigiata, several of the reef slope patches were *Chlorodesmis major.* As their effects on corals were indistinguishable, both species are treated collectively (as *Chlorodesmis spp.).* Although *Chlorodesmis* does have basal rhizomes, they do not form the extensive horizontal filaments seen in typical turfing (prostrate and creeping) morphologies (e.g. *A. tenue, C. huysmansii*, see Price and Scott 1992 for further explanation).

3.2.2. Experiment 1: Corallophila huysmansii

In order to examine the ability of *C. huysmansii* to colonize and kill live coral tissue, I compared the effects of this algal species on coral tissue mortality with the effect of other mixed turfing and crustose coralline algae, attempting to "infect", or induce colonization of, healthy *P. cylindrica* branches with both types of algae. Nine *P. cylindrica* branches (approximately 2 cm thick and 6 cm long) with *C. huysmansii* present were carefully cut off using a small hand-saw, and attached to nine healthy coral branches, using cable ties (*C. huysmansii* treatment). Similarly, nine other dead coral branches, overgrown by mixed algal turfs and coralline algae, were attached onto healthy coral branches (mixed algal treatment), adjacent to (~30 cm apart) one of the branches infected by *C. huysmansii*. "Infected" branches were approximately two meters apart. The effect of the algae on the coral was estimated as the area (in mm^2) of coral tissue mortality caused by the algal infection, measured using vernier calipers every 5-8 weeks for 6-7 months. The experiment was run at two different times of year, to assess temporal or seasonal variability in the interaction. The first period was from August 1998 to March 1999 and the second period was from May to November 1999.

Algal overgrowth in these experiments was generally relatively short-lived (3-4 months). To investigate whether this reflects intrinsic seasonality or senescence of the alga, a number of *C. huysmansii*-overgrown branches were collected and transplanted to determine their longevity in aquaria. Branches were anchored by gluing to clay tiles, transplanted and maintained under running seawater at the James Cook University aquarium and algal condition regularly observed for 6 months (concurrently with the second field experiment: May to November 1999).

3.2.3. *Experiment 2: Hypnea pannosa*

The effects of *H. pannosa*, on *P. cylindrica*, was assessed by comparing coral growth and mortality in quadrats in which the alga was naturally present or experimentally removed. Sixteen permanent quadrats (50 x 50 cm) were marked within *P. cylindrica* colonies that have extensive mats of *H. pannosa* alga growing within the coral branches. The alga was removed from eight randomly selected quadrats (*H. pannosa* removal treatment) and was left intact on the other eight quadrats as control (*H. pannosa* present).

To compare coral growth and tissue mortality between treatments, 4 individual branches were chosen randomly within each quadrat and marked with plastic labels attached by cable ties onto the basal part of the branch. Coral tissue mortality was estimated for the tagged coral branches as the change in area (mm square) of dead coral tissue. Coral growth was estimated as linear skeletal extension, measured from the marker (cable tie) to the tip of each coral branch. This experiment ran for 1.5 years from April 1998 to October 1999.

3.2.4. *Experiment 3: Chlorodesmis* spp.

The potential effects of the filamentous green algae, *Chlorodesmis spp.* on surrounding corals were investigated by monitoring *Chlorodesmis spp.* patches, to identify any apparent stresses or impacts. 15 small permanent quadrats (14.5 x 21.5 cm) containing patches of *Chlorodesmis spp.* surrounded live corals were marked on each of the reef flat and reef slope at Rib Reef, and monitored using a Nikonos V camera with 28mm lens and close-up kit. Quadrats were photographed, algal filament heights measured manually, and qualitative observations of coral condition noted every two to three months for 18 months, from September 1998 to March 2000.

3.2.5. Data analyses

Data analyses for experiments 1 and 2 involved simple one way ANOVAs. All data were tested for homogeneity of variance (Cochran's test), outliers, and independence and normality of residuals. Based on these tests, data transformation was unnecessary for experiment 1. Data for experiment 2 were log-transformed, because temporal changes differed by orders of magnitude between treatments, resulting in heteroscedasticity in the untransformed data. Qualitative observations of *Chlorodesmis spp.* effects only are presented, since no significant coral tissue mortality was recorded in that study.

3.3. Results

3.3.1. Experiment 1 Corallophila huysmansii

C. huysmansii was able to colonize and overgrow live *P. cylindrica* tissue, and overgrowth by even relatively sparse filaments of *C. huysmansii* appeared to cause considerable damage to underlying and adjacent coral tissue (e.g. Fig. 3.1). Coral tissue became bleached, swollen, and subsequently died even up to several mm from algal filaments. The experimental results provide strong evidence that overgrowth by *C. huysmansii* was the direct cause of coral tissue death. Coral tissue mortality was significantly higher on the *C. huysmansii* infection treatment than on the corals infected by mixed algal turfs, during both periods (Fig. 3.4 and Table 3.1). Within about one

Fig. 3.4. Graphs showing coral tissue (cm^2) mortality on *P. cylindrica* branches "infected" by *C. huysmansii* and mixed algal turfs. Data are means of total coral tissue death (cm^2 ± S.E.) of 9 replicates.

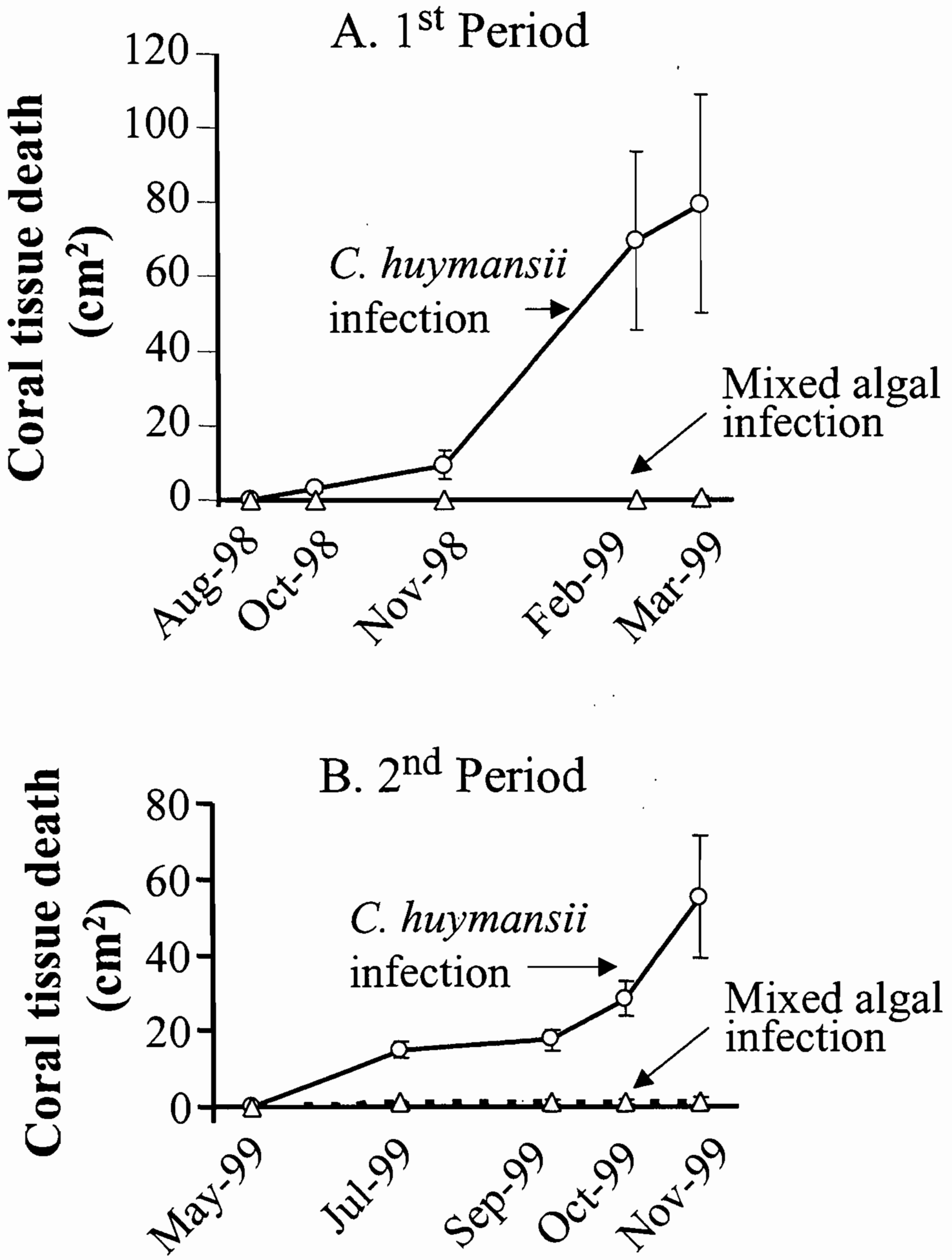


Table 3.1. Analyses of variance of the effect of different algal infections on tissue mortality of the branching coral, *P. cylindrica*. Data are transformed with ^{10}Log (n+1), and analysed independently for the first and second periods.

Source	d.f.	Mean-Square	F-ratio	P
First period (Aug-98 to Mar-99				
Treatment	1	38.0	46.2	< 0.001
Residual	16	0.8		
Second period (May to Nov-99)				
Treatment	1	24.7	22.7	< 0.001
Residual	16	1.1		

month after *C. huysmansii* branches were placed in contact with healthy coral branches, the alga had colonized and overgrown the healthy coral tissue. Although relatively little coral tissue had died within that time, the rest of the overgrown tissue was clearly severely stressed. Coral tissue mortality appeared to generally follow overgrowth, but with a delay of up to several months; dead coral tissue was occupied subsequently by mixed-species, filamentous algal turfs. Thus, although Fig. 3.4 shows an increase in coral mortality toward the end of both experimental periods, algal colonization had generally ceased by that time, and only a very few coral branches still had small amounts of *C. huysmansii* filaments growing on live coral tissue. Algal overgrowth of new, live coral tissue generally ceased within two to six months. Comparison of the two experimental periods suggest that the time course of colonization was similar at both times of year, with little seasonal difference (Fig. 3. 4 A & B). Interestingly, in contrast to the field experiments, *C. huysmansii* transplanted to aquaria continued to grow well over new coral substrate for up to 6 months, and attained upright filament heights longer than those in the field.

In contrast to the *C. huysmansii* treatment, the mixed algal turfs and crustose corallines were relatively poor competitors with the healthy *P. cylindrica*. Coral branches in the mixed algal treatment showed only minor tissue mortality during the first month, and otherwise generally remained healthy throughout the study periods. In a few cases, the coral tissue even overgrew the mixed algal communities on the experimentally attached dead coral branches.

3.3.2. Experiment 2: Hypnea pannosa

The presence of *H. pannosa* had minimal effects on both coral tissue mortality and coral growth during this experiment. Coral tissue mortality in both treatments was minimal, indicating that *H. pannosa* had not caused significant damage to underlying coral tissue. Coral tissue underneath the algal mat was generally healthy, although a little darker in colour, with only a few, minor tissue lesions (Fig. 3.3). Quantitative results are not given because tissue mortality was insufficient to quantify. Although growth (or linear skeletal extension) of *P. cylindrica* branches was very slightly higher in the absence of *H. pannosa* than in plots with the alga present, this difference was very small and not significant (Fig. 3.5 and Table 3.2).

3.3.3. Experiment 3 Chlorodesmis spp

Coral tissue in direct contact with *Chlorodesmis spp.* filaments showed minimal tissue damage even after 18 months of monitoring. Direct observations showed that longer algal filaments (5-10 cm in length), although very soft, would constantly brush adjacent coral tissue, as the filaments moved with water motion, with the frequent consequence that coral polyps in the vicinity of the filaments were retracted, and the tissue showed minor stress symptoms such as pale coloration or a pink speckled appearance.

Both photographic monitoring and filament height measurements showed that *Chlorodesmis spp.* patches undergo a dramatic cycle in standing crop, with a periodic loss and reappearance or regrowth of most macroscopic filaments. Although the periodicity of this cycle is difficult to determine from intermittent photographs/visits, and appeared to vary between patches, it appears that individual patches can undergo at least one complete cycle within 4-6 months (e.g. Fig. 3.2). Of the 15 *Chlorodesmis* patches initially marked in each zone, after 18 months, 12 were still present on the reef slope, and 6 on the reef flat.

Figure 3.5. Graph showing growth rate of the branching coral, *Porites cylindrica*, in plots with *H. pannosa* present or experimentally removed. Data are means of coral growth rate (± SE) of 32 replicates (averaged over 4 plots).

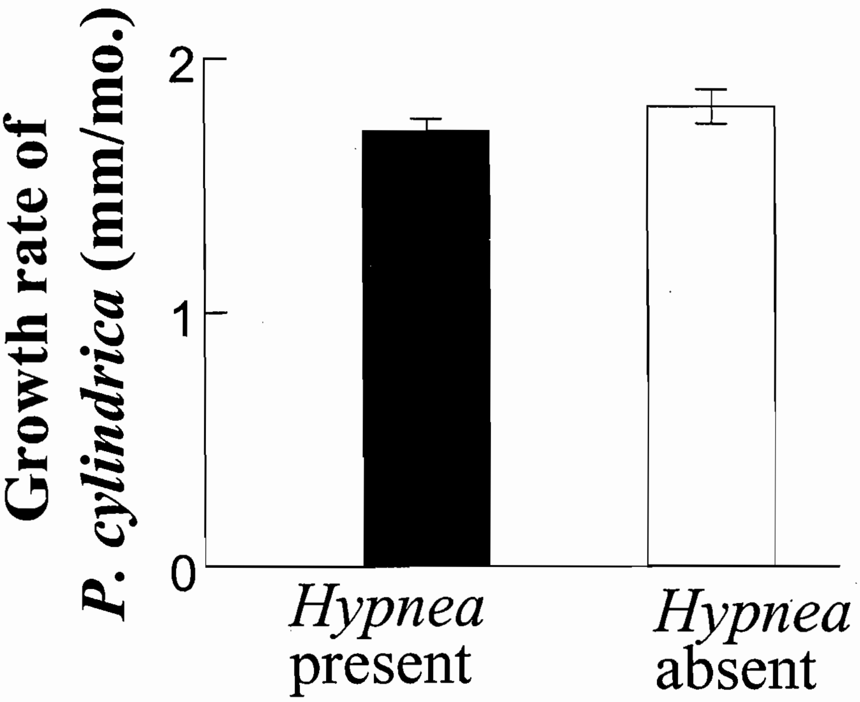


Table 3.2. Analyses of variance of the effect of *H. pannosa* on the growth rate of the branching coral, *P. cylindrica*. Homogeneity of variance test is shown as Cochran's C, the critical value of C here is 0.26; data are untransformed.

Source	d.f.	Mean-Square	F-ratio	P
Treatment	1	0.15	1.34	0.253
Plot	7	0.12	1.02	0.429
Treatment * Plot	7	0.10	0.93	0.492
Residual (n=4)	48	0.11		
Cochran's C = 0.24				

Cochran's C = 0.24

3.4. Discussion

The results of this study provide further demonstration of the considerable variation in process and outcomes of coral-algal interactions, as previously discussed (e.g. Chapter 2; McCook et al. 2001). The different algal taxa examined in this study demonstrate strongly contrasting effects on the corals, with one filamentous taxa causing severe coral tissue damage even at some distance from the filaments, and another causing negligible damage. It appears that much of this variation can be interpreted in terms of the properties of the algae, and the consequent mechanisms by which they affect the adjacent coral tissue. Thus although corticated algae are generally more robust than filamentous taxa, *H. pannosa* is a relatively fragile example of the corticated functional group (Littler 1980; Steneck and Dethier 1994), and its relatively porous, reticulate structure and translucent thallus apparently do not limit water flow (with associated gas and nutrient exchange) or light availability sufficiently to seriously inhibit coral performance. *Chlorodesmis,* although generally longer and more robust than *C. huysmansii*, does not have a turfing growth habit; and may be limited in its ability to vegetatively overgrow and colonise new substrate. Although it appears to cause polyp retraction, the effect is minor, perhaps because the softness of the filaments, and because the seasonal dieback provides adjacent coral with an opportunity to recover.

In contrast, the relatively delicate filaments of *C. huysmansii* can colonise and kill coral tissue very effectively. As for *A. tenue*, the apparent ability of *C. huysmansii* to kill coral tissue relatively distant from its fine filaments (Fig. 3.1), raises the possibility of allelochemical effects (c.f. de Nys et al. 1991 for soft coral). Although again I do not have direct evidence, it is difficult to explain the nature of the effect by any of the other mechanisms by which algae are known to inhibit corals. The turfing growth habit of *C. huysmansii* allows it to rapidly invade new substrate, but this alone can not explain the ability to colonize live coral tissue, as many of the taxa present in the mixed algal turfs have similar growth habits. Thus the factor that provides *C. huysmansii* with the ability to colonize live coral tissue is critical to the competitive effectiveness of this taxa. The interpretation of the variability in coral-algal interactions in terms of algal properties and functional groups is discussed more fully in the General Discussion, Chapter 7.

The relatively short life-span of *C. huysmansii* in the field experiments is intriguing. The greater longevity in aquaria, along with the occasional occurrence of large patches of *C. huysmansii* overgrown *P. cylindrica*, suggests that the dieback in the field is not due to intrinsic seasonality or senescence, but to other factors. It may be that the longevity of *C. huysmansii* in aquaria reflects competitive advantages conferred by the lack of herbivores, or elevated nutrient conditions, but such ideas remain strictly speculative without further evidence.

CHAPTER 4. Effects of competition and herbivory on interactions between a hard coral and a brown alga

4.1. Introduction

As outlined in the Introduction (Chapter 1), interactions between herbivory and coral-algal competition may be critical to benthic community structure of coral reef. The significance of herbivores in controlling algal abundance on coral reefs has been widely discussed (Hay 1981; Hay 1984; Lewis 1985; Lewis 1986; Hughes 1994a; McCook 1996; McCook 1997), and 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).

Although a number of studies have suggested the importance of herbivory to coral-algal competition (e.g. Sammarco 1982; Lewis 1986; Hughes 1994a), only two have manipulated both herbivory and algal abundance (Miller and Hay 1996; Miller and Hay 1998), and only one previous study has directly examined effects of corals and algae on each other (McCook 2001). In this chapter, I experimentally tested the effects of the brown alga, *Lobophora variegata* on the branching hard coral *Porites cylindrica* (Fig. 4.1), the reciprocal effects of the coral on growth of the algae, and simultaneously tested those effects under different levels of herbivory.

4.2. Materials and Methods

4.2.1. Study site

This study was conducted on the reef slope (7-8 m depth) at Cannon Bay (Fig. 2.1; 18°41.1' S 146°35.2'E), Great Palm Island, Great Barrier Reef, Australia, close to the site used in Chapter 2. The site was dominated by colonies of *P. cylindrica* (~ 65% cover, based on four 20 m line-intercept transects). These colonies reach two metres 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. 4.1). Other macroalgae also were 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 (pers. obs.; also Russ 1984). Sea-urchins were rarely observed in this zone.

4.2.2. Experimental design

To test the hypotheses that the algal-coral interaction is competitive, and influenced by herbivory, I simultaneously manipulated competitors and herbivores in a nested factorial design (Fig. 4.2). 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; (ii) the effect of *P. cylindrica* on *L. variegata* by comparing

Fig. 4.1. A) Colony of *Porites 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 *Lobophora 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 one 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.

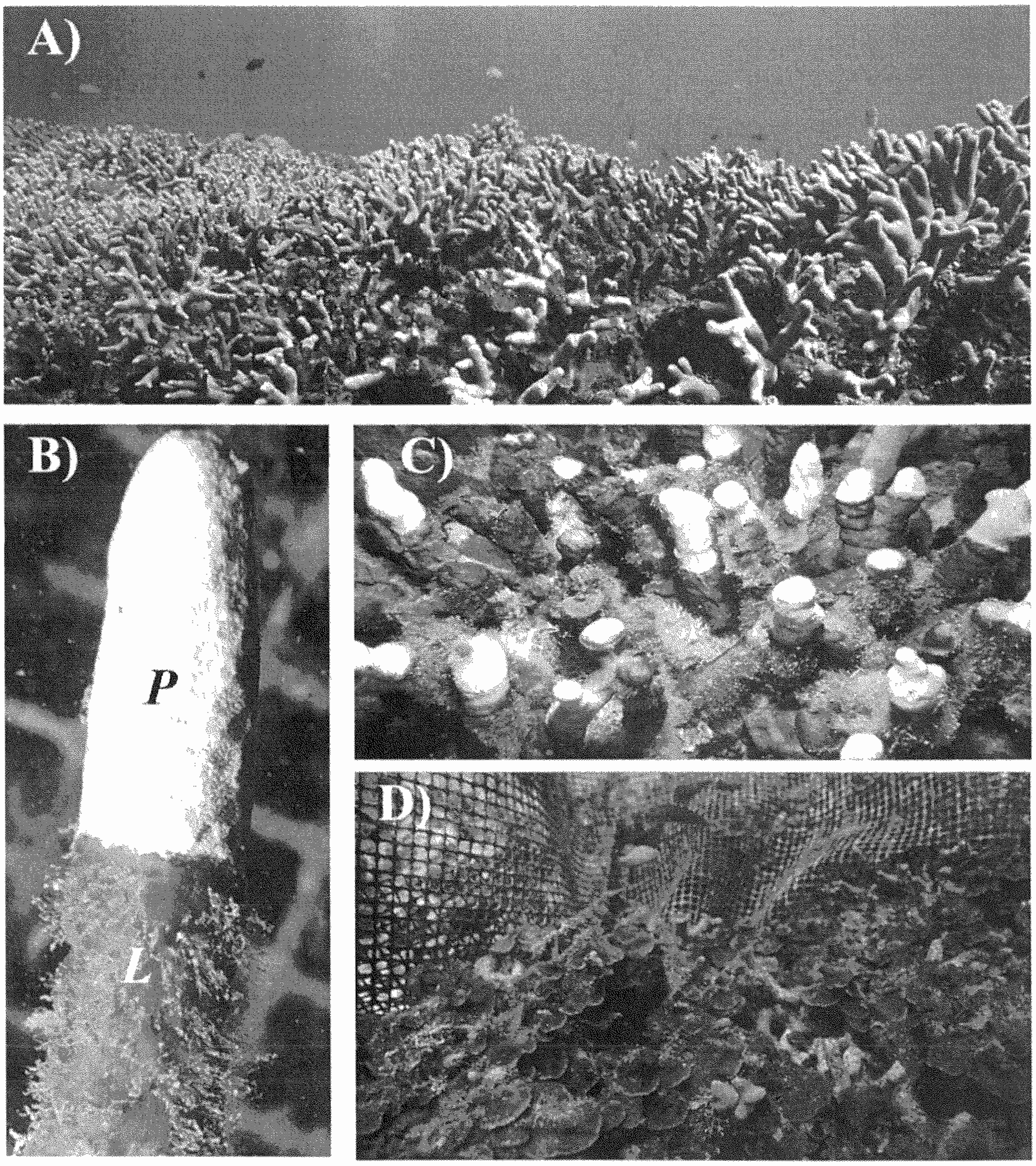


Fig. 4.2. **Experimental design**. A nested factorial design involving 2 treatment factors (herbivore treatment and competitor treatments), with competitor treatments nested within colony plots.

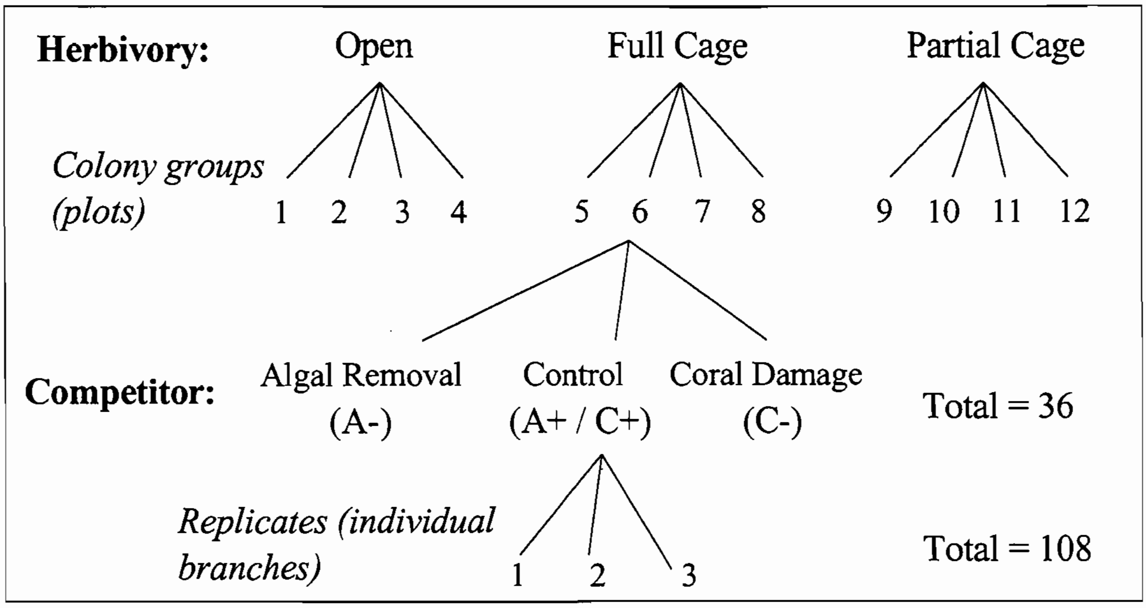
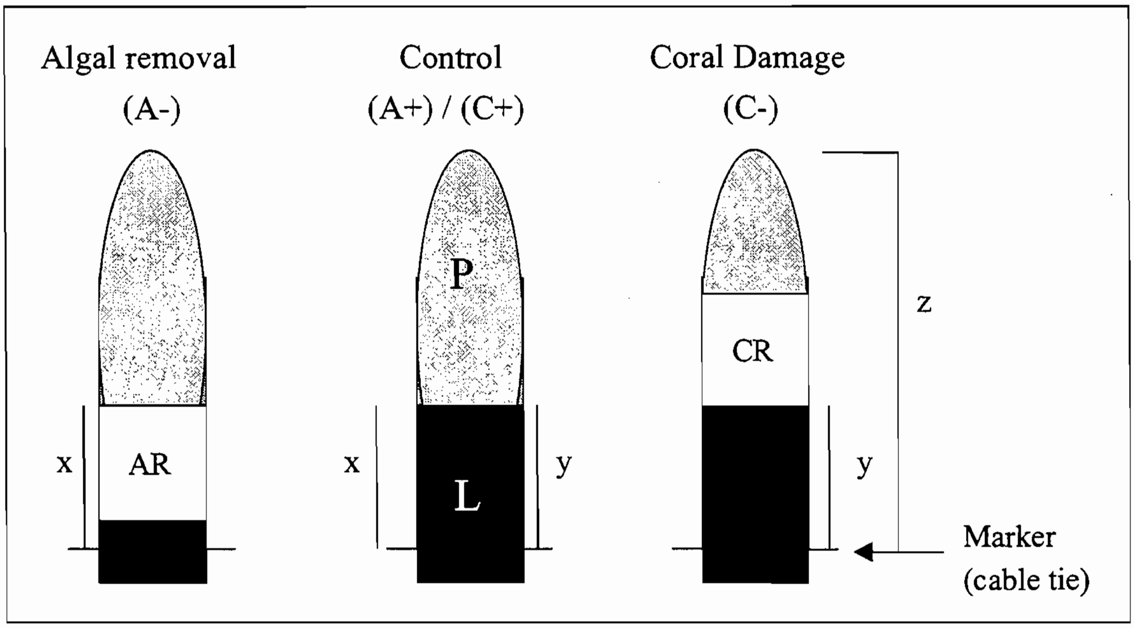


Fig. 4.3. **Method.** The effect of *L. variegata* on *P. cylindrica* was assessed by comparing coral mortality or skeletal extension in the presence of the alga (A+; control) with that in the absence of alga (A-). The effect of *P. cylindrica* on *L. variegata* was assessed by comparing algal growth 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.



algal growth on damaged coral and control (coral present) treatments (Fig. 4.3). I chose a nested factorial over a full factorial design (Fig. 4.2) 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 six 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. 4.3) could be measured subsequent to such overgrowth.

4.2.3. General approach and methods

There were twelve similar plots 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 cm x 25 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. 4.1 C) and randomly allocated to competitor treatments (Fig. 4.2). Each branch was labelled with a plastic tag attached to the base with a plastic cable tie.

4.2.3.1. Herbivore treatments

Herbivore exclusion cages were 75 cm by 75 cm x 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.

4.2.3.2. 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. 4.2 B "A-"). In the first period, algal removal was undertaken at two to three months intervals, whereas in the second period, algal removal was only done at the beginning of the experiment. 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 two to three months 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.

4.2.3.3. Measurements and data analysis

Three response variables were measured (i) coral mortality; (ii) coral skeletal extension; and (iii) algal growth (Fig. 4.3). Coral 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 2-factor nested ANOVA, with plots nested within herbivory treatment (Fig. 4.2), followed by post hoc Tukey's HSD test, using Systat^{TM} 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. Magnitudes of effects were estimated by the percentage of sums of squares (% SST) attributed to treatments. 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.

4.3. Results

4.3.1. The effects of herbivores and L. variegata on coral mortality

Tissue mortality of *P. cylindrica* was significantly affected by both herbivore and competition (*L. variegata*) treatments in both periods (Fig. 4.4 and Table 4.1). 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, and herbivore treatments had no effect on coral 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 mortality was significantly higher in the presence of

Fig. 4.4. 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 ± S.E.M) of 12 replicates averaged over plots (see Fig. 4.2). 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.

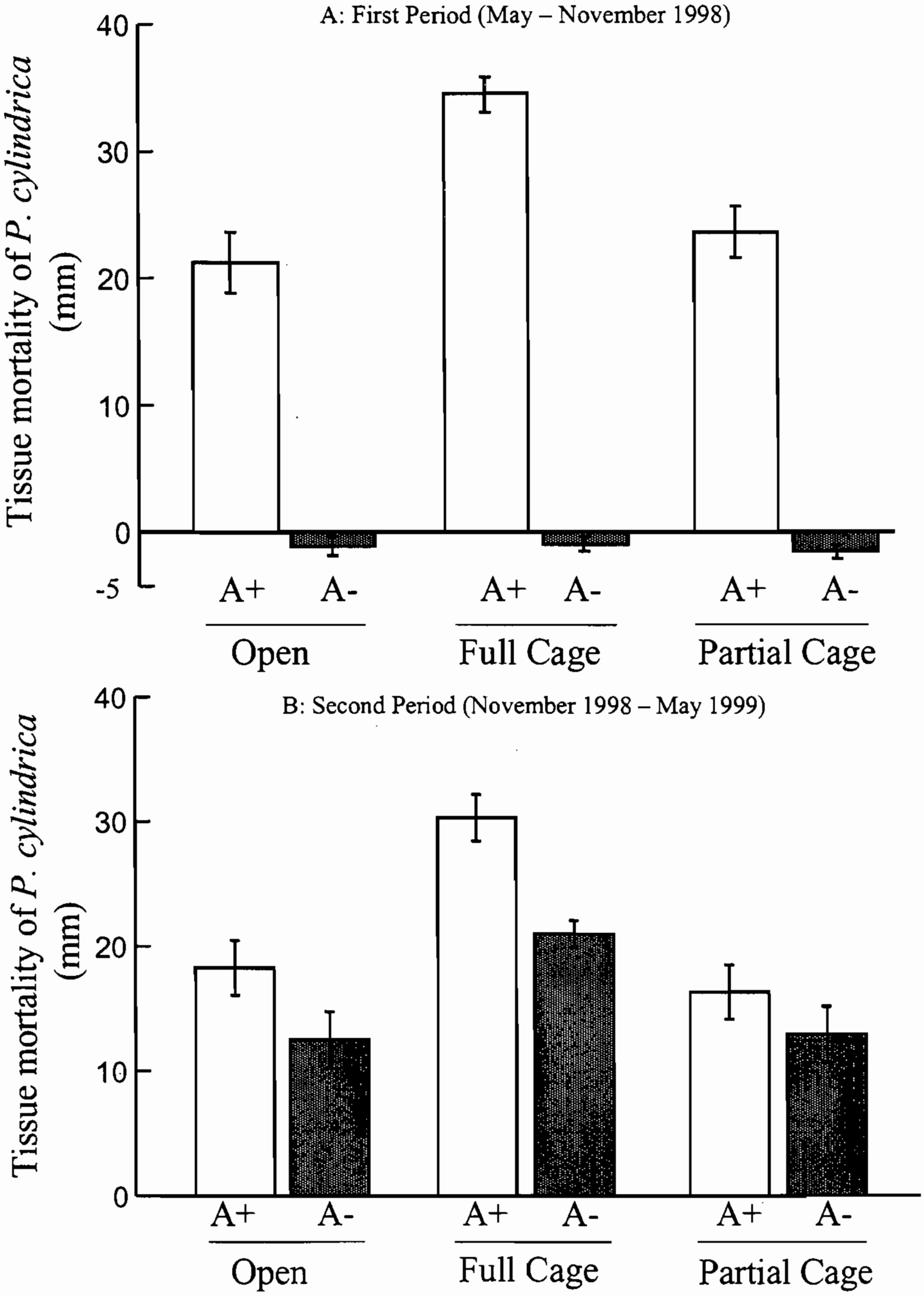


Table 4.1. Analysis of variance the effects on coral tissue mortality of herbivory and competition with *L. variegata*.

Source	df	Mean-Square	F-ratio	P	%SST	Conclusion
First Period (May – Nov ’ 98)						
Herbivory	2	365.95	6.99	0.015	4%	
Competitor	1	15842.00	333.14	0.000	83%	
C * H	2	325.26	6.84	0.016	3%	Significant*
Plot(H)	9	52.35	1.10	0.444	2%	
C * Plot(H)	9	47.55	2.17	0.041	2%	Significant
Residual (n=3)	48	21.95			5%	

Cochran’s C = 0.18

* 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

Second Period (Nov ’98 – May ’99)						
Herbivory	2	1096.358	14.673	0.001	29%	Cage > open ≈ partial
Competitor	1	1196.420	14.665	0.004	16%	Algal removal > control
C * H	2	113.149	1.387	0.299	3%	
Plot(H)	9	74.721	0.916	0.551	9%	
C * Plot(H)	9	81.582	1.545	0.160	10%	
Residual (n=3)	48	52.813			34%	

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

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 mortality (Fig. 4.4 A). Competitor treatments in the first period accounted for much more (83%) of total variation (%SST) than did herbivore treatments (4%).

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 when herbivores were present (Fig. 4.4 B). However, in contrast to the first period, there was no significant interaction between herbivore and competitor treatments, and herbivore treatment in the second period accounted for more of the total variation (29% SST) than did competitor treatments (16%). 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 mortality. Table 4.1 also indicates a significant interactive effect of competition with plot in the first period, which implies that the effect of competition in this period varied between the plots. This may be due to natural variation or initial differences between the plots, which unavoidably included a range of colony shapes and initial algal abundance. Post hoc Tukey's HSD test on herbivory treatments revealed that coral 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. 4.1 D). Such overgrowth was rare in uncaged plots.

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

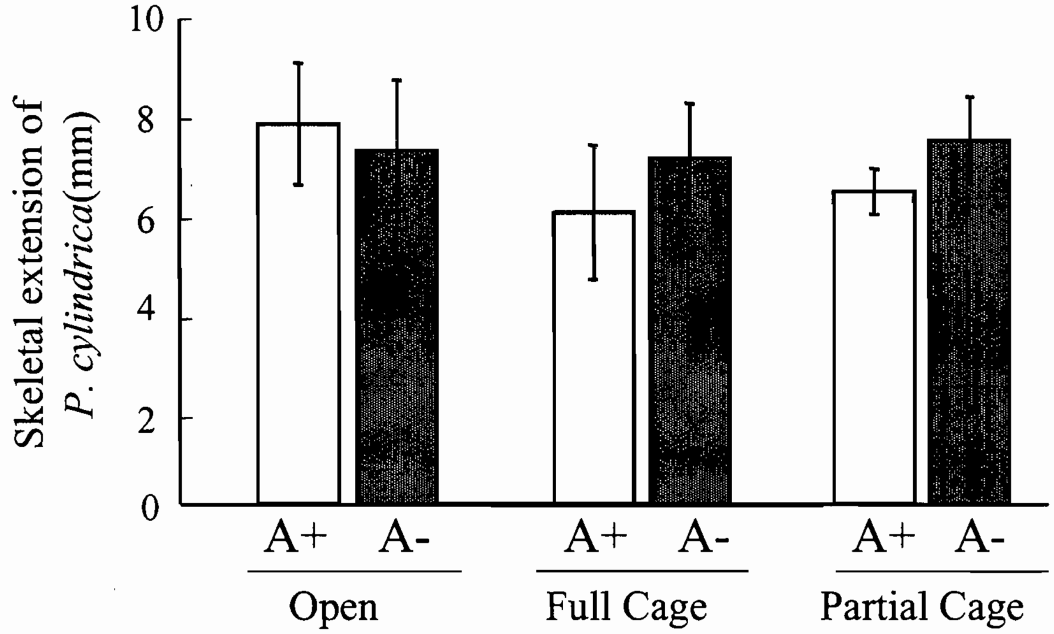
Coral skeletal extension was not significantly affected by any treatments in the first period (Fig. 4.5 A, Table 4.2), whereas in the second period, the presence of algae significantly reduced coral skeletal extension (Fig. 4.5 B, Table 4.2). Fig. 4.5 A suggests a similar but non-significant trend for 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.

4.3.3. *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 4.3 and Fig. 4.6). 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 magnitude of effects of competition treatments (0-25% reduction in algal growth, 4-8% SST) were less than those of herbivore exclusion (approximately 50% reduction in algal growth, 45-50% SST). Although the interaction between the two factors was not significant (Table 4.3), ANOVAs within herbivore treatments indicated 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 partial cages). This suggests that inhibition of algal growth by corals was stronger in the absence of herbivores (Fig. 4.6).

Fig. 4.5. 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 ± S.E.M) of 12 replicates.

A: First Period (May – November 1998)



B: Second Period (November 1998 – May 1999)

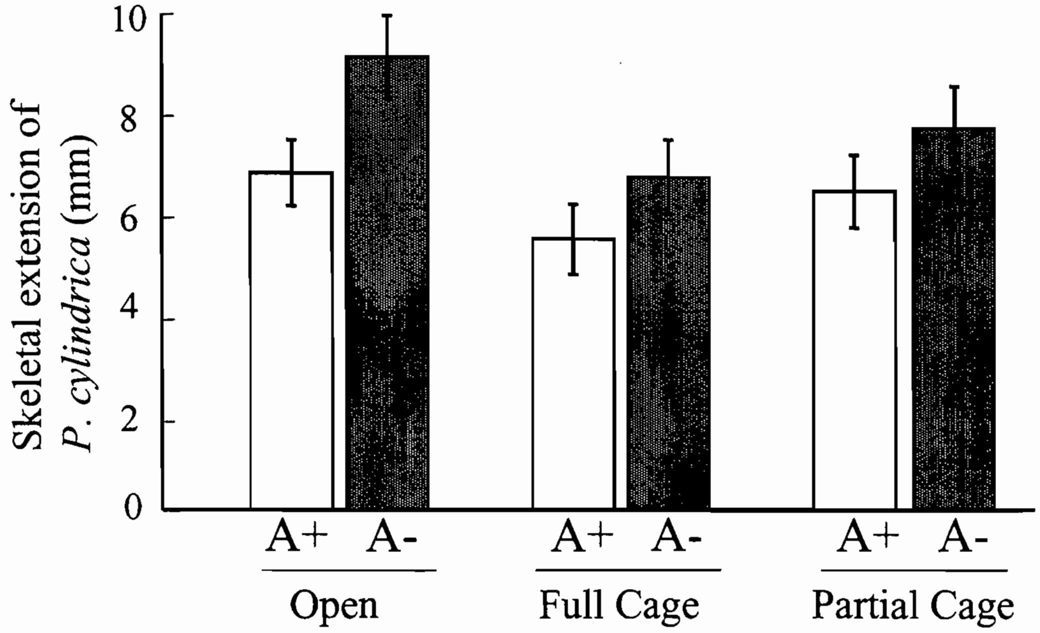


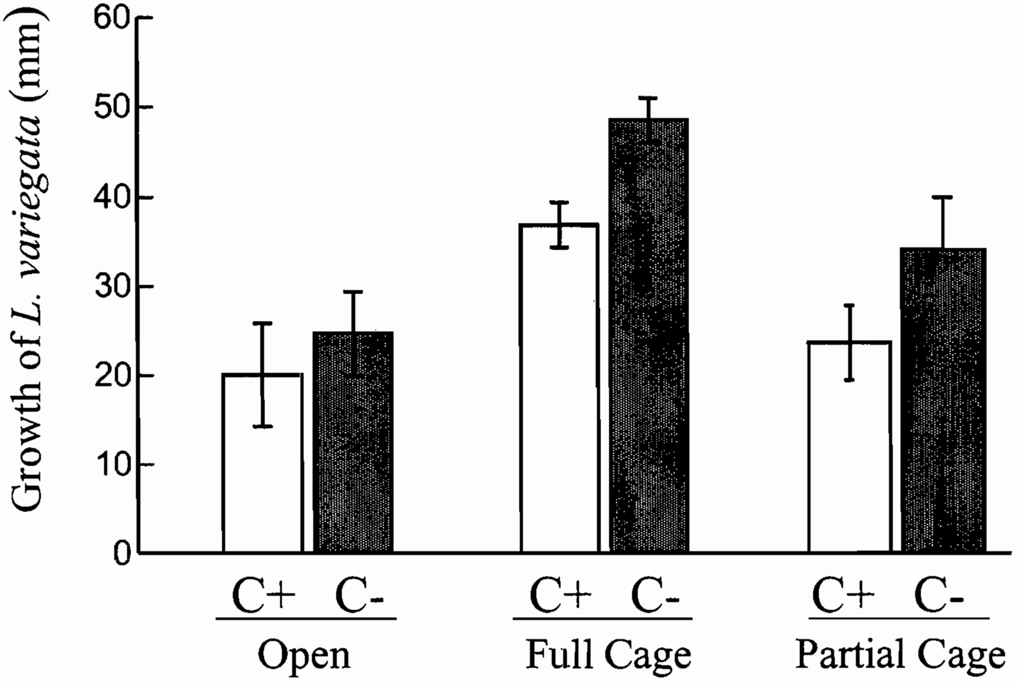
Table 4.2. Analysis of variance of the effects on coral skeletal extension of herbivory and competition with *L. variegata*.

Source	df	Mean-Square	F-ratio	P	%SST	Conclusion
First Period (May – Nov' 98)						
Herbivory	2	3.608	0.498	0.624	0.6%	No significant treatment effects
Competitor	1	3.337	0.474	0.508	0.3%	
C * H	2	3.233	0.459	0.646	0.5%	
Plot(H)	9	7.249	1.030	0.483	5.4%	
C * Plot(H)	9	7.036	0.760	0.653	5.3%	
Residual (n=3)	48	21.948			87.9%	
Cochran's C = 0.104						
Second Period (Nov '98 – May '99)						
Herbivory	2	22.531	2.259	0.160	8%	
Competitor	1	50.000	10.128	0.011	9%	Algal rem. > control
C * H	2	2.531	0.513	0.615	1%	
Plot(H)	9	9.975	2.020	0.155	17%	
C * Plot(H)	9	4.937	0.767	0.647	8%	
Residual (n=3)	48	6.441			57%	
Cochran's C = 0.08						

Note as for Table 4.1.

Fig. 4.6. 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 ± S.E.M) of 12 replicates.

A: First Period (May – November 1998)



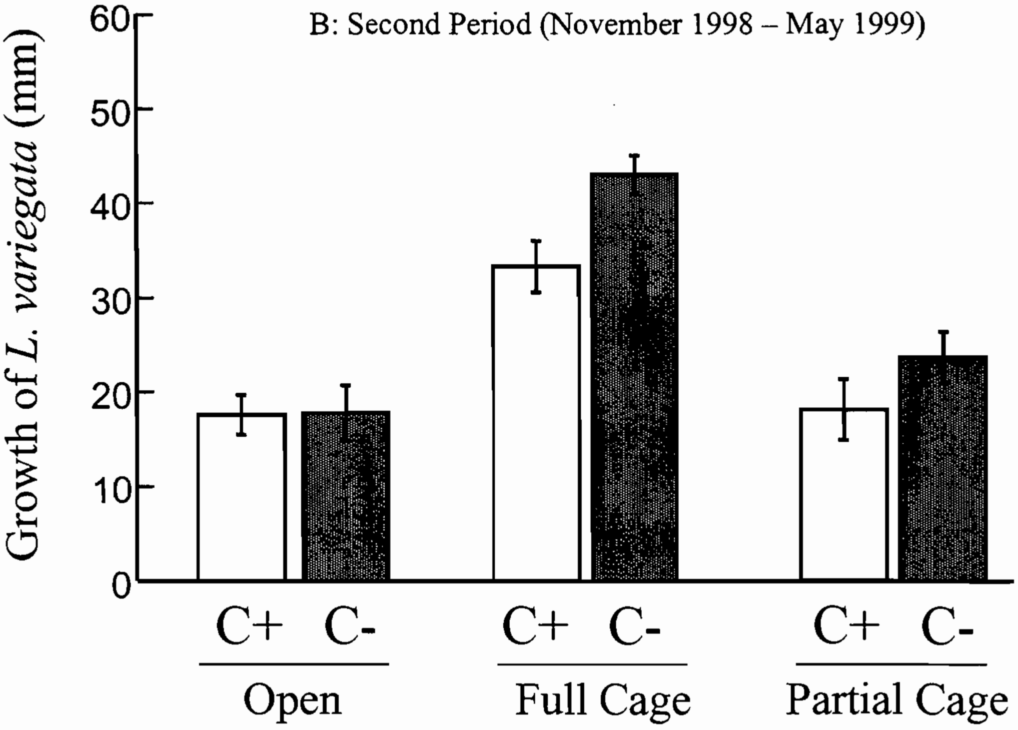

B: Second Period (November 1998 – May 1999)

Table 4.3. Analysis of variance of the effects on *L. variegata* growth of herbivory and competition with *P. cylindrica*.

Source	df	Mean-Square	F-ratio	P	% SST	Conclusion
First Period (May – Nov' 98)						
Herbivory	2	2686.774	12.576	0.002	45%	Cage > open ≈ partial
Competitor	1	938.889	10.454	0.010	8%	Coral rem. > control
C * H	2	215.524	2.400	0.146	4%	
Plot(H)	9	213.646	2.379	0.106	16%	
C * Plot(H)	9	89.813	1.741	0.105	7%	
Residual (n=3)	48	51.580			21%	
Cochran's C = 0.13						
Second Period (Nov '98 – May l'99)						
Herbivory	2	2926.097	40.562	0.000	50%	Cage > open ≈ partial
Competitor	1	475.347	5.702	0.041	4%	Coral rem. > control
C * H	2	138.347	1.660	0.243	2%	
Plot(H)	9	72.139	0.865	0.584	6%	
C * Plot(H)	9	83.366	1.081	0.349	6%	
Residual (n=3)	48	77.125			32%	
Cochran's C = 0.16						

Note as for Table 4.1.

The complete algal overgrowth observed after 12 months herbivore exclusion (Fig. 4.1 D) also resulted in a change in algal growth form, from the creeping morphology of algae attached to the coral branches, to foliose, horizontal fronds. This foliose form was rare in plots exposed to herbivores.

4.4. Discussion

The results of this chapter are significant because they provide direct, causal evidence for a specific example 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 Table 7.1). 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. 4.4 A), 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 4.2). 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. 4.5), 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 4.3 and Fig. 4.6), 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 mortality: Fig. 4.4 and Fig. 4.5). 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 Ruyter 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 Table 7.1), indicated by damaged margins of algal blades; and chemical (allelopathic) defence. I could not distinguish between these two possible mechanisms in my study: I 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. 4.6) suggests 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. 4.6) than on coral mortality (approximately 40% reduction: Fig. 4.4), and, significantly, herbivory had no effect on coral mortality when the algae had been removed. Together, this provides strong evidence that the effects of herbivores on the 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; Sammarco 1982; Connell 1983; Lewis 1986; Hughes 1989; Done 1992; Miller and Hay 1996; Miller and Hay 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 (McClanahan et al. 1999; Hughes et al. 1999; McCook 1999; c.f. Lapointe 1997).

It appears that the caging treatments provided effective herbivore exclusions, with minimal caging artifacts. Partial cage treatments were consistently not significantly different from 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. 4.6 and Table 4.3), and caging effects on coral skeletal extension were not significant (Table 4.2 and Fig. 4.5). Similarly, the patterns of coral skeletal extension among caging treatments (Table 4.2 and Fig. 4.5) 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 six-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).

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 1994a; 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 (McCook pers. com.). 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 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.

CHAPTER 5. The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*)

5.1. Introduction

The recent controversy over the relative importance of "bottom-up" (e.g. Lapointe 1997; 1999) and "top-down" (Hughes 1994a; Hughes et al. 1999; Aronson and Precht 2000) factors in controlling macroalgal blooms hinges to a large extent on the impact of these factors on the balance between algal production and algal consumption (McCook 1999). In particular, there is evidence that on reefs with healthy populations of herbivores, herbivore consumption often closely matches changes in algal production, so that increases in algal production or growth do not generally result in increased accumulation of algal biomass (Hatcher and Larkum 1983; Carpenter 1986; Hatcher 1988; Russ and McCook 1999; McCook 1999).

Despite the controversy, there have been few studies which simultaneously address more than one factor, especially experimentally (Hatcher and Larkum 1983; Miller and Hay 1996; 1998; Miller et al. 1999; Smith et al. 2001; Thacker et al. 2001), and, in particular, very few that specifically demonstrate competition using unconfounded, multifactorial experimental tests (Chapter 1). This makes it difficult to compare the relative importance of different factors. The scarcity of multifactorial studies is particularly unfortunate given that the three processes appear *a priori* to be interdependent: accumulation of nutrient-induced algal growth depends on herbivore consumption rates, and the effects of both factors on coral abundance depend largely on coral-algal competition.

The present study addressed this issue by simultaneously testing factorial combinations of the effects, on corals, of nutrients, herbivory, and competition with algae. This not only provides i. a direct comparison of the relative magnitude of each effect, but ii. does so for more than one level of the other factors, and most importantly, iii. the interaction terms in such a factorial experiment provide a direct test of the mechanisms by which the processes may interact. Thus, for example, the effects of nutrients and herbivores on corals are tested in the presence and absence of the algal competitor, indicating whether the effects of these factors depend on competition or influence the coral directly. I chose the naturally co-occurring brown alga *Lobophora variegata* (creeping or crustose morphology) and the branching scleractinian coral *Porites cylindrica* for this experiment (see Chapter 4), since it provides an ideal experimental unit, allowing logistically simple manipulations of competitors, herbivores and nutrients. As discussed in Chapter 4, *L. variegata* is relatively common and widespread on both the GBR and the Caribbean (Diaz-Pulido and Diaz 1997, and references therein; Littler and Littler 2000).

5.2. Materials and Methods

5.2.1. Experimental design and approach

I used a nested, fully factorial experimental design, with three factors: (1) competitor treatment, with two levels: *L. variegata* naturally present (unmanipulated) and *L. variegata* removal; (2) herbivory, with two levels: open plots, exposed to natural levels of herbivory, and caged plots, with herbivores excluded; (3) nutrient treatments, with three levels: control or ambient water, medium, and high pulsed nutrient additions. For each combination of treatments I used four replicate plots (nested within the factorial treatment combinations) and two replicate coral-algal branches (experimental units) for each plot. Each plot consisted of a steel frame to which the two branches were attached. The coral-algal branches were collected from reef slope colonies at Cannon

Bay on Great Palm Island, and transplanted to the reef slope at the Orpheus Island Research Station for the experiment, which ran from February to May 2000. Transplantation to the research station provided access to aquarium facilities for the nutrient treatments.

5.2.2. Study sites

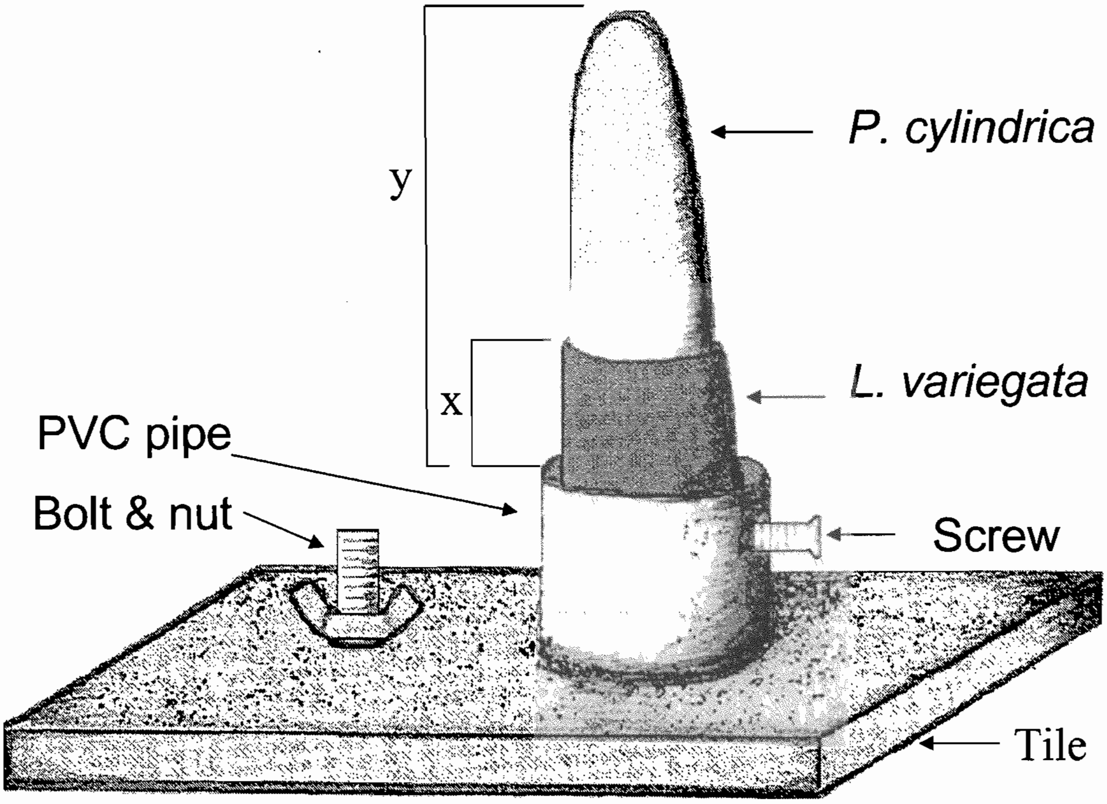
The specimens were collected from the reef slope (6-7 m depth) at Cannon Bay (Fig. 2.1; 18°41.1' S 146°35.2'E), Great Palm Island, on the inshore central Great Barrier Reef (GBR), (see Chapters 2 & 4 for more detailed description of this site). The brown alga *L. variegata* was the most common of several macroalgae growing within the branches of *P. cylindrica.* The alga usually occupied and overgrew the basal parts of coral branches and formed distinct patches among the *P. cylindrica* colonies along the reef slope.

The experimental site was on the reef slope at Pioneer Bay, Orpheus Island, also in the Palm Island group (Fig 2.1; 18°36.423' S 146°29.359' E; close to the site used in Chapter 2), at similar depth to the original habitat of the specimens (6m). This site consists of mostly dead coral rubble of branching *Acropora* and *Millepora tenella* (apparently killed during the 1998 mass bleaching event). Both *P. cylindrica* and *L. variegata* occurred naturally in this area.

5.2.3. Specimen selection and preparation

Coral branches were selected to have relatively uniform size (~ 6 cm long and ~ 1.5 cm diameter) and to have similar amounts of *L. variegata* (~ 2.5 cm) growing in a creeping, adherent morphology on the basal part of the branch. Branches were cut off using a small hand-saw, clamped to the attachment plates (Fig. 5.1), placed in large plastic bins (~65 litre "Nally" bins) underwater, brought up the research vessel, and then

Fig. 5.1. Experimental units. Branches of *Porites cylindrica* with naturally occurring *Lobophora variegata* growing around the base of the branch were selected and transplanted to the study site. The *L. variegata* has a creeping morphology, growing closely adherent to and overlying dead coral skeleton, with only 1-2 mm overlap between the top edge of the *L. variegata* and the bottom margin of live coral tissue. Each coral-algal branch or unit was clamped, by a stainless steel screw, into a short length of PVC pipe, which was glued onto terra cotta tiles. The tile was attached to a steel frame with a bolt and wing nut, and the steel frames were anchored to the bottom. This method allowed specimens to be removed and reattached readily for the nutrient pulse treatments. Coral tissue mortality was estimated by the change in position of the border between live and dead coral tissue (x), relative to a reference point (the PVC pipe); i.e. mortality here refers to upward retreat of the bottom of the live coral. Coral skeletal extension (y) was measured as the change in distance from coral tip to the reference marker; thus extension refers to upward growth.



transported under running seawater to the experimental site at Orpheus Island (~ 1 hour travel). Specimens were maintained underwater at all times during both the transplantation process and the experimental procedures.

5.2.4. Experimental treatments

The competition treatment simply involved careful removal of all *L. variegata* from randomly selected branches, with half the branches left intact. The herbivore exclusion treatment involved large cages (40 x 40 x 25 cm) made of 12-mm plastic mesh (Nylex, "Trical" high density polyethylene), as used by McCook (1996; 1997). The mesh was attached to the steel frames, to which two coral-algal branches had been attached (i.e. plots). Open plots consisted of frames with no mesh. Limitations on the number of specimens available meant that it was not feasible to include a partial cage treatment to test for caging artifacts and still use a fully factorial combination of all three factors (this would have required another 48 coral branches). As previous experiments in this area (Russ 1987; Russ and McCook 1999), including several using the same mesh (McCook 1996; 1997) and even using the same coral and algal species (Chapter 4) have found minimal caging artifacts, I felt that the benefits of the factorial design outweighed the risks of caging artifacts.

Nutrient manipulations involved pulsed addition of nutrients for a 24 h period every 2-3 weeks for 3 months, using reagent-grade ammonium chloride and sodium-dihydrogen phosphate (e.g. Schaffelke and Klumpp 1998b). Although pulsed application of nutrients does not simulate long-term, constant eutrophication, it does simulate the major nutrient inputs experienced by inshore reefs of the GBR, which involve flood plumes delivering short-lived pulses of high nutrient concentrations; it is also logistically far simpler to sustain and measure the nutrient elevations (Schaffelke, 1999). Three levels of nutrients were applied: (1) controls, using ambient seawater at

Orpheus Island (average concentrations 0.1 μM ammonium and 0.08 μM phosphate); (2) medium, an addition of 5 μM ammonium and 0.5 μM phosphate; and (3) high, an addition of 10 μM ammonium and 1 μM phosphate. Nutrient pulses were given either on the Research Vessel *Harry Messel* or at Orpheus Island Research Station using a separate, 10-litre plastic bucket for each two branches. The buckets were aerated to ensure adequate water movement and mixing and the water was replaced every 3-4 hours to maintain relatively constant nutrient levels. Shade cloth was used to minimize stress to the corals. The effectiveness of the nutrient manipulations was tested by measuring tissue nutrient levels in *L. variegata*. Algal tissue was removed from the base of *P. cylindrica* at the end of the experiment, after applying the 24 h nutrient pulse. Samples were dried at 60°C for 36 hours, ground and concentration (% dry weight) of carbon and nitrogen were determined with a Perkin Elmer CHN Analyser. Phosphorus was determined using ICP Analysis.

5.2.5. Measurement and data analyses

Two response variables were measured. Tissue mortality of *P. cylindrica* was calculated as the change in height of the border between live and dead coral tissue relative to a reference point (Fig. 5.1). Coral growth or linear extension of the branch was measured as the growth of the coral tip from the reference point (Fig. 5.1). All measurements were made using vernier calipers, to the nearest 0.5 mm. Note that in treatments with alga present, the coral tissue mortality is equivalent to algal growth, since the top edge of the alga corresponds to the bottom edge of the live coral.

Data analyses involved a 3-factor, nested ANOVA, followed by *post hoc* SNK tests. Where the interaction between treatments was significant, analyses (ANOVA and SNK tests) were repeated within levels of each treatment factor. In order to minimize the risks of overlooking relatively small nutrient effects (i.e. Type II error), nutrient effects on coral tissue mortality (or equivalently on algal growth, see above) were specifically tested within the caged, alga present treatment combination, as it is this treatment combination that any nutrient effects are most likely to be measurable. Magnitudes of the effects were estimated by the percentage of sums of squares (% SST) attributed to treatments. All data were tested for homogeneity of variance (Cochran's test), outliers, and independence and normality of residuals (graphically). Based on these tests, no data transformation was needed for the analyses.

5.3. Results

5.3.1. Coral tissue mortality

Coral tissue mortality data indicated a significant interaction between effects of the competitor, *L. variegata* and herbivory, while the effect of nutrients and other interactions were not significant (Fig. 5.2 and Table 5.1). Separate analyses carried out to explain the significant interaction indicated that (i) within the algal removal treatment, no differences were detected in coral mortality between open and caged treatments ($P = 0.910$, < 1% SST); (ii) where alga was present, coral tissue mortality was significantly higher in caged compared to open treatments ($P < 0.001$, 56% SST); (iii) coral tissue mortality was always higher in the presence of alga compared to treatments where the alga had been removed, for all levels of herbivory treatments ($P < 0.001$ in all cases, 42% and 89% SST for open and caged treatments respectively). Indeed, in the absence of the alga, coral tissue generally regrew downward over the bare skeleton. Competition generally accounted for a relatively high proportion of the total variability in the experiment, herbivory a small proportion, and nutrient treatments very little (<1%).

Fig. 5.2. Graph showing total mortality of coral tissue under different experimental treatments. Data are means of the total coral tissue mortality (mm ± S.E.M) of 8 replicates (averaged over 4 plots). Note that coral tissue mortality for *L. variegata* removal was almost always negative as a result of downward coral tissue regeneration after algal removal.

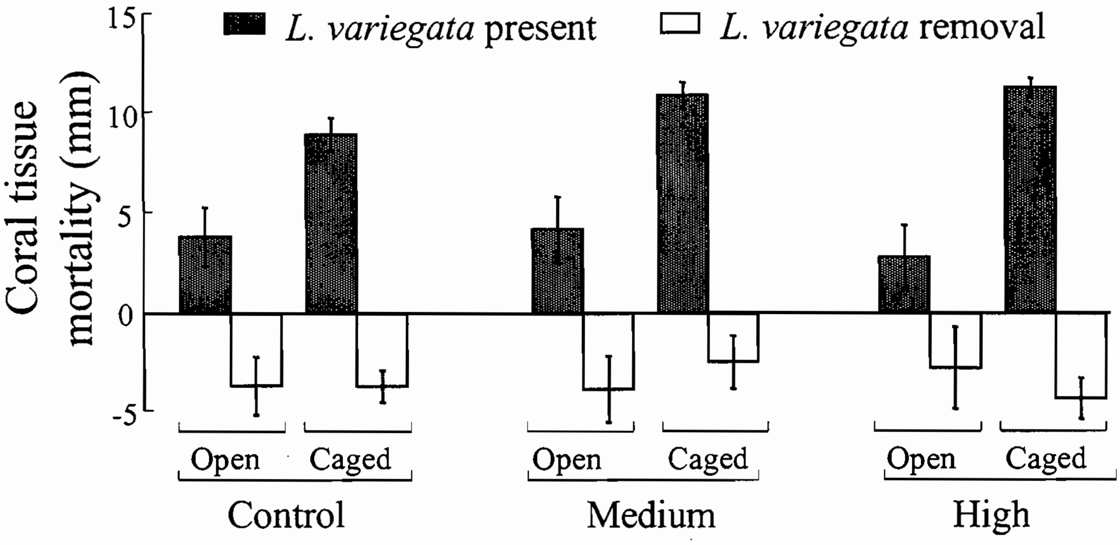


Table 5.1. Analysis of variance of the effect of nutrient, herbivory and competitor (*L. variegata*) on tissue mortality of *P. cylindrica*. Cochran's test indicates the homogeneity of variance (C critical value = 0.212). Data are not transformed.

Source	d.f.	Mean-Square	F-ratio	P	% SST	Conclusion
Nutrient (N)	2	6	0.5	0.629	< 1	ns
Herbivory (H)	1	280	22.4	< 0.001	6	Significant
Competitor (C)	1	2678	214.1	< 0.001	61	Significant
N * H	2	5	0.4	0.674	< 1	ns
N * C	2	1	0.1	0.924	< 1	ns
H * C	1	300	24.0	< 0.001	7	Significant*
N * H * C	2	15	1.2	0.306	< 1	ns
Plot (N*H*C)	36	13	1	0.503	10	ns
Residual	48	13			14	
Cochran's C = 0.158						

* see text for explanation

Although the effects of nutrients on coral tissue mortality were not significant in the overall analysis (Table 5.1), I also specifically tested for nutrient effects within the caged, alga present treatment. This test, which amounts to a test of nutrient effects on algal growth, did indicate a small effect of nutrient treatments (Table 5.2). *Post hoc* SNK tests indicated that coral tissue mortality (in caged, algal removal treatments) was significantly higher in both medium and high nutrient treatments than at control levels ($P < 0.05$), whereas there was no significant difference between medium and high nutrient treatments.

5.3.2. Coral growth rate

The growth rates of coral tips (skeletal extension) were not significantly affected by any of the treatments (Fig. 5.3 and Table 5.3). Further, separate analyses within each level of all factors did not indicate any differences in coral growth amongst treatments ($P > 0.2$ in all cases).

5.3.3. Algal tissue nutrients

Algal tissue levels of both nitrogen and phosphorus were significantly enhanced in response to the nutrient pulse treatments (Fig. 5.4; $P < 0.001$ and 0.005 for N and P respectively, whether expressed as % of dry weight or as C:N and C:P ratios). *Post hoc* SNK test indicated that for % of dry weight, tissue nitrogen and phosphorus were significantly higher for high ($P < 0.01$, $P < 0.05$) and medium ($P < 0.01$ in all cases) nutrient treatments than in control treatment, but that medium and high nutrient treatments were not statistically different ($P > 0.05$ both for N and P). Although not statistically significant, it is interesting that tissue nitrogen showed an increasing trend at the higher level, whereas tissue phosphorus appeared to be saturated (Fig. 5.4).

Table 5.2. Analysis of variance of nutrient effect within full cage and algal present treatments, on tissue mortality of coral *P. cylindrica*. Cochran's test indicates the homogeneity of variance (C critical value = 0.541). Data are not transformed.

Source	d.f.	Mean-Square	F-ratio	P	% SST	SNK test
Nutrient	2	13.300	6.224	0.020	28%	high ≅ medium > control
Plot (Nutrient)	9	2.137	0.523	0.832	20%	
Error (n=2)	12	4.084			52%	
Cochran's C = 0.225						

Fig. 5.3. Graph showing total coral skeletal extension under different experimental treatments. Data are means of total coral skeletal extension (mm ± S.E.M) of 8 replicates.

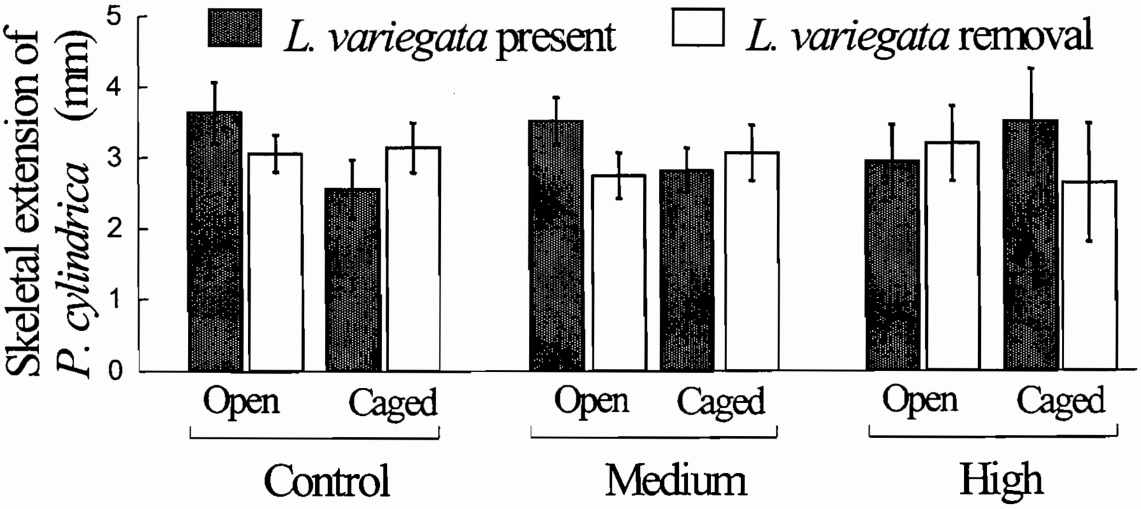
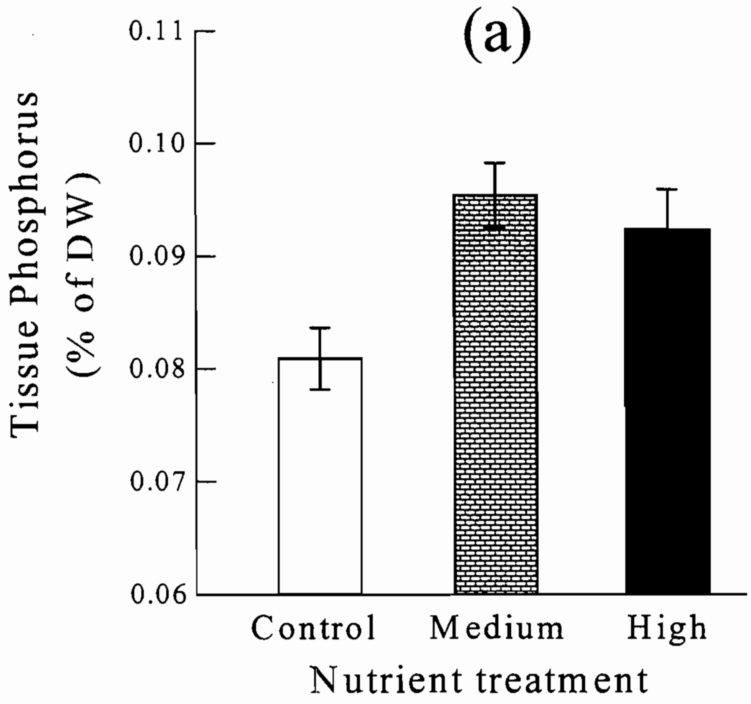
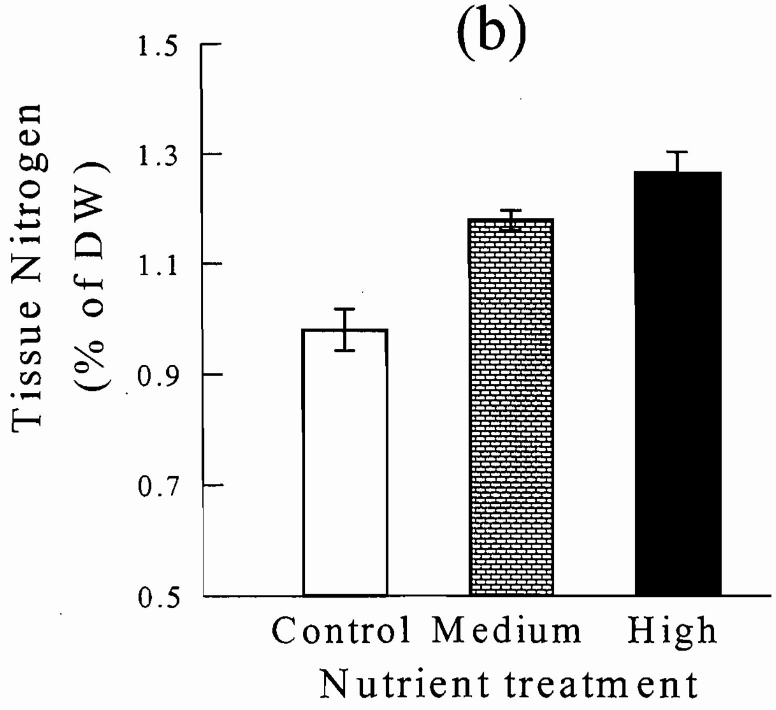


Table 5.3. Analysis of variance of the effect of nutrient, herbivory and competitor (*L. variegata*) on skeletal extension of *P. cylindrica*. Other notes as Table 5.1.

Source	d.f.	Mean-Square	F-ratio	P	% SST	Conclusion
Nutrient (N)	2	0.04	0.02	0.978	< 1	ns
Herbivory (H)	1	1.26	0.74	0.396	1	ns
Competitor (C)	1	0.83	0.48	0.491	1	ns
N * H	2	0.50	0.30	0.746	1	ns
N * C	2	0.22	0.13	0.881	< 1	ns
H * C	1	0.77	0.45	0.506	< 1	ns
N * H * C	2	3.20	1.88	0.168	4	ns
Plot (N*H*C)	36	1.71	1.11	0.369	42	ns
Residual	48	1.54			51	
Cochran's C = 0.119						

Fig. 5.4. Graphs showing algal tissue nutrient levels, expressed as percentage of dry weight of nitrogen (a) and phosphorus (b), for *L. variegata* tissue under different nutrient treatments. Data are means (± S.E.M) of 8 replicates.





5.4. Discussion

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

The experimental demonstration that the coral tissue mortality at the interaction border was dependent on overgrowth by the alga provides critical proof that the interaction is competitive: i.e. that coral tissue mortality is caused by algal overgrowth, rather than algal overgrowth responding to coral tissue mortality due to some unknown cause (section 1.2). The strength of the competitive inhibition is demonstrated by the tissue growth or recovery (downward) over the bare skeleton which consistently occurred in the absence of the algal competitor (Fig. 5.2). The strength of this competitive interaction is further demonstrated by the high proportion of variation explained by the competition treatment, and by the strong competitive effects at all levels of the other treatment factors (herbivory and nutrients).

L. variegata has been previously observed overgrowing scleractinian corals (de Ruyter van Steveninck et al. 1988; Hughes 1994a; Littler and Littler 2000), and appears to have relatively severe effects on corals compared to other macroalgae (such as filamentous turfs or upright macrophytes: e.g. Tanner 1995; McCook 2001; Lirman

2001). These different effects are likely to result from differences in the mechanisms involved in coral-algal competitive interactions, and differences in algal growth strategies (General Discussion; Chapter 7).Thus, the outcomes of this study are to some extent specific to the particular combination of coral and algal species (as well as the particular herbivore and nutrient regimes at the experimental site). However, it is worth noting that *P. cylindrica* is very common coral species in Indo-Pacific and *Lobophora variegata* is a very widespread and common species in both the Indo-Pacific and Caribbean (Chapter 4).

Experimental exclusion of large herbivores led to a significant increase in coral tissue mortality (Fig. 5.2), although the magnitude of this effect was smaller than the competitor treatment, and critically, exclusion cages had no effects when the algal competitor was experimentally removed. This interaction, by demonstrating that the effects of exclusion cages were dependent on the overgrowth by the algal competitor, provides strong evidence that herbivores affected coral abundance indirectly, by removing their algal competitors. Although a number of herbivore exclusion experiments have previously suggested the importance of indirect effects of herbivory on corals via competition with macroalgae, most have not directly demonstrated competition (Vine 1974; Sammarco 1982; Fitz et al. 1983; Hay and Taylor 1985; Lewis 1986; Stachowicz and Hay 1999; Lirman 2001). Although two studies have previously demonstrated the competitive mechanism of the herbivore effect (Miller and Hay 1996; 1998), one of these found that herbivore-control of algal competitors was partially offset by the direct effects of parrotfish grazing on the corals themselves (Miller and Hay 1998), in contrast to my results.

The importance of these herbivore effects, in preventing algal overgrowth of the corals, is emphasized by the magnitude of effects on coral tissue mortality, which increased by more than 50 % in just 3 months in plots in which herbivores were excluded. Thus, although *L. variegata* frequently overgrows the basal parts of *P. cylindrica* branches (see also Littler and Littler 2000), herbivory probably plays an important role in preventing the coral branches from being completely overgrown by the alga. Herbivore mediation of algal competition appears critical to the persistence and survival of these corals (Chapter 4).

Although overall nutrient effects on coral tissue mortality were not significant, and very small compared to the effects of the competitor (*L. variegata*) and herbivory (Fig. 5.2 and Table 5.1), addition of nutrients did significantly increase coral tissue mortality within full cages when *L. variegata* was present (Table 5.2). Further, algal tissue nutrient levels were significantly enhanced in nutrient addition treatments (Fig. 5.4). These results are important, since together they demonstrate that the nutrient treatments in this experiment were effective, not only in increasing nutrient supply to the algae (tissue nutrient data), but also in doing so sufficiently to enhance algal growth (Table 5.2). Further, the relatively small difference between medium and high nutrient treatments suggests that pulse concentrations were sufficient to be near to saturating growth responses (at this pulse frequency), again suggesting that the relatively small effect of the nutrient treatments does not represent ineffective treatments, but genuinely represents a relatively weak effect compared to the much larger effects of competition and herbivory. It appears that *L. variegata* growth was not strongly limited by nutrient supply.

Interestingly, the lack of nutrient enhancement of coral tissue mortality in the absence of *L. variegata* shows that the effect was not a direct effect on the physiology of the corals (c.f. Simkiss 1964; Kinsey and Davies 1979; Stambler et al. 1991; Ferrier-Pages et al. 2000), but an indirect effect of enhanced growth of the algal competitor

(Miller and Hay 1996). Whilst this conclusion supports the accepted mechanism of the "bottom-up" view of nutrient effects on corals (in the absence of herbivores), it emphasizes the importance of the competitive interaction to that effect. As the strength of coral-algal competitive interactions may vary considerably (Miller 1998; McCook et al. 2001), the strength of the bottom up effects on corals (where expressed) will presumably also vary.

However, the expression of nutrient effects on algal competitiveness was strongly dependent on exclusion of herbivores. Presumably herbivore removal of algal biomass masked any differences in intrinsic algal growth rates, leaving no differences in *net* algal growth to accumulate as increased algal biomass, and hence increased algal competitiveness. Algal competitiveness is a function of biomass, not growth rates, and algal biomass can only accumulate if tissue production exceeds total losses, including losses to herbivores (Hatcher and Larkum 1983; McCook 1999). Thus, the results of this study support the argument that algal abundance (and hence competitiveness) on coral reefs is often regulated by consumption rates, rather than growth rates, and consumption rates often respond to absorb any changes in production (Hatcher and Larkum 1983; Steneck 1988; Carpenter 1997; Russ and McCook 1999; McCook 1999). For example, after an apparent, large-scale nutrient pulse, Russ and McCook (1999) reported a five-fold increase in production of epilithic algal communities, but this increase was closely matched by increased algal consumption, resulting in no changes to algal standing crop. As nutrient enhancement affects algal growth, it can only affect algal competitiveness when that increased growth exceeds the consumption capacity of herbivores.

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

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

In contrast to the effects on coral tissue mortality at the interaction border, none of the treatments significantly affected the growth of coral branch tips (Fig. 5.3 and Table 5.3). Overall growth rates of *P. cylindrica* in this study were relatively normal compared to growth rate measured in the original habitat (unpub. data). As in Chapter 4, The lack of competitive effects of the alga on coral branch growth is presumably due to the physical separation between the alga and the coral tips, as the upper border of the algal blades during this study period remained more than 2 cm from coral tips throughout the experiment. This separation would therefore also explain the lack of any indirect effects, through the algal competitor, of herbivory or nutrients on coral growth. However, no direct effect of nutrients on coral growth was apparent either, despite previous evidence that nutrient enhancement may cause reductions in coral growth (Simkiss 1964; Kinsey and Davies 1979; Stambler et al. 1991; Ferrier-Pages et al. 2000). This result should be interpreted cautiously, since the length of this experiment (3-months) might be insufficient for nutrient effects on coral growth to become apparent (Hoegh-Guldberg et al. 1997). If such effects did occur, they may strongly influence coral competitive abilities, especially in synergy with increased algal growth. The absence of any consistent effects of the caging treatment on coral growth supports the suggestion that caging artifacts were minimal. Finally, the lack of treatment effects on growth at the branch tips means that the effects on coral tissue mortality at the interaction border are approximately equivalent to the overall effect of the treatments on the net growth of the coral.

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

CHAPTER 6. An unusual coral-algal interaction: *Sargassum* canopy reduces coral bleaching damage along a water quality gradient on inshore reefs

6.1. Introduction

As outlined in Chapter 1, coral reef degradation is often characterised as a decline in coral abundance and an increase in fleshy macroalgal abundance. Many inshore reefs of the Great Barrier Reef (GBR) have abundant beds of large brown macroalgae (seaweeds) on the reef flat, often dominated by species of *Sargassum* (McCook et al. 1997). There have been concerns that the abundance of these seaweeds signifies increased terrestrial input of sediments and nutrients, and that the seaweeds outcompete and kill coral populations (Bell 1992; Bell and Elmetri 1995). However, the assumption that these algal beds are detrimental to corals is based on very little rigorous evidence, mostly for very different algal taxa or assemblages (Chapter 1). There has been no study that specifically tested the effect of these canopy forming seaweeds on coral populations.

To test for such effects, large plots were established and maintained at several sites on two inshore reefs from which the *Sargassum* canopy had either been removed or left intact. However, the focus of the experiment was partially diverted by the mass bleaching events of early 1998. In mid-February 1998, I noticed considerable bleaching of corals at both reefs, and so took the opportunity to examine the effect of the *Sargassum* canopy on coral bleaching.

Coral bleaching involves the disappearance of microalgal symbiotic zooxanthellae from the coral tissues, in response to stress (Brown 1997; Glynn and D'Croz 1990). Large-scale coral bleaching events on the GBR region have previously been associated with extreme floodwaters (e.g. van Woesik et al. 1995) and high air and seawater temperature (e.g. Jones et al. 1997). During January 1998, exceptional weather conditions and flooding apparently caused widespread bleaching of marine organisms, especially corals, on inshore reefs over much of the GBR region (Berkelmans and Oliver 1999; Hoegh-Guldberg 1999). This present study aimed to test the effect of the canopy forming macroalgae on coral bleaching and recovery rates along a water quality gradient on inshore reefs.

6.2. Methods

6.2.1. Study sites

This study was conducted on the reef flat at two fringing reefs on the inshore, central Great Barrier Reef. The reefs were chosen to represent a gradient in influence of terrestrial sources of nutrients and sediments (Fig. 2.1). Goold Island (18° 10.7' S 146° 10.1' E), north of Hinchinbrook Island, is ~ 15 km from the mainland, is surrounded by shallow, muddy turbid waters, with high levels of resuspended fine, terrigenous sediments and is directly in the path of flood plumes from the Herbert River. Cannon Bay (18°41.1' S 146°35.2' E) at Great Palm Island is further offshore (~ 35 km), is surrounded by deeper waters, with carbonate sediments, and is rarely exposed to flood plumes. Measurements of inorganic and organic nutrients, Chlorophyll a, suspended sediments, turbidity and salinity were generally higher at Goold Island than at Cannon Bay (see McCook 2001 and references therein for more detail). It should be emphasized that comparisons among reefs amount to a natural experiment, and that the reefs differ in numerous aspects besides availability of nutrients etc. Thus these comparisons can only indicate whether outcomes are consistent with possible roles of water quality, but can neither prove nor disprove any such effects.

Macroalgal beds are abundant on both reefs and sometimes form a thick canopy up to 1-2 meters high, with ~ 90% cover (in summer). The beds are dominated by Fucales, predominantly several species of *Sargassum*, but also including *Hormophysa cuneiformis*, *Turbinaria* spp and *Cystoseira trinodis*. Despite this canopy, the plots had a relatively high initial cover of live corals growing as understory, beneath the canopy (up to 70% before bleaching events), especially at Goold Island (McCook 1999).

6.2.2. Experimental design and methods

The experiment involved a two factor, nested design, with 2 reefs (Goold Island and Cannon Bay) and 2 canopy treatments, with two sites nested within each reef, and two replicate plots of each treatment at each site. The effects of the macroalgal canopy on corals were examined by comparing coral in the presence and absence of the algal canopy. Within each reef, two sites were chosen (~ 200 m apart) to assess spatial variability within reefs. Each site contained two replicate plots for each treatment. The experimental plots were relatively large area (5 x 5 m) to minimize edge effects. Algae were removed by carefully cutting away the major canopy forming macroalgae at the holdfasts, with minimal disturbance to the substrate. This treatment had already been maintained for other studies for 18 months when the coral bleaching occurred in February 1998, and was repeated approximately every two months for the duration of the current study (8 months).

The study involved two phases. The first examined the effects of the *Sargassum* canopy on the proportion of corals bleached, the second tested for canopy effects on the recovery of corals from the bleaching in order to determine the extent to which any bleaching effects were transient or persisted as long-term impacts.

6.2.2.1. Phase 1. Bleaching damage

Corals bleaching in both *Sargassum* canopy (control) and removal plots was recorded (at genus level) on 12th February, 1998, using four 5 m line intercept transects, spaced evenly 1m apart, within each of the experimental plots (to the nearest cm). The condition of each coral colony was categorized as either bleached or healthy. For partially bleached coral colonies, proportions of bleached and healthy colonies were measured and recorded separately. The proportion of corals bleached was estimated by the cover of bleached colonies as a percentage of the total cover of colonies (bleached or healthy).

6.2.2.2. Phase 2. The recovery rate of selected bleached corals

Recovery of bleached corals was monitored using selected bleached colonies, approximately every two months, from March 1998 until all selected corals had either died or fully recovered (November 1998). This experiment was limited to corals that were bleached (i.e. had lost some or all of their zooxanthellae resulting in pale or white coloration) but still alive (e.g. polyps visible, and/or no algal turf overgrowth) on 28th March 1998.

Individual bleached corals were selected and tagged using numbered plastic tags, attached with stainless steel screws. Corals were selected to have similar initial degrees of bleaching in all treatments and sites. There were few genera with sufficient, bleached colonies present at both reefs to allow optimal between-reef comparisons. Tagged corals were selected from the four genera (*Porites, Favia, Favites and Pocillopora*) which were most abundant at both reefs. However, as even these were relatively rare at Great Palm Island, I also tagged colonies of *Montipora* at that reef, to ensure adequate comparison between the two treatments within Great Palm Island.

6.2.3. Data analyses

The extent of coral bleaching (phase 1) was compared at both the overall coral population and genus level. Data analysis of corals overall involved a two-factor nested ANOVA, with sites nested within reefs with replicate plots. To explore variation between genera in contributing to the overall effect, I chose eight of the most dominant coral genera at each reef and graphically compared the individual bleaching rate within each genus. The effect of the canopy on coral recovery (phase 2) was analysed as the proportional recovery of the selected bleached corals within each plot, using the same ANOVA design as in phase 1. Magnitudes of effects were estimated by the percentage of sums of squares (% SST) attributed to treatments. All data were tested for homogeneity of variance (Cochran's test), outliers, and independence and normality of residuals (graphically). Based on these tests, no data transformation was needed for analyses.

6.3. Results

6.3.1. Phase 1: Bleaching damage

The frequency and severity of coral bleaching was markedly reduced under the macroalgal canopy, even within colonies (Fig. 6.1). At both reefs, the percentage of corals bleached was significantly higher in the plots from which the *Sargassum* canopy had been experimentally removed, compared to the plots with an intact algal canopy (Fig. 6.2 and Table 6.1). Overall, 20% of corals were bleached under "normal" conditions (control treatment) for these reefs, compared to 36% where the *Sargassum* canopy had been experimentally removed. Although the average bleaching rate at Great Palm Island (37%) was higher than that at Goold Island (19%) (Fig. 6.2), this difference was not statistically significant (Table 6.1; this may reflect limited power of the study).

Fig. 6.1. Photograph showing reduced bleaching on coral tissue which was shaded by *Sargassum* canopy: the right side (arrow) of the *Porites* sp. shown was underneath the *Sargassum* canopy, and was not bleached, whereas the right side was not shaded and was bleached.

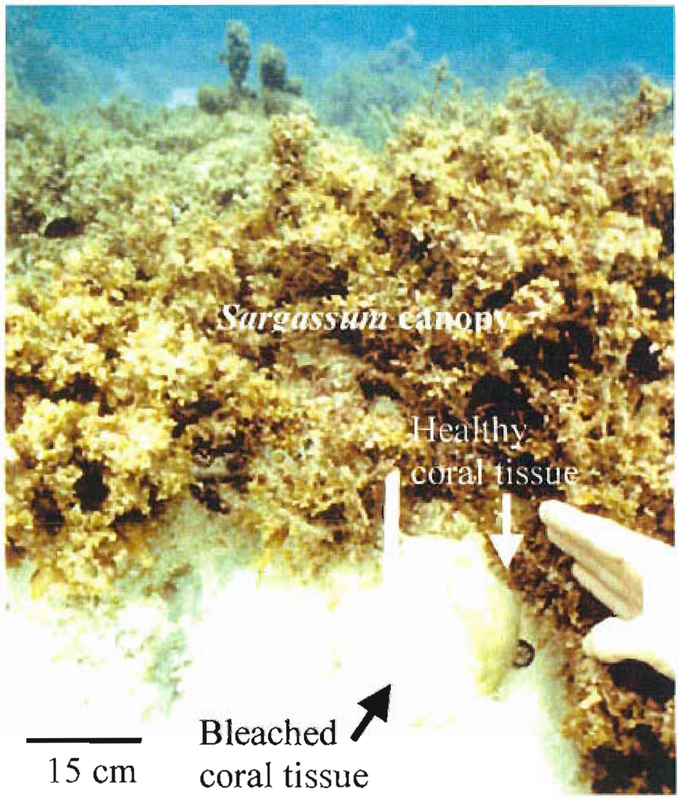


Fig. 6.2. Graph showing proportion of percent cover of all coral tissue considered bleached (means ± S.E.M. of 8 plot replicates) in plots with *Sargassum* canopy removed (Removal Treatment) or left intact (Control Treatment), shown separately for reefs at Goold Island; and Cannon Bay at Great Palm Island.

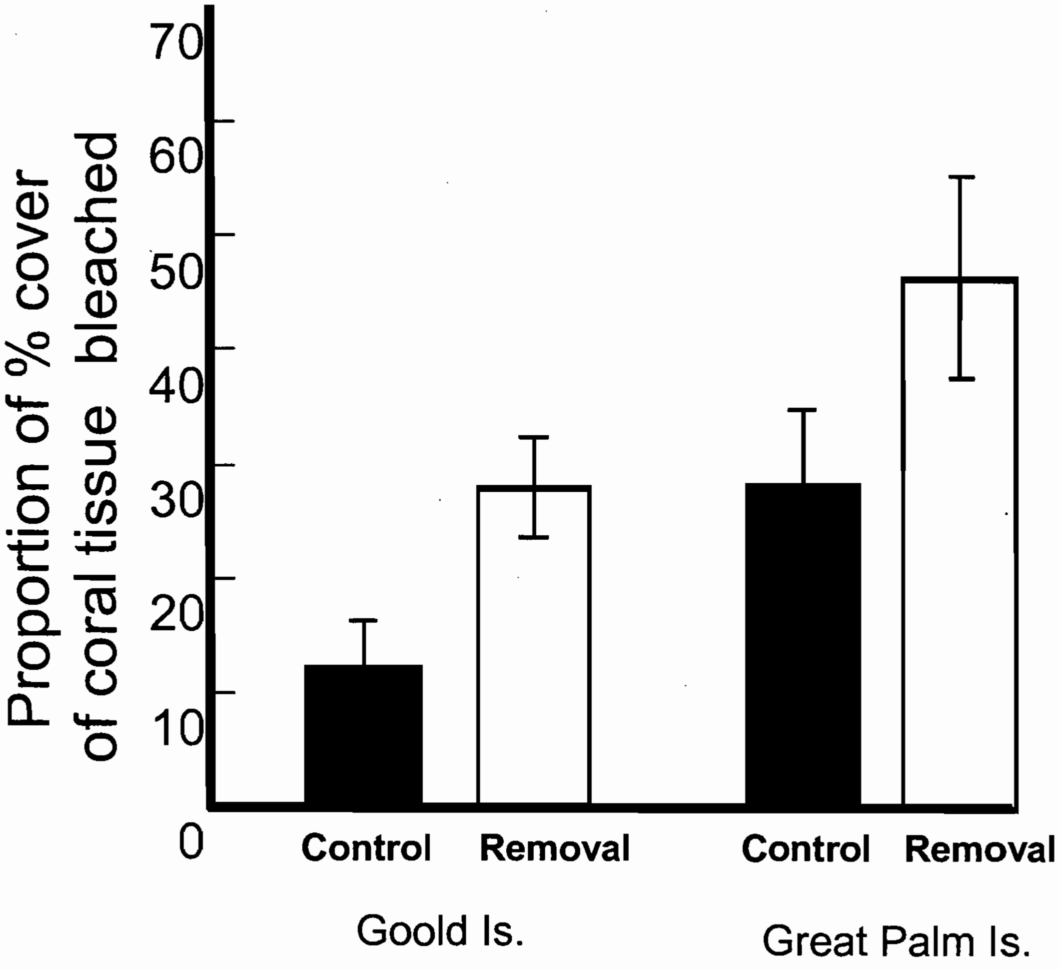


Table 6.1. Analysis of variance of the effects *Sargassum* canopy on the percentage of corals bleached. Homogeneity of variance test is shown as Cochran's C, the critical value for C is 0.68; data are not transformed.

Source	df	Mean-Square	F-ratio	P	%SST	Conclusion
Reef	1	1201	5.5	0.134	32%	ns
Treatment	1	1124	19.3	0.048	30%	Rem. > Ctr.
Reef * Treatment	1	2	0.1	0.883	< 1%	ns
Site(Reef)	2	219	3.7	0.210	12%	ns
Treatment*Site(Reef)	2	58	0.6	0.590	3%	ns
Residual	8	103			22%	
Cochran's C = 0.26						

The effects of the algal canopy were consistent at the two reefs and between sites within reefs, and between reef differences were consistent for both treatments (i.e interaction effects between treatments and sites and reefs were small and not significant). Spatial variation between sites within reefs also was relatively small and not significant.

Bleaching rates within genera at both reefs (Fig. 6.3A and 6.3B) indicate that the canopy effects were consistent in direction across most genera, with most genera showing reduced bleaching under the canopy. However, there is considerable variation in the magnitude of these effects between coral genera. For example, at Goold Island, bleaching rates of *Porites, Acropora and Favites* appeared to be most strongly protected by the canopy, whereas *Galaxea* showed little difference between treatments. In contrast, at Great Palm Island, *Porites, Pocillopora* and *Goniastrea* appeared to be most strongly affected by the treatments. In addition to the treatment effects, there was also within treatment variation between coral genera in terms of their susceptibilities to the bleaching effect. For instance, *Acropora* seemed to be the most susceptible to bleaching compared to other coral taxa, especially at Great Palm Island where almost 100% of the *Acropora* were bleached.

6.3.2. Phase 2: The recovery of selected bleached corals

Of the corals recorded as severely bleached in Phase 1, qualitative observation suggested that most had died by the commencement of phase 2. Of the tagged, bleached colonies on both reefs, most were able to recover from bleaching within eight months (Fig. 6.4), although qualitative observations suggest that a significant proportion of more severely bleached corals were already moribund by the commencement of this study (and hence excluded from these results). Although there was very little difference

Fig. 6.3. Graphs showing proportion of percent cover of bleached corals within coral genera (means ± S.E.M of 8 plot replicates) for both treatments, *Sargassum* canopy present (control) and *Sargassum* canopy removal. Eight most abundant genera were chosen for each reef; A. Goold Island, and B. Canon Bay, Great Palm Island.

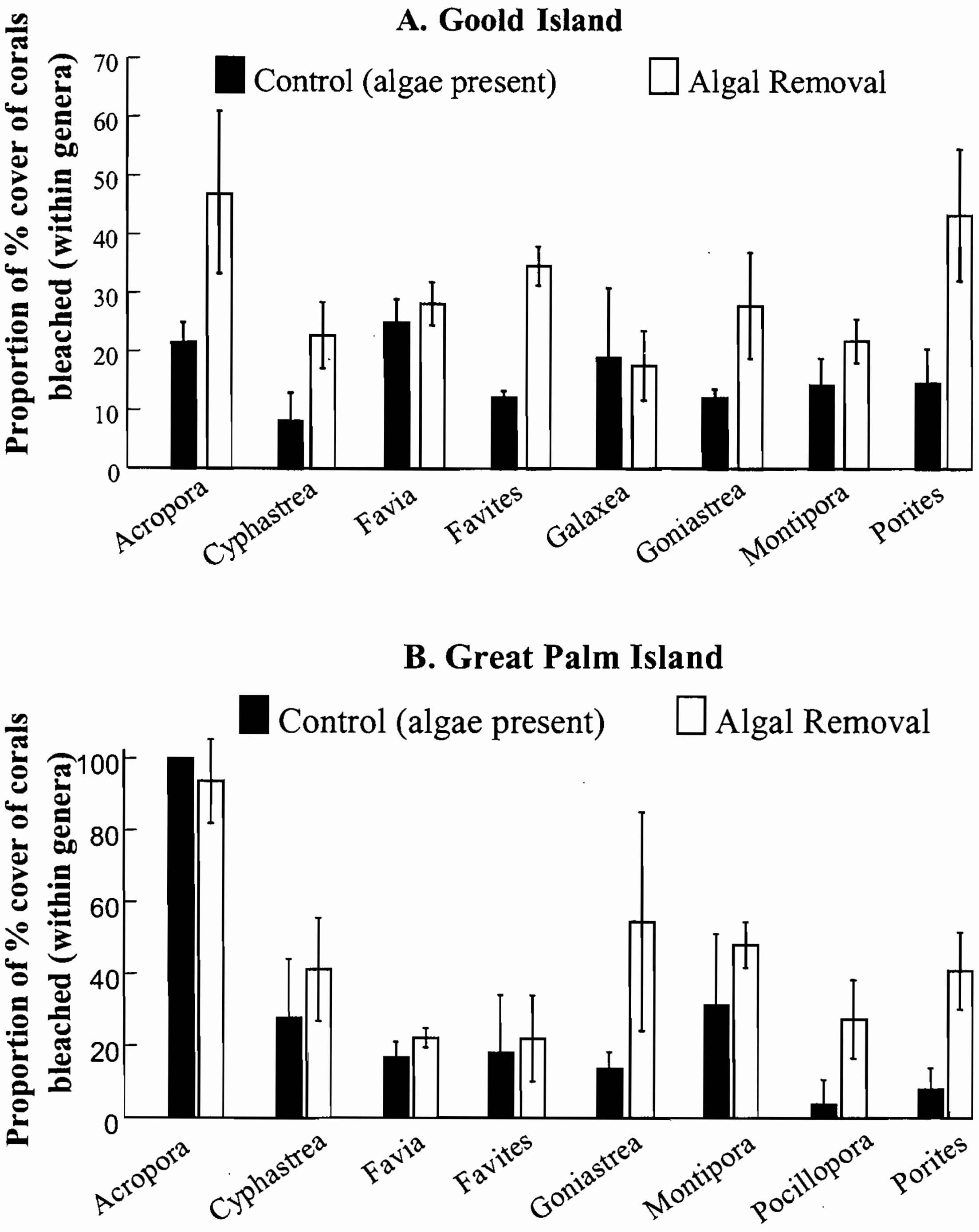
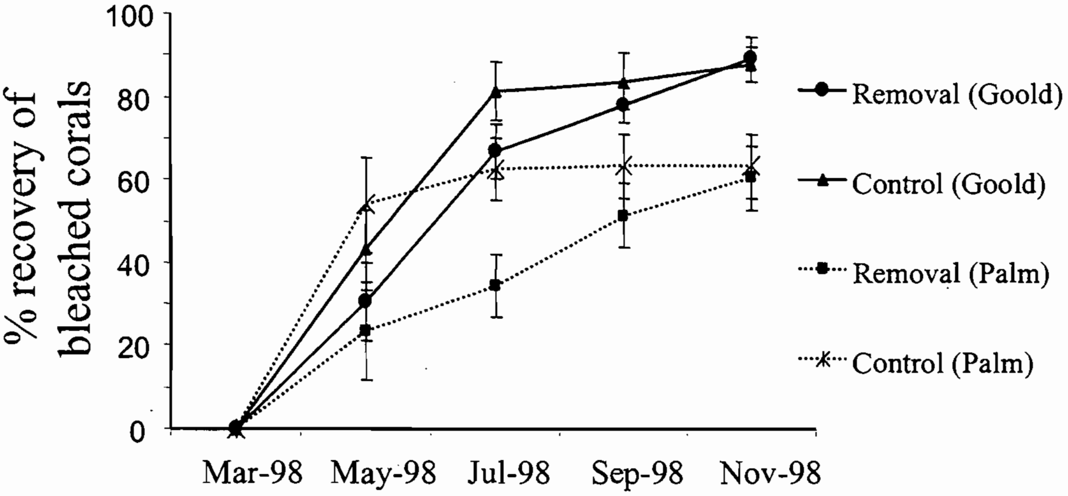


Fig. 6.4. The averages of recovery rates (means ± S.E.M) of the selected bleached corals within each treatment and reefs (n = 27 for each treatment at Goold Island, while at Great Palm Island n = 21 for Removal treatment and n = 25 for Control treatment), n = number of individual coral colonies tagged.



in final recovery rates between the two treatments (Table 6.2), there was a tendency for earlier recovery of bleached coral in plots with the *Sargassum* canopy intact (control plots). However, ignoring differences in generic composition of the selected corals, average recovery across all taxa was considerably higher for both treatments at Goold Island (88%) than at Cannon Bay (62%), although this effect is confounded by the a priori differences in generic composition of the selected corals. Only one genus, *Porites*, had sufficient replicate colonies at both reefs to allow meaningful statistical comparison between reefs within genus. Although average recovery of *Porites* tended to be higher at Goold Island than at Great Palm Island (Fig. 6.5), this difference was not statistically significant (P = 0.15, Kruskal-Wallis test).

In general, there was little variation in the overall recovery rate of the tagged bleached corals within and between the two reefs (Fig. 6.5). The coral genera *Porites, Favia* and *Favites* at Goold Island showed relatively high recovery rates (~ 90%). In comparison, recovery of *Pocillopora* was very poor at this reef, although this result is based on only two colonies (as only two bleached but living colonies were found within the experimental plots). The Favid corals at Great Palm Island also showed very high recovery rates, while *Pocillopora, Porites,* and *Montipora* show moderate recovery. Although *Acropora* was not individually monitored (as most colonies had already died when this phase commenced), it appeared that recovery rate of this taxa, especially at Great Palm Island, was very low.

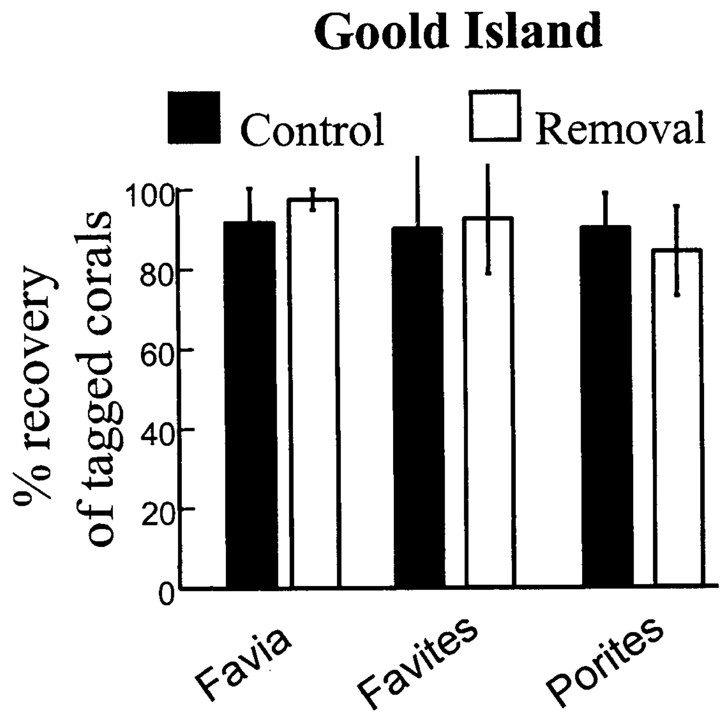
Most of the bleached corals had either recovered or died by July 1998, approximately four months after the bleaching, with the exception of corals in the control plots at Great Palm Island, which recovered more slowly. Thirty nine percent of the tagged corals reached full recovery by May 1998, indicating that most of the surviving corals needed about two to five months to regain their normal microalgal

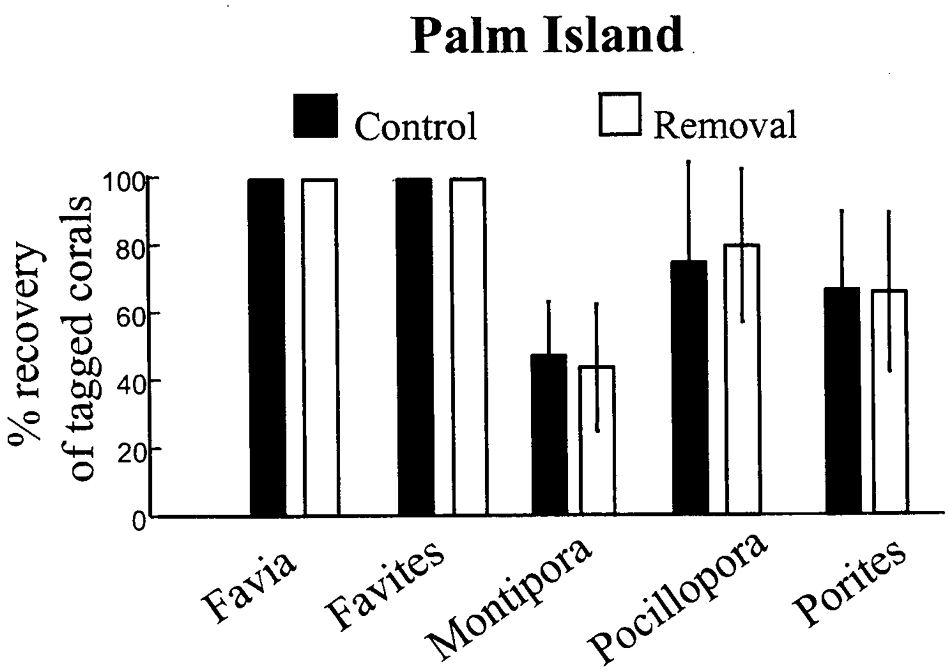
Table 6.2. Analysis of variance of the effects *Sargassum* canopy on the recovery rates of selected bleached corals, at the end of the experiment. Note as for Table 6.1.

Source	df	Mean-Square	F-ratio	P	%SST	Conclusion
Reef	1	2819	44.6	0.022	66%	Goold > Palm
Treatment	1	2	< 0.1	0.914	< 1%	ns
Reef * Treatment	1	16	0.1	0.773	< 1%	ns
Site(Reef)	2	63	0.4	0.695	3%	ns
Treatment*Site(Reef)	2	144	1.1	0.365	7%	ns
Residual	8	126			24%	

Cochran's C = 0.49

Fig. 6.5. Graph showing the percentages of the recovery rates of selected corals (means ± S.D.) of each coral genera (based on number of colonies).


Goold Island


Palm Island

endosymbionts (zooxanthellae). Coral deaths from bleaching mostly took place within the first one or two months and the skeletons of those dead corals were rapidly colonised by filamentous algal turfs.

6.4. Discussion

The results of this study are significant for several reasons. Firstly, they provide an unusual example of macroalgae benefiting or protecting corals, rather than competing with them, as generally assumed. Thus the results demonstrate the considerable variability possible in coral-algal interactions. Secondly, the results provide indications of the potential variability in bleaching and recovery rates, between locations, habitats, and taxa, and specifically suggest that bleaching damage on inshore reefs of the GBR may have been ameliorated by the widespread and abundant canopy-forming algal beds. Thirdly, they show that the effects of this disturbance on the corals were not consistent with the idea that corals are more vulnerable on reefs more strongly influenced by terrestrial runoff.

The increase in overall coral bleaching in plots from which the normally abundant canopy of macroalgae had been experimentally removed suggests that the algal canopy actually provided protection from the factors that caused the coral bleaching. The likely causes of this bleaching include low salinity, high temperature, and high UV light intensity (Gates 1990; Glynn and D'Croz 1990; Brown and Ogden 1993; Brown 1997; Podesta and Glynn 1997); light intensity is considered to have a particularly crucial role in coral bleaching (Brown 1997; Jones et al. 1998). Therefore it seems likely that the macroalgal canopy reduces damage to the corals primarily by decreasing exposure to high UV light intensities. The algal canopy would reduce UV light by shading, as shaded corals were generally less affected by the bleaching (e.g.

beneath tabulate corals, pers. obs.). The canopy may have also reduced temperature stress, either by shading, or by trapping a boundary layer of cooler water. It is also possible that this boundary layer reduced coral stress from low salinity floodwater plumes, although salinity was apparently not a widespread contributor to the 1998 mass bleaching on the GBR. Evidence is available from temperate areas for similar effects of algal canopies: such canopies can dramatically reduce thermal stress (e.g. Salles et al. 1996) and water movement (McCook and Chapman 1991). Similar effects may have contributed to the more rapid recovery of corals under the canopy (Fig. 6.4). It is important to recognize that, given that the effect of the algae appeared to depend on the canopy, and that the entire coral population at these sites consists of colonies small enough to be covered by the algal canopy, the effect is likely to be limited to corals small enough to be protected by such a canopy.

It appears likely that the effects of the canopy on bleaching would persist as a long-term effect on coral mortality. Although the effects on recovery had disappeared by ten months (Fig. 6.4), this refers to the recovery of similarly bleached corals in each treatment. As more corals were bleached in the canopy removal treatment, the net bleaching damage and mortality would remain higher in that treatment. Further, although such a severe bleaching event represents an relatively rare cause of coral mortality (but see also Hoegh-Guldberg 1999), so that the beneficial effects of the algae observed here are probably exceptional, it is worth emphasising that the 1998 bleaching event probably represents the major cause of coral mortality on these reefs over a relatively long-time scale. As such, the protection provided by the algae, however exceptional, may have real, long-term consequences and significance for coral community structure.

The variability in bleaching effect (Figs. 6.3) suggests that some coral genera are more susceptible to bleaching than others. In particular, the branching *Acropora* spp. seem to be most strongly affected (see also Davies et al. 1997; Spencer et al. 2000). For example, at Great Palm Island almost 100 % of *Acropora* were bleached (Fig 6.3B), while other taxa were approximately 20-40% bleached. Previous studies have suggested that bleaching-related mortality is generally higher in branching species, particularly *Acropora*, than in many massive corals (Davies et al. 1997; Berkelmans and Oliver 1999). Further, the protection provided by the algal canopy, although fairly general, did vary considerably in extent among genera. This raises the possibility of a synergistic effect of the bleaching event and the algal canopy on long-term coral community composition. Most bleaching related coral mortality at these sites occurred within one to two months after the bleaching event. This is consistent with the observations of Berkelmans and Oliver (1999), who reported that bleaching-related mortality took place after 5-19 weeks.

In contrast to the general expectation that corals in more eutrophic conditions are more stressed (e.g. Tomascik and Sander 1987) and are thus more vulnerable to any natural disturbances, the overall coral bleaching damage in this study was higher and recovery lower at Great Palm Island than at Goold Island (Fig. 6.2 and 6.3). Although Goold Island is more strongly influenced by terrestrial inputs of sediments and nutrients, coral survival was consistently better at that reef than at Cannon Bay, as previously found for massive corals competing with filamentous algal turfs on the same reefs (McCook 2001). In combination with the higher abundance of corals at Goold Island (McCook 1999), the available direct evidence is not consistent with the suggestion that terrestrial runoff places corals at greater risk from competition with benthic algae on inshore reefs.

In summary, the results of this study provide an exceptional example of a coral-algal interaction in which benthic macroalgae actually benefit the corals, thereby demonstrating the full extent of possible variability in outcomes and processes of coral-algal interactions. These results should certainly not be taken as indicating that macroalgal canopies are generally beneficial to coral populations, since the context for the effects reported here was an exceptional and rare event. The results by no means disprove the potential processes by which corals may be inhibited by abundant macroalgae, but they certainly provide further evidence that abundant macroalgae should not be assumed uniformly detrimental to inshore reefs without much more information. Macroalgae clearly have more diverse potential effects on corals than have been reported (see General Discussion) and this diversity may have important long-term ecological and environmental consequences.

CHAPTER 7. General Discussion

7.1. Variable outcomes of coral-algal interactions between species and between functional groups

The outcomes of coral algal interactions involving different algal species and/or types (Chapters 2-6) appear to be highly variable, varying between strong, and partially reciprocal competitive inhibition of corals by algae (Chapters 4 & 5) to negligible (Chapters 2 & 3) or even beneficial or protective effects (Chapter 6). For example, although most filamentous algae studied had negligible effects on corals, and were apparently unable to colonise live coral tissue, I identified two species, *A. tenue* and *C. huysmansii*, that were able to do so, with lethal effects on the coral tissue (Chapters 2 and 3). The corticated red alga, *H. pannosa,* appeared to cause very minor damage to the coral tissue (Chapter 3). In contrast, the creeping foliose brown alga, *L. variegata* could effectively overgrow and kill corals (Chapters 4 and 5). Interestingly, although canopies of leathery algae (e.g. *Sargassum* spp., *Cystoseira* spp) could reduce coral recruitment and growth (unpub. data, see also McCook et al. 2000a), these canopy forming macroalgae could also benefit the corals by reducing the effects of bleaching damage (Chapter 6). As reviewed in Chapter 1, several studies have previously demonstrated differing effects of macroalgae on corals (e.g. Fishelson 1973; Potts 1977; Hughes 1994a; Tanner 1995; McCook 2001). However, the results presented in this thesis considerably extend the range of taxa, algal and coral types, and outcomes that have been studied, and provide clear experimental evidence for the causality of the range of effects observed. Taken together, the studies thus provide an opportunity to explore the nature of the variability in the interaction, and how it relates to the properties of the competing organisms.

For example, as illustrated in the above overview, the outcomes of coral-algal interaction in this thesis varied, not only between algal functional groups (e.g. Littler 1980; Steneck and Dethier 1994), but also between taxa within the same functional groups. Between functional groups, there was considerable difference in the effects of the general mixed filamentous algal turfs, which had relatively minor or no effect on corals (Chapters 2 and 3), compared to the creeping foliose alga *Lobophora* that could effectively overgrow and kill corals (Chapters 4 and 5). However, there was also a dramatic contrast within the filamentous algal functional group, between the lethal effects of the two filamentous red algal species, *A. tenue* and *C. huysmansii*, and the relatively benign effects of mixed algal turfs or the large filamentous green alga *Chlorodesmis* spp (Chapters 2 and 3). Indeed, the results of the canopy removal experiment, in which the same algal canopy protected established corals from bleaching (Chapter 6) and inhibited growth of established corals and recruitment of new corals (unpubl. data), demonstrates a marked contrast in the interaction between the same taxa under different circumstances (bleaching c.f. normal conditions) or life-stages (established corals c.f. recruits).

Although it is clear that extrinsic factors, such as nutrients, herbivores (e.g. Chapters 2, 4, and 5) or disturbances such as bleaching (Chapter 6; McCook et al. 2000b), can have major effects on competitive outcomes, it is also clear from the studies presented here that there is considerable variability in the interaction that is intrinsic to the competing taxa. As this variability must derive from properties of the algae and corals, it worthwhile to reflect on the properties most likely to be relevant to the interaction. In order to do this, it is necessary to consider the possible mechanisms by which corals and algae can affect each other.

Review of the literature suggests that there are limited numbers of mechanisms by which algae can directly inhibit corals and vice versa, as summarised in Table 7.1. There are 6 distinct mechanisms by which algae are able to directly compete with corals for space or light, as well as a number of indirect processes, not discussed here. Although various studies refer to energetic or metabolic costs of interactions as a competitive process (leading to e.g. reduced growth or reproduction), these costs are actually consequences of the interaction, not a kind of competition.

This mechanistic approach, by clarifying the processes of coral-algal competition, provides a basis for interpreting the variability in the outcomes of that competition. For example, the differences in competitive interactions among different algal functional groups can be largely understood in terms of the differences in potential mechanisms by which the algae can affect the corals. A creeping, foliose alga (e.g. *L. variegata*, Chapters 4 & 5) will be able to effectively smother and shade underlying corals, in contrast to filamentous algae (Chapters 2 & 3) and canopy forming leathery macrophytes (e.g. *Sargassum* species with a small attachment holdfast and no vegetative dispersal; Chapter 6). Many of the ecological properties that define the algal functional groups (size, robustness, calcification, growth rates) are strongly related to the alga's potential for the competitive mechanisms in Table 7.1, so it is not surprising that functional groups provide a strong basis for interpreting the variability in coral-algal competition. In a recent review, this approach was extended to list, for each combination of algal functional group and coral life-form, the subset of mechanisms in Table 7.1 by which algae might inhibit corals (Table 6 in McCook et al. 2001). As outlined in that review, this tabulation apparently provides a useful framework to understand the broader patterns of coral algal competition, and suggests some useful

Table 7.1. Mechanisms for competition between corals and algae.

Adapted from Schoener (1983), Carpenter (1990), Olson and Lubchenco (1990), Lang and Chornesky (1990), Karlson (1999), modified for corals and algae specifically. [1] Shading or overtopping may include establishment of dense canopy, with numerous effects on the chemical and physical conditions, hydrodynamics, etc. [2] Whiplash, often cited as damaging corals, will generally also be very detrimental to the softer algal tissue. [3] Allelopathic chemical effects have been demonstrated on soft corals (de Nys et al. 1991) and hard corals (Littler and Littler 1997a; see Figures 2.2 & 3.1). [4] Canopy forming macrophytes will actually occupy little of the substrate, but may still form an effective barrier to coral settlement. [5] Epithelial sloughing and mucus secretion are defence mechanisms against epibiotic colonisation, rather than mechanisms for expansion (Lang and Chornesky 1990; Littler and Littler 1999; pers. obs.).

Algal inhibition of corals	Coral Inhibition of algae	Includes:	Categories
Overgrowth	Overgrowth	smothering;	direct, interference, overgrowth (Chapters 4 & 5)
Shading[1]	Shading	overtopping;	indirect, exploitative, consumptive (Chapter 6)
Abrasion	Abrasion	whiplash[2];	direct, interference, encounter (Chapter 3)
	Stinging, etc	including sweeper tentacles & polyps, mesenterial filaments	direct, interference, encounter
Chemical[3]	Chemical	allelopathy	direct, interference, chemical (Chapters 2 and 3)
Pre-emption / Recruitment barrier[4]	Space Pre-emption		direct, exploitative, consumptive (Chapter 6)
Epithelial sloughing[5]	Mucus secretion		defensive mechanism

general patterns. For example, it seems that coral recruits are likely to be vulnerable to more of the mechanisms in Table 7.1 than established corals.

However, as noted above, the mechanisms listed in Table 7.1 also provide a basis for interpreting the variation within algal functional groups. For example the only apparent way that *A. tenue* and *C. huysmansii* can be so effective at colonising and killing coral tissue, even killing tissue some distance from the filaments (Figures 2.2 & 3.1), compared to all the other species in the filamentous algal turfs, is by means of secondary metabolites (allelochemicals) that enable them to overgrow and kill the corals.

Using this approach, I have synthesized the results of this thesis in Table 7.2 by listing all the algal taxa studied; the relevant algal functional groups; the potential mechanisms involved in the interaction; and the effects of those mechanisms on the corals. The interpretation of the patterns among filamentous algae as indicating allelopathic effects were outlined above. The creeping, adherent morphology of *L. variegata,* combined with a relatively robust and opaque thallus, would effectively block light and water flow, so the alga may be expected to be very effective at smothering and killing corals. The contrasting effects of *H. pannosa,* also a corticated alga, can be interpreted in terms of the relatively brittle and porous (reticulate) and translucent thallus structure, making it relatively ineffective at blocking light and water flow, with the consequence that it had relatively minor effects on overgrown corals. Most of the effects of the leathery macrophytes (last row in Table 7.2) can be attributed to their canopy-forming structure, which means that they directly overgrow relatively little substrate, but provide shade and may affect water flow. Although this canopy may generally be detrimental to coral growth, and recruitment, in the specific case

Table 7.2. Summary of the different studies on this thesis, and including the potential mechanisms and possible effects of different types of algae on corals. Algal functional groups are based on Littler 1980; Littler and Littler 1984; Steneck and Dethier 1994.

Algae involved	Functional group	Potential mechanism	Effect on corals
Mixed algal turfs	Filamentous (turf)	Vary	No major effect
Corallophila huysmansii	Filamentous (turf)	Allelochemical	Coral mortality
Anotrichium tenue	Filamentous (turf)	Allelochemical? And sediment trapping	Coral mortality
Chlorodesmis spp	Filamentous (not turfing)	Abrasion	No major effect
Lobophora variegata	Creeping corticate foliose	Overgrowth	Coral mortality
Hypnea pannosa	Corticated macrophyte	Shading/overgrowth	No major effect/minor tissue damage
Sargassum spp *Cystoseira* spp & *Turbinaria* spp	(Canopy forming) Leathery macrophytes	Shading/overtopping/ physical barrier	Reduced coral bleaching

documented here it appears that the shading provided protection from bleaching. Thus it appears understanding the mechanisms by which corals and algae interact (Tables 7.1 & 7.2) can provide an effective approach for interpreting and integrating the variable processes and outcomes of coral-algal interactions, both in this thesis and, presumably, on a wider basis.

7.2. The importance of interactions between nutrients, herbivory and coral-algal competition: the processes by which algae overgrow corals.

Both top-down and bottom-up explanations for coral reef phase shifts depend on coral-algal competition. The results in Chapters 4 and 5 not only provide much needed direct comparisons of the effects of all three factors and their relative importance, but also demonstrate the value of factorial experiments in exploring the interactions between these factors, and hence the process of algal replacement of corals. These experiments (Chapters 4 & 5) strongly support the mechanistic view, summarised by McCook (1999, see also Hatcher and Larkum 1983; Szmant 1997) and shown in Fig. 1.1. According to this perspective, if increased nutrient supply enhances daily algal growth or production rate, this can only enhance the standing crop of algal abundance or biomass, and consequently enhance algal competitive overgrowth of corals, *if* algal losses from the herbivore consumption remain unchanged. Empirically, this is only the case where herbivores are scarce; in general on coral reefs, algal consumption can increase dramatically to match production, leaving little algal production to accumulate as increase in biomass (e.g. Hatcher and Larkum 1983; Russ and McCook 1999), and thereby obviating any competitive consequences for corals. In contrast, changes in algal consumption by herbivores can result in dramatic changes in algal abundance. The key distinction in this perspective is that algal consumption and production are not independent, nor reciprocally dependent: consumption will track production (when herbivores are sufficiently abundant), but not vice versa. However, sufficient reduction in herbivores will allow excess production to accumulate as increased standing biomass of algae. Finally, Fig. 1.1 shows that the competitive consequences, for coral populations, of any change in algal abundance, due either to increased production or decreased consumption, will depend critically on the nature of the competitive interaction between corals and algae.

The experiments in this thesis clearly demonstrate that the effects of herbivores and nutrients on coral mortality are largely depended on algal overgrowth (competition). Although widely accepted, the demonstration, throughout this thesis, of the considerable variation in the nature and strength of these competitive effects demonstrates the potential variation in consequences for corals (McCook et al. 2001). Although the experiments in Chapters 4 and 5 demonstrated marked effects of *L. variegata* on the corals, the contrasting and often minor effects of other algae on corals ((e.g. general algal turfs Chapters 2, 3 and McCook 2001, *Hypnea pannosa* Chapter 3, *Sargassum*: Chapter 6) suggest that both nutrients and herbivores would have little effect on the corals in those situations. Clearly the strength of both top-down and bottom-up processes will depend on the nature of the competitive interaction, which will vary considerably with the taxa involved, and the circumstances (McCook et al. 2001).

When algae were effective competitors with corals (Chapters 4 and 5), the marked effect of herbivores on algal overgrowth provides strong evidence for the importance of herbivores to competitive outcomes. Thus, these results not only support the critical role of herbivory in controlling macroalgal abundance on these reefs (Sammarco 1983; McCook 1996; McCook 1997; Russ and McCook 1999) and on coral reefs more generally (Sammarco 1982; Lewis 1986; Hughes 1994a; Miller and Hay

1998), but also demonstrate effects of herbivores on corals as a consequence of the effects on macroalgal competitors (Miller 1998). Although widely assumed, there is surprisingly little direct evidence demonstrating this process.

Herbivores can have large effects on these competitive interaction *at all levels of nutrients*, whereas nutrient enhancement may have relatively small effects on algal growth, and those effects were critically dependant on herbivore access: nutrient effects on algal growth were only expressed as increased algal biomass (and consequent increased competitiveness with corals) *when herbivores were excluded.* Thus the results of these two experiments provide valuable support for the mechanistic perspective in Fig. 1.1 and outlined above. Interactions between nutrient and herbivore effects are not reciprocal: herbivore effects can overwhelm any nutrient effects, whereas nutrient effects do depend on herbivory. The effects of both processes on corals depend on changes in algal abundance and competitiveness.

It is also important to note that even where nutrient effects are greatest (in the absence of herbivores and presence of algal competitors) those effects were relatively small compared to those of competition and herbivory. This further emphasises the need for studies which demonstrate nutrient enhancement of algal growth to be placed in an appropriate ecological context: not only may the nutrient effects depend on the intensity of processes such as competition and herbivory, but the effects may be relatively minor anyway.

Overall, the experiments provide clear support for the above view of the mechanisms in Fig. 1.1, and all chapters demonstrate the variability inherent in the critical step of coral-algal competition. Thus, it is important to recognise that the overall outcomes of these processes will depend not only on circumstances such as levels of herbivory or nutrients, but also on the coral and algal taxa involved (McCook et al.

2001). Although the studies reported here demonstrate a wide range of outcomes, they are by no means comprehensive, and the patterns found should not be taken as general. In particular, the results in other chapters show that the *L. variegata – P. cylindrica* interaction, although an excellent experimental combination, does not represent a general paradigm.

Importantly, the results of the factorial experiments also demonstrate the value of viewing the top-down and bottom-up perspectives from a process-oriented perspective, which addresses the mechanisms by which different factors can operate, rather than simply continuing to apply empirical tests to the apparent dichotomy. Although small-scale experiments such as these should not be directly scaled up to community level changes such as phase shifts, the results do demonstrate the value of understanding and testing the mechanisms and processes involved, and the relationships between them. This mechanistic approach can provide a broader basis for the interpretation and management of phase shifts. For example, as indicated in Fig. 1.1, many natural disturbances (e.g. bleaching, storm damage, crown-of-thorns outbreaks) may kill corals, which subsequently become overgrown by algae. Such events will result in similar outcomes to top-down and bottom-up mediated change but the causality is reversed: decreased coral abundance is the cause, not the consequence, of increased algal abundance (Fig. 1.1). Such distinctions may have important consequences for the interpretation of coral-algal phase shifts in the context of reef degradation.

7.2.1. Implications for interpretation and management: Coral algal competition in the context of reef degradation.

The processes of how variable herbivores, nutrients, and disturbances may affect competitive outcomes between coral and algae have important implications for the interpretation, prediction and management or prevention of reef degradation or phase shifts and management (Hatcher and Larkum 1983; Hodgson 1994; Hughes 1994b; McCook 1999). For example, on the GBR, increased inputs of terrestrial sediments and nutrients may make relatively minor direct contributions to algal overgrowth of coral populations (McCook et al. 1997; Umar et al. 1998; Russ and McCook 1999) but this contribution may be most significant on inshore reef flats where herbivores are scarce. Changes in terrestrial sediment or nutrient inputs may potentially have serious *indirect* effects (McCook 1999). These impact may not occur directly or immediately, but as failure for the reef to recover from independent natural and anthropogenic disturbances, such as coral bleaching, cyclones or freshwater kills (Kinsey 1988; van Woesik and Done 1997; McCook et al. 2000b). Human impacts on water sediments and nutrients may affect coral algal competition indirectly by affecting herbivore abundance and distribution (e.g. Williams 1982).

McCook (1999) argues that there are several risks associated with such scenarios. For example, over-simplistic understanding of the potential mechanisms by which anthropogenic changes in runoff can cause reef degradation may lead to false rejection of a human impact: if it can be shown that coral mortality resulted from natural events rather than runoff enhanced algal overgrowth, then it may be asserted that the degradation is natural, even if there is a failure to recover as a direct result of water quality changes. Management strategies which focus on simple, single causes of degradation (e.g. eutrophication) may ignore other critical processes (such as herbivory, or the need for coral recruitment). The potential for herbivores to absorb increased algal production may even preclude recognition of human impacts on ecosystem function until the system is severely stressed. The variability inherent in coral-algal competition and other processes may have considerable consequences in terms of predicting the outcomes of specific circumstances: a reef with abundant *Sargassum* overtopping healthy coral populations may have far less dire prospects than a reef overgrown by abundant *Lobophora*. Changes in these processes may amount to critical human impacts, but may only be apparent at relatively large temporal and spatial scales, making them very difficult to detect or predict (McCook et al. 2000b). Understanding the processes, variability and interactions between herbivores, nutrients, disturbances, and coral-algal competition has real consequences in terms of interpretation and management of changes in coral-algal dynamics and reef degradation.

7.3. Summary

- Most filamentous algal turfs have relatively minor effects on corals, but *Anotrichium tenue* and *Corallophila huysmansii* are dramatic exceptions to this pattern, being able to overgrow and kill live coral tissue. Available evidence suggests that the most likely mechanism for this ability involved allelochemical substances produced by the algae, although this was not directly demonstrated. In addition, *A. tenue* filaments appear to trap sediments, mucus and detritus, increasing the extent of damage to underlying coral tissue.
- The larger filamentous alga, *Chlorodesmis fastigiata,* although very conspicuous and abundant on Indo-Pacific reefs, also had relatively little effect on coral tissue mortality.
- A corticated red algae, *Hypnea pannosa*, observed living within *P. cylindrica* branches, did not have a major impact on underlying coral tissue, although this alga occupied the branched coral for over a year.

- The foliose creeping macroalga *Lobophora variegata* was a highly effective competitor with *P. cylindrica* corals, since its growth strategy (adherent creeping morphology) could directly overgrow corals, killing underlying coral tissue.
- Although *L. variegata* was the competitive dominant in this interaction, the coral also competitively inhibited the growth of the alga.
- Although large, canopy forming leathery macrophytes can accumulate relatively high biomass with the potential to shade corals, under the unusual circumstances of a large and severe bleaching event, the algae in fact provided protection to corals from bleaching damage.
- Experimental exclusion of herbivores resulted in increased (net) growth of *L. variegata* and consequent overgrowth and death of coral tissue.
- Factorial manipulation of herbivory and nutrients and competition showed that coral algal competition was regulated by herbivore control of algal abundance, and that nutrient enhancement was minor and only influenced algal abundance and hence competitiveness when herbivores were reduced.

7.4. Conclusion

In general, coral algal interactions are widespread on coral reefs, but the competitive outcomes vary with the coral and algal taxa and/or groups involved, and with ecological factors, including nutrient, herbivore and disturbance regimes. This variability may have significant consequences in the context of reef degradation, making it difficult to predict and manage the outcomes and consequences of coral-algal dynamics under varying circumstances.

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Appendix A. Classification of studies according to their levels of evidence on coral-algal competition.

Table 1. Comparison of studies which directly test effects of algae and corals on each other.
Summary table of key aspects of published experimental studies of coral-algal competition (see text; studies are organised by the type of study or evidence, and then chronologically). Impacts are summarised as A. the impacts of algae on corals; and C. the impact of corals on algae; in each case impacts are summarised as: -: negative (competitive); 0: no impact; +: facilitatory or beneficial. Note that both corals and algae will often be mutually inhibitory, but since many studies did not consider the impacts of corals on algae, the impacts represent a biased sample. Methods and evidence listed are only those relevant to this table. Any limitations noted refer only to the interpretative context of this table, and are therefore not to be taken as criticisms of the studies (in most cases the limitations were unavoidable and acknowledged by the authors). The final rows summarise studies of coral recruitment or recovery from experimental lesions, which I have reinterpreted in terms of competition. Algal functional groups are modified from Steneck & Dethier (1994) and abbreviations are: Filamentous (Filament); Foliose; Corticated Foliose, Creeping or Upright (Cort Foliose Creep or Upright); Corticated Macrophytes (Cort Macro); Leathery Macrophytes (Leathery); Articulated Calcareous (Artic Calc); Crustose. Creeping and upright corticated foliose algae refer to the growth habit, often variable within a genotype. CCA = crustose coralline algae; GBR = Great Barrier Reef; *A.* = *Acropora; Ag.* = *Agaricia.*

Reference	Location, region	Impacts, Methods & Evidence			Comments	Algal Taxa / Functional Group	Coral Taxa / Lifeform
		A	C				
Hughes (1989)	Rio Bueno, Jamaica, Caribbean	-		Macroalgal removal treatment & natural encounters; coral bleached or dead where in contact with macroalgae; macroalgae outcompeted coral by overgrowth.	Expt. design not specified but results clearcut.	Unspecified / "Fleshy algae"	*Ag.* spp. + 20 spp listed / Most forms
Coyer et al. (1993)	California, temperate Pacific rocky kelp bed	-		Coral transplantation to different algal abundance; overgrowth of corals after 1 year, corals damaged by brushing; 10 years.	Temperate location; non-reef building coral; results clearcut.	*Cystoseira; Dictyota;* CCA; Kelp holdfast / Leathery; Cort Foliose; Crustose	*Balanophilia* / Solitary (small)
Tanner (1995)	Heron Is., GBR	- 0		Algal removal treatment & natural encounters; energetic cost to corals from algal contact; algae reduced cover, growth and fecundity of some corals but not all, and, importantly, did not affect survival.	Clearcut experiment, limited by low cover of both algae and coral - may underestimate effects.	Various*: / Artic Calc; Crustose; Filament; Leathery; Cort Macro; Cort Foliose	A. brueggemannia; A. cuneata; Pocillopora damicornis / Branching
Miller and Hay (1996)	Nth Carolina, temperate Atlantic; in- offshore gradient	-		Algal removal, coral transplantation, herbivore exclusion, & nutrient enrichment; algae inhibited growth and recruitment of coral, due to shading or abrasion.	Temperate location; non-reef building coral; results clearcut.	Various**/ Leathery; Cort Foliose; Filament; Cort Macro	*Oculina arbuscula* / Branching; Recruits

Table 1 *continued*

Miller and Hay (1998)	Florida, Caribbean	-		Corals transplanted to herbivore exclusion cages with & without algae present; coral growth reduced in presence of algae.	Coral growth rate differences may be slightly confounded by different predator bite rates on corals.	Various *** / Cort Foliose; Artic Calc; Cort Macro; Filament	*Porites porites* / Branching
Jompa and McCook (1998)	Inshore, central GBR; 2 sites 2 reefs: in–off shore gradient	+		Canopy algal removal; algal canopy protected corals from bleaching damage (shading?)	Demonstrates variable impacts of macroalgal beds.	*Sargassum* / Leathery	Diverse / Diverse;
McCook (2001)	Inshore, central GBR	0	-	Removal of massive corals or turf algae along gradient of terrestrial runoff: corals inhibited turf growth more than vice versa; coral success not related to nutrient or sediment inputs.		Various (listed) / Filament	*Porites lobata* / Massive
Recruitment study:							
Heyward and Negri (1999)	Lizard I., GBR & Ningaloo, W. Aust.	+		Calcified red algae induced metamorphosis / settlement of coral larvae	Demonstrates positive impacts of algae on coral. Not intended to address competition.	*Lithophyllum, Hydrolithon, Neogoniolithon, Amphiroa Mesophyllum, Peyssonnelia* / Crustose; Artic. Calc.	*A. millepora;* various / recruits
Lesion Studies							
Bak et al. (1977)	SW Curacao, Caribbean		-	Algal turfs which initially colonised experimental lesions on corals were overgrown by the coral.	Not intended to address coral-algal competition but demonstrates coral overgrowth of colonising algae.	Unspecified / Filament	*Ag. agaricites; Montastrea annularis* / Foliose & Massive
Meesters and Bak (1993); Meesters et al. (1994; 1997)	Curacao, Caribbean	-	-	Colonisation of experimental lesions by algae influenced but did not generally prevent coral overgrowth of the algae. Duration and type of algal colonisation affected recovery.	As above	Unspecified / Filament	*Montastrea annularis; Porites astreoides; Meandrina meandrites* / Massive
Van Woesik (1998)	Okinawa, Japan	-	-	As above	As above	Unspecified; *Padina* / Filament; Cort Foliose	*Porites* / Massive

* *Halimeda, Peyssonnelia, Chlorodesmis fastigiata, Turbinaria, Sargassum, Amphiroa, Caulerpa, Hypnea, Enteromorpha, Padina*

** *Sargassum; Lobophora; Dictyota; Dictyopteris; Zonaria; Ectocarpus; Chondria; Hypnea*

*** *Dictyota, Halimeda, Laurencia, Coelothrix, Galaxaura, Amphiroa, Stypopodium* and filamentous reds.

Table 2. Comparison of experiments which indirectly examine coral-algal competition using herbivore manipulations
Impacts, methods, evidence, comments, functional groups and abbreviations as for Table 1. Note that impact summaries (column A) assume that effects on coral are direct results of increased algae, in turn resulting from herbivore manipulations, and ignore the potential confounding factors (see text). As such experiments can not detect impacts of corals on algae, these are not summarised. [1]Comparisons using damselfish territories as herbivore reductions are confounded by the complex effects of damselfish on composition of algae, coral injury, coral recruitment, nutrient conditions, etc (e.g. Kaufman 1977; Russ 1987).

Reference	Location, Region	Impacts, Methods & Evidence A		Comments	Algal Taxa / Functional Group	Coral Taxa / Lifeform
[1]Vine (1974)	Harvey Reef, Red Sea	-	Settlement plates caged, uncaged and in damselfish territories; observed that invertebrate (incl. coral) recruitment was reduced where algae abundant.	No data given for corals; [1]Damselfish effects confound herbivore exclusion with other effects.	Unspecified / Filament	Unspecified / Recruits
Sammarco (1980; 1982)	Discovery Bay, Jamaica, Caribbean	- 0	*Diadema* density manipulations & removals; no effect of algae on coral recruitment but some effect on survival of recruits and cover of adults; coral recruits overgrew CCAs.	Differences among and between taxa in competitive outcomes; *Diadema* removal alone led to increased coral abundance.	32 spp. listed / Filament; Artic Calc; Crustose	*Ag.* spp.; *Porites* spp. + 15 spp. listed/ Branching; Massive; Foliose; Sub-massive; Recruits
[1]Sammarco and Carleton (1981)	Britomart, GBR	- 0	Settlement plates inside and outside territories & cages; coral recruits shaded by filamentous algae, but no effect of caging on recruitment.	[1]Damselfish effects confounded.	*Palmophyllum; Polysiphonia; Ceramium Gracilariopsis* / Crustose (not calcified); Filament	*A.* & *Seriatopora* + 10 spp. listed / Recruits
Fitz et al. (1983)	St. Croix, Caribbean	- 0	Caged and exposed settlement panels; algal growth in cages reduced coral settlement in one size class, but not in 2 others.	Variable effects.	Unspecified / Various	*Ag.* & *Porites* / Recruits
Hay and Taylor (1985)	St. Thomas, Caribbean	-?	*Diadema* removal; decreased cover of "benthic invertebrates" following algal growth.	Coral cover initially low.	*Dictyota* / Cort Foliose	Unspecified / Unspecified
Lewis (1986)	Carrie Bow, Belize, Caribbean	-	Herbivore reduction by fences; increased algal biomass killed and bleached corals.	Although significant, decline in coral cover only 2%.	Various* / Cort Foliose (Creep; Upright);Leathery; Cort Macro; Filament	*Porites astreoides* / Massive
Stachowicz and Hay (1999)	N. Carolina, temperate Atlantic	-	Removal of symbiotic herbivorous crab led to algal overgrowth (& invertebrates).	Temperate, non-reef building coral.	*Sargassum; Dictyota; Codium; Ectocarpus* / Leathery; Cort Foliose; Cort Macro; Filament	*Oculina arbuscula* / Branching
Lirman (2001)	Florida, Caribbean	-	Algal additions and cages led to inhibition and polyp retraction in corals.	Algal addition treatment unclear.	*Halimeda* & *Dictyota* / Artic Calc; Cort Foliose	3 coral species / Massive

* *Padina; Dictyota; Turbinaria; Gelidiella* + 26 spp. listed

** *Montastrea faveolata; Porites astreoides; Siderastrea siderea*

Table 3. Comparison of evidence for coral-algal competition based on natural experiments and correlations in abundance.
Studies are organised chronologically within approach or theme. Although more studies could be included, the list has been limited to those which specifically invoke coral-algal competition, have been cited in that context, or which I consider noteworthy. "Natural experiment" refers to studies with a specific comparison, but where treatments were not allocated or applied by the researchers; in some cases they are human impacts such as fishing pressure or eutrophication. In most cases, the *Diadema* die-off occurred against a background of overfishing. Where possible, the outcome (O) of the interaction is summarised as: A – Algae overgrew corals; B – No change; C – Corals overgrew algae; impacts are not summarised as causality is intrinsically confounded (see text). Methods, evidence, comments, functional groups and abbreviations as for Table 1. [1]Comparisons using damselfish territories are confounded (see Table 2). Most natural experiments also include or imply negative correlations in abundance of corals and algae. Except where noted, all correlation studies listed indicate inverse relationships between cover of algae and corals, although not necessarily identified as such by authors.

Reference	Location, region	O	Outcomes, Methods & Evidence	Algal Taxa / Functional Group	Coral Taxa / Lifeform
Natural experiment (Algae):					
Crossland (1981)	H. Abrolhos, W. Australia	B	Algae present or absent; coral growth reduced when algae present.	*Sargassum* & *Turbinaria; Eucheuma* & *Laurencia* / Leathery; Cort Macro	*A.* and *Pocillopora* / Branching
Natural experiments (Herbivory):					
[1]Potts (1977)	Heron Is., GBR	A B	Colonisation of coral transplants by damselfish; variable outcome: generally reduced coral growth and survival, but at times growth increased. Confounded by complex effects[1].	Unspecified / Filament	*A. palifera* / Branching
Littler and Littler (1997b)	Great Astrolabe Reef, Fiji	A C	High & low fishing pressure; coral recruits could overgrow turfs, but turfs could also exclude recruits. Temporal & spatial correlation, cover.	~24 spp. listed / Filament; Cort Macro; Artic Calc	*A.* / Branching?; Recruits
Ruyter van Steveninck and Bak (1986)	Curacao, Caribbean	A	*Diadema* die-off; cover through time; corals & algae generally but not always inversely related.	*Lobophora; Dictyota; Halimeda; Valonia; Wrangelia;* turfs / Cort Foliose; Art Calc; Filament; Crustose	*Ag. agaricites* + 21 spp listed/ Foliose; Massive; Branching; Encrusting
Liddell and Ohlhorst (1986)	Jamaica, Caribbean	B	*Diadema* die-off; cover before and after, along depth gradient; changes in coral cover variable, even increased.	*Dictyota*; *Lobophora; Halimeda* + 7 spp. listed/ Cort Foliose; Artic Calc; Filament; Leathery; Foliose	Unspecified; *A.* / Branching

Table 3 *continued*

Natural experiments (Herbivory and Disturbance):					
Hughes (1989; 1994a; 1996)	Rio Bueno, Jamaica	A	*Diadema* die-off and hurricane: Temporal and spatial neg. correlations in algal and coral cover, and coral recruitment. Effects variable with coral lifeform.	*Dictyota; Padina; Halimeda; Lobophora* & others / Filament; Crustose; Cort Foliose (Creep; Upright); Artic Calc; Leathery	*Ag.* spp. + 20 spp listed / Most forms
Goreau (1992)	Jamaica, Caribbean	A	*Diadema* die-off, hurricane, eutrophication (review); algae increased with coral decreases.	*Lobophora; Ceramium; Dictyota; Chaetomorpha; Halimeda; Sargassum* / Cort Foliose; Filament; Artic Calc; Leathery	55 spp. listed / Most forms
Steneck (1994)	Discovery Bay, Jamaica; St. Croix, Caribbean	A B	*Diadema* die-off, hurricane, temporal and spatial neg. correlations in cover of varying strength, also recruits.	*Dictyota; Laurencia; Lobophora* / Cort Foliose; Cort Macro; Crustose	8 spp. listed / Branching; Massive; Foliose
Shulman and Robertson (1996)	Panama, Caribbean	A	*Diadema* die-off, bleaching; temporal neg. correlation of cover of corals and algae over 7 yrs; some corals no change.	*Dictyota; Halimeda* / Cort Foliose; Artic Calc	*Ag. agaricites; Ag. tenuifolia; Porites* spp.; *Millepora* spp. / Foliose; Massive; Digitate
Rogers et al. (1997)	Virgin Islands, Caribbean	A	Hurricane, herbivorous fish; decrease in corals and increase in algae over 7 yrs.	*Dictyota; Liagora;* / Cort Foliose; Cort Macro	*Montastrea annularis; Ag. agaricites; Siderastrea siderea; Montastrea cavernosa / Massive; Foliose*
Natural experiments (Disturbance):					
Connel et al. (1997)	Heron Is. and Jamaica	A	Cyclones; v. long term (30 yrs), neg. correlations in algal and coral cover and coral recruitment.	Unspecified	Unspecified + Recruits
Banner (1974)	Kaneohe Bay, Hawaii	A	Eutrophication gradient: Categorisation of algal and coral abundances, showing inverse relationship.	*Dictyosphaeria cavernosa* / Foliose	*Porites compressa* / Digitate
Smith et al. (1981)	Kaneohe Bay, Hawaii	A	Eutrophication gradient & before - after diversion: Algal biomass, cover of corals and algae. Little relevant data included.	*Dictyosphaeria cavernosa* / Foliose	*Porites compressa* / Digitate

Table 3 *continued*

Hunter and Evans (1995)	Kaneohe Bay, Hawaii	A C	Nat. Expt. spatial & temporal correlations, cover; several reversals in abundance; coral not inversely related to algae at some sites.	*Dictyosphaeria cavernosa* / Foliose	5 spp. listed / Most forms
Birkeland (1977)	Panama, Pacific		Oligotrophic and upwelling areas; survival of recruits higher with less algae; Filamentous algae trap sediments which kill corals.	Unspecified / Filament	Unspecified / Recruits
Wittenberg and. Hunte (1992)	Barbados, Caribbean		Eutrophication gradient; higher coral juvenile size and survival where algae and sediments less abundant.	Unspecified	*Porites; Diploria; Ag. agaricites* / Massive; Foliose
Genin et al. (1995)	Gulf of Eilat, Red Sea		Eutrophication gradient; Coral condition inversely related to abundance of algal bloom.	*Enteromorpha* / Filament	* / Branching; Massive
Miller and Hay (1996)	Nth Carolina, Atlantic		Inshore-offshore gradient; temperate; algal cover inversely related to coral abundance.	See Table 1	See Table 1
Spatial and temporal correlations:					
Coles (1988)	Arabian Gulf	B	Spatial & temporal correlations in cover	*Dictyota; Lobophora; Sargassum* / Cort Foliose; Leathery	5 spp. listed/ Branching; Massive
Van den Hoek (1978)	Curacao, Caribbean		Spatial correlation in cover: depth etc gradients	Various (all listed) / All groups	Various (all listed) / Most forms
Morrissey (1980)	Inshore, central GBR		Spatial correlation in cover: reef flat zones	Various (all listed) / All groups	Various (all listed) / Massive; Foliose; Branching
Benayahu and Loya (1981)\	Gulf of Eilat, Red Sea		Spatial correlation in cover; among 9 locations	Unspecified	Various / Branching; Massive
Sheppard (1988)	Red Sea, Arabian Sea, the Gulf		Spatial correlation in cover, along stress gradient	*Sargassum; Turbinaria; Hormophysa* / Leathery	46 spp. listed / Most forms
Stimson et al. (1996)	Kaneohe Bay, Hawaii		Spatial correlation in cover	*Dictyosphaeria cavernosa* / Foliose	*Porites compressa* / Digitate
McCook (1999)	Inshore, central GBR		Spatial correlation in cover: coral cover *not* inversely related to algal canopy within or between reefs.	*Sargassum* / Leathery	Various

**Stylophora pistillata, A.* spp., *Pocillopora verrucosa, Favia, Favites, Porites* spp. *Fungia granulosa, Fungia horrida, Ctenactis echinata*

Table 4. Comparison of direct observations of coral-algal interactions or contacts.

Studies which provide relatively detailed and small scale descriptions or photographs of coral-algal interactions. Methods, evidence, comments, functional groups and abbreviations as for Table 1, outcomes (O) as for Table 1.

Reference	Location, region	Methods & Evidence		Algal Taxa / Functional Group	Coral Taxa / Lifeform
		O			
Fishelson (1973)	Eilat, Red Sea	C	(Photograph) Coral regeneration by overgrowth of areas colonised by algae.	Various; esp. *Dichotrix; Sphacelaria; Lobophora* / Filament; Cort Foliose (Creep)	* / Branching; Massive
Banner (1974)	Kaneohe Bay, Hawaii	A	(Photograph) Algal overgrowth of corals.	*Dictyosphaeria cavernosa* / ~ Foliose	*Porites compressa* / Digitate
Birkeland (1977)	Panama, Pacific	A	(Photograph) Algae reduce recruit survival & trap sediment.	Unspecified / Filament	Unspecified / Recruits
Bak and Engel (1979)	Curacao, Caribbean	A	(Photograph) Algal overgrowth of 20 % recruits.	*Porolithon* & unspecified/ Crustose; Filament	*Ag. agaricites* + 21 species listed; / Recruits
Lewis (1986)	Belize, Caribbean	A	(Photograph) see Table 2.	See Table 2	See Table 2
Hughes et al. (1987); Hughes (1994a)	Jamaica, Caribbean	A	(Photograph) Algal overgrowth of corals.	See Table 3	See Table 3
de Ruyter van Steveninck et al. (1988)	Curacao, Caribbean		(Photograph) Algal growth reduced in close proximity to corals.	*Lobophora* / Cort Foliose (Creep)	*Ag.; Meandrina; Mycetophyllia; Stephanocoenia* / Foliose; Massive; Encrusting
James et al. (1988)	Bahamas, Atlantic; St. Croix, Barbados, Antilles, Caribbean	A	(Photograph) *Peyssonnelia* overgrows and kills corals.	*Peyssonnelia* / Crustose	*A. cervicornis; Acropora palmata; Montastrea annularis* / Branching; Massive
Lapointe (1989)	Caribbean	A	(Photograph) Algal overgrowth of coral.	*Cladophoropsis; Cladophora* / Filament	Unspecified
Stimson et al. (1996)	Kaneohe Bay, Hawaii	A	(Photograph) Algal overgrowth of coral.	*Dictyosphaeria cavernosa* / Foliose	*Porites compressa* / Digitate

Table 4 *Continued*

Keats et al. (1997)	Indo-Pacific	A	(Photograph) CCA overgrowth of coral.	*Pneophyllum conicum* / Crustose	*Porites* spp. / Massive
Littler and Littler (1997b)	Great Astrolabe Reef, Fiji	A C	(Photograph) Coral recruits overgrew turfs; turfs overgrew adult corals.	See Table 3	See Table 3
Littler and Littler (1997a)	Caicos Island, Caribbean	A	(Photograph) Algae killed coral tissue allelochemically.	*Dasyopsis spinuligera* / Filament or Cort Macro?	*Madracis decactis* / Digitate
Antonius (1999)	Belize +?, Caribbean	A	(Photograph) Crust overgrowth of coral.	Metapeyssonnelia corallepida	*Millepora complanata*
Finckh (1904)	Funafuti Atoll, Pacific	A	Algal overgrowth of corals.	*Lithothamnion* / Crustose	*Pocillopora; Heliopora; Porites* / Branching
Smith et al. (1981)	Kaneohe Bay, Hawaii	A	Algal overgrowth of corals.	*Dictyosphaeria cavernosa* / Foliose	*Porites compressa* / Digitate
Chadwick (1988)	Kaneohe Bay, Hawaii	A	Algal overgrowth of coral.	*Dictyosphaeria cavernosa* & CCA / Foliose; Crustose	*Fungia scutaria* / Mushroom
Wittenberg and Hunte (1992)	Barbados, Caribbean	A	Algal overgrowth of juvenile corals.	Unspecified	*Porites astreoides; Ag. agaricites; Diploria sp.* / Massive; Foliose
Tanner (1995)	Heron Is., GBR	B	Contact with algae reduced coral growth.	See Table 1	See Table 1
Shulman and Robertson (1996)	Panama, Caribbean	A	Bleaching of corals underneath algae.	See Table 3	See Table 3
Lirman (2001)	Florida, Caribbean	A	Polyp retraction and overgrowth near algae.	See Table 2	See Table 2

* *Stylophora pistillata, Pocillopora danae, A., Favia favus, Platygyra lamellina, Favites* spp., *Goniastrea pectinata, Lobophyllia corymbosa, Millepora dichotoma, Porites lutea*

Appendix B: Abstracts of manuscripts published, accepted or submitted for publication extracted from this thesis

Coral Reefs (19): 400 - 417

Competition between corals and algae on coral reefs: A review of evidence and mechanisms

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Abstract

Despite widespread acceptance of that competition between scleractinian corals and benthic algae is important to the structure of corals reef communities, there is little direct experimental evidence that corals and algae do compete, and very little data on the processes and causality of their interactions. Most available evidence is observational or correlative, with intrinsic risks of confounding causality. This paper reviews and categorise available evidence, concluding that competition between corals and algae probably is widespread on coral reefs, but also that the interaction varies considerably. Widespread replacement of corals by algae may often indicate coral mortality due to external disturbances, rather than competitive overgrowth, but may lead to competitive inhibition of coral recruitment, with consequences for reef recovery. We list eight specific processes by which corals and algae may affect each other, and suggest life history properties that will influence which of these interactions are possible. We proposes of a matrix for algal effects on corals, which list the subset of processes possible for each combination of coral life form and algal functional group. This table provides a preliminary framework for improved understanding and interpretation of coral-algal interactions.

Appendix B: (Continued)

Journal of Experimental Marine Biology & Ecology. 271(1):25-39

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

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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 competitor 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.

Appendix B: (Continued)

Limnology & Oceanography. 47(2):527-534

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

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Abstract

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

Marine Ecology Progress Series: *(in press)*

Contrasting effects of filamentous turf algae on corals: Massive *Porites* are unaffected by mixed species turfs, but are killed by the red alga *Anotrichium tenue*

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Abstract

Coral algal competition is an important process on coral reefs, especially during reef degradation, when abundant corals are often overgrown by benthic macroalgae. Despite the widespread assumption that macroalgae are able to out-compete corals for space, there have been very few experimental studies testing the nature of this interaction. This study compared the effects of a filamentous red alga, *Anotrichium tenue,* with those of mixed-species, filamentous algal turfs, on massive *Porites* corals on inshore reefs of the central Great Barrier Reef, Australia. We compared mortality of coral tissue in plots with *A. tenue* naturally present on live coral tissue, plots in which *A. tenue* was naturally present but experimentally removed, and plots where mixed algal turfs were naturally present but *A. tenue* was not. The results indicate that *A. tenue* caused coral tissue mortality by actively overgrowing and killing live coral tissue. Removing the algae removed the effect. In contrast, the general, mixed-species algal turfs did not cause any coral tissue death. We suggest that two particular traits of *A. tenue* may facilitate its effects on the corals. First, unlike most filamentous turf species present, it was able to overgrow live coral tissue, perhaps due to allelochemical effects. Second, individual algal filaments trap relatively large amounts of coral mucus and sediments, apparently increasing the damage to underlying coral tissue. Surveys indicated that *A. tenue* primarily affected massive *Porites spp.*, that overgrowth effects were not site specific, but that occurrence of infected corals was not widespread. In particular, distribution patterns were not consistent with an effect of terrestrial runoff. This study provides evidence of an exceptionally lethal effect on corals by a single species of filamentous alga, and emphasizes the variability of coral-algal competitive outcomes, even within a functional group.

Appendix B: (Continued)

Marine Ecology Progress Series: *(in review)*

CORAL-ALGAL COMPETITION: MACROALGAE WITH DIFFERENT PROPERTIES HAVE DIFFERENT EFFECTS ON CORALS

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ABSTRACT

Competition between hard corals and macroalgae is a key ecological process on coral reefs, especially during reef degradation, which often involves a "phase shift" from coral to algal dominated reefs. However, there are relatively few published studies exploring the variability in this interaction. This paper expands the range of documented coral-algal interactions by comparing the mechanisms and outcomes of interactions involving three different algal species, as well as general, mixed algal turfs. Mixed filamentous turfs had relatively minor effects on corals. However, the turfing, filamentous red alga *Corallophila huysmansii* provides a dramatic exception to this pattern, being able to settle on, overgrow and kill live coral tissue, perhaps due to allelochemical production by the algae, although this was not directly demonstrated. The larger filamentous alga, *Chlorodesmis fastigiata* ("Turtle weed"), conspicuous and abundant on Indo-Pacific reefs, had relatively little effect on coral tissue, resulting in polyp retraction but little other noticeable effect. A corticated red algae, *Hypnea pannosa*, frequently observed living within colonies of the branching coral *P. cylindrica*, did not have a major impact on underlying coral tissue, even over a year, apparently because the relatively translucent and porous thallus structure does not strongly inhibit coral tissue function. Together, these results demonstrate the considerable potential variability in both process and outcome of coral-algal competition. That variability can be effectively interpreted in terms of the limited number of mechanisms by which algae can affect corals, largely a consequence of the properties of the algae. Given the central importance of coral-algal competition to the process of coral reef phase shifts, understanding the variability and complexity in that competition will have important implications for the prediction and consequences of such phase shifts.